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A LATE CAMBRIAN (SUNWAPTAN) SILICIFIED TRILOBITE FAUNA FROM NEVADA

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ABSTRACT

At Barton Canyon, Cherry Creek Range, east-central Nevada, a two-meter interval of the Bullwhacker Member of the Late Steptoean–Sunwaptan Windfall Formation has yielded abundant silicified sclerites. This Late Sunwaptan (Late Cambrian) assemblage, assigned to the informal *Bowmania lassieae* Fauna, is correlative with the *Prosaukia pyrene* Subzone of Texas, and with the uppermost *Illaenurus* Fauna of southern Alberta. At least 15 species are present, and these represent 14 genera; *Cherrycreekia* and *Glaberaspis* are new. New species are *Prosaukia oldyelleri, Sunwaptia plutoi, Euptychaspis dougali, Eurekia rintintini, Bowmania lassieae, Cherrycreekia benjii,* and *Glaberaspis scoobydooi.*

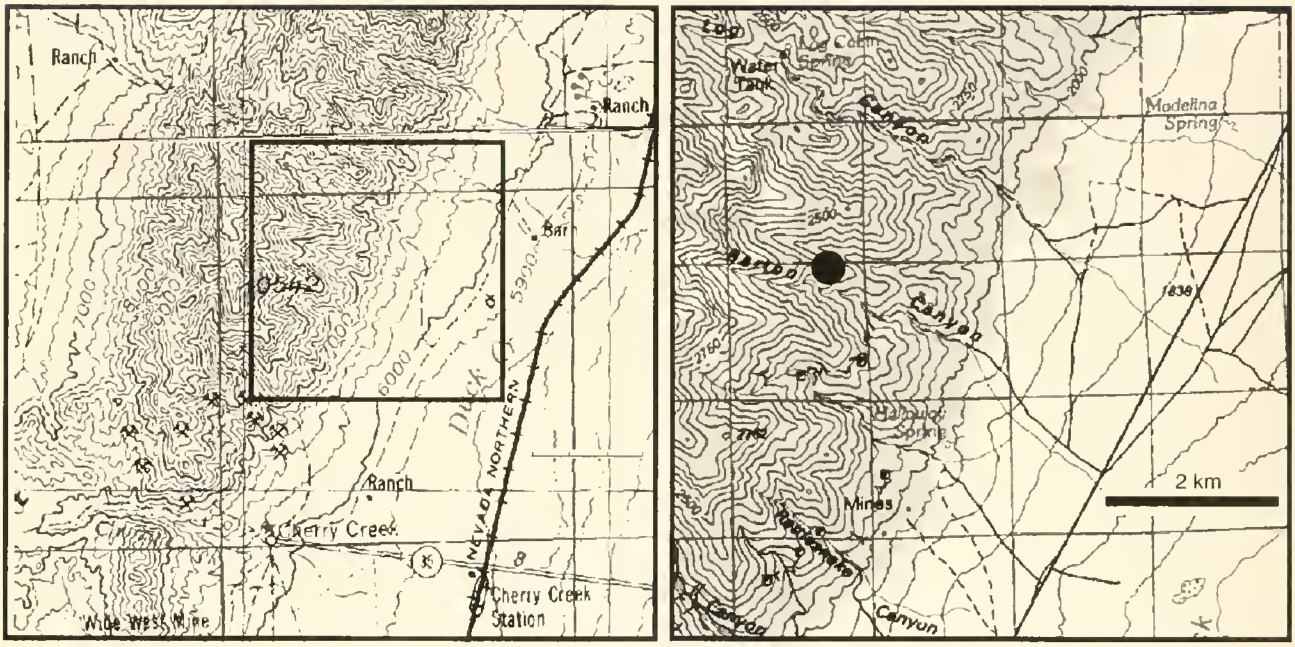
INTRODUCTION

North American silicified trilobites of Ordovician age were studied intensively in the 1950s by Evitt (1951), Ross (1951), Hintze (1953), Whittington and Evitt (1954) and Whittington (1956, 1959), and the morphologic and ontogenetic information provided by this work contributed greatly to the understanding of the phylogenetic relationships of post-Cambrian groups. In contrast, silicified faunas are virtually unknown in the Cambrian (see Ludvigsen, 1982, for an important exception) and their phylogenetic potential is largely untapped. Here we document a new silicified fauna from a Late Cambrian (Sunwaptan) sequence in the Cherry Creek Range of east-central Nevada. Although it lacks early ontogenetic stages, the fauna provides new insight into the morphology of a variety of genera. The fauna is also of significance because, although the trilobites of the underlying Steptoean stage have received considerable attention (Palmer, 1960, 1962, 1965), Sunwaptan trilobites of the Great Basin are essentially undocumented (see Taylor, 1976, for an exception).

The fauna was collected from a two-meter interval of the upper Bullwhacker Member of the Windfall Formation (Text-fig. 1) on the eastern side of the Cherry Creek Range, about 10 km north of the town of Cherry Creek (Text-fig. 2). The measured section runs along the crest of the ridge that forms the north side of Barton Canyon. Here, the upper Bullwhacker is composed of thin-bedded, fossiliferous calcareous sandstones and sandy bioclastic grainstones, with minor oolitic pack- and grainstones, intrarudites and thrombolitic microbial buildups (Text-fig. 3). The fauna includes 15 species, six of which are new.

ACKNOWLEDGMENTS

This a joint study; the order of authorship is alphabetical and does not indicate seniority. Support by the National Science Foundation through grant EAR-9973065 is gratefully acknowledged. We thank Pete Palmer for suggesting the Cherry Creek section as a locality with potential for recovery of silicified faunas, and Brian Chatterton and Bruce Lieberman for helpful reviews.

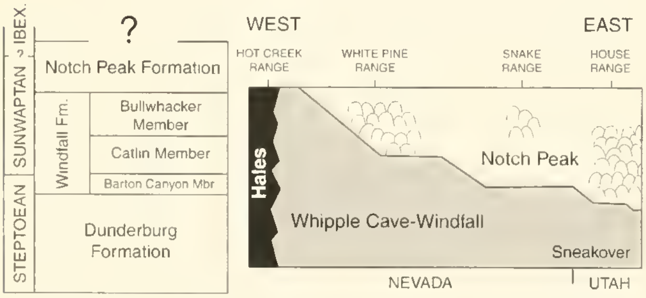


Text-figure 1.—A. Steptoean–Early Ibexian lithostratigraphy, Cherry Creek Range. B. Correlation of lithostratigraphic units immediately to the south of the study area, along an east-west transect from the House Range (west-central Utah) to the Hot Creek Range (central Nevada) (modified from Osleger and Read, 1993).

STRATIGRAPHIC AND ENVIRONMENTAL SETTING

STRATIGRAPHY

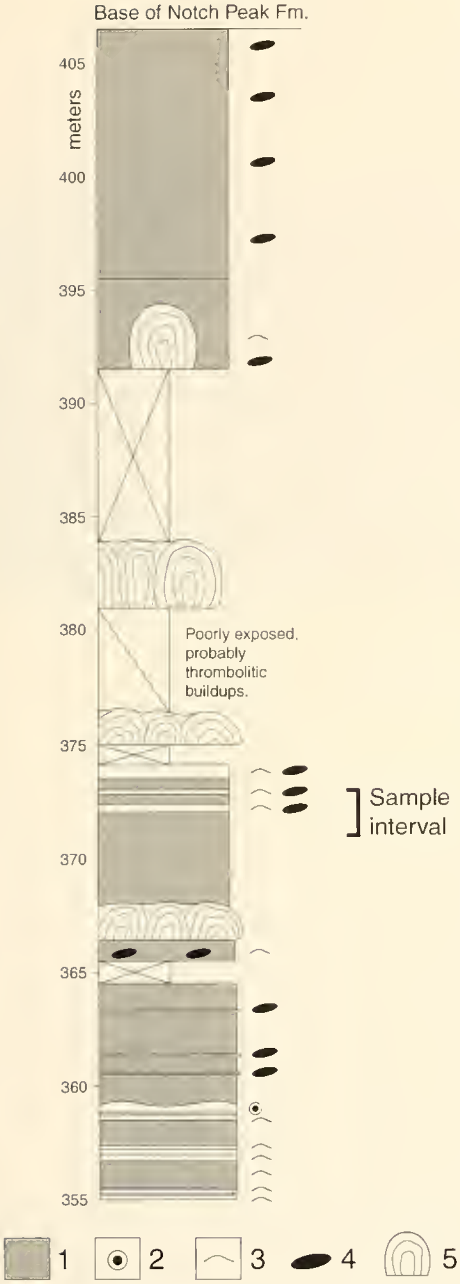
The Windfall Formation (Nolan *et al.*, 1956) was established in the Eureka Mining District of east-central Nevada for a sequence of carbonates that overlies the shales and interbedded carbonates of the Dunderberg Formation. The formation has also been recognized to the east and northeast of Eureka, in the Cherry Creek, northern Egan, and northern Schell Creek ranges (Palmer, 1971). Nolan *et al.* (1956) divided the Windfall into, in ascending order, the Catlin and Bullwhacker members. In the type area, the Catlin is composed of two distinct lithologies. The lower nine meters consists of thick-bedded, light-colored lime mudstones, and this is succeeded by about 75 meters of thin-bedded cherty carbonates. Farther to the east, in the northern Schell Creek Range, Young (1960) assigned the lower, light-colored carbonates to the Barton Canyon Limestone (named for, and well exposed at, the sample locality of this study), effectively restricting the Catlin to the overlying cherty carbonates. Subsequent workers (*e.g.*, Palmer, 1965, 1971) have followed Young in separating the Barton Canyon from the Catlin, and the three-fold division of the Windfall Formation is used herein (Text-fig. 1A).



Text-figure 2.—Locality Map, showing the measured section along the ridge at the north side of Barton Canyon, Cherry Creek Range.

The upper boundary of the Windfall Formation in the Cherry Creek Range is placed immediately below the base of a massive, cliff-forming unit that is composed of stacked thrombolitic and stromatolitic microbial buildups (Text-fig. 4). In previous work, Adair (1961) placed this buildup-bearing interval at the base of the "Pogonip Group." More recently, Osleger and Read (1993) interpreted a correlative interval of buildups farther to the south, in the White Pine Range, as a tongue of the Notch Peak Formation. In its type area of the southern House Range, Utah, the Notch Peak includes a thick interval of buildups (Hintze, 1973; Hintze *et al.*, 1988), and Osleger and Read's interpretation is followed herein.

The Barton Canyon Limestone yields faunas of the *Elvinia* Zone, with the base of the *Irvingella major* Zone (basal Sunwaptan) lying about 10 cm below the top of the member (Palmer, 1965; Adrain and Westrop,



Text-figure 3.—Stratigraphic column through the upper Bullwhacker Member, Barton Canyon, Cherry Creek Range, showing the interval that yielded the trilobite faunas described herein. Scale in meters above the base of the Catlin Member. The entire Bullwhacker is about 270 m in thickness at this locality. 1, sandy bioclastic limestone and calcareous sandstone; 2, wave-rippled oolitic grainstone; 3, bioclastic rudstone; 4, intraclastic rudstone; 5, thrombolitic microbial buildups.

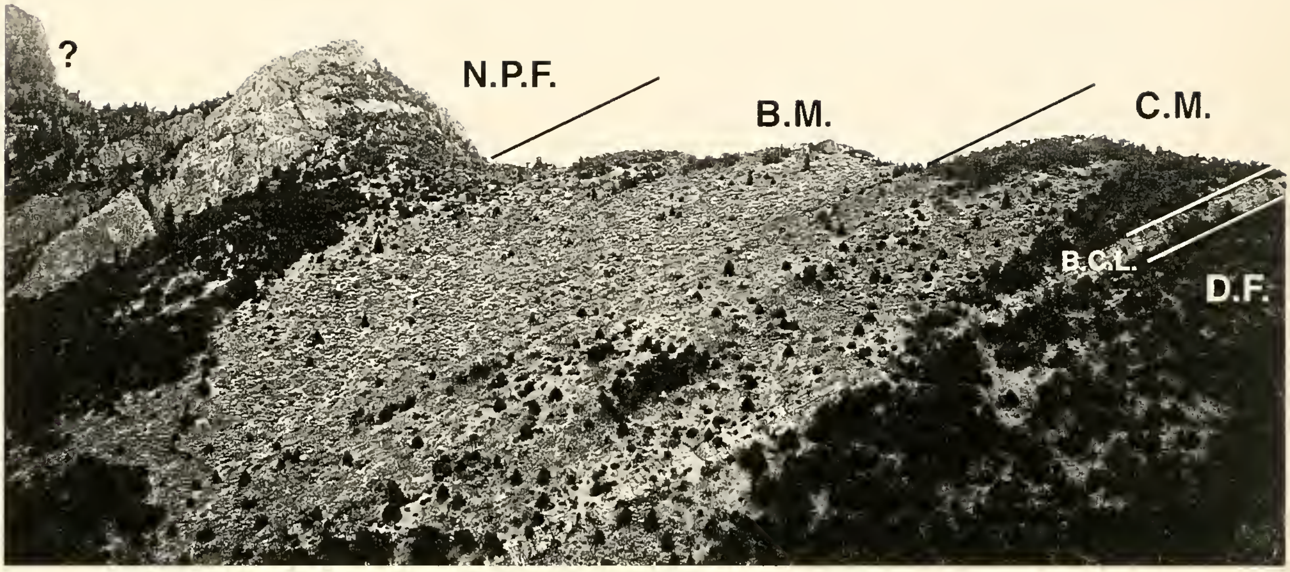
unpublished data). The basal few centimeters of the Catlin Member contains a fauna that includes *Elvinia roemeri* (Shumard, 1861), and this is followed by a 15-m interval with undescribed species of *Loganellus* Devine, 1863, *Wujiajiania*? Lu and Lin, 1980, and *Drumaspis* Resser, 1942 (Adrain and Westrop, unpublished data). The remainder of the Catlin is unfossiliferous, but the faunas of the lower 100 m of the Bullwhacker resemble the deep subtidal assemblages of the Rabbitkettle Formation of northwestern Canada (Ludvigsen, 1982; Westrop, 1995), and include *Idiomesus* Raymond, 1924, *Yukonaspis* Kobayashi, 1936a, *Tatonaspis* Kobayashi, 1935, *Parabriscoia* Kobayashi, 1935, *Hungaia* Walcott, 1914, *Elkanaspis* Ludvigsen, 1982, *Naustia* Ludvigsen, 1982 and *Eurekia* Walcott, 1916. The upper Bullwhacker includes the fauna described herein, and its age and correlation are discussed below.

The base of the Notch Peak Formation is a 50-cm-thick bed of sandy, cross-bedded bioclastic rudstone that provides the foundation for the overlying microbial buildups. The trilobite fauna of this rudstone includes *Eurekia longifrons* Westrop, 1986b and *Meniscocoryphe platycephala* (Kobayashi, 1935), and demonstrates that the Windfall–Notch Peak boundary correlates with the *Saukiella junia* Subzone of Oklahoma (Stitt, 1971, 1977) and Texas (Longacre, 1970), and the *Proricephalus wilcoxensis* Fauna of Alberta (Westrop, 1986b).

The buildup-bearing interval assigned to the Notch Peak Formation is overlain by a thick interval of largely unstudied carbonates. The lower 25 m consist mostly of bioturbated lime mudstones, with chert horizons appearing about 20 m above the top of the buildups. A silicified trilobite fauna was recovered 24.15 m above the top of the buildups, and this contains *Apoplanias* Lochman, 1964, *Symphysurina* Ulrich, *in* Walcott, 1924, and *Parakoldinioidia stitti* Fortey, 1983. It likely correlates with the upper *Missisquoia* or lower *Symphysurina* zones (*e.g.*, Stitt, 1977), an interval which lies near the top of the Notch Peak Formation in west-central Utah (Hintze *et al.*, 1988).

SEDIMENTARY FACIES

The thin-bedded, cherty lime mudstones and shales of the Catlin Member record a sharp deepening following the deposition of the shallow subtidal limestones of the Barton Canyon Limestone (see Brady and Rowell, 1976, for interpretation of the Barton Canyon Limestone and correlatives). The contact between the Catlin and the Bullwhacker Member is not exposed, and the latter is at least 270 m thick. The lower 100 m of the Bullwhacker consists of thin-bedded, unbioturbated lime mudstones with thin, dolomitic partings, and closely resembles the deep shelf facies of the Rabbitkettle Formation of northwest Canada (*e.g.*, Ludvigsen, 1982, fig. 12D; Westrop, 1995, text-fig. 3). In higher parts of the Bullwhacker, lime mudstones are extensively bioturbated and dolomite-mottled, sug-



Text-figure 4.—Skyline along ridge immediately to the north of the measured section, showing topographic expression of the Windfall and Notch Peak formations. D.F., Dunderburg Formation; B.C.L., Barton Canyon Limestone; C.M., Catlin Member; B.M., Bullwhacker Member; N.P.F., Notch Peak Formation; ?, unstudied cliff-forming carbonates of the "Pogonip Group." Stratigraphic thickness from the base of the Catlin Member to the top of the lower, resistant cliff formed by the Notch Peak buildup complex is 514.5 m.

gesting shallower, more oxygenated, subtidal conditions. In the upper 60 m of the Bullwhacker (Text-fig. 3), bioturbated lime mudstones are minor components of a succession that includes sandy bioclastic grainstones and calcareous sandstones. Shallow subtidal conditions (above storm wave base) are indicated by intraclastic rudstones ("flat pebble conglomerates") and pebbly intraclastic grainstones. Wave-rippled oolitic grainstones and thrombolitic buildups (1.5–3 m in thickness) also point to shallow-water conditions.

The Bullwhacker Member may be interpreted as recording upward-shoaling from deep subtidal conditions, culminating with the appearance of the thick, microbial buildup complex recorded by the Notch Peak Formation. The appearance of quartz sand and silt in the upper Bullwhacker (about 20 m below the fauna described herein) may be of more than local significance. Osleger (1995; Osleger and Read, 1993) suggested that a sequence boundary could be recognized within the lower *Saukia* Zone throughout southern Laurentia (Virginia–Tennessee, Oklahoma, Texas and west-central Utah). The biostratigraphic control presented by Osleger (1995) is limited, but the calcareous sandstones and sandy carbonates of the Bullwhacker may be an expression of the same sea-level fall.

AGE AND CORRELATION OF THE FAUNA

The assemblage described here is assigned to an informal biostratigraphic unit, the *Bowmania lassieae* n. sp. Fauna. Several species occur in other parts of North America, including *Illaenurus montanensis* Kobayashi, 1935, *Cherrycreekia benjii* n. sp., and *Corbinia implumis* Winston and Nicholls, 1967. At Wilcox Peak, southern Alberta (Westrop, 1986b, text-fig. 31), *I. montanensis* and *C. benjii* have been recorded from the upper part of the *Illaenurus* Zone, where they are separated by less than two meters of strata. *Proricephalus scapane* (Longacre, 1970) occurs with *C. benjii* in Alberta and is also present in the *Prosaukia pyrene* Subzone of the Wilberns Formation, central Texas (Longacre, 1970).

Corbinia implumis is known from two figured specimens (Winston and Nicholls, 1967, pl. 9, fig. 3; Longacre, 1970, pl. 3, fig. 13) from Texas that, according to boundaries defined by Longacre (1970, pp. 11–12), occur in the *P. pyrene* Subzone. In Alberta, this species extends from the upper *Illaenurus* Zone into the overlying *Proricephalus wilcoxensis* Fauna (Westrop, 1986b).

Although the biostratigraphic data support a correlation with the upper *Illaenurus* Zone of Alberta and the *Prosaukia pyrene* Subzone of Texas, we have not assigned the fauna from the silty and sandy carbonates of the upper Bullwhacker to either of these units. Quantitative analyses of Late Sunwaptan trilobite abundance and distribution (Ludvigsen and Westrop, 1983a; Westrop, 1986b, 1995, 1996) have demonstrated profound facies control, especially in carbonate environments. Assemblages track lithofacies changes (*e.g.*, Westrop, 1996, fig. 9), and this provides unequivocal evidence for the existence of environmentally controlled trilobite biofacies. Ludvigsen and Westrop (1983a; see also Ludvigsen *et al.*, 1986) advocated the use of separate zonations for different facies belts, and argued that correlation between zonations is best achieved through occurrences of relatively rare, widespread species. In contrast, Loch *et al.* (1993) ignored the complexities of facies control, and attempted to force all shallow-water facies into a single "standard" zonation based on the succession in southern Oklahoma and central Texas. They noted that the first occurrences of *Calvinella tenuisculpta* Walcott, 1914, a species that occurs at the base of the *Saukiella serotina* Subzone in Oklahoma, and *Stenopilus glaber* (Westrop, 1986b) are within three meters of each other in Alberta. From this, they concluded that the *Stenopilus glaber* Fauna of the latter region and the *Saukiella serotina* Subzone were equivalent. *Calvinella tenuisculpta* is, however, very rare in the Mistaya Formation (nine cranidia from three collections represent less than two percent of the trilobites recovered from the *S. glaber* Fauna; Westrop, 1984), so that it is unlikely that the first appearance in Alberta is synchronous with that in Oklahoma. As noted by Loch *et al.* (1993), *C. tenuisculpta* and *S. glaber* make their first occurrence in the same collection in a section at Mt. Murchison. They fail to mention, however, that this is the *only* collection from the Mistaya Formation at that locality, and is separated from the closest underlying sample by more than 100 meters (Westrop, 1986b, fig. 24). As such, it says nothing about the order of appearance of these species. Similarly, their (Loch *et al.*, 1993, p. 503) observation that the eponymous species is absent from the *S. glaber* Zone at Chaba Creek is irrelevant because the single collection from that locality contains only four trilobite sclerites (Westrop, 1984). Finally, the species that can be used to assign their section at Mt. Wilson to the *Saukiella serotina* Subzone are either poorly preserved, very rare (e.g., *Euptychaspis kirki* Kobayashi, 1935, is represented by only one cranidium; Loch *et al.*, 1993, Appendix 1) or misidentified (the larger of the two cranidia assigned to "*Briscoia*" *llanoensis* Winston and Nicholls, 1967, by Loch *et al.* [1993, fig. 6.18] shows a clearly defined anterior border and short preglabellar field that is not present on material from the type area in Texas [Winston and Nicholls, 1967, pl. 10, figs. 1, 3, 5]). Thus, although an approximate correlation between Alberta and Oklahoma-Texas is possible (Westrop, 1986b), use of a common zonal nomenclature implies a degree of accuracy that is not supported by the available data.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Our approach to systematic treatment of fossils is essentially that laid out by Smith (1994), and our species concept corresponds to what he defined as "phena." Morphological terminology follows Whittington (1997). Specimens are reposited in the Paleontology Repository, Department of Geoscience, University of Iowa, with specimen numbers prefixed SUI. Trilobites were photographed using a Leitz Aristophot macrophotography system and Kodak Technical Pan film. Negatives were scanned using a Polaroid negative scanner to produce digital images, which were manipulated using Adobe Photoshop.

Class **TRILOBITA** Walch, 1771

Family **DIKELOCEPHALIDAE** Miller, 1889

Discussion.—The problematic nature of many dikelocephalid genera has been discussed often over the last 25 years (*e.g.* Taylor, *in* Taylor and Halley, 1974; Ludvigsen and Westrop, 1983b; Westrop, 1986b) but little progress has been made. The large number of taxa involved and their broad geographic distribution (*e.g.*, Shergold, 1975; Ergaliev, 1980; Peng, 1984, 1992) make revision of the Dikelocephalidae a daunting task that is well beyond the scope of this study.

Genus **DIKELOCEPHALUS** Owen, 1852

Type species.—*Dikelocephalus minnesotensis* Owen, 1852, p. 574.

Discussion.—The presence of a pair of posterolateral pygidial spines has generally been considered to be a diagnostic character of *Dikelocephalus* Owen (*e.g.*, Westrop, 1986b; Hughes, 1994). Apart from the absence of marginal spines, pygidia of several species currently assigned to Briscoia Walcott, 1924, (*e.g.*, Westrop, 1986b, pl. 2, figs. 3, 4) differ little from those of Dikelocephalus. It is also clear that the holaspid ontogenetic development of the frontal area in cranidia of Briscoia, in which the distinction between the preglabellar field and anterior border is lost (*e.g.*, Westrop, 1986b, pl. 2, figs. 1, 5, 6, 7) is similar to that of *Dikelocephalus.* Indeed, as noted by Westrop (1986b, p. 29), only the more anteriorly positioned palpebral lobe separates cranidia of *Briscoia* from *Dikelocephalus*, but similarly positioned palpebral lobes occur in a variety of other dikelocephalid genera (*e.g.*, Longacre, 1970, pl. 4, figs. 16, 17; Taylor and Halley, 1974, pl. 2, fig. 2; Westrop, 1986b, pl. 4, figs. 1, 10). Thus, even if well-developed pygidial spines and posteriorly positioned palpebral lobes are apomorphies of *Dikelocephalus*, recognition of the genus may create paraphyly in *Briscoia*.

Resolution of this problem must await a comprehensive revision of the Dikelocephalidae.

Dikelocephalus minnesotensis Owen, 1852
Plate 1, figures 1–26

Dikelocephalus minnesotensis Owen, 1852, p. 574, pl. 1, figs. 1, 2 (only), pl. 1a, figs. 3, 6; Hughes, 1994, p. 53, pls. 1–8, pl. 10, figs. 14, 15, pl. 11 (see for complete synonymy); Stitt and Straatman, 1997, p. 86.

Figured material.—One cranidium (SUI 99042), two pygidia (SUI 99048, 99051), one hypostome (SUI 99043), four librigenae (SUI 99045–99047) and two thoracic segments (SUI 99049, 99050).

Discussion.—Hughes (1994), in his analysis of phenotypic variation in the type area of the Upper Mississippi Valley, advocated a broad species concept for *Dikelocephalus minnesotensis*. At least one other species, *D. freebergensis* Feniak (*in* Bell *et al.*, 1952; Hughes, 1994, pl. 9, figs. 3–5, 17–19), may be represented in the Sunwaptan of the Upper Mississippi Valley (see Hughes, 1994, p. 57). It differs from *D. minnesotensis* in such pygidial features as longer, stouter marginal spines and a more transverse posterior pygidial margin.

Pygidia from the Bullwhacker Member (Pl. 1, figs. 13, 18, 19, 22–26) possess a fourth axial ring that is poorly differentiated from the terminal piece and fall within the range of variation of specimens of *D. minnesotensis* illustrated by Hughes. The pygidial doublure (Pl. 1, fig. 26) is very broad, and has a prominent medial notch beneath the terminal piece of the axis. In contrast, the doublure of *Prosaukia oldyelleri* n. sp. (Pl. 3, figs. 1, 18) is narrower, with an anterior margin that is bluntly rounded medially and extends forward only as far as the end of the postaxial ridge. A doublure similar to that of *P. oldyelleri* is also present in pygidia of *Calvinella palpebra* Ludvigsen (1982, fig. 58J) and, judging from the position of the faint paradoublural furrow or inflexion on the pleural field, in *Hoytaspis speciosa* (Walcott) (Ludvigsen and Westrop, 1983b, pl. 15, figs. 11–13), *P. corrugata* Rasetti (1959, pl. 54, figs. 6, 7) and *P. stosei* (Walcott) (Rasetti, 1959, pl. 54, fig. 17).

The associated cranidium (Pl.1, figs. 1–4) is much smaller than any that have been illustrated previously. It has a shorter frontal area than most larger holaspids from the Upper Mississippi Valley (*e.g.*, Hughes, 1994, pl. 2, figs. 2, 3, pl. 3, figs. 1–6), although Hughes (1994, p. 26, figs. 18, 19) demonstrated substantial variability in frontal area length. A distinct anterior border and border furrow is present, and similar features can be seen on small cranidia from the Upper Mississippi Valley (*e.g.*, Labandeira and Hughes, 1994, fig. 1.3). In this respect, it resembles small holaspids of *Briscoia* (Westrop, 1986b, pl. 2, fig. 5). Finally, the palpebral lobe is relatively long (Pl. 1, fig. 1; equal to slightly more than half of glabellar length), and this is consistent with Hughes's (1994, p. 32, fig. 24) conclusion that palpebral lobe length is size-dependant.

The hypostome of *D. minnesotensis* (Pl. 1, figs. 5, 6, 8) can be identified with confidence because of the association with complete cephala in Wisconsin (Ulrich and Resser, 1930, pl. 10, fig. 2). The expansion of the flat lateral border opposite the median furrow is particularly distinctive. Hypostomal borders of other dikelocephalids are variable. Some are similar to, but narrower than, those of *Dikelocephalus* (*e.g.*, Shergold, 1991, pl. 4, figs. 7, 20), whereas others are convex and rim-like (*e.g.*, Ulrich and Resser, 1933, pl. 36, fig. 14). A comparable range in morphologies, from flat and somewhat expanded (Westrop, 1986b, pl. 7, fig. 9, pl. 8, fig. 16) to convex rims (Westrop, 1986b, pl. 8, fig. 4), is seen among species of such outgroups as the ptychaspidid *Ptychaspis* Hall, 1863, so that character polarities are uncertain.

Genus **PROSAUKIA** Ulrich and Resser, 1933

Type species.—*Dikelocephalus misa* Hall, 1863, p. 144.

Discussion.—As discussed by Ludvigsen and Westrop (1983b, p. 30) and Westrop (1986b, p. 32), *Prosaukia* and *Saukiella* Ulrich and Resser, 1933, are to some extent gradational and could prove to be synonyms. Part of the problem stems from the fact that *Saukiella* currently includes two groups of species that differ in the structure of the frontal area. The type species, *Saukiella pepinensis* (Owen, 1852) (Ulrich and Resser, 1933, pl. 32, figs. 1–4, pl. 33, fig. 22; Longacre, 1970, pl. 5, figs. 10, 11), and *S. junia* (Walcott, 1914) (Winston and Nicholls, 1967, pl. 9, figs. 8, 10, 12, 14; Longacre, 1970, pl. 5, figs. 13–17, 19, 20) both possess long frontal areas in which the preglabellar field is barely developed. In contrast, *S. pyrene* (Walcott, 1914) (Ulrich and Resser, 1933, pl. 34, pl. 35, fig. 1; Longacre, 1970, pl. 5, figs. 1–7), *S. fallax* (Walcott, 1914) (Longacre, 1970, pl. 5, figs. 1, 3) and *S. serotina* Longacre (1970, pl. 6, figs. 1–3) are characterized by short, subequally divided frontal areas that are comparable to those of *Prosaukia* (*e.g.*, Longacre, 1970, pl. 4, figs. 19–21; Ludvigsen and Westrop, 1983b, pl. 11, figs. 1–8; Westrop, 1986b, pl. 4, figs. 8–11, 13). Indeed, of the criteria suggested by Longacre (1970, p. 49), only the confluent border furrows of the librigenae separate *S. pyrene* (*e.g.*, Ulrich and Resser, 1933 pl. 34, pl. 35, figs. 2, 3, pl. 36, figs. 7–9) from *Prosaukia hartti* (Walcott, 1879) which has border furrows that do not meet (Ludvigsen and Westrop, 1983b, pl. 11, fig. 10). Character polarities, however, are uncertain because both states occur in outgroups to the Dikelocephalidae (for examples of isolated border furrows similar to those of *P. hartti*, see Ludvigsen, 1982, fig. 58N, fig. 59S, T; Westrop, 1986b, pl. 7, fig. 5, pl. 8, fig. 5; confluent border furrows occur in *Keithiella depressa* [Rasetti, 1944], see Ludvigsen and Westrop, 1983b, pl. 16, fig. 8). Among dikelocephalid genera, confluent border furrows are present in *Calvinella* (Walcott, 1914) (Ulrich and Resser, 1933, pl. 37, figs. 22, 24, 27, 28, 31, 32; Ludvigsen, 1982, fig. 58F) and *Tellerina* Ulrich and Resser (1933, pl. 44, figs. 4, 19), whereas isolated furrows occur in *Parabriscoia* (Palmer, 1968, pl. 15, fig. 1). Thus, librigenal border morphology is ambiguous and does not demonstrate monophyly of *Saukiella*.

As a tentative first step toward a revision of the dikelocephalid genera, we suggest restriction of *Saukiella* to *S. pepinenis* and *S. junia*, with frontal area proportions (long frontal area with very short preglabellar field) as a potential apomorphy. *Saukiella pyrene*, *S. fallax*, and *S. serotina* are transferred to *Prosaukia*, and the diagnosis of Ludvigsen and Westrop (1983b) is followed herein.

Prosaukia oldyelleri, new species

Plate 2, figures 1–39, Plate 3, figures 1–41

Diagnosis.—A species of *Prosaukia* with small marginal spines on anteriormost pleura of pygidium. Anterior end of palpebral lobe reaches glabella, so that palpebral furrow joins axial furrow. Short, narrow frontal area has subtriangular anterior border.

Description.—Strongly convex subrectangular glabella occupies about 85 percent of cranidial length and slightly less than 60 percent of cranidial width across palpebral lobes. Axial and preglabellar furrows are finely etched grooves, and are bowed outward at S1 and S2 lobes, especially in larger cranidia; glabella is weakly constricted opposite anterior ends of palpebral lobes. Longitudinal profile of glabella is gently convex between posterior margin and anterior tips of palpebral lobes, but curves steeply downward anteriorly. Occipital furrow is narrow (sag.), roughly transverse groove. S1 furrows are curved gently backward and connected across glabella, although become somewhat shallower medially. S2 furrows also curved backward although are well defined only near axial furrows; may be connected across glabella in some individuals. Frontal area is short and narrow, with maximum width equal to about 70 percent of cranidial width across palpebral lobes; unequally divided into short preglabellar field and longer, convex, subtriangular anterior border by shallow, forwardly curved border furrow. Long, flat, strongly curved palpebral lobes are centered slightly in front of anterior tips of S1 furrows and extend from occipital furrow to mid-point of frontal glabellar lobe; separated posteriorly from glabella by narrow strips of fixigenae but abut glabella anteriorly. Palpebral furrow is finely etched groove that merges with axial furrow anteriorly; palpebral lobe may be subequally divided by barely perceptible furrow that parallels palpebral furrow. Posterior branches of facial sutures diverge sharply backward. Anterior branches moderately divergent near palpebral lobe, curving gradually inward to become nearly parallel at anterior border furrow before converging abruptly inward along anterior cranidial margin. Posterior fixigenae narrow, strap-like; in anterior view, flexed downward at about 30 degrees. Posterior border furrow very shallow, finely etched groove. Glabella, interocular fixigenae and anterior border have sculpture of terrace ridges; palpebral lobes and preglabellar field are smooth. Occipital ring may carry minute occipital spine.

Librigenae separated by median suture. Long, slender genal spine curves gently inward; equal to about 275 percent of length of librigenal field. Moderately inflated librigenal field separated from convex posterior and lateral border by shallow, confluent border furrows. Eye socle consists of two wire-like bands separated by finely etched longitudinal furrow. Inner edge of doublure lies beneath lateral border furrow but diverges posteriorly from posterior border furrow, so that doublure narrows laterally away from genal angle. Genal spine, borders, doublure and librigenal field carry sculpture of terrace ridges.

Pygidium subelliptical in outline, with length about 66 percent of maximum width; pair of minute marginal spines located slightly anterior of posterior tip of axis. Convex axis accounts for about half of pygidial height in lateral view, and about 40 percent of pygidial width at anteriormost axial ring; tapers backward and occupies slightly more than 75 percent of pygidial length; post-axial ridge terminates close to pygidial border. Axial furrows are shallow grooves. Four subequal axial rings and rounded terminal piece separated by subtransverse axial ring furrows; semielliptical articulating half-ring equal to about 75 percent of length of anteriormost axial ring. Pleural field nearly flat at axial furrow but flexed downward, becoming nearly flat at pygidial margin. Inner edge of doublure underlies point of downward flexure of pleural field and does not reach posterior end of axis. Pleural and interpleural furrows well defined and curve outward and backward to terminate just short of pygidial margin; degree of curvature decreases in successive furrows so that posteriormost are nearly straight. Apart from anteriormost, convex anterior and posterior pleural bands subequal in length. Pleural field and doublure carry fine terrace ridges that roughly parallel pygidial margin; axis also with terrace ridges.

Holotype.—A cranidium (SUI 99054; Pl. 2, figs. 3, 4, 7, 11) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range, Nevada.

Figured material.—Eleven cranidia (SUI 99052–99062), four librigenae (SUI 99063, 99064, 99080, 99081), and 14 pygidia (SUI 99065–99079).

Etymology.—Named for Old Yeller.

Discussion.— *Prosaukia oldyelleri* n. sp. is unusual in possessing palpebral lobes whose anterior tips abut the glabella. The typical dikelocephalid condition has the anterior end of the palpebral lobe separated from the glabella by a strip of fixigena of variable width (*e.g., Prosaukia* [Rasetti, 1959, pl. 54, figs. 4, 5, 9, 16, 22; Longacre, 1970, pl. 4, figs. 19–21; Taylor and Halley, 1974, pl. 2, figs. 15–17; Ludvigsen and Westrop, 1983b, pl. 10, figs. 1, 3; Westrop, 1986b, pl. 4, figs. 8–11]; *Calvinella* Walcott, 1914 [Nelson, 1951, pl. 110, fig. 21; Longacre, 1970, pl. 4, figs. 16, 17; Taylor and Halley, 1974, pl. 2, figs. 2, 3]; *Saukia* Walcott, 1914 [Westrop, 1986b, pl. 3, figs. 8, 9, 11]; *Hoytaspis* Ludvigsen and Westrop [1983b, pl. 14, fig. 1, 8]; *Saukiella* Ulrich and Resser, 1933 [Longacre, 1970, pl. 5, figs. 10, 12, 17]; *Stigmaspis* Nelson, 1951 [Westrop, 1986b, pl. 4, figs. 1, 3–5]; *Tellerina* Ulrich and Resser, 1933 [Nelson, 1951, pl. 112, figs. 5, 12]; *Briscoia* Walcott, 1924 [Walcott, 1925, pl. 20, fig. 1; Westrop, 1986b, pl. 2, figs. 1, 5–7, 10]; *Parabriscoia* Kobayashi, 1935 [Palmer, 1968, pl. 15, figs. 2, 5; Westrop, 1995, pl. 1, figs. 28]; *Elkia* Walcott, 1924 [Walcott, 1925, pl. 18, figs. 1, 2]; *Dikelocephalus* Owen, 1952 [Hughes, 1994, pl. 2, figs. 1–3, 6, 7]; *Lophosaukia* Shergold, 1972 [Shergold, 1975, pl. 18, fig. 1; Peng, 1992, fig. 24B]; *Mictosaukia* Shergold, 1975 [Robison and Pantoja-Alor, 1968, pl. 104, figs. 13, 18; Shergold, 1975, pl. 24, fig. 10; Peng, 1992, fig. 24H]; *Anderssonella* Kobayashi, 1936b [Shergold, 1975, pl. 20, fig. 4]; *Galerosaukia* Shergold [1975, pl. 22, fig. 9]; *Caznaia* Shergold [1975, pl. 25, fig. 1]; *Platysaukia* Kobayashi, 1960 [Shergold, 1991, pl. 3, fig. 8]; *Eosaukia* Lu, 1954 [Shergold, 1991, pl. 5, fig. 21]). Although the anterior branches of the facial sutures are sharply divergent, the position of the palpebral lobes of *P. oldyelleri* results in a relatively narrow frontal area that also differs from typical dikelocephalids. Only *Osceolia osceola* (Hall, 1863) (Nelson, 1951, pl. 110, fig. 9) and at least some specimens of *Prosaukia pyrene* (Walcott, 1914) (*e.g.*, Ulrich and Resser, 1933, pl. 34, pl. 35, fig. 1; Nelson, 1951, pl. 110, fig. 4) have palpebral lobes in a position that is similar to *P. oldyelleri*. *Osceolia osceola*, however, is differentiated readily by a much longer frontal area on the cranidium and a pygidium (Nelson, 1951, pl. 110, fig. 10) that lacks interpleural furrows and has very long, stout marginal spines on the anteriormost pleura. *Prosaukia pyrene* has less strongly divergent anterior branches of the facial sutures, and an arcuate anterior border that results in an evenly rounded anterior cranidial margin.

The minute marginal spines on the anteriormost pleura and associated embayment of the lateral margin separate pygidia of *P. oldyelleri* from those of all previously described members of *Prosaukia*, although similarly sized spines could perhaps be overlooked or destroyed in preparation of "crackout" pygidia of other species. The only other spinose species is *P. spinula* Taylor (*in* Taylor and Halley, 1974, pl. 2, figs. 18, 20), but in that species, a single median spine is present.

Apart from the absence of marginal spines, pygidia of *P. pyrene* (Longacre, 1970, pl. 5, fig. 8) are very similar to those of *P. oldyelleri*. The type species, *P. misa* (Hall, 1863) (Westrop, 1986b, pl. 4, fig. 14), possesses pygidia that differ from those of *P. oldyelleri* and *P. pyrene* in having an axis composed of three, rather than four, axial rings plus terminal piece, whereas *P. hartti* (Walcott, 1879) (Ludvigsen and Westrop, 1983b, pl. 11, fig. 12) has five rings and a terminal piece.

The thoracic segment illustrated on Plate 17 (figs. 41, 46, 50) probably belongs to a dikelocephalid trilobite. We hesitate to assign it to *P. oldyelleri* because the coarse granules on the pleural bands and along the posterior margin of the axial ring are not present on any of the sclerites that can be confidently attributed to this species.

Family **PTYCHASPIDIDAE** Raymond, 1924

Subfamily **PTYCHASPIDINAE** Raymond, 1924

Discussion.—The genera of the Ptychaspidinae are in need of revision. Among North American representatives of the subfamily, monophyly of *Idiomesus* Raymond, 1924, is supported by substantial eye reduction or loss. *Keithia* Raymond, 1924, is defined by an expanded, bulb-shaped glabella that partly or completely overhangs the anterior border. *Proricephalus* Westrop, 1986a, (and its probable synonym *Plectrella* Ludvigsen and Westrop, *in* Ludvigsen *et al.*, 1989) can be diagnosed on the structure of the frontal area. The status of *Ptychaspis* Hall, 1863, and *Keithiella* Rasetti, 1944, is less certain. These genera have been separated by the expression of the anterior border and border furrow (*e.g.*, Longacre, 1970; Westrop, 1986b; Ludvigsen *et al.*, 1989). *Keithiella* possesses a convex anterior border and firmly impressed anterior border furrow, whereas *Ptychaspis* is characterized by an undifferentiated frontal area. By comparison with outgroups in the Dikelocephaloidea (*e.g.*, Westrop, 1986b, pl. 5, figs. 1, 2, 6), the condition in *Keithiella* is most likely plesiomorphic. The frontal area morphology of *Ptychaspis* is, however, shared with *Idiomesus*. Thus, it is possible that both *Ptychaspis* and *Keithiella* are paraphyletic. Any phylogenetic analysis will need to consider Australian and Chinese representatives of the subfamily, including *Asioptychaspis* Kobayashi, 1933 (regarded as a synomym of *Ptychaspis* by Shergold, 1991), *Changia* Sun, 1924, and *Quadraticephalus* Sun, 1924.

Genus **IDIOMESUS** Raymond, 1924

Type species.—Idiomesus tantillus Raymond, 1924, p. 397.

Idiomesus levisensis (Rasetti, 1944)
Plate 4, figures 1–20, 22, 23

Stigmametopus levisensis Rasetti, 1944, p. 257, pl. 37, figs. 8, 9.
Idiomesus levisensis (Rasetti). Taylor, 1976, p. 686, pl. 3, figs. 12, 13 (see for complete synonymy); Ludvigsen and Westrop, 1986, p. 305, pl. 20, figs. 5, 6D (see for synonymy); Ludvigsen, Westrop and Kindle, 1989, p. 32, pl. 20, figs. 8–13; Westrop, 1995, p. 24, pl. 7, fig. 24.

Figured material.—Six cranidia (SUI 99082–99088) and three librigenae (SUI 92089–92091).

Discussion.—The spindle-shaped glabella with S2 and S3 lateral glabellar furrows is characteristic of *Idiomesus levisensis* (Rasetti) (see Taylor, 1976, p. 686; Ludvigsen and Westrop, 1986). The librigena, illustrated here for the first time (Pl. 4, figs. 19, 20, 22, 23), carries a long, gently curved genal spine that contrasts with the minute spine of *I. tantillus* Raymond (Ludvigsen, 1982, fig. 54R)

Subfamily **MACRONODINAE** Westrop, 1986a

Genus **SUNWAPTIA** Westrop, 1986a

Type species.—Sunwaptia carinata Westrop, 1986a, p. 218.

Discussion.—Pygidial morphology offers potential synapomorphies for the Macronodinae (Adrain and Westrop, 2001, fig. 8), so that the discovery of the pygidium of *Sunwaptia* (Pl. 5, figs. 21–32) is of phylogenetic significance. As in *Macronoda* (Lochman, 1964, pl. 14, figs. 14, 18, 19, 21, 22; Westrop, 1986b, pl. 11, figs. 6, 7; Loch *et al.*, 1993, fig. 6.24), it is subtriangular in outline, with a long axis and narrow pleural fields. Moreover, *Sunwaptia* and *Macronoda* possess pits in the border furrow, and this character is an unequivocal synapomorphy. *Sunwaptia* differs in that the pits are overlain by swollen protuberances that extend inward from the border. The two genera also differ in the segmentation of the pygidial axis. The axis of *Sunwaptia plutoi* n. sp. has three or four axial rings, with a long terminal piece that occupies at least one-third of axial length. In contrast, pygidia of *Macronoda* have multisegmented axes, with up to at least 14 poorly defined axial rings (Loch *et al.*, 1993, p. 512).

Sunwaptia plutoi, new species
Plate 4, figures 21, 24–26, Plate 5, figures 1–32

Diagnosis.—A species of *Sunwaptia* in which fixigenal ridge is poorly defined or absent. Palpebral lobe relatively small. Anterior cranidial arch weak.

Description.—Cranidium subsemielliptical in outline, with length equal to 60 percent maximum width; posterior margin curved backward, so that posterior tips of fixigenae extend back well beyond occipital ring. Glabella strongly convex and accounts for about 75 percent of cranidial height in anterior view; bulb shaped in outline, and occupies about 90 percent of cranidial length and nearly 50 percent of cranidial width across palpebral lobes. Longitudinal profile horizontal between posterior margin and S1 furrow, becoming arched strongly upward at frontal lobe before curving almost vertically downward at anterior. Axial and preglabellar furrows moderately impressed grooves. Occipital furrow deeply incised, transverse; occipital ring equal to about 15 percent of glabellar length and with posterior margin bowed gently backward. S1 firmly impressed transverse groove; L1 transverse band, roughly equal in length to occipital ring. Frontal lobe suboval in outline and strongly inflated, with maximum height in lateral view equal to 150–175 percent of height of L1; maximum width opposite palpebral ridge and equal to 130–145 percent of width of L1. Anterior border furrows shallow, diverging forward from anterior corners of glabella to anterior corners of cranidium; anterior border nearly flat medially but arched strongly downward in anterior view in all but smallest cranidium (Pl. 5, fig. 9). Palpebral lobe ill-defined inflated area at abaxial end of conspicuous, gently curved, wall-like palpebral ridge; located in front of mid-length of anterior glabellar lobe. Anterior branches of facial suture run forward and inward from palpebral lobe; posterior branches diverge gradually backward before curving slightly inward near posterior corner of cranidium. Posterior fixigena broad, maximum width equal to about 300 percent of interocular fixigena; slopes steeply upward from axial furrow, creating broad, arcuate, depressed area from palpebral ridge to S1 furrow; reaches maximum convexity behind palpebral lobe before flexing downward to lateral cranidial margin. Some individuals show low fixigenal ridge extending for short distance posterolaterally from palpebral lobe (Pl. 4, figs. 25, 26). Posterior border furrow deeply incised, slot-like, and curves gently backward from axial furrow; posterior border convex, curving gently backward and expanding distally, so that length is less than length of occipital ring at axial furrow but is subequal at posterior corner. Well-preserved cranidia (Pl. 5, figs. 1, 4, 5) with coarse tubercles along crest of glabella, becoming finer along the sides; larger tubercles perforated by large pore. Near axial furrow, glabella mostly smooth, as is adjacent portion of posterior fixigena. Outer parts of posterior fixigena with closely spaced fine tubercles and scattered coarser tubercles.

Librigena with short, broad-based, subtriangular genal spine. Librigenal field broad and moderately inflated. Lateral border furrow moderately impressed, running parallel to border posteriorly, then diverges from border, curving backward and inward as shallow paradoublural furrow; posteriorly, border furrow ill defined, marked by change in slope. Lateral border convex, best defined anteriorly, and merges with rim-like posterior border at tip of genal spine. Outer edge of weakly convex doublure follows anterior border and paradoublural furrows. Sculpture of very fine terrace ridges on doublure; remainder of librigena smooth.

Pygidium subtriangular in outline, with length slight less than 70 percent of maximum width. Axis long, extending back to border and narrow, accounting for about 25 percent of maximum pygidial width; parallel sided to gently tapered anteriorly but with terminal piece expanded posteriorly, and strongly convex, standing well above pleural fields. Four axial rings and long terminal piece separated by firmly impressed, forwardly curved ring furrows; successive rings decrease slightly in length, so that posteriormost about 75 percent length of anteriormost; terminal piece accounts for about 40 percent of axis length. Articulating half-ring short, equal to 25 percent of length of adjacent axial ring, with very gently curved anterior margin; articulating furrow also gently curved and firmly impressed. Pleural field triangular in outline and flexed downward from axis; crossed by three pairs of firmly impressed, oblique pleural furrows; interpleural furrows barely perceptible on broad pleural bands. Border narrow, convex rim; border furrow with four pairs pits that are overlain by swollen protuberances that extend inward from the border. Doublure narrow, convex, so that border is subcircular in cross-section. Dorsal surface of pygidium smooth except for coarse terrace ridges on border.

Holotype.—A cranidium (SUI 99092; Pl. 4, figs. 21, 24–26) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Six cranidia (SUI 99092–99097), three librigenae (SUI 99098–99100), and four pygidia (SUI 99101–99104).

Etymology.—Named for Pluto Pup.

Discussion.—*Sunwaptia plutoi* n. sp. is very similar to the type species, *Sunwaptia carinata* Westrop (1986a, figs. 4A–E; 1986b, pl. 11, figs. 9–13), from the Mistaya Formation of Alberta, but clearly differs in that the fixigenal ridge extending from the palpebral lobe to the posterior border furrow is poorly defined, extending for only a short distance from palpebral lobe (*e.g.*, Pl. 4, figs. 25, 26), or absent (*e.g.*, Pl. 5, figs. 10, 14, 17). Other differences in *S. plutoi* include a somewhat longer L1 glabellar lobe, a less pronounced anterior arch, and a smaller palpebral lobe. The smallest cranidium (Pl. 5, figs. 8, 9) has a transverse, rather than arched, anterior margin, and appears to have a faint anterior border furrow and rim-like border.

Subfamily **EUPTYCHASPIDINAE** Hupé, 1953

Discussion.—Ingroup relationships of both the Euptychaspidinae and Macronodinae have been discussed recently by Adrain and Westrop (2001). As currently conceived, the Euptychaspidinae is confined to the Upper Sunwaptan (*sensu* Ludvigsen and Westrop, 1985) of North America, although Briggs *et al.* (1988) and Edgecombe (1992) suggested that *Curiaspis* Sdzuy, 1955, from the Leimitz Shale of Germany, might be an Ordovician ptychaspidid. Among the Ptychaspididae, glabellar structure of *Curiaspis* (Sdzuy, 1955, p. 7, figs. 11–16) is most similar to *Euptychaspis*, sharing transglabellar S1 and S2 furrows and a rounded anterior lobe. It has comparable palpebral lobes, but lacks the ridge-like extensions of the border on the occipital ring, which carries a conventional spine. Unlike *Euptychaspis* (and any other dikelocephaloidean), *Curiaspis* is proparian, with a short, slender genal spine. The relationship between *Curiaspis* and the euptychaspidines is uncertain, although discovery of the pygidium may clarifiy the affinities of this genus.

Calvipelta Westrop, 1986b, a small, effaced, blind trilobite from the Late Sunwaptan of Alberta, may prove to be a euptychaspidine. The poorly defined, parallel-sided glabella shares features with *Euptychaspis* (Pl. 6, figs. 1, 2, 4, 8; see also Ludvigsen, 1982, fig. 58K–M, Q, V, W). Although not connected across the glabella, distinct S1 and S2 lateral furrows are present, and the frontal lobe may be slightly expanded (Westrop, 1986b, pl. 41, figs. 33–35). In addition, the posterior border is curved backward to merge with the occipital ring. This resembles the structure of the occipital ring in *Euptychaspis*, in which the posterior border is extended backward as ridge (Pl. 6, figs. 1, 2, 4, 8; see also Ludvigsen, 1982, fig. 58K–M). The external surface of the pygidial exoskeleton appears to have been entirely effaced (Westrop, 1986b, pl. 41, fig. 36), but internal molds show that the axial, axial ring and pleural furrows were expressed on the ventral surface. The axis is similar in width to that of *Euptychaspis* (*e.g.*, Pl. 6, fig. 39), but the pleural field is broader. The pleural field is, however, more closely comparable to that of *Larifugula leonensis* (Winston and Nicholls, 1967) (Ludvigsen, 1982, fig. 67R), which was assigned to the Euptychaspidinae by Adrain and Westrop (2001).

Genus **EUPTYCHASPIS** Ulrich *in* Bridge, 1931

Type species.—Euptychaspis typicalis Ulrich *in* Bridge, 1931, p. 218.

Discussion.—Euptychaspis has to this point consisted of three named species: *E. typicalis*, the type species, *E. kirki* Kobayashi, 1935, and *E. jugalis* Winston and Nicholls, 1967. *Euptychaspis frontalis* Longacre, 1970, has been assigned to *Kathleenella* Ludvigsen, 1982. The holotype of *Euptychaspis trematocus* Hu, 1973, appears to be a shumardiid, and the pygidium associated by Hu (1973, pl. 2, fig. 14) appears to represent a missisquoiid.

Euptychaspis typicalis is known in its type occurrence in the Eminence Dolomite of Missouri from a tiny, retouched photograph (Ulrich in Bridge, 1931, pl. 19, fig. 7) of a dolomitic internal mold of cranidium lacking its occipital spine and posterior fixigenae, along with two stylized line drawings (Ulrich in Bridge, 1931, pl. 19, figs. 5, 6). The types have never been revised, and no other material from the Eminence Dolomite has ever been figured. Documentation of the types of *Euptychaspis kirki* is equally poor. The two incomplete, poorly preserved cranidia (Kobayashi, 1935, pl. 10, figs 4, 5) from the Windfall Formation in the Eureka mining district, Nevada, have never been revised, and no other material from this unit has ever been illustrated. *Euptychaspis jugalis* is known from a tiny stereopair photograph of a single incomplete cranidium (Winston and Nicholls, 1967, pl. 9, fig. 13) from the San Saba Member of the Wilberns Formation, Texas. Longacre (1970, pl. 3, fig. 18) figured another stereopair of a large cranidium from the type area but it is so poorly preserved that it is far from clear that it is actually conspecific with Winston and Nicholls' holotype.

Taken together, the type material of the species assigned to *Euptychaspis* provide a woefully inadequate basis for comparison. Nevertheless, the names *E. typicalis* and *E. kirki* have been used for many occurrences of *Euptychaspis*, in widely separated regions of Laurentia, and both species have come to be regarded as biostratigraphically important. Material has been assigned to *Euptychaspis typicalis* from Texas (Dake and Bridge, 1932; Winston and Nicholls, 1967; Longacre, 1970), Maryland (Rasetti, 1959), Oklahoma (Stitt, 1971), New York State (Taylor and Halley, 1974), the Mackenzie Mountains (Ludvigsen, 1982), and the southern Canadian Rocky Mountains (Westrop, 1986b). Similarly, *Euptychaspis kirki* has been reported from Texas (Winston and Nicholls, 1967; Longacre, 1970), Oklahoma (Stitt, 1971), and the Mackenzie Mountains (Westrop, 1995). The species have also been used to support the trilobite biostratigraphy of potential Cambrian-Ordovician boundary stratotype sections in western Utah (*e.g.*, Miller *et al.*, 1982; see also Hintze *et al.*, 1988; Loch *et al.*, 1999), though no specimens have ever been figured.

Close examination of the range of intra-sample variation in these reports suggests that pervasive morphological differences exist between some samples from different regions, and that in the case of both *E. typicalis* and *E. kirki*, a plexus of related species has been confused as a single species, largely on the basis of inadequate documentation. We will deal with the species regarded as *Euptychaspis kirki* in a forthcoming work. Here we document an unequivocal new species that would have been assigned under previous practice to the broad wastebasket of *E. typicalis*. The status of other occurrences assigned to *E. typicalis* is discussed below.

Euptychaspis dougali, new species
Plate 6, figures 1–44

Diagnosis.—S1 only weakly impressed medially in most specimens; S2 restricted to notches adjacent to the axial furrows, not impressed medially and not forming a single transverse furrow; L1 and L2 lacking sharp, scarp-like anterior and posterior margins; eye ridge not discernible dorsally or ventrally; interocular fixigenae broad; genal spine very long; pygidium with three axial rings.

Description.—Cranidium subpentagonal in outline, with length (excluding occipital spine) equal to about 60 percent of width at posterior; strongly convex with height opposite palpebral lobes equal to about half of cranidial length (excluding occipital ring). Glabella parallel sided, well rounded anteriorly, strongly convex and raised well above adjacent fixigenae at L1 lobe; occupies about 80 percent of cranidial length (excluding occipital ring) and 40 percent of cranidial width between the palpebral lobes. In front of occipital ring, longitudinal profile of glabella curves steadily downward so that anterior part of anterior lobe weakly raised above surrounding fixigenae. Axial and preglabellar furrows narrow but well-defined grooves. Composite occipital ring includes slender, steeply inclined occipital spine equal to about 60 percent of preoccipital glabellar length; ring and spine enclosed by raised rims that are extensions of posterior border and that join beneath posterior tip of spine. Occipital furrow finely etched groove, transverse or bowed gently forward. S1 furrow transglabellar (Pl. 6, fig. 4, 22), deepest at axial furrow but shallow medially. S2 lateral furrow well incised, narrow (tr.), extending inward for about 15 percent of glabellar width, and not connected across glabella. L1 lobe convex, subtransverse band and slightly wider (tr.) than occipital ring. L2 lobe subequal in length and width to L1. Frontal lobe weakly inflated, well rounded anteriorly, and accounts for about 50 percent of preoccipital glabellar length. Frontal area slopes forward to terminate at minute triangular border that is little more than expanded sculptural ridge. Palpebral area of fixigenae nearly flat. Palpebral lobe semielliptical, upturned flap, length about one-third of preoccipital glabellar length; palpebral furrow finely etched groove. Anterior branches of facial suture initially gently convergent before swinging sharply inward along anterior cranidial margin; posterior branches diverge gradually backward. Convex posterior border slightly shorter (exsag.) than L1 lobe and separated from fixigena by firmly impressed border furrow. Doublure beneath border short near axial furrow but increases in length (exsag.) distally. Frontal area with coarse, irregular sculptural ridges that are roughly parallel to cranidial margin. With exception of smooth cranidial furrows, posterior border and ridge along occipital spine, remainder of cranidium has sculpture of irregular, coarse anastomosing ridges. Sculpture not expressed on ventral surface (Pl. 6, fig. 3).

Librigenae with long genal spine narrowing backward and gently curved distally; length somewhat more than twice length of genal field. Genal field convex, accounting for more than half of height of librigena in lateral view, with distinct eye socle overlain by visual surface of eye. Posteriorly, librigenal field merges with broad, anterior end of carinate ridge extending along entire length of genal spine. Lateral border furrow is broad shallow groove; lateral border convex and steeply downsloping. Posterior border furrow firmly impressed and does not join lateral border; extends along inner edge of genal spine as narrow, weakly concave band that lacks sculpture. Narrow, tubular doublure beneath borders and raised above adjacent doublure of genal spine. Genal field, borders and spine with coarse, weakly anastomosing sculptural ridges that run roughly parallel to margin; border furrows and doublure smooth.

Pygidium elliptical in outline with length about 60 percent of maximum width; strongly convex, with height in posterior view equal to about half of pygidial width. Posterior margin with narrow, upward medial embayment. Axis and very narrow pleural field enclosed by narrow, rim-like ridges that extend backward and inward from anterior pygidial margin to join behind axis. Convex axis tapers gently backward and occupies about 65 percent of pygidial length; width at anterior axial ring equal to slightly less than 40 percent of maximum pygidial width. Three axial rings subequal in length and separated by finely etched, transverse ring furrows. Forwardly curved articulating half ring bounded posteriorly by transverse, finely etched articulating furrow. Pleural field with firmly impressed pleural furrow at anterior; remaining pleural and interpleural furrows shallow to barely perceptible. Broad posterior border slopes steeply downward from ridges bounding axis and pleural field. Border carries sculpture of anastomosing terrace ridges whereas axis has coarser anastomising ridges; pleural fields and pygidial furrows smooth.

Holotype.—A cranidium (SUI 99105; Pl. 6, figs. 1, 5, 11, 12, 22) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Seven cranidia (SUI 99105–99110, 99115, 99119), seven librigena (SUI 99111–99114, 99116–99118, 99122, 99123), and two pygidia (SUI 99120, 99121).

Etymology.—After Dougal, of the Magic Roundabout.

Discussion.—The most striking feature of *Euptychaspis dougali* is the presence of S2 furrows that are not connected across the glabella. A transglabellar S2 furrow is clearly present in Ulrich's photographed type specimen of *Euptychaspis typicalis* (Ulrich *in* Bridge, 1931, pl. 19, fig. 7). Moreover, in all reasonably well-known cranidia that have been assigned to *E. typicalis* (Rasetti, 1959, pl. 52, figs. 11–13; Winston and Nicholls, 1967, pl. 9, fig. 17; Longacre, 1970, pl. 4, fig. 9; Stitt, 1971, pl. 6, fig. 19; Taylor in Taylor and Halley, 1974, pl. 2, figs 4–6; Ludvigsen, 1982, fig. 58K, Q, V; Westrop, 1986b, pl. 10, figs 22, 23), both S1 and S2 are transglabellar and expressed in the central body of the glabella as distinct, unsculptured, transverse trenches. Both L1 and L2 are convex, transverse bands that extend across the glabella and whose anterior and posterior margins are sharply defined at a vertical, scarp-like break in slope. Opposite the notch-like S2 of *E. dougali*, the glabellar sculpture of coarse, anastomosing ridges extends without interruption across the central area of the glabella. S1 is generally more weakly developed in *E. dougali* than in any cranidia assigned to *E. typicalis*. Although this furrow is clearly transverse (confirmed by the presence of a furrow in ventral view, Pl. 6, figs. 3, 22), it is much deeper and notch-like near the axial furrow and very shallow to nearly indistinct (*e.g.*, Pl. 6, fig. 2) medially. In several specimens, the glabellar sculpture runs medially across S1 essentially without interruption. This glabellar morphology is unique within the genus, and it alone serves to differentiate *E. dougali* from all other occurrences of *Euptychaspis*. The species differs in detail in other ways from various taxa assigned to *E. typicalis*, and to clarify these contrasts it is necessary to evaluate each of these occurrences:

The type material of *E. typicalis* is totally inadequate and cannot be meaningfully compared with other taxa. *Euptychaspis typicalis* should be restricted to its type specimens, until such time as it is revised on the basis of new and better material.

Occurrences in Texas (Winston and Nicholls, 1967; Longacre, 1970) and Oklahoma (Stitt, 1971) are so poorly documented that they, too, cannot be meaningfully compared with other taxa. Until such time as they are adequately described, with more cranidia, knowledge of librigena and pygidia, etc., they should be regarded as *Euptychaspis* cf. *typicalis*. For the same reasons, two cranidia from Maryland (Rasetti, 1959) should also be placed in open nomenclature.

We regard occurrences of *Euptychaspis* from the Whitehall Formation of New York (Taylor *in* Taylor and Halley, 1974) and the Rabbitkettle Formation of northwest Canada (Ludvigsen, 1982) as each representing a distinct species, but we are reluctant to formally name them in the present state of knowledge. The Whitehall material is known from three cranidia, a librigena, and a pygidium (Taylor and Halley, pl. 2, figs. 4–11). It differs from what little is known of *E. typicalis* most prominently in the fact that its L1 is substantially wider than its L2 (this also distinguishes it from all other material assigned to *E. typicalis*). Further, its anterior glabellar bulb is wider and more inflated than in any other material assigned to *E. typicalis*. It has a prominent eye ridge, not visible on Ulrich's photograph of *E. typicalis* or on any other specimens that have been assigned to the species. Finally, it has very small, subsemicircular palpebral lobes. Additional comparisons are made with other taxa below.

The species from the Rabbitkettle Formation is known from three cranidia, two librigenae, and a pygidium, all silicified (Ludvigsen, 1982, fig. 58K–W). It differs from the Whitehall species in the possession of an L1 that is subequal in width to L2, a considerably less laterally inflated anterior glabellar lobe, longer (exsag.) palpebral lobes, librigena with a much shorter genal spine, a pygidium with two as opposed to three clearly developed axial rings, and in the absence of distinct eye ridges. Caution must obviously be exercised in pygidial comparisons, as each species is represented by only one specimen. However, work in progress on silicified faunas of the Notch Peak Formation of western Utah indicates that in large pygidial samples of *Eupytchaspis*, there is no intrasample variation in axial ring number. Indeed, there is no documented example of variation in this feature in any species of *Euptychaspis*. The two cranidia from the Mistaya Formation of the southern Canadian Rocky Mountains illustrated by Westrop (1986b) are comparable in all available details to the Rabbitkettle material (including the presence of fine anastomosing sculpture at the base of the occipital spine) and may well prove conspecific.

Euptychaspis dougali shares with the Whitehall species a pygidium with three distinct axial rings and a very similar librigena with a long genal spine. In addition to its glabellar autapomorphies, *E. dougali* differs in that its L1 is subequal to, or even narrower than, its L2, its anterior glabellar bulb is less inflated, it lacks eye ridges, it lacks a very sharp break in slope of the frontal area (demarcated in the Whitehall species by a prominent, transverse sculptural ridge), and it has longer, larger palpebral lobes with a much less prominent palpebral furrow. *E. dougali* can be differentiated from the Rabbitkettle species (in addition to its glabellar autapomorphies) in the possession of a more transverse versus more rounded anterior cranidial margin in dorsal view (this could be affected by distortion of the Rabbitkettle specimens), relatively wider interocular fixigena, less well impressed palpebral furrow, much longer genal spine, and a pygidium with three versus two axial rings. The pygidium of *E. dougali* has a prominent median notch in its posterior margin (Pl. 6, fig. 44) that is not present in the Rabbitkettle specimen (Ludvigsen, 1982, fig. 58S), but this apparent difference could be influenced by photographic orientations and should be confirmed on the basis of additional specimens.

Family **ILLAENURIDAE** Vogdes, 1890

Genus **ILLAENURUS** Hall, 1863

Type species.—*Illaenurus quadratus* Hall, 1863, p. 176.

Illaenurus montanensis Kobayashi, 1935

Plate 7, figures 1–37, Plate 8, figures 1–35

Illaenurus montanensis Kobayashi, 1935, p. 48, pl. 10, figs. 1, 2; Westrop, 1986b p. 70, pl. 34, figs. 13–15 (see for complete synonymy).

Diagnosis.—A species of *Illaenurus* with divergent anterior branches of facial sutures; in large individuals, width at anterior end of cranidium exceeds width across palpebral lobes.

Discussion.—As revised by Westrop (1986b, pp. 69–71), *Illaenurus* falls into two stratigraphically segregated groups of species that differ in cranidial length. A lower group, comprising *I. priscus* Resser, 1942, (Westrop, 1986b, pl. 34, figs. 1–5) and *I. holcus* Westrop (1986b, pl. 34, figs. 6–10), is characterized by relatively short cranidia. The stratigraphically higher species, *I. quadratus* Hall, 1863, (Westrop, 1986b, pl. 33, figs. 1–7) and *I. montanensis* Kobayashi, 1935, (Westrop, 1986b, pl. 34, figs. 13–15) have longer cranidia. The material illustrated here conforms to the current concept of *Illaenurus montanensis* by possession of strongly divergent, anterior branches of the facial sutures. Like cranidia from Alberta (Westrop, 1986b, pl. 34, fig. 14), width at the anterior end of the cranidium of large individuals of *I. montanensis* from Nevada exceeds width across the palpebral lobes. Cranidia from Alberta possess punctae along the axial furrows and frontal area that are absent from cranidia illustrated herein. *Illaenurus quadratus* is characterized by subparallel to weakly divergent anterior branches of the sutures and, consequently, the anterior portion of the cranidium is relatively narrower.

Sclerites other than the cranidium have not been illustrated previously. Small librigenae (Pl. 8, figs. 5, 12, 14–16) have long, gently curved genal spines and conspicuous, convex lateral borders. During ontogeny, this spine is reduced to a small, thorn-like structure (Pl. 8, figs. 1, 2, 4, 6) and is lost almost completely in the largest individuals (Pl. 8, fig. 13). The lateral border is lost posteriorly, but is retained as a rim anteriorly (*e.g.*, Pl. 8, figs. 1, 2, 10). The doublure is narrow, and at least one specimen (Pl. 8, figs. 1, 7) suggests that a functional rostral suture was present. In contrast, *I. priscus* Resser (Westrop, 1986b, pl. 33, figs. 14, 15) appears to have had yoked cheeks.

The pygidium of *I. montanensis* has not been described previously. It is subelliptical in outline, with length slightly less than 40 percent of maximum width, and is moderately convex, with height along midline (posterior view) a little less than 25 percent of pygidial width; anterior corners have well-defined articulating facets. The lateral profile is evenly curved upward. The axis is weakly convex and differentiated from the pleural field in posterior view only by a change in slope. The axial ring furrows are completely effaced. The pleural field is effaced except for one pair of pleural furrows at anterior. The doublure occupies about 33 percent of pygidial length and maintains a roughly even width; the anterior margin is weakly undulose. The external surface of the pygidium is smooth except for terrace ridges near, and parallel to, the posterior margin.

Figured material.—Thirteen cranidia (SUI 99124–99137), eleven librigenae (SUI 99138–99149), one thoracic segment (SUI 99154), and five pygidia (SUI 99150–99153, 99155).

Family **CATILLICEPHALIDAE** Raymond, 1937

Genus **TRIARTHROPSIS** Ulrich, *in* Bridge, 1931

Type species.—*Triarthropsis nitida* Ulrich, *in* Bridge, 1931, p. 214.

Triarthropsis limbata Rasetti, 1959
Plate 9, figures 1–25, 28, 32, 33

Triarthropsis limbata Rasetti, 1959, p. 382, pl. 52, figs. 1–8; Ludvigsen, 1982, p. 74, fig. 57U (see for complete synonymy).

Figured material.—Seven cranidia (SUI 99156–99161, 99170) and seven librigenae (SUI 99162–99169).

Discussion.—Wide fixigenae and, on several specimens, a poorly defined anterior border furrow, are shared with *Triathropsis limbata* Rasetti (1959, pl. 52, figs. 1–8). Rasetti's types are variable in glabellar outline but tend to have a somewhat more tapered anterior lobe than the cranidia illustrated herein. Rasetti (1959, p. 382) described faint median furrows on the anterior lobes of his specimens, although they are not evident in his photographs. *Triarthropsis nitida* Ulrich (*in* Bridge, 1931, pl. 19, figs 3, 4; Rasetti, 1959, pl. 55, figs. 6–13; Westrop, 1986b, pl. 39, figs. 8–13) has narrower fixigenae and lacks an anterior border and border furrow. In addition, specimens from Pennsylvania (*e.g.*, Rasetti, 1959, pl. 55, fig. 12) and Alberta (*e.g.*, Westrop, 1986b, pl. 39, figs. 8, 10, 12) have paired tubercles on the fixigenae and glabella.

Triarthropsis marginata (Rasetti, 1945, pl. 60, figs. 9–13; Ludvigsen *et al.*, 1989, pl. 35, figs. 17–19), *T.* cf. *marginata* (Westrop, 1986b, pl. 39, figs. 6, 7) and *T. casca* Ludvigsen and Westrop (*in* Ludvigsen *et al.*, 1989, pl. 35, figs. 20–27) all differ from *T. limbata* in having much shorter frontal areas and palpebral lobes that are located close to the glabella. The poorly known *T. princetonensis* Kobayashi, 1935, (Winston and Nicholls, 1967, pl. 11, fig. 26) differs from *T. limbata* on the basis of the subrectangular glabella that is poorly differentiated from a short anterior border, and palpebral lobes that are centered opposite the S2 glabellar furrow, rather than the L2 lateral lobe.

Librigenae (Pl. 9, figs. 12–25) include some specimens that are yoked. They possess long genal spines and convex lateral borders that carry sculpture of coarse terrace ridges. The librigenal field is narrow and also carries terrace ridges. Similar librigenae have been attributed to *T. nitida* Ulrich (Rasetti, 1959, pl. 55, fig. 9; Westrop, 1986b, pl. 39, fig. 13), and those of *Peracheilus spinosus* (Rasetti, 1945) (Ludvigsen *et al.*, 1989, pl. 34, fig. 17) differ in having a shorter, more slender genal spine and a more convex librigenal field. *Theodenisia gibba* (Rasetti, 1944) (Ludvigsen *et al.*, 1989, pl. 32, fig. 10) has a librigena with sculpture of coarse terrace ridges and a stout genal spine, but the lateral border is not differentiated from the librigenal field.

Triarthropsis sp. 1

Plate 9, figures 26, 27, ?29, 30, 31, 34–38

Figured material.—Three cranidia (SUI 99171–99173) and three librigenae (SUI 99174–99176).

Discussion.—A few cranidia differ from *Triarthropsis limbata* (Pl. 9, figs. 1–11) in having a shorter frontal area and narrower preocular fixigenae. In these respects, they resemble cranidia of T. *marginata* (Rasetti, 1945, pl. 60, figs, 9–13; Ludvigsen *et al.*, 1989, pl. 35, figs. 17–19), *T.* cf. *marginata* (Westrop, 1986b, pl. 39, figs. 6, 7), *T. casca* Ludvigsen and Westrop (*in* Ludvigsen *et al.*, 1989, pl. 35, figs. 20–27) and *T. princetonensis* Kobayashi, 1935, (Winston and Nicholls, 1967, pl. 11, fig. 26). All of these differ from *T.* sp. 1, however, in having smaller palpebral lobes that are located very close to the glabella. In addition, the palpebral lobes of *T. princetonensis* are located farther forward on the cranidium and the anterior end of the glabella is poorly differentiated from the frontal area. Librigenae of *T.* sp. 1 (Pl. 9, figs. 34, 35, 37, 38) are similar to those of *T. limbata* (Pl. 9, figs. 12–25), differing in possessing a much longer posterior segment of the the facial suture that corresponds to a wider posterior fixigena (Pl. 9, fig. 26, 27). Also, the border furrow of *T.* sp. 1 is shallower than on similarly sized librigenae of *T. limbata.*

Family **EUREKIIDAE** Hupé, 1953

Discussion.—Ludvigsen and Westrop (*in* Ludvigsen *et al.*, 1989) suggested that the Eurekiidae could be assigned to the Remopleuridoidea. Although some characters (*e.g.*, size and position of the palpebral lobes) lend support to this view, new information on the structure of the thorax (Pl. 11, figs. 30–35, Pl. 12, figs. 1–5) suggests that eurekiids are not remopleuridoideans. Thoracic segments of *Eurekia* are strongly arched with a well-defined fulcrum and wide inner portion of the pleura; articulation is fulcrate. In contrast, remopleuridoideans have a fulcrum close to the axial furrow and, consequently, very narrow inner portion of the pleura (Whittington, 1997); articulation includes well-developed fulcral processes and sockets (Chatterton and Ludvigsen, 1976, pl. 1, figs. 16–19, 23, 25–29, 31, 49). The Eurekiidae are regarded herein as of uncertain affinities.

Although the broader relationships of the Eurekiidae are uncertain, they may be related to such Early Sunwaptan genera as *Monocheilus* Resser, 1937, and *Stigmacephalus* Resser, 1937. Westrop (1986b) considered such a relationship unlikely, but there are striking similarities in glabellar furrow morphology and size and position of the palpebral lobes between small cranidia of *Monocheilos* (*e.g.*, Westrop, 1986b, pl. 15, figs. 7, 8) and eurekiids. Restudy of the poorly known *Maladia* Walcott, 1924, generally regarded as an early member of the Eurekiidae (*e.g.*, Longacre, 1970), may be helpful in evaluating eurekiid relationships.

Genus **EUREKIA** Walcott, 1916

Type species.—*Ptychoparia* (*Euloma*)? *dissimilis* Walcott, 1884, p. 409 (see Taylor, 1978).

Eurekia rintintini, new species

Plate 10, figures 1–32, Plate 11, figures 1–35, Plate 12, figures 1–29

Diagnosis.—A species of *Eurekia* with sculpture of closely spaced, irregular, star-shaped tubercles over external surface of cranidium, librigenal field, thoracic pleurae, and axis and pleural field of pygidium. Cranidium with distinct preglabellar field that is subequal in length to anterior border. Large pygidium with five pairs of long, widely spaced, tapered marginal spines.

Description.—Cranidium (excluding posterior fixigenae) subrectangular in outline, with width between the palpebral lobes equal to cranidal length; maximum width across posterior fixigenae slightly more than 150 percent of width between palpebral lobes. Convex glabella raised well above level of palpebral lobes and occupies a little more than 80 percent of cranidial length; width is 55 percent cranidial width across palpebral lobes. Occipital ring raised above rest of glabella in lateral view; longitudinal profile of preoccipital glabella curved, with curvature increasing sharply in front of palpebral lobes. Glabellar outline subrectangular; rounded anteriorly. Axial furrows firmly impressed and bowed gently outward, so that maximum glabella width is at S1 furrow or L2 lobe. Occipital furrow well-incised groove, subtransverse medially but deflected forward near axial furrows; occipital ring occupies slightly less than 25 percent of glabellar length. Firmly impressed S1 furrow curves backward and inward from axial furrow. L1 lobe subcircular in outline and slightly shorter than occipital ring; width equal to about 25 percent of glabellar length. S2 furrow as deep as, but less strongly curved than, S1 furrow. L2 lobe equal in length to occipital ring. Frontal lobe accounts for about 27 percent of glabellar length. Frontal area subequally divided into downsloping preglabellar field and upturned, triangular anterior border that is strongly arched in anterior view (Pl. 10, fig. 4); anterior border furrow may be transverse (Pl. 10, figs. 1, 22), forwardly curved (Pl. 10, fig. 16) or bowed gently backward (Pl. 10, fig. 3). Interocular fixigenae narrow, roughly equal in width to palpebral lobe, and upwardly sloping. Palpebral lobe flat to gently upsloping, arcuate band centered opposite L2 lobe; extends from midpoint of L1 to posterior end of frontal lobe. Palpebral furrow finely etched groove. Anterior branches of facial suture weakly convergent, nearly straight before swinging abruptly inward along anterior cranidial margin. Posterior branches diverge at almost 90 degrees to axial furrow, then curve almost straight back. Posterior fixigenae narrow, nearly transverse bands flexed downward at about 45 degrees; bisected by firmly impressed posterior border furrow; posterior border expands abaxially, so that distal width is twice width at axial furrow. Cranidial furrows, inner half of palpebral lobe and preglabellar field lack sculpture; glabella, fixigenae, and anterior border carry sculpture of closely spaced, irregular, star-shaped tubercles; outer part of palpebral lobe has network of anastomosting ridges that produce an irregularly punctate appearance.

Hypostome shield shaped in outline with width about 75 percent of length; posterior margin well rounded and anterior margin bowed gently forward. Convex, subelliptical median body divided unequally by barely perceptible median furrow into crescentic posterior lobe and roughly oval anterior lobe; latter accounts for about 60 percent of median body length. Lateral and posterior borders narrow, convex rims separated from median body by finely etched border furrows; width of posterior border about 50 percent width of lateral border. Anterior border wall-like, directed ventrally well below level of adjacent portions of lateral borders. Anterior wings triangular in outline, flexed dorsally at about 30 degrees; width about 30 percent of hypostome length. Posterior wings narrow, vertically directed prongs with tips curved gently forward. Sculpture of terrace ridges confined to borders and anterior wings.

Librigenae separated by median suture and carry small, thorn-like genal spine. Librigenal field tall, accounting for about 75 percent of librigenal field in lateral view, and slopes steeply downward from eye socle. Socle consists of two bands separated by shallow longitudinal furrow; upper band slightly narrower than lower band. Convex, tube-like border separated from librigenal field by broad, shallow border furrow; inner edge of doublure lies beneath border furrow; panderian notch present near posterior end of doublure. Librigenal field with sculpture of closely spaced, irregular, star-shaped tubercles and coarse, longitudinal ridges on border; doublure with fine terrace ridges.

Thorax of at least 11 segments; tapers gradually backward, so that width at posterior is about 67 percent width at anterior. Axis occupies about 35 percent of segment width in dorsal view; strongly arched, accounting for about 45 percent of segment height in anterior view. Axial furrows shallow, ill-defined grooves. Subelliptical articulating half-ring depressed slightly below rest of ring; firmly impressed articulating furrow transverse medially but curved forward near axial furrows. Pleura with well-defined fulcrum. Inner portion of pleura horizontal; outer portion slopes steeply downward from fulcrum to terminate at short, blunt spine. Well-incised, narrow, nearly transverse pleural furrow divides pleura into subequal anterior and posterior pleural bands; outer portion of anterior band with narrow, subtriangular facet. Facet and articulating half-ring smooth; pleural spine with terrace ridges. Sculpture of closely spaced, irregular, star-shaped tubercles on remainder of segment.

Pygidium subelliptical in outline, with length (excluding marginal spines) slightly more than 50 percent of width; triangular facet at anterior corner. Five pairs of tubular marginal spines that decrease in size posteriorly; posteriormost pair about 33 percent of length of anteriormost. Spines become longer, more slender, distinctly tapered, more pointed, and more widely spaced during holaspid ontogeny (compare Pl. 12, figs. 7, 8, 11, 15, 16 and Pl. 12, figs. 19–21, 23–27). Axis strongly convex, raised well above pleural field, and accounts for about 65 percent of pygidial height in posterior view; in dorsal view, occupies slightly less than 90 percent of pygidial length and about 33 percent of maximum pygidal width; tapers gradually backward, with width at anterior ring about 150 percent of width at terminal piece. Axial furrows broad, clearly defined grooves. Three axial rings and rounded terminal piece; anteriormost ring with conspicuous, semielliptical articulating half-ring and deep, transverse articulating furrow. Rings decrease in length posteriorly, so that first ring is almost twice length of third; terminal piece accounts for about 20 percent of axial length. Two anterior ring furrows firmly impressed, but third furrow shallower. Pleural fields convex, downsloping. Narrow, slot-like pleural and interpleural furrows become shallower and indistinct toward rear; only two pairs usually evident. Subequal anterior and posterior pleural bands usually evident only opposite first axial ring. Doublure narrow, with anterior edge extending to posterior end of axis. Pleural field and axis with sculpture of irregular tubercles; marginal spines carry terrace ridges.

Holotype.—A cranidium (SUI 99178; Pl. 10, figs. 2, 5, 8, 9) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Twelve cranidia (SUI 99177–99187, 99193), seven hypostomes (SUI 99188–99192, 99195, 99196), five librigenae (SUI 99194, 99197–99200), one thoracopygon (SUI 99203), two isolated thoracic segments (SUI 99201, 99202), and eight pygidia (SUI 99204–99211).

Etymology.—Named for Rin Tin Tin.

Discussion.—Irregular, star-shaped turbercles similar to those of *Eurekia rintintini* n. sp. are scattered over external surfaces of *Eurekia* sp. 1 from the Rabbitkettle Formation of the Mackenzie Mountains (Westrop, 1995, pl. 6, fig. 1), although their true morphology cannot be determined on internal molds. *Eurekia* sp. 1 differs from *E. rintintini* in lacking a preglabellar field.

Eurekia longifrons Westrop (1986b, pl. 6, figs. 1–5), from the Mistaya Formation of Alberta, is the only other species with a distinct preglabellar field. This feature is relatively longer than that of *E. rintintini*, and is equal to roughly twice the length of the anterior border. *Eurekia longifrons* also possesses conventional, rounded tubercles on the cranidium and has narrower, less strongly curved palpebral lobes than *E. rintintini*. Pygidia of these two species possess similar marginal spines, but can be differentiated on the basis of sculpture. The type species of *Eurekia*, *E. dissimilis* (Walcott, 1884) (Taylor, 1978, text-fig. 1) from the Windfall Formation of Nevada, is much more strongly convex than *E. rintintini*, so that the anterior third of the glabella slopes steeply downward and partly overhangs the anterior border. *Eurekia ulrichi* (Rasetti, 1945) (Ludvigsen, 1982, fig. 61A–Q), from northern and eastern Canada, has a finely tuberculate sculpture and lacks a preglabellar field. The pygidium of this species has shorter, less tapered marginal spines than *E. rintintini*, and has faint pleural and axial ring furrows posteriorly. The hypostome attributed to *E. ulrichi* is very similar to that of *E. rintintini*, and corroborates the assignment. *Eurekia eos* (Hall, 1863) (Taylor, 1978, pl. 1, figs. 1–17, pl. 2, figs. 1–17), a species that has been reported widely over North America, and *E. bacata* Ludvigsen (1982, fig. 62A–J), from the Rabbitkettle Formation of the Mackenzie Mountains, both differ from *E. rintintini* in lacking a preglabellar field. In addition, the pygidia are differentiated readily from *E. rintintini*. *Eurekia eos* has short, closely spaced, bluntly ended marginal spines (see also Westrop, 1986b, pl. 6, fig. 11), whereas *E. bacata* has a broad axis that overhangs the posterior pygidial axis. Finally, *Eurekia plectocanthus* Loch (*in* Loch *et al.*, 1993, fig. 6.2, 3, 5–7), from the Survey Peak Formation, Alberta, is based upon inadequate material and is probably best restricted to the types. It appears to have possessed an anteriorly rounded glabella that is quite different from the subquadrate glabella of *E. rintintini*.

Genus **CORBINIA** Walcott, 1924

Type species.—*Corbinia horatio* Walcott, 1924, p. 55.

Corbinia implumis Winston and Nicholls, 1967
Plate 13, figures 1–28

Corbinia implumis Winston and Nicholls, 1967, p. 86, pl. 9, fig. 3; Westrop, 1986b, p. 78, pl. 6, figs. 6, 7 (see for complete synonymy).

Bayfieldia binodosa (Hall). Stitt and Straatman, 1997, fig. 9.17 (only).

Diagnosis.—A species of *Corbinia* with coarsely granulose sculpture on cranidium; pygidium with sculpture restricted to terrace ridges on or near marginal spines. Only anterior axial ring and pleural furrows impressed firmly; remaining furrows shallow to barely perceptible. Terminal piece of axis has pair of gently rounded protuberances. Bluntly rounded marginal spines are closely spaced.

Description.—Cranidium (excluding posterior fixigenae) subrectangular in outline, with width across palpebral lobes equal to about 95 percent of length; width across palpebral lobes 67 percent of width across posterior fixigenae. Glabella tapers forward, gently rounded anteriorly and slightly constricted at L1; occupies about 85 percent of cranidial length and 60–70 percent (lower values in smaller cranidia) of cranidial width between palpebral lobes; strongly convex and raised well above palpebral lobes in anterior view. Lateral profile of glabella curved, with occipital ring barely raised above level of L1; degree of curvature increases in front of palpebral lobes. Axial and preglabellar furrows narrow, but clearly defined, grooves. Occipital furrow firmly impressed, transverse medially but curved forward near axial furrow; bifurcates distally, so that occipital ring is composite with small, gently inflated antero-lateral lobe. Occipital ring occupies about 17 percent of cranidial length. S1 and S2 lateral furrows are barely perceptible on even small cranidia (Pl. 13, figs. 3, 4) and not expressed on ventral surfaces (Pl. 13, fig. 11). Short frontal area with distinct preglabellar field equal to 20–30 percent of anterior border length; border furrow may be transverse or bowed gently backward, so that outline of border may be subtriangular (Pl. 13, fig. 3) to transversely subelliptical. Border gently upturned in lateral view and moderately arched in anterior view. Palpebral lobes flat to weakly upturned, arcuate bands centered opposite L2; length decreases somewhat through holaspid ontogeny from 45 percent of glabellar length in smaller cranidia to 36 percent in large specimens. Palpebral furrow finely etched groove. Interocular fixigenae narrow, equal in width to palpebral lobe; anterior and posterior tips of palpebral lobes separated from glabella by very narrow strips of fixigenae. Anterior branches of facial sutures very weakly divergent before swinging inward along anterior cranidial margin. Posterior branches initially weakly divergent before diverging abruptly along nearly transverse path; swing backward at anterior tips of posterior fixigenae and are subparallel near posterior margin of cranidium. Posterior fixigenae narrow, nearly transverse bands flexed downward at about 45 degrees; bisected by firmly impressed posterior border furrow (shallower in largest cranidum); posterior border expands abaxially, so that distal width is twice width at axial furrow. Most small cranidia with sculpture of closely spaced, fine tubercles over entire surface; on largest cranidium (Pl. 13, fig. 1), tubercles subdued, more widely scattered, and confined to glabella.

Fixigenae separated by median suture and with very short, sharply pointed genal spine. Eye socle simple, arcuate band. Tall librigenal field slopes steeply downward from socle to broad, shallow anterior border furrow. Anterior border convex, tubular; outer edge of doublure lies beneath border furrow and is deflected by panderian notch near posterior margin of librigena. Sculpture of closely spaced, fine tubercles on librigenal field; coarse, longitudinal ridges on border.

Pygidium subelliptical in outline with length slightly less than half of width; narrow, triangular facet at anterior corner. Five pairs of short, bluntly pointed, closely spaced marginal spines that become progressively more curved inward and reduced slightly in size toward rear; posteriormost pair expressed only as rounded protuberances. Axis convex, gently tapered and long, occupying almost entire pygidial length; width at anterior ring about 35 percent of maximum pygidial width. Axis strongly convex, occupying about 75 percent of pygidial height in posterior view. Two axial rings and long terminal piece that carries pair of ill-defined, rounded protuberances at posterior; terminal piece occupies 40 percent of axis length. Anteriormost ring includes conspicuous, semielliptical articulating half-ring and firmly impressed articulating furrow. Two transverse axial ring furrows; posteriormost very shallow and barely perceptible on some specimens. Pleural field flexed steeply downward, becoming flatter near margin. Two pairs of pleural furrows expressed as narrow grooves on most specimens; interpleural furrows weak. Subequal anterior and posterior pleural bands well defined opposite anteriormost axial ring, but indistinct on remainder of pleural field. Medially, outer edge of doublure reaches posterior end of axis; doublure expands abaxially, so that width at anterior corner of pygidium almost twice width behind axis. Surface smooth except for terrace ridges on and near marginal spines, doublure, and posterior tip of terminal piece.

Figured material.—Four cranidia (SUI 99212–99215), one librigena (SUI 99216), and three pygidia (SUI 99217–99219).

Discussion.—Westrop (1986b) restricted the type species of *Bayfieldia*, *B. tumifrons* Clark, 1924, to the incomplete holotype (Westrop, 1986b, pl. 6, fig. 8), and suggested that *Bayfieldia binodosa* (Hall, 1863) should be assigned to *Corbinia* Walcott, 1924. Pygidia (Hall, 1863, pl. 7, fig. 47) and cranidia (Clark, 1924, pl. 4, fig. 7; see Winston and Nicholls, 1967, p. 84 for discussion) of *C. binodosa* are preserved as sandstone internal molds and have never been illustrated photographically, so that this species is difficult to interpret. Cranidia of *C. implumis* Winston and Nicholls (1967, pl. 9, fig. 3) are coarsely granulose, whereas cranidia from Texas (Winston and Nicholls, 1967, pl. 9, fig. 1) that have been attributed to *C. binodosa* are smooth. Although Longacre (1970; see also Stitt, 1971) argued that *C. binodosa* and *C. implumis* were synonyms, Westrop (1986b) suggested that the distinction between them should be maintained. The material illustrated herein supports the latter view. Cranidia (Pl. 13, figs. 1–15) closely resemble the holotype of *C. implumis* (Winston and Nicholls, 1967, pl. 9, fig. 3), differing only in having an anterior border furrow that is less strongly curved backward posteriorly. The coarsely granulose sculpture is retained through a broad size range, although it is more subdued in the largest (Pl. 13, fig. 1, 15) and smallest (Pl. 13, figs. 4, 10) specimens. Pygidia of C. *implumis* have not been described previously but are quite distinct from those attributed to *C. binodosa*, including Hall's (1863, pl. 7, fig. 47) type. On the dorsal surface (Pl. 13, figs. 18, 19, 21, 24), pygidia of the former species have one well-defined anterior axial ring, and a second ring that is separated from the terminal piece by a faint ring furrow. Pleural furrows also become progressively effaced toward the rear. Expression of axial ring and pleural furrows is equally poor on ventral surfaces (Pl. 13, fig. 27) and, therefore, these features will be ill defined on internal molds. In contrast, Hall (1863, p. 160) noted the presence of three axial rings and a terminal piece in the axis of *C.? binodosa*, and described well-defined ribs on the pleural field. Pygidia attributed to this species by other workers (*e.g.*, Grant, 1965, pl. 15, fig. 18; Winston and Nicholls, 1967, pl. 9, fig. 2; Stitt, 1971, pl. 5, fig. 7) all possess three pairs of firmly impressed pleural furrows that define convex pleural bands. In addition, these pygidia are relatively narrower than those illustrated herein.

Pygidia of the type species of *Corbinia*, *C. horatio* Walcott, 1924 (Westrop and Ludvigsen, 1986, fig. 2.6–

2.8), are closely comparable to those of *C. implumis* in the degree of effacement. *Corbinia implumis* has rounded, closely spaced marginal spines, whereas those of *C. horatio* are widely spaced and sharply pointed. In addition, *C. horatio* lacks the pair of rounded protuberances that are present on the terminal piece of the axis of *C. implumis* (*e.g.*, Pl. 13, figs. 18, 24), and the pleural field carries granulose sculpture. Cranidia of *C. horatio* from Walcott's type lot (Westrop and Ludvigsen, 1986, fig. 2.1, 2.2, 2.5, 2.9) are mostly exfoliated, but demonstrate that the external surface of the fixigena, frontal area, and at least part of the glabella was smooth. This species is also unique in the very small size of the palpebral lobes (*e.g.*, Westrop and Ludvigsen, 1986, fig. 2.9; Westrop, 1986b, pl. 5, fig. 15). Our cranidia of *C. implumis* cover a broad size range and demonstrate that the relative length of the palpebral lobe was reduced during holaspid ontogeny. Only the largest cranidium (Pl. 13, fig. 1) has a palpebral lobe that approaches the size of that of *C. horatio*.

The cranidia of *C. implumis* show the bifurcating occipital furrow and inflated lateral portion of the occipital ring (*e.g.*, Pl. 13, fig. 3) that was included in the diagnosis of *Bayfieldia* by Longacre (1970, p. 36). However, the phylogenetic significance of this feature, which is poorly expressed in *C. horatio*, is unclear because it also occurs in "*Bayfieldia*" *simata* Winston and Nicholls, 1967, (especially "*B.*" *simata* "var. A" Winston and Nicholls, 1967, pl. 9, fig. 24 [regarded herein as a separate species]) and, apparently, *Maladia* Walcott, 1924 (Walcott, 1925, pl. 16, figs. 23, 24).

Family **ENTOMASPIDIDAE** Ulrich, *in* Bridge, 1931

Genus **HETEROCARYON** Raymond, 1937

Type species.—*Heterocaryon platystigma* Raymond, 1937, p. 1119.

Heterocaryon vargum Westrop, 1986b
Plate 14, figures 1–33

Heterocaryon vargum Westrop, 1986b, p. 80, pl. 40, figs. 4–6 (see for complete synonymy); Loch *et al.*, 1993, fig. 6.10.

Figured material.—Five cranidia (SUI 99220–99224), seven librigenae (SUI 99225–99230, 99232), and two pygidia (SUI 99231, 99233).

Discussion.—Cranidia from the Bullwhacker Member (Pl. 14, figs. 1–16) are closely comparable to silicified specimens from the Rabbitkettle Formation, northwest Canada (Ludvigsen, 1982, fig. 55A–F, H, L) assigned to *Heterocaryon vargum* Westrop, 1986b, a species known from two cranidia from the Mistaya Formation of the southern Canadian Rocky Mountains. Pygidia illustrated herein (Pl. 14, figs. 26, 27, 29–33) are somewhat longer than those from the Rabittkettle Formation, and have a weak medial indentation (Pl. 14, figs. 30, 33) in the ventral margin of the steeply sloping border. Ludvigsen (1982, fig. 55G) illustrated a single incomplete librigena. New material illustrated herein (Pl. 14, figs. 17–19) demonstrates that the species, like *Bowmania* (Pl. 16, figs 18, 21, 22; Ludvigsen, 1982, fig. 54F; Westrop, 1995, pl. 14, fig. 5), possessed yoked librigenae.

Genus **BOWMANIA** Walcott, 1924

Type species.—*Arethusina americana* Walcott, 1884, p. 62.

Discussion.—In his revision of the genus, Ludvigsen (1982, p. 69) included the presence of marginal cephalic spines on the librigenae in the diagnosis of *Bowmania*. *Bowmania lassieae* n. sp. from the Bullwhacker Member at Cherry Creek has a fringe of closely crowded, very short spines, and possession of a row of elongate spines can now be interpreted as a probable autapomorphy of the type species, *B. americana* (Walcott, 1884). Librigenae are unknown for other species currently assigned to the genus. Ludvigsen (1982, p. 72) noted that highly spinose librigenae occurred with cranidia of *Bowmania pennsylvanica* Rasetti, 1959, in the Frederick Limestone of Maryland. The types of *B. pennsylvanica*, however, are from the Conococheague Formation and lack librigenae; cranidia from the Frederick Limestone are poorly preserved and only "tentatively attributed to the species" (Rasetti, 1959, p. 396). Thus, the nature of the librigenae of *B. pennsylvanica* remains uncertain.

The dorsal pygidial margins of *B. americana* (Ludvigsen, 1982, figs, 53K, 54H–L: Westrop, 1995, pl. 14, figs. 7, 9, 11) and *B. bridgei* (Rasetti, 1952, pl. 117, fig. 13) have narrow, nearly continuous raised rims, composed of low, closely spaced subrectangular pleural spines, and Ludvigsen (1982, p. 69) included this trait (misconstrued as a "pygidial border") in his diagnosis. In the pygidium of *B. lassieae* (Pl. 17, figs. 1–16, 18–20, 23, 25, 26, 28) the pleural spines are less crowded, and are similar to those of *Heterocaryon vargum* (see above) (Pl. 14, figs. 26, 29, 30–33).

Bowmania lassieae, new species
Plate 15, figures 1–30, Plate 16, figures 1–30, Plate 17, figures 1–16, 18–20, 23, 25, 26, 28

Diagnosis.—A species of *Bowmania* with a very subdued fringe of small spines along cephalic margin; occipital spine absent in all but smallest holaspids. Anterior cranidial border long, convex, with length roughly equal to occipital ring. Cranidial sculpture of closely spaced tubercles augmented by fine pits. Pygidial border formed by incompletely fused, square-tipped marginal spines.

Description.—Cranidium subtrapezoidal in outline, with forwardly curved anterior margin; length 80 percent of width across palpebral lobes, and maximum width across posterior fixigenae 125 percent of width at palpebral lobes. Posterior cranidial margin curved weakly (Pl. 15, fig. 1) to strongly (Pl. 15, fig. 2) backward, so that lateral tips of posterior fixigenae extend back slightly to well behind occipital ring. Glabella parallel sided and well rounded anteriorly, with length 67 percent of cranidal length and width 33 percent of cranidial width across palpebral lobes; strongly convex and stands well above level of fixigenae; in most specimens, accounts for about half of cranidial height in anterior view. Longitudinal profile of glabella weakly convex between occipital furrow and anterior tips of palpebral lobes, then sloping forward to become nearly vertical at preglabellar furrow. Axial and preglabellar furrows shallow grooves. Finely etched occipital furrow is transverse medially but curved forward near axial furrow. Occipital ring accounts for slightly more than 20 percent of glabellar length; may bear large median tubercle or, in smallest individuals, minute, thorn-like occipital spine. Firmly impressed S1 furrow short and oblique, terminating close to axial furrow; S2 similar but more transverse. L1 about twice length of L2 and occupies about 20 percent of glabellar length; frontal lobe accounts for nearly 40 percent of glabellar length. Long frontal area with inflated, steeply sloping preglabellar field and shorter, gently convex anterior border; border occupies 33–40 percent of frontal area length. Anterior border furrow well-incised groove and curved forward, roughly parallel to anterior cranidial margin. Small, semicircular, gently upsloping palpebral lobe centered opposite L2 or, less commonly, S2 and equal to about 25 percent of glabellar length; differentiated from broad, gently inflated interocular fixigenae by change in slope. Convex palpebral ridge curved gently forward and reaches glabella near mid-length of frontal lobe. Anterior branches of facial sutures weakly convergent before swinging inward along anterior cranidial margin. Posterior branches moderately divergent, but curve inward at posterior border furrow. Posterior fixigenae with firmly impressed posterior border furrow and convex posterior border; near axial furrow, border equal to about seven percent of cranidal length and increases somewhat in length distally. Surfaces of fixigenae and preglabellar field finely pitted and carry closely spaced tubercles that are perforated by median pores in large cranidia. Similar tubercles present on glabella, anterior and posterior border and palpebral ridges, and scattered fine tubercles on inner part of palpebral lobe.

Librigenae yoked anteriorly and carry long genal spines that curve gently outward and backward, and may be flexed upward distally; spine equal to 325 percent of length of librigenal field. Eye socle of two narrow bands separated by finely etched groove; upper band slightly smaller than lower band. Librigenal field tall, accounting for about 65 percent of librigenal height in lateral view, and slopes steeply downward from socle to borders. Lateral and posterior borders broad, shallow, confluent grooves. Lateral and posterior borders convex; doublure also convex and outer edge lies beneath border furrow. Librigenal field with pitted sculpture augmented with "pitted" tubercles similar to those on cranidium. Tubercles also present on lateral and posterior borders, and continue along proximal 33 percent of genal spine; remainder of genal spine finely granulose. Doublure carries fine terrace ridges.

Thoracic segment with very long, gently inclined axial spine; spine about 14 times length of rest of segment. Axis narrow, equal to slightly more than 20 percent of segment width, and convex, accounting for about 50 percent of segment height. Articulating half-ring slightly more than half of length of axial ring; articulating furrow transverse. Inner portion of pleura horizontal; outer portion flexed gently downward at fulcrum and teminates at slender spine. Pleural furrow transverse, finely etched groove and divides pleura into subequal anterior and posterior pleural bands. Pleurae and axial ring with sculpture of fine tubercles; tubercles present on proximal part of axial spine but grade into granulose scupture distally.

Pygidium subelliptical in outline, with length about 50 percent of maximum width. Axis long and narrow, occupying about 80 percent of pygidial length and 25 percent of maximum pygidial width; convex, standing well above pleural field and accounting for about 60 percent of pygidial height. Six axial rings and rounded terminal piece; anterior ring with semielliptical articulating half-ring, equal to about 50 percent of length of ring and transverse, finely etched articulating furrow. Ring furrows also transverse and finely etched. Pleural fields weakly arched in posterior view; flat near axis but flexed gently downward distally. At least four pairs of well-incised pleural furrows define subequal pleural bands. Anterior furrow nearly transverse before curving gently backward near border. Other furrows are increasingly oblique toward rear, and posteriormost does not reach border. Interpleural furrows finely etched and parallel to pleural furrows. Pygidial rim formed by closely crowded, square-tipped pleural spines. Border descends steeply from rim. Doublure extends inward medially to posterior edge of axis, but widens abaxially to become about 200 percent of medial width at anterior corners of pygidium. Sculpture of fine tubercles on axial rings and pleural bands; on some segments, sculpture is missing on some anterior pleural bands.

Holotype.—A cranidium (SUI 99234; Pl. 15, figs. 1, 4, 7, 12, 13) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Fifteen cranidia (SUI 99234–99248, 99250), four librigenae (SUI 99251, 99253–99255), one thoracic segment (SUI 99249), and nine pygidia (SUI 99256–99264).

Etymology.—Named for Lassie.

Discussion.—The type species of *Bowmania, B. americana* (Walcott, 1884) is known from a single cranidium from the Eureka mining district of Nevada. Specimens from various regions of Laurentia have been assigned to it, but more data from Nevada are required to properly evaluate the true range of variation of the species. Material from elsewhere (Ludvigsen, 1982, fig. 53K–S, fig. 54A–O; Westrop, 1995, pl. 14, figs. 1–14), is variable in sculpture, frontal area length, and glabellar proportions, but all cranidial morphs are characterized by the presence of an occipital spine and a shorter anterior border than *B. lassieae*; librigenae have fringe of long marginal spines (Ludvigsen, 1982, figs. 53P, 54F, G, M–O; Westrop, 1995, pl. 14, figs. 5, 12). The type lot of *B. pennsylvanica* Rasetti (1959, pl. 55, figs. 1–5) apparently varies somewhat in cranidial sculpture (Taylor *in* Taylor and Halley, 1974, p. 21), but all specimens are characterized by very short anterior borders. The cranidum identified as *B.* cf. *B. pennsylvanica* by Taylor (*in* Taylor and Halley, 1974, pl. 2, figs. 12–14) also has a short anterior border, and the preglabellar field descends steeply from the anterior end of the glabella. *Bowmania sagitta* Winston and Nicholls (1967, pl. 10, figs. 19, 20) has a medially pointed anterior margin, which gives the cranidium a subpentagonal outline.

The less crowded pygidial pleural spines separates the pygidium of *B. lassiae* (Pl. 17, figs. 1–16, 18–20, 23, 25, 26, 28) from all other species of the genus for which this sclerite is known (*e.g.*, Rasetti, 1952, pl. 117, fig. 13; Ludvigsen, 1982, figs, 53K. 54H–L; Westrop, 1995, pl. 14, figs. 7, 9, 11).

Family **PLETHOPELTIDAE** Raymond, 1925

Discussion.—The most recent evaluation of the Plethopeltidae was presented by Ludvigsen and Westrop (*in* Ludvigsen *et al.*, 1989, p. 56). Of the characters listed in their diagnosis, the terminations of the thoracic pleurae appear to be the most robust of the potential synapomorphies that define the group. *Plethopeltis* Raymond, 1913, has distinctive, square-tipped segments with ill-defined spines that appear to be continuations of the anterior pleural bands (Ludvigsen *et al.*, 1989, pl. 45, figs. 9–11, pl. 46, fig. 2, 3). Identical thoracic tips are present in *Leiocoryphe* Clark, 1924 (Ludvigsen *et al.*, 1989, pl. 48, fig. 11, pl. 49, figs. 7, 11, 12) and on all but the three anterior segments of *Stenopilus pronus* Raymond, 1924 (Stitt, 1976, pl. 2, fig. 1).

A wide range of pygidia have been attributed to species assigned to *Plethopeltis* (*e.g.*, Rasetti, 1959, pl. 53, figs. 3, 5, 7, 10, 13; Stitt, 1971, pl. 6, figs. 13, 14, 18, pl. 8, fig. 14; Westrop, 1986b, pl. 36, figs. 7, 10, 12, 13, pl. 37, figs. 6, 8–10, 14, 15; Ludvigsen *et al.*, 1989, pl. 45. figs. 2, 9, 10, pl. 46, figs. 12, 14, 18, 19), suggesting that the current classification captures only a fraction of the phylogenetic structure that might be retrieved from a detailed analysis of the Plethopeltidae. Recognition of *Plethometopus* Ulrich, in Bridge, 1931, and *Plethopeltis* as differently effaced grades, however, as advocated by Loch *et al.* (1993), does not address this issue and merely creates paraphyly in *Plethopeltis*. Further revision is needed, but is beyond the scope of this monograph.

CHERRYCREEKIA, new genus

Type species.—Cherrycreekia benjii, new species.

Diagnosis.—A genus of? Plethopeltidae with cranidial outline bluntly pointed at anterior. Librigenae with long, slender, outwardly curved genal spine. Pygidium with short axis reduced to single axial ring and terminating at conspicuous ridge that is directed steeply upward and backward. Pleural and interpleural furrows absent.

Etymology.—For the Cherry Creek Range.

Assigned species.—Bynumiella? oklahomensis Resser, 1942; *Cherrycreekia benjii* n. sp.

Discussion.— *Cherrycreekia* resembles several variably effaced, mostly small and probably polyphyletic Sunwaptan trilobites, including *Calvipelta* Westrop, 1986b and *Pugionicauda* Westrop, 1986b. Westrop (1986b) initially assigned them to the family Kingstoniidae but later (Westrop, 1992) argued that differences in the structure of the occipital ring cast doubt on a relationship with such genera as *Kingstonia* Walcott, 1924, and *Bynumia* Walcott, 1924. As discussed above, *Calvipelta* may prove to be an effaced euptychaspidine, but the affinities of *Pugionicauda* remain uncertain.

Cranidia from the Mistaya Formation, Alberta, (Westrop, 1986b, pl. 41, figs. 11–13) are clearly conspecific with those illustrated herein (Pl. 18, figs. 1–23, 29, 30). In discussing the affinities of this species, Westrop (1986b) made comparisons with *Acheilus* Clark, 1924, (see Ludvigsen, 1986), but noted that differences in the size and position of the palpebral lobes made an assignment to that genus questionable. Also, the glabella of *Acheilus* is subrectangular in outline (Ludvigsen *et al.*, 1989, pl. 37, figs. 6, 12), whereas *C. oklahomensis* (Resser, 1942) (Westrop, 1986b, pl. 41, fig. 8) has a glabella that is tapered anteriorly. Thus, while comparisons between effaced taxa are fraught with difficulty, the available information makes a close relationship between *Cherrycreekia* and *Acheilus* unlikely.

Cherrycreekia is most likely a member of the family Plethopeltidae. The new silicified material (Pl. 18, figs. 1–23) shows that the cranidial outline of *Cherrycreekia* is very similar to that of *Plethopeltis* (*e.g.*, see Ludvigsen, 1982, fig. 56T–V; Ludvigsen and Westrop, 1983b, pl. 19, figs. 1–5, 8, 9; Westrop, 1986b, pl. 36, figs. 1, 2, 14, 16, 17, 19, pl. 37, figs. 1–3, 11–13), and differs only in the bluntly pointed, rather than evenly rounded, anterior cranidial margin (*e.g.*, Pl. 18, fig. 16) and the less divergent posterior branches of the facial sutures. The long, slender, outwardly curved genal spines differ from the short, stout spines that are developed in *Plethopeltis* (*e.g.*, Ludvigsen and Westrop, 1983b, pl. 18, figs. 7, 8, 13, pl. 19, fig. 10; Westrop, 1986a, pl. 36, fig. 5; Ludvigsen *et al.*, 1989, pl. 45, fig. 11, pl. 46, fig. 1); other plethopeltid genera possess rounded genal angles (*e.g.*, Ludvigsen *et al.*, 1989, pl. 47, fig. 3, pl. 48, figs. 3, 9, pl. 49, fig. 22, pl. 50, figs. 1, 2).

Square-tipped thoracic segments (Pl. 17, figs. 48, 49) similar to those of *Plethopeltis* and *Leiocoryphe* (*e.g.*, Ludvigsen *et al.*, 1989, pl. 45, figs. 9–11, pl. 46, fig. 2, 3, pl. 48, fig. 11, pl. 49, figs. 7, 11, 12) may belong to *Cherrycreekia* and provide strong support for an assignment to the Plethopeltidae.

The pygidium of *Cherrycreekia* has a distinctive ridge at the posterior end of the short axial lobe that must have docked with the cephalic doublure during enrollment. Although a wide diversity of plethopeltid tails have been described (*e.g.*, Rasetti, 1959, pl. 3, figs. 3, 5, 7, 13, 18, 19, 20, 21, 28–30; Stitt, 1971, pl. 4, fig. 10, pl. 6, figs. 13, 14, 18, pl. 8, fig. 14; Westrop, 1986b, pl. 36, figs. 7, 10, 13, pl. 37, figs. 6, 8, 9, 14; Ludvigsen *et al.*, 1989, pl. 45, figs. 2, 9, pl. 46, figs. 3, 12, 14, 18, 19, pl. 47, figs. 5, 6, 8, 9, 11–14, pl. 48, figs. 5, 18–20, pl. 49, figs. 3, 7, 11, 12, 19), none possesses a comparable structure. Ridge-shaped structures that presumably functioned in enrollment also occur on pygidia of the euptychasidine, *Euptychaspis* (Pl. 6, figs. 37–39, 42–44; see also Taylor and Halley, 1974, pl. 2, fig. 11; Ludvigsen, 1982, fig. 58S–U; Westrop, 1995, pl. 7, fig. 21), but are much lower than in *Cherrycreekia*. In both genera, the down-sloping region of the pygidium outside of the ridge is unfurrowed, and carries a sculpture of anastomosing terrace ridges or coarser ridges. Despite these general similarities, we are confident the pygidium of *Cherrycreekia* is correctly assigned. Sclerites of *Cherrycreekia* do not occur in association with cranidia and librigenae of euptychaspidines. There are numerous differences in the structure of the cranidia and librigenae between *Euptychaspis* and *Cherrycreekia*, so that pygidial similarities are reasonably interpreted as homoplasious. It is also worth noting that several features of the pygidium of *Cherrycreekia* also occur in some plethopeltids, including the overall outline and the convex, down-sloping pleural field with sculpture of terrace ridges (*e.g.*, Rasetti, 1959, pl. 53, figs. 17–19).

Cherrycreekia benjii, new species

Plate 18, figures 1–30, Plate 19, figures 1–11, 17,
?Plate 17, figures 48, 49

Acheilus? cf. *oklahomensis* (Resser, 1942). Westrop, 1986b, p. 83, pl. 41, figs. 11–13 (only; fig. 10 = *Calvipelta spinosa*).

Diagnosis.—A species of *Cherrycreekia* with glabella effaced anteriorly and with long, slender occipital spine.

Description.—Cranidium subrectangular in outline, with bluntly pointed anterior margin; width across palpebral lobes slightly greater than preoccipital length. Long, slender occipital spine directed gently upward at about 10 degrees and equal to at least 50 percent of preoccipital cranidial length. Lateral cranidial profile gently convex between occipital furrow and anterior tips of palpebral lobes, then slopes evenly downward at about 45 degrees to anterior cranidial margin. Cranidial furrows largely effaced, with very shallow, subparallel axial furrows expressed only between posterior margin and anterior tips of palpebral lobes. Glabella moderately arched posteriorly, occupying about 60 percent of width between palpebral lobes, but undifferentiated from fixigena in front of palpebral lobes. Faint, transverse occipital furrow evident on most specimens; occipital ring subtriangular, length (excluding spine) equal to slightly more than 25 percent of preoccipital cranidial length. Palpebral lobes semielliptical flaps, horizontal or gently down sloping; differentiated from down-sloping interocular field centered slightly behind cranidial mid-length; length equal to about 75 percent of occipital ring length. Anterior branches of facial sutures initially subparallel, then curve smoothly inward to become nearly tranverse at midline; posterior branches diverge for short distance before becoming subparallel. Posterior fixigenae subtriangular in outline and flexed downward at about 45 degrees; posterior border furrow obsolete. External surface of cranidium smooth.

Librigena with long, stout, gently tapered, slightly advanced genal spine curved outward and backward; length about 160 percent length of remainder of librigena. Eye socle composed of two parallel bands separated by shallow, transverse groove; upper band somewhat smaller than lower band. Librigenal field slopes steeply downward almost to cranidial margin; lateral border very narrow rim separated from librigenal field by finely etched groove. Doublure narrow, gently convex and maintains even width. External surface of librigena smooth, except for coarse terrace ridges on border.

Pygidium subelliptical in outline, with length about 80 percent of maximum width; strongly convex, with distinct arch in posterior margin; lateral margins straight, oblique, and broad posterior margin well rounded. Axis very short, equal to about 25 percent of pygidial length, and bounded posteriorly by tall, wall-like ridge extending upward and backward to terminate well above level of axis; in posterior view, ridge has inverted v-shape. Single transverse axial ring and subequal articulating half-ring with gently curved anterior margin; articulating furrow shallow, nearly transverse groove. Pleural field unfurrowed and flexed steeply down to posterior margin; border and border furrow absent. Doublure narrow, gently convex and maintains even width along posterior margin; length equal to 10 percent of pygidial length. Pleural field with sculpture of anastomosing terrace ridges; ridge at end of axis may have small node at apex.

Holotype.—A cranidium (SUI 99276; Pl. 18, figs. 1, 2, 5, 10, 12) from the Bullwhacker Member, Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Eight cranidia (SUI 99276–99282, 99286), three librigenae (SUI 99284, 99285, 99287), three pygidia (SUI 99288–99290) and, possibly, one thoracic segment (SUI 99268).

Etymology.—Named for Benji.

Discussion.— *Cherrycreekia oklahomensis* (Resser, 1942) (Westrop, 1986b, pl. 41, figs. 8, 9; see also Stitt, 1971, pl. 7, fig. 15) differs from *C. benjii* n. sp. in the absence of an occipital spine, and by possession of a more nasute anterior cranidial margin. *Cherrycreekia oklahomensis* is also less effaced, so that the glabella is outlined completely by axial and preglabellar furrows on both the dorsal surface of the exoskeleton (Stitt, 1971, pl. 7, fig. 15) and on internal molds (Westrop, 1986b, pl. 41, figs. 8, 9). Faint S1 lateral furrows and a more firmly impressed occipital furrow are present, as are palpebral ridges.

As discussed above, cranidia from the Mistaya Formation, Alberta, assigned by Westrop (1986b) to *Acheilus* cf. *oklahomensis* (Resser, 1942), are unquestionably conspecific with *C. benji.* Westrop (1986b, pl. 41, fig. 10) also attributed a small, exfoliated pygidium with a long axis to this species, but it most likely belongs to *Calvipelta spinosa* Westrop, 1986b, which occurs through the same stratigraphic interval (Westrop, 1986b, fig. 31).

GLABERASPIS, new genus

Type species.—*Glaberaspis scoobydooi,* new species.

Diagnosis.—A blind, isopygous genus of ?Plethopeltidae with semielliptical pygidium with long, narrow axis that consists of four axial rings and terminal piece. Convex cranidium with conspicuous occipital ring that is curved strongly backward. Where evident, glabella is forwardly tapered and subtriangular in outline.

Etymology.—From *glaber,* hairless, bald, smooth, and *aspis,* shield, in reference to the strongly effaced cranidium of this species.

Assigned species.—*Leiocoryphe occipitalis* Rasetti, 1944; *Leiocoryphe longiceps* Rasetti, 1963; *Bynumiella vescula* Stitt, 1971; *Glaberaspis scoobydooi* n. sp.

Discussion.—In their revision of the plethopeltid genera, Ludvigsen and Westrop (*in* Ludvigsen *et al.,* 1989) assigned *Leiocoryphe occipitalis* Rasetti and *L. longiceps* Rasetti only questionably to that genus in the absence of information of the pygidium. Cranidia of both of these species, and a related new species from the Bullwhacker Member, differ from those of *Leiocoryphe* in possessing conspicuous, backwardly curved occipital rings. The new species has a pygidium (Pl. 19, figs. 24–39) that differs markedly from all previously described plethopeltid pygidia, and provides the basis for the establishment of a new genus. The pygidium of *Glaberaspis scoobydooi* n. gen. and sp. is semielliptical in outline, with a long, well-defined axis that consists of four axial rings and a terminal piece. Cranidia and pygidia show a comparable size range, suggesting that it was isopygous. In contrast, *Leiocoryphe* is micropygous with an effaced lenticular pygidium whose axis is broad and convex (Ludvigsen *et al.,* 1989, pl. 48, fig. 11, pl. 49, figs. 3, 4, 7, 11, 12).

Although the dorsal surface of the cranidium of *Glaberaspis* is effaced, the ventral surface of the exoskeleton shows the barely perceptible outline of an anteriorly tapered, subtriangular glabella (Pl. 19, figs. 16, 19; the dark, triangular areas near the posterior margins of the cranidia are shadows created by flash photography). Taylor (1976) suggested that *Bynumiella vescula* Stitt (1971, pl. 7, figs. 16–18) should be assigned at least questionably to *Leiocoryphe.* The well-defined occipital ring and anteriorly tapered, subtriangular glabella, however, both suggest that this species is related to *G. scoobydooi*. Differences between these two species are discussed below.

Like *Leiocoryphe* and *Glaberaspis*, *Meniscocoryphe* Ludvigsen and Westrop (in Ludvigsen *et al.*, 1989) is blind, and possesses broad, short, transversely semi-elliptical pygidia. Although expressed only on the ventral surface of the exoskeleton, the long, narrow axis of *Mensicocoryphe* (*e.g.*, Ludvigsen *et al.*, 1989, pl. 49, fig. 19) appears to consist of at least four segments and, in this respect, resembles the pygidium of *Glaberaspis*. Pygidia of *Meniscocoryphe* (*e.g.*, Stitt, 1971, pl. 4, fig. 10; Westrop, 1986b, pl. 38, fig. 21; Ludvigsen *et al.*, 1989, pl. 49, figs. 19, pl. 50, fig. 3) encompass a similar size range as associated cranidia and it is possible that this genus, like *Glaberaspis*, was isopygous.

Both *Stenopilus* and *Plethopeltis* differ from *Glaberaspis* in possessing eyes. Cranidia of *Stenopilus* (*e.g.*, Ludvigsen *et al.*, 1989, pl. 47, figs. 1–4, 7, 16–22, pl. 48, figs. 1–3, 8, 9, 13–16) are comparable to *Glaberaspis* in the degree of effacement, but are more strongly arched longitudinally. The effaced pygidia of *Stenopilus* are typically short and possess broad, convex axes (*e.g.*, Ludvigsen *et al.*, 1989, pl. 47, figs. 5, 6, 9, 12–14, pl. 48, figs. 4–6, 12). The glabella of *Plethopeltis* is defined by axial furrows at least posteriorly and, where fully expressed, is very gently tapered and rounded anteriorly (*e.g.*, Ludvigsen and Westrop, 1983b, pl. 18, figs. 1–3, 9, 12, pl. 19, figs. 1, 6, 8, 11, 13). In late meraspids of *Plethopeltis hastatus* (Westrop, 1986b, pl. 38, fig. 14), however, the glabella is subtriangular in outline, and resembles *Glaberaspis* much more closely. Although most species of *Glaberaspis* possess posteriorly rounded occipital rings, *G.* cf. *G. occipitalis* from the Shallow Bay Formation (Ludvigsen *et al.*, 1989, pl. 49, figs. 17, 18) has a tapered, posteriorly pointed occipital ring and distinct occipital furrow that closely resembles those of some species of *Plethopeltis* (*e.g.*, Westrop, 1986b, pl. 36, figs. 8, 9, pl. 37, fig. 6; Ludvigsen *et al.*, 1989, pl. 46, figs. 6, 8, 13)

In the absence of information on the thoracic segments, assignment of *Glaberaspis* (and *Meniscocoryphe*) to the Plethopeltidae must be tentative. It is also worth making comparisons with *Clelandia* Cossman, a genus whose affinities are currently uncertain. Westrop (1986b) commented on the similarities between some species of this genus and *G. vescula*. The glabella of the type species, *C. typicalis* (Resser, 1942) (Westrop, 1986b, pl. 41, figs. 20–30) is strongly tapered and subtriangular in outline. Lateral glabellar furrows are effaced on the external surface of the exoskeleton but, as in *G. vescula* (*e.g.*, Stitt, 1971, pl. 7, figs., 17, 18), they are expressed on internal molds as ill-defined pits that are connected across the glabella by a shallow furrow (*e.g.*, Westrop, 1986b, pl. 41, figs. 23, 24). Pygidia of *Clelandia* are quite different from those of *Glaberaspis* or any other plethopeltid (Norford, 1969).

Glaberaspis scoobydooi, new species
Plate 19, figures 12–16, 18–39

Diagnosis.—A species of *Glaberaspis* with conspicuous, posteriorly rounded occipital rings that lacks an occipital furrow. Glabella is poorly defined on ventral surface of exoskelton.

Description.—Cranidium subelliptical in outline, with width between posterior corners of fixigenae 90–95 percent of length; strongly convex with highest point at posterior end of occipital ring; lateral profile gently curved upward and steeping in slope along anterior third of cranidium. All cranidial furrows completely effaced on dorsal surface; strongly tapered, subtriangular glabella outline barely perceptible on ventral surface. Occipital rings conspicuous, occupying about 30 percent of cranidial length and about 70 percent of maximum cranidial width; posterior margin curved strongly backward. Palpebral lobes absent. In dorsal view, sutures converge forward in smooth curve. In anterior view, each branch of the sutures appears gently curved upward, meeting on midline, so that anterior tip of cranidium is pointed (Pl. 19, fig. 20). External surface of cranidium is smooth.

Pygidium semielliptical in outline with length 67–80 percent of maximum width (lower proportions in smaller pygidia). In posterior view, axis and pleural fields weakly arched, with very weakly concave lateral margins descending steeply. Axis long, narrow, tapered gradually backward, and gently convex, occupying 33–43 percent of pygidial width at anterior (lower proportions in smaller pygidia), and nearly 95 percent of pygidial length in dorsal view. Axial furrows very shallow grooves. Axial rings and ring furrows ill defined on dorsal surfaces of larger pygidia; ventral surfaces of larger pygidia and dorsal surfaces of some small individuals show four axial rings and rounded terminal piece separated by nearly transverse axial furrows. Pleural field crossed by faint, oblique pleural furrows. Border in form of narrow rim at base of steeply descending flanks of pygidium. External surface of pygidium is smooth.

Holotype.—A cranidium (SUI 99291; Pl. 19, figs. 12, 14, 19, 20) from the Bullwhacker Member of the Windfall Formation, Barton Canyon, Cherry Creek Range.

Figured material.—Three cranidia (SUI 99291–99293) and five pygidia (SUI 99294–99298).

Etymology.—Named for Scooby-Doo.

Discussion.—The conspicuous, well-rounded occipital ring of *Glaberaspis scoobydooi* is shared with *G. occipitalis* (Rasetti, 1944), a species that has been reported from the south-central United States (*e.g.*, Bell and Ellinwood, 1962; Stitt, 1971) and eastern Canada (Rasetti, 1944; Ludvigsen *et al.*, 1989). However, all cranidia assigned previously to the latter species (Bell and Ellinwood, 1962, pl. 59, fig. 4; Stitt, 1971, pl. 4, fig. 13; Ludvigsen *et al.*, 1989, pl. 49, figs. 15, 16) possess a well-defined occipital furrow on both testate and exfoliated surfaces, whereas the furrow is absent on *G. scoobydooi*. In addition, the occipital ring is the most elevated portion of the cranidium of *G. scoobydooi* (Pl. 19, figs. 14, 18, 21), whereas stereopairs of *G. occipitalis* (*e.g.*, Stitt, 1971, pl. 4, fig. 13) indicate that the central portions of the cranidium are strongly convex and are elevated above the occipital ring. *Glaberaspis* cf. *G. occipitalis* from the Shallow Bay Formation of western Newfoundland (Ludvigsen *et al.*, 1989, pl. 49, figs. 17, 18) has a tapered, posteriorly pointed occipital ring and distinct occipital furrow, and probably represents an undescribed species. *Glaberaspis longiceps* (Rasetti, 1963, pl. 130, figs. 21–26) has a relatively narrower cranidium than *G. scoobydooi* and is much more convex, so that the anterior end slopes almost downward in lateral view. In addition, an occipital furrow is expressed on at least larger individuals (Rasetti, 1963, pl. 130, fig. 25).

Glaberaspis vescula (Stitt, 1971, pl. 7, figs. 16–18; see also Taylor, 1976, pl. 3, fig. 21) bears a superficial resemblance to *G. scoobydooi*, but shows an anteriorly tapered glabella on testate (Stitt, 1971, pl. 7, fig. 16) and exfoliated surfaces (Stitt, 1971, figs. 17, 18; Westrop, 1986b, pl. 41, fig. 31). Stitt (1971, p. 23) describes "very faint" palpebral lobes and furrows, although they are not evident in his photographs (1971, pl. 7, figs. 16–18). Examination of the holotype (OU 6519) and paratypes (OU 6520, OU 6521), housed at the Oklahoma Museum of Natural History, showed that these features are not present. The apparent deflection in the suture on the left side of the holotype (Stitt, 1971, pl. 7, fig. 16) is actually a broken surface, and the sutures form a smooth curve in lateral view. At least parts of the lateral cranidial margins of the paratypes have been damaged during preparation and do not show the true course of the facial sutures.

Family **UNCERTAIN**

GEN. AND SP. INDET.

Plate 17, figures 51–53

Figured material.—One cranidium (SUI 99275)

Discussion.—A single cranidium is characterized by a narrow, convex, gently tapered, anteriorly rounded glabella with three pairs of shallow lateral furrows. Palpebral lobes are long, extending from the occipital furrow to the S3 furrow, and are separated from narrow fixigenae by finely etched palpebral furrows. The short frontal area lacks an anterior border and border furrow.

The long palpebral lobes invite comparison with genera of the Dikelocephalidae or, perhaps, Eurekiidae. However, dikelocephalids typically possess conspicuous, transglabellar S1 furrows throughout the holaspid ontogeny (*e.g.*, Pl. 2, figs. 2, 13, 15, 34), whereas the cranidium described herein has weak lateral furrows only. Some eurekiids have lateral furrows that approach those of our cranidium (*e.g.*, Ludvigsen, 1982, fig. 61A–F), but those species with long palpebral lobes are characterized by very narrow interocular fixigenae (*e.g.*, Westrop, 1986b, pl. 6, fig. 15).

UNASSIGNED SCLERITES

Plate 17, figures 17, 21, 22, 24, 27, 29–47, 50

Discussion.—Thoracic segments with narrow pleurae and extremely long axial spines (Pl. 17, figs. 17, 21, 22, 24, 27, 29, 30, 34, 36) are presumably from the posterior part of a thorax. Similar segments occur at the end of the thoraces of articulated individuals of *Yukonaspis* from the lower Bullwhacker Member at Cherry Creek (Adrain and Westrop, unpublished data), although other sclerites of this genus have not been recovered from the samples described herein.

Hypostomes have been attributed to very few Sunwaptan trilobites. Eurekiid (Ludvigsen, 1982; Pl. 11, figs. 1–11), plethopeltid (Westrop, 1986b, pl. 36, fig. 3, pl. 37, fig. 16; Ludvigsen *et al.*, 1989, pl. 46, fig. 15) dikelocephalid (Pl. 1, figs. 5, 6, 8; Ulrich and Resser, 1933, pl. 26, fig. 6, pl. 31, fig. 2, pl. 35, fig. 5, pl. 36, fig. 13, pl. 37, fig. 3; Shergold, 1991, pl. 3, fig. 11, pl. 4, figs. 7, 14, 20) and ptychaspidid (Lochman and Hu, 1959, pl. 58, fig. 25; Westrop, 1986b, pl. 7, fig. 9, pl. 8, figs. 4, 16) hypostomes have been documented and, on this basis, the specimens illustrated herein are unlikely to belong to *Prosaukia, Euptychaspis, Sunwaptia, Corbinia, Cherrycreekia* or *Glaberaspis*.

The hypostomes are similar in outline, convexity and shape of the median body, expression of the median furrow and the morphology of the lateral and posterior borders. They differ in size and position of the anterior and posterior wings. On the basis of size, the larger specimens illustrated herein (Pl. 17, figs. 33, 35, 37, 40, 42, 45) might belong to *Illaenurus montanensis*.

A single pygidium (Pl. 17, figs. 31, 38, 43) is convex with a well-defined axis of three rings and a terminal piece, weakly furrowed pleural field, narrow posterior border and a well-defined median embayment of the posterior margin in posterior view. Only two genera, *Triarthropsis* and Gen. Uncertain, are potential candidates for this pygidium, as all others occur with pygidia that are assigned with confidence. Although a wide variety of pygidia have been attributed to catillicephalids (*e.g.*, Ludvigsen *et al.*, 1989, pl. 32, figs. 21, 22, 28, 29, pl. 34, figs. 13, 28, 29, pl. 35, fig. 7), the specimen illustrated herein is unlikely to belong to either species of *Triarthropsis* present in our collections. The pygidia associated with holotype of *T. limbata* Rasetti in Virginia (Rasetti, 1959, pl. 52, figs. 5–8) are quite different, with long, multi-segmented axes and pleural fields traversed by up to six pairs of firmly impressed pleural and interpleural furrows. The pygidia that occur with cranidia of *T. nitida* Ulrich (Rasetti, 1959, pl. 55, figs. 6–8) are comparable to those of *T. limbata* and are unlike our specimen.

As noted earlier, under the discussion of *Prosaukia oldyelleri*, dikelocephalid thoracic segments (Pl. 17, figs. 41, 46, 50) are left unassigned because they possess sculpture of coarse granules that is not matched in either of the species described herein. A librigena (Pl. 17, fig. 47) also belongs to a dikelocephalid trilobite but differs from those of *P. oldyelleri* (Pl. 2, figs. 35, 37–39; Pl. 3, figs. 33, 41) in having a shorter, more slender and rapidly tapering genal spine.

REFERENCES CITED

Adair, D.H.

1961. Geology of the Cherry Creek District. Unpublished M.S. thesis, University of Utah, 122 pp.

Adrain, J.M., and Westrop, S.R.

2001. Stratigraphy, phylogeny, and species sampling in time and space. *In* Fossils, Phylogeny and Form: An Analytical Approach. J.M. Adrain, G.D. Edgecombe and B.S. Lieberman, *eds.*, Kluwyer Academic Press/Plenum Publishers, New York, pp. 291–322.

Bell, W.C., and Ellinwood, H.L.

1962. Upper Franconian and lower Trempealeauan Cambrian trilobites and brachiopods, Wilberns Formation, central Texas. Journal of Paleontology, vol. 36, pp. 385–423.

Bell, W.C., Feniak, O.W., and Kurtz, V.E.

1952. Trilobites of the Franconia Formation, southeast Minnesota. Journal of Paleontology, vol. 26, pp. 175–198.

Brady, M.J., and Rowell, A.J.

1976. Upper Cambrian subtidal blanket carbonate of the Cordilleran miogeocline, eastern Great Basin. Brigham Young University Geological Studies, vol. 23, pp. 153–163.

Bridge, J.

1931. Geology of the Eminence and Cardareva Quadrangles. Missouri Bureau of Geology and Mines, Second Series, vol. 24, 228 pp.

Briggs, D.E.G., Fortey, R.A., and Clarkson, E.K.N.

1988. Extinction and the fossil record of arthropods. *In* Extinction and Survival in the Fossil Record. G.P. Larwood, *ed.*, Clarendon Press, Oxford, pp. 171–209.

Chatterton, B.D.E., and Ludvigsen, R.

1976. Silicified Middle Ordovician trilobites from the South Nahanni River area, District of Mackenzie, Canada. Palaeontographica (Abt. A), vol. 154, 106 pp, 22 pls.

Clark, T.H.

1924. The paleontology of the Beekmantown Series at Lévis, Quebec. Bulletins of American Paleontology, vol. 10, no. 41, 134 pp., 9 pls.

Dake, C.L., and Bridge, J.

1932. Faunal correlation of the Ellenburger limestone of Texas. Geological Society of America Bulletin, vol. 43, pp. 725–747.

Devine, T.

1863. Description of a new trilobite from the Quebec Group. Canadian Naturalist and Geologist, vol. 8, pp. 95–98.

Edgecombe, G.D.

1992. Trilobite phylogeny and the Cambrian-Ordovician "event": Cladistic reappraisal. *In* Extinction and Phylogeny. M.J. Novacek and Q.D. Wheeler, *eds.*, Columbia University Press, New York, pp. 144–177.

Ergaliev, G.K

1980. Trilobites of the Middle and Upper Cambrian of Malyi Karatau. Kazakhstan SSR Academy of Sciences, K.I. Satpaev Institute of Geological Sciences, Alma Ata [in Russian], 211 pp.

Evitt, W.R.

1951. Some Middle Ordovician trilobites of the families Cheiruridae, Harpidae and Lichidae. Journal of Paleontology, vol. 25, pp. 587–616.

Fortey, R.A.

1983. Cambrian-Ordovician trilobites from the boundary beds in western Newfoundland and their phylogenetic significance. Special Papers in Palaeontology, vol. 30, pp. 179–211.

Grant, R.E.

1965. Faunas and stratigraphy of the Snowy Range Formation (Upper Cambrian) in southwestern Montana and northwestern Wyoming. Geological Society of America Memoir 96, 171 pp., 15 pls.

Hall, J.

1863. Preliminary notice of the fauna of the Potsdam Sandstone. 16th Annual Report of the Regents of the University of the State of New York on the condition of the Cabinet of Natural History, pp. 119–222.

Hintze, L.F.

1953. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey, Bulletin 48, 249 pp., 28 pls.

1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah. Brigham Young University Geology Studies, vol. 20, pp. 3–36.

Hintze, L.F., Taylor, M.E., and Miller, J.F.

1988. Upper Cambrian-Lower Ordovician Notch Peak Formation in western Utah. United States Geological Survey Professional Paper 1393, 30 pp.

Hu, C.-H.

1973. Description of basal Ordovician trilobites from the Deadwood Formation, northern Black Hills, South Dakota. Proceedings of the Geological Society of China, vol. 16, pp. 85–95.

Hughes, N.C.

1994. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. Smithsonian Contributions to Paleobiology 79, 89 pp., 10 pls.

Hupé, P.

1953. Classification des trilobites. Annales de Paléontologie, vol. 39, pp. 61–169.

Kobayashi, T.

1933. Upper Cambrian of the Wuhutsui Basin, Liaotung, with special reference to the limit of Chaumitien (or Upper Cambrian), of eastern Asia, and its subdivision. Japanese Journal of Geography and Geology, vol. 11, pp. 55–155.

1935. The *Briscoia* fauna of the late Upper Cambrian in Alaska with descriptions of a few Upper Cambrian trilobites from Montana and Nevada. Japanese Journal of Geography and Geology, vol. 12, pp. 39–57.

1936a. Cambrian and Lower Ordovician trilobites from northwestern Canada. Journal of Paleontology, vol. 10, pp. 157–167.

1936b. Notes on the nomenclature of some Cambro-Ordovician genera. Journal of the Geological Society of Japan, vol. 43, p. 922

1960. The Cambro-Ordovician formations and faunas of South Korea, Part VII. Palaeontology VI. Supplement to the Cambrian faunas of the Tsuibon Zone with notes on some trilobite genera and families. Journal of the Faculty of Science University of Tokyo, Section 12 (2), pp. 329–420.

Labandiera, C.C., and Hughes, N.C.

1994. Biometry of the late Cambrian trilobite *Dikelocephalus* and its implications for trilobite systematics. Journal of Paleontology, vol. 68, pp. 492–517.

Loch, J.D., Stitt, J.H., and Derby, J.R.

1993. Cambrian-Ordovician boundary interval extinctions: implications of revised trilobite and brachiopod data from Mount Wilson, Alberta, Canada. Journal of Paleontology, vol. 67, pp. 497–517.

Loch, J.D., Stitt, J.H., and Miller, J.F.

1999. Trilobite biostratigraphy through the Cambrian-Ordovician boundary interval at Lawson Cove, Ibex, western Utah, U.S.A. *In* Quo vadis Ordovician—Short papers of the Eighth International Symposium on the Ordovician System. Acta Universitatis Carolinae, Geologica, vol. 43, pp. 13–16.

Lochman, C.

1964. Upper Cambrian faunas from the subsurface Deadwood Formation, Williston Basin, Montana. Journal of Paleontology, vol. 38, pp. 33–60.

Lochman, C., and Hu, C.H.

1959. A *Ptychaspis* faunule from the Bear River Range, southeastern Idaho. Journal of Paleontology, vol. 33, pp. 404–427.

Longacre, S.A.

1970. Trilobites of the Upper Cambrian Ptychaspid Biomere, Wilberns Formation, central Texas. Paleontological Society Memoir 4, 70 pp., 6 pls.

Lu, Y.H.

1954. Upper Cambrian trilobites from Santu, southeastern Kueichou. Acta Palaeontologica Sinica, vol. 2, pp. 136–152.

Lu, Y.H. and Lin, H.L.

1980. Cambro-Ordovician boundary in western Zhejiang and the trilobites contained therein. Acta Palaeontologica Sinica, vol. 19, pp. 118–135.

Ludvigsen, R.

1982. Upper Cambrian and Lower Ordovician trilobite biostratigraphy of the Rabbitkettle Formation, western District of Mackenzie. Life Sciences Contributions, Royal Ontario Museum 134, 187 pp., 70 figs.

1986. Revision of *Acheilus* and *Theodenisia* (Late Cambrian, Trilobita). Journal of Paleontology, vol. 60, pp. 61–67.

Ludvigsen, R., and Westrop, S.R.

1983a. Trilobite biofacies in the Cambrian-Ordovician boundary interval in northern North America. Alcheringa, vol. 7, pp. 301–319.

1983b. Franconian trilobites of New York State. New York State Museum Memoir 23, 83 pp., 19 pls.

1985. Three new Upper Cambrian stages for North America. Geology, vol. 13, pp. 139–143.

1986. Classification of the Late Cambrian trilobite *Idiomesus* Raymond. Canadian Journal of Earth Sciences, vol. 23, pp. 300–307.

Ludvigsen, R., Westrop, S.R., and Kindle, C.H.

1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. Palaeontographica Canadiana 6, 175 pp., 50 pls.

Ludvigsen, R., Westrop, S.R., Pratt, B.R., Tuffnell, P.A., and Young, G.A.

1986. Paleoscience 3. Dual biostratigraphy: zones and biofacies. Geoscience Canada vol. 13, pp. 139–154.

Miller, J.F., Taylor, M.E., Stitt, J.H., Ethington, R.L., Hintze, L.F., and Taylor, J.F.

1982. Potential Cambrian-Ordovician boundary stratotype sections in the western United States. *In* The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations. M.G. Bassett and W.T. Dean, *eds.*, National Museum of Wales, Geological Series, no. 3, pp. 155–180.

Miller, S.A.

1889. North American geology and paleontology for the use of amateurs, students and scientists. Western Methodist Book Concern, Cincinnati, Ohio, 718 pp.

Nelson, C.A.

1951. Cambrian trilobites from the St. Croix Valley. Journal of Paleontology, vol. 25, pp. 765–784.

Nolan, T.B., Merriam, C.W., and Williams, J.S.

1956. The stratigraphic section in the vicinity of Eureka, Nevada. United States Geological Survey Professional Paper 276, 77 pp.

Norford, B.S.

1969. The Early Canadian (Tremadocian) trilobites *Clelandia* and *Jujuyaspis* from the southern Rocky Mountains of Canada. Geological Survey of Canada Bulletin, vol. 182, pp. 1–15.

Osleger D.

1995. Depositional sequence on Upper Cambrian carbonate platforms: Variable sedimentologic responses to allogenic forcing. *In* Sequence Stratigraphy and Depositional Response to Eustatic, Tectonic and Climatic Forcing. B.U. Haq, *ed.*, Kluwer Academic Press, Amsterdam, pp. 247–276.

Osleger, D., and Read, J.F.

1993. Comparative analysis of methods used to define eustatic variations in outcrop: Late Cambrian interbasinal sequence development. American Journal of Science, vol. 293, pp. 157–216.

Owen, D.D.

1852. Report of the Geological Survey of Wisconsin, Iowa and

Minnesota. Lippencott, Grambo and Co., Philadelphia, 638 pp.

Palmer, A.R.

1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada. United States Geological Survey Professional Paper 334C, pp. 53–109, 11 pls.

1962. *Glyptagnostus* and associated trilobites in the United States. United States Geological Survey Professional Paper. 374F. 49 pp., 6 pls.

1965. Trilobites of the Late Cambrian Pterocephaliid Biomere in the Great Basin, United States. United States Geological Survey Professional Paper 493, 105 pp., 23 pls.

1968. Cambrian trilobites of east-central Alaska. United States Geological Survey Professional Paper 559-B, 105 pp., 15 pls.

1971. The Cambrian of the Great Basin and adjacent areas, western United States. *In* The Cambrian of the New World. C. H. Holland, *ed.*, Wiley, New York, pp. 1–78.

Peng, S.

1984. Cambrian-Ordovician boundary in the Cili-Taoyuan border area, northwestern Hunan with descriptions of relative trilobites. *In* Stratigraphy and paleontology of systematic boundaries in China. Cambrian-Ordovician boundary, 1, pp. 285–405. Anhui Science and Technology Publishing House.

1992. Upper Cambrian biostratigraphy and trilobite faunas of the Cili-Taoyuan area, northwestern Hunan, China. Australasian Association of Paleontologists Memoir 13, 119 pp., 63 figs.

Rasetti, F.

1944. Upper Cambrian trilobites from the Lévis Conglomerate. Journal of Paleontology, vol. 18, pp. 229–258.

1945. New Upper Cambrian trilobites from the Levis Conglomerate. Journal of Paleontology, vol. 19, pp. 462–478.

1952. Cephalic structures in the Upper Cambrian trilobite *Entomaspis*. Journal of Paleontology, vol. 26, pp. 797–802.

1959. Trempealeauian trilobites from the Conococheague, Frederick and Grove limestones of the central Appalachians. Journal of Paleontology, vol. 33, pp. 375–399.

1963. Additions to the Upper Cambrian fauna from the conglomerate boulders at Lévis, Quebec. Journal of Paleontology, vol. 37, pp. 1009–1017.

Raymond, P.E.

1913. A revision of the species which have been referred to the genus *Bathyurus*. Geological Survey of Canada, Memoir of the Victoria Museum, vol. 1, pp. 51–69.

1924. New Upper Cambrian and Lower Ordovician trilobites from Vermont. Proceedings of the Boston Society of Natural History, vol. 37, pp. 389–466.

1925. Some trilobites of the lower Middle Ordovician of eastern North America. Museum of Comparative Zoology, Bulletin 67, pp. 1–180, 10 pls.

1937. Upper Cambrian and Lower Ordovician Trilobita and Ostracoda from Vermont. Geological Society of America Bulletin, vol. 48, pp. 1079–1146.

Resser, C.E.

1937. Third contribution to the nomenclature of Cambrian trilobites. Smithsonian Miscellaneous Collections, vol. 103, no. 5, 136 pp., 21 pls.

1942. New Upper Cambrian trilobites. Smithsonian Miscellaneous Collections, vol. 103, no. 5, 136 pp., 21 pls.

Robison, R.A., and Pantoja-Alor, J.

1968. Tremadocian trilobites from the Nochixtlan region, Oaxaca, Mexico. Journal of Paleontology, v. 42, pp. 767–800.

Ross, R. J.

1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. Peabody Museum of Natural History, Yale University, Bulletin 6, 161 pp, 36 pls.

Sdzuy, K.

1955. Die Fauna der Leimitz-Schiefer (Tremadoc). Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft 492, 74 pp., 8 pls.

Shergold, J.H.

1972. Late Upper Cambrian trilobites from the Gola Beds, western Queensland, Australia. Bureau of Mineral Resources of Australia, Bulletin 112, 89 pp., 19 pls.

1975. Late Cambrian and Early Ordovician trilobites from the Burke River Structural Belt, western Queensland. Bureau of Mineral Resources of Australia, Bulletin 153, 251 pp., 58 pls.

1991. Late Cambrian and Early Ordovician trilobite faunas and biostratigraphy of the Pacoota Sandstone, Amadeus Basin, central Australia. Bureau of Mineral Resources of Australia, Bulletin 237, pp. 15–77, 9 pls.

Shumard, B.F.

1861. The Primordial zone of Texas with descriptions of new fossils. American Scientist (2nd Series), vol. 32, pp. 213–221.

Smith, A.B.

1994. Systematics and the Fossil Record: Documenting Evolutionary Patterns. Blackwell Science, Oxford, 223 pp.

Stitt, J.H.

1971. Late Cambrian and earliest Ordovician trilobites, Timbered Hills and Lower Arbuckle groups, western Arbuckle Mountains, Murray County, Oklahoma. Oklahoma Geological Survey Bulletin 110, 83 pp., 8 pls.

1976. Functional morphology and life habits of the Late Cambrian trilobite *Stenopilus pronus* Raymond. Journal of Paleontology, vol. 50, pp. 561–576.

1977. Late Cambrian and earliest Ordovician trilobites, Wichita Mountains area, Oklahoma. Oklahoma Geological Survey Bulletin 124, 79 pp., 6 pls.

Stitt, J.H., and Straatmann, W.M.

1997. Trilobites from the upper part of the Deadwood Formation (Upper Franconian and Trempealeauan stages, Upper Cambrian), Black Hills, South Dakota. Journal of Paleontology, vol. 71, pp. 86–102.

Sun, Y-C.

1924. Contribution to the Cambrian faunas of China. Palaeontologia Sinica, ser. B, fasc. 4, 109 pp., 5 pls.

Taylor, M.E.

1976. Indigenous and redeposited trilobites from Late Cambrian basinal environments of central Nevada. Journal of Paleontology, vol. 50, pp. 668–700.

1978. Type species of the Late Cambrian trilobite *Eurekia* Walcott, 1916. Journal of Paleontology, vol. 52, pp. 1054–1064.

Taylor, M.E., and Halley, R.B.

1974. Systematics, environment and biogeography of some Late Cambrian and Early Ordovician trilobites from eastern New York State. United States Geological Survey Professional Paper 834, 38 pp., 4 pls.

Ulrich, E.O., and Resser, C.E.

1930. The Cambrian of the Upper Mississippi Valley. Part 1, Trilobita, Dikelocephalinae and Osceolinae. Milwaukee Public Museum Bulletin 12, pp. 1–122, pls. 1–23.

1933. The Cambrian of the Upper Mississippi Valley. Part 2, Trilobita, Saukiinae. Milwaukee Public Museum Bulletin 12, pp. 123–306, pls. 24–45.

Vogdes, A.W.

1890. A bibliography of Palaeozoic Crustacea from 1698–1889, including a list of North American species and a systematic arrangement of genera. United States Geological Survey Bulletin 63, 177 pp.

Walch, J.E.I.

1771. Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürkigkeiten der Natur., vol. 4, pt. 3. Paul Jonathan Felstecker, Nürnburg, 184 pp., 81 pls.

Walcott, C.D.

1879. Descriptions of new species of fossils from the Calciferous Formation. 32nd Annual Report of the New York State Museum of Natural History, pp. 129–131.

1884. Paleontology of the Eureka district. United States Geological Survey Memoir 8, 298 pp., 24 pls.

1914. *Dikelocephalus* and other genera of the Dikelocephalinae. Smithsonian Miscellaneous Collections, vol. 57, no. 13, pp. 345–512.

1916. Cambrian geology and paleontology, 3. Cambrian trilobites. Smithsonian Miscellaneous Collections, vol. 64, no. 3, pp. 157–258, 14 pls.

1924. Cambrian geology and paleontology, 5, part 2. Cambrian and Ozarkian trilobites. Smithsonian Miscellaneous Collections, vol. 75, no. 2, pp. 56–60, 6 pls.

1925. Cambrian geology and paleontology, 5, part 3. Cambrian and Ozarkian trilobites. Smithsonian Miscellaneous Collections, vol. 75, no. 3, pp. 61–146, 24 pls.

Westrop, S.R.

1984. Late Cambrian and earliest Ordovician trilobites, southern Canadian Rocky Mountains, Alberta. Unpublished Ph.D. thesis, University of Toronto, 990 pp.

1986a. New ptychaspidid trilobites from the Upper Cambrian Mistaya Formation of southern Alberta. Canadian Journal of Earth Sciences, vol. 23, pp. 214–221.

1986b. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. Palaeontographica Canadiana 3, 179 pp., 41 pls.

1992. Upper Cambrian (Marjuman-Steptoean) trilobites from the Port au Port Group, western Newfoundland. Journal of Paleontology, vol. 66, pp. 228–254.

1995. Sunwaptan and Ibexian (Upper Cambrian-Lower Ordovician) trilobites of the Rabbitkettle Formation, Mountain River region, northern Mackenzie Mountains. Palaeontographica Canadiana, 12, 75 pp., 15 pls.

1996. Temporal persistence and stability of Cambrian biofacies: Sunwaptan (Upper Cambrian) trilobite faunas of North America. Paleogeography, Paleoclimatology, Paleoecology, vol. 127, pp. 33–46.

Westrop, S.R., and Ludvigsen, R.

1986. Type species of the Ibexian trilobite *Corbinia* Walcott, 1924. Journal of Paleontology, vol. 60, pp. 68–75.

Whittington, H.B.

1956. Silicified Middle Ordovician trilobites: the Odontopleuridae. Museum of Comparative Zoology, Harvard University, Bulletin 114, pp. 159–288, 24 pls.

1959. Silicified Middle Ordovician trilobites: Remopleuridae, Trinucleidae, Raphiophoridae, Endymioniidae. Museum of Comparative Zoology, Harvard University, Bulletin 121, pp. 371–496, 36 pls.

1997. Morphology of the exoskeleton. *In* Treatise on invertebrate paleontology. R.L. Kaesler, *ed.*, Part O, Revised, Trilobita 1, by H.B. Whittington *et al.*, Geological Society of America and University of Kansas Press, pp. 1–67.

Whittington, H.B., and Evitt, W.R.

1954. Silicified Middle Ordovician trilobites. Geological Society of America Memoir 59, 137 pp., 33 pls.

Winston, D., and Nicholls, H.

1967. Late Cambrian and Early Ordovician faunas from the Wilberns Formation of central Texas. Journal of Paleontology, vol. 41, pp. 66–96.

Young, J.C.

1960. Structure and stratigraphy in the north-central Schell Creek Range. Intermountain Association of Petroleum Geologists Guidebook to the Geology of east-central Nevada.

PLATES

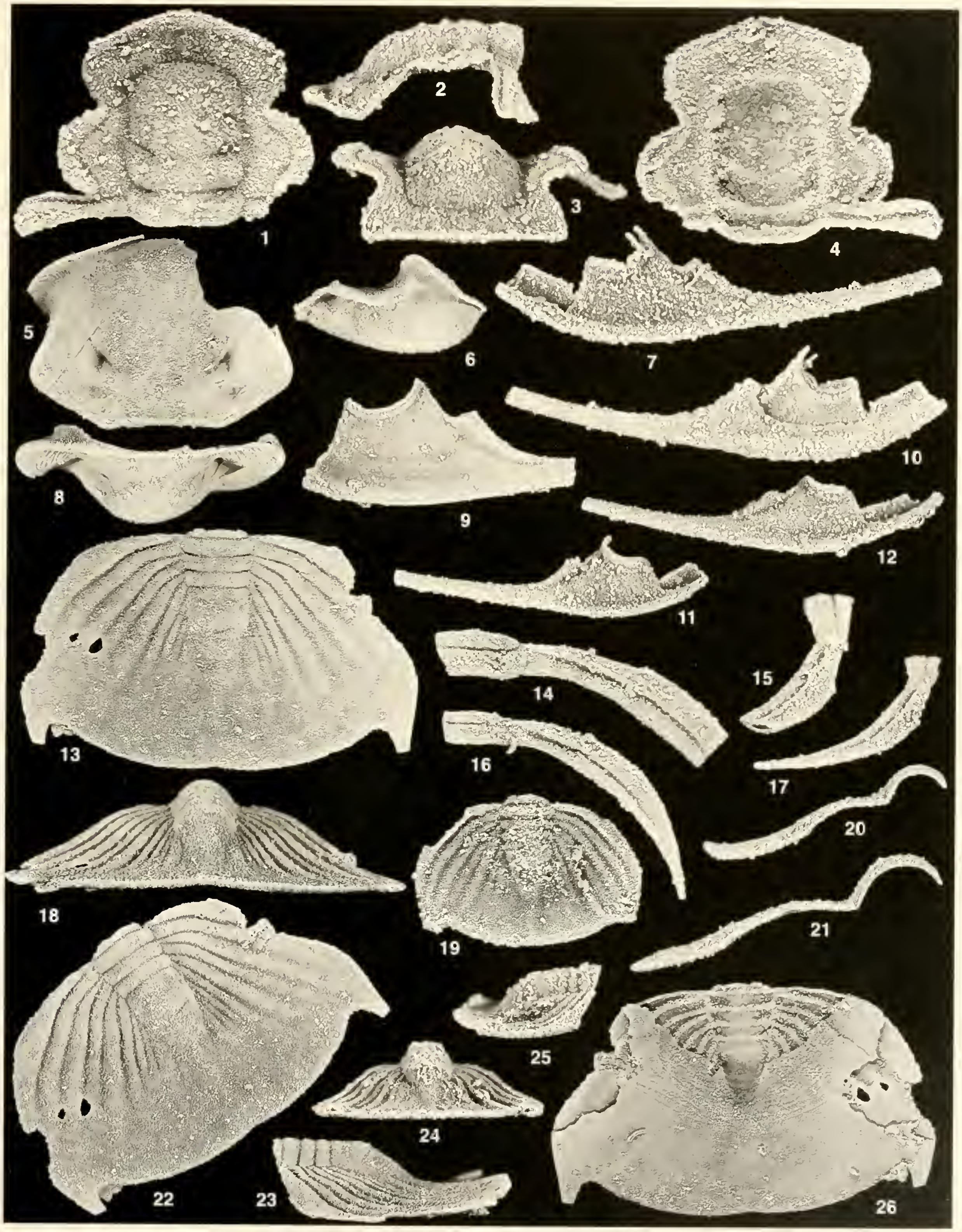
Explanation of Plate 1

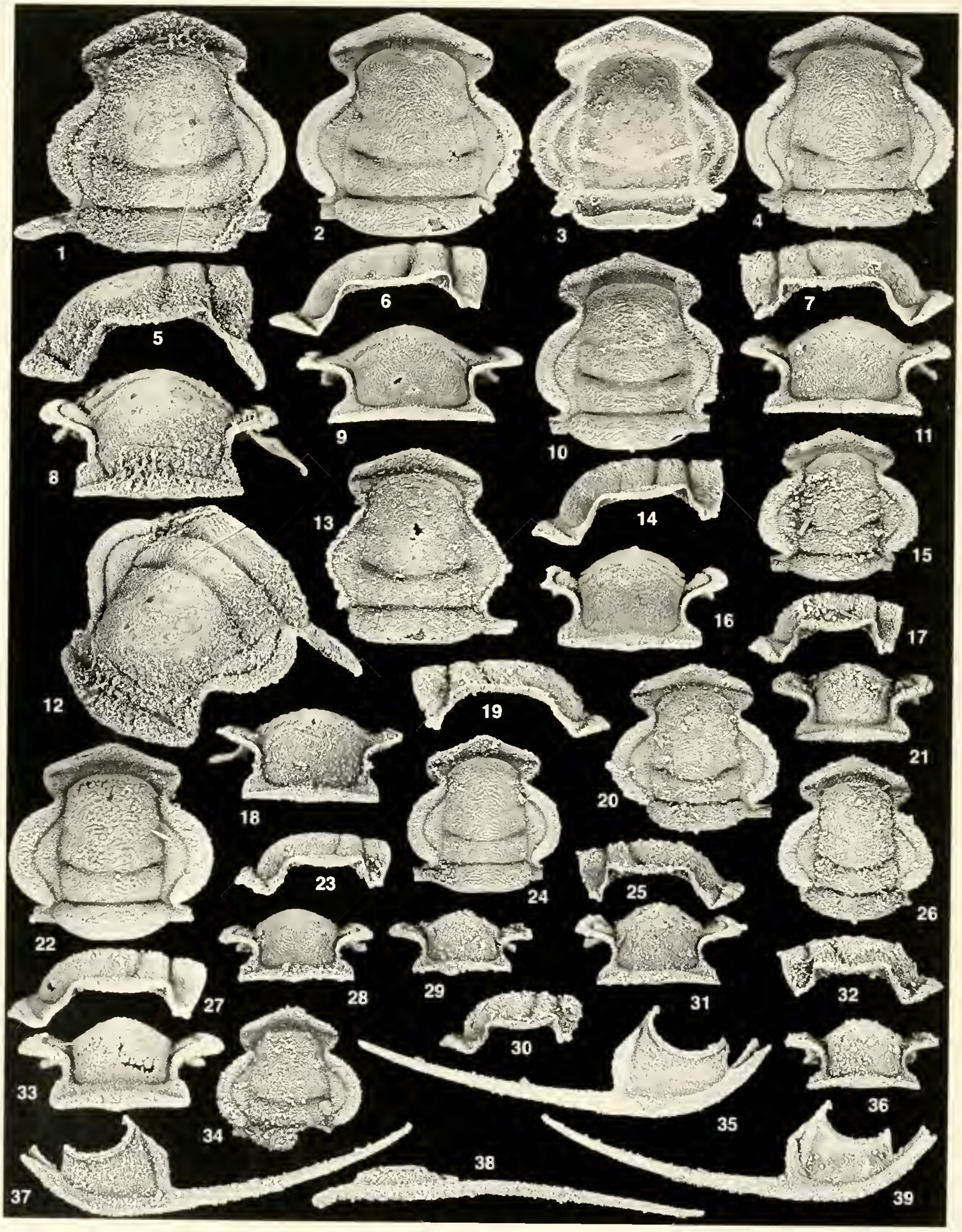
Figure Page

1–26. *Dikelocephalus minnesotensis* Owen, 1852. 10

- 1–4. Cranidium, SUI 99042, dorsal, left lateral, anterior, and ventral views, ×15.
- 5, 6, 8. Hypostome, SUI 99043, ventral, right lateral, and posterior views, ×4.
- 7, 10. Left librigena, SUI 99044, external and internal views, ×12.
- 9. Left librigena, SUI 99045, external view, ×10.
- 11. Right librigena, SUI 99046, external view, ×12.
- 12. Right librigena, SUI 99047, external view, ×10.
- 13, 18, 22, 23, 26. Pygidium, SUI 99048, dorsal, posterior, oblique, lateral and ventral views, ×3.
- 14, 15, 21. Thoracic segment, SUI 99049, dorsal, right lateral, and anterior views, ×7.5.
- 16, 17, 20. Thoracic segment, SUI 99050, dorsal, right lateral, and anterior views, ×7.5.
- 19, 24, 25. Pygidium, SUI 99051, dorsal, posterior, and right lateral views, ×10.

PLATE 1

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EXPLANATION OF PLATE 2

Figure Page

1–39. *Prosaukia oldyelleri* new species. 11

1, 5, 8, 12. Cranidium, SUI 99052, dorsal, left lateral, anterior, and oblique views, ×4.

2, 6, 9. Cranidium, SUI 99053, dorsal, left lateral, and anterior views, ×7.5

3, 4, 7, 11. Cranidium, **holotype,** SUI 99054, ventral, dorsal, right lateral, and anterior views, ×7.5

10, 14, 16. Cranidium, SUI 99055, dorsal, left lateral, and anterior views, ×7.5.

13, 18, 19. Cranidium, SUI 99056, dorsal, anterior, and right lateral views, ×7.5.

15, 17, 21. Cranidium, SUI 99057, dorsal, left lateral, and anterior views, ×10.

20, 25, 31. Cranidium, SUI 99058, dorsal, right lateral, and anterior views, ×7.5.

22, 27, 33. Cranidium, SUI 99059, dorsal, left lateral, and anterior views, ×15.

23, 24, 28. Cranidium, SUI 99060, left lateral, dorsal, and anterior views, ×7.5.

26, 32, 36. Cranidium, SUI 99061, dorsal, right lateral, and anterior views, ×7.5.

29, 30, 34. Cranidium, SUI 99062, anterior, left lateral, and dorsal views, ×7.5.

35. Right librigena, SUI 99063, external view, ×7.5.

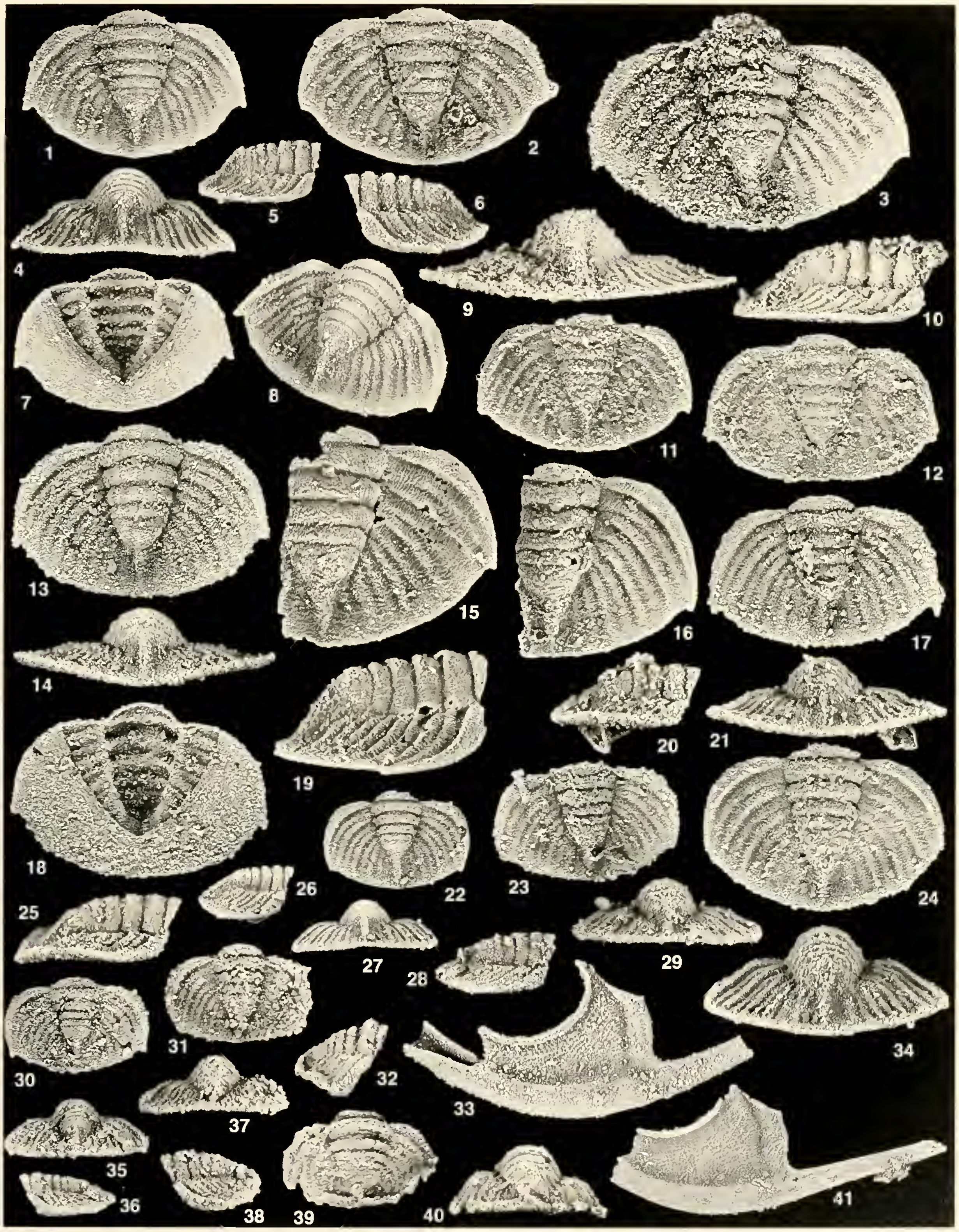
37–39. Left librigena, SUI 99064, external, ventrolateral, and internal views, ×7.5.

EXPLANATION OF PLATE 3

Figure Page

1–41. *Prosaukia oldyelleri* new species. 11

1, 4, 5, 7, 8. Pygidium, SUI 99065, dorsal, posterior, right lateral, ventral, and oblique views, ×7.5.
2, 6. Pygidium, SUI 99066, dorsal and left lateral views, ×7.5.
3, 9, 10. Pygidium, SUI 99067, dorsal, posterior, and right lateral views, ×7.5.
11. Pygidium, SUI 99068, dorsal view, ×10.
12. Pygidium, SUI 99069, dorsal view, ×7.5.
13, 14, 18, 25. Pygidium, SUI 99070, dorsal, posterior, ventral, and right lateral views, ×7.5.
15, 19. Pygidium, SUI 99071, dorsal and right lateral views, ×10.
16. Pygidium, SUI 99072, dorsal view, ×10.
17, 20, 21. Pygidium, SUI 99073, dorsal, right lateral, and posterior views, ×10.
22, 26, 27. Pygidium, SUI 99074, dorsal, right lateral, and posterior views, ×10.
23, 28, 29. Pygidium, SUI 99075, dorsal, right lateral, and posterior views, ×10.
24, 34. Pygidium, SUI 99076, dorsal and posterodorsal views, ×10.
30, 35, 36. Pygidium, SUI 99077, dorsal, posterior, and left lateral views, ×12.
31, 37, 38. Pygidium, SUI 99078, dorsal, posterior, and left lateral views, ×15.
32, 29, 40. Transitory pygidium, SUI 99079, right lateral, dorsal, and posterior views, ×15.
33. Left librigena, SUI 99080, external view, ×7.5.
41. Left librigena, SUI 99081, external view, ×5.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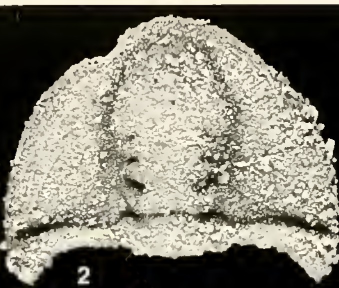
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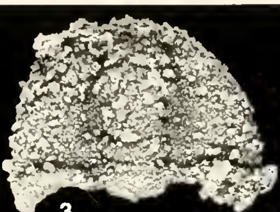
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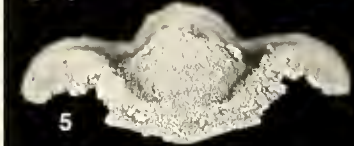
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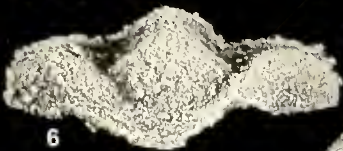
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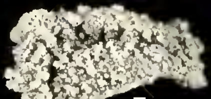
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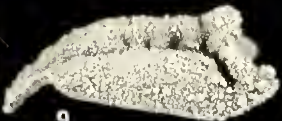
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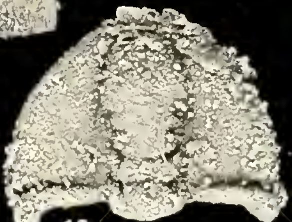
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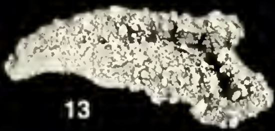
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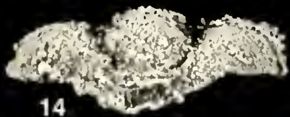
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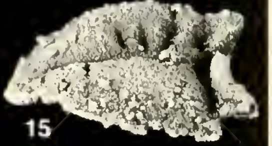
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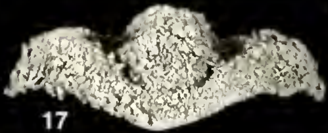
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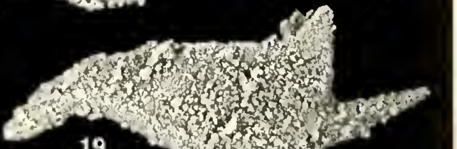
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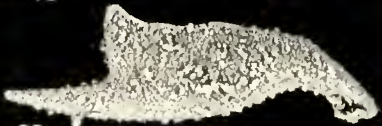
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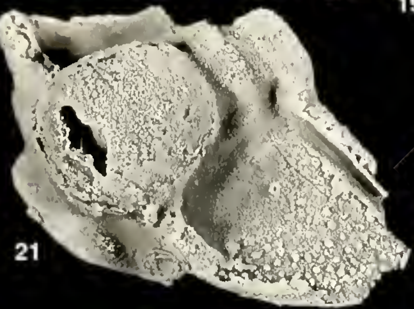
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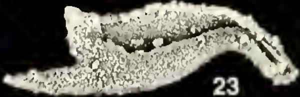
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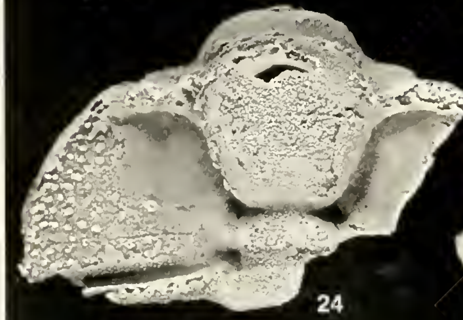
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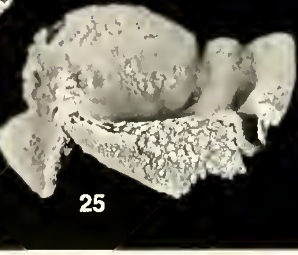
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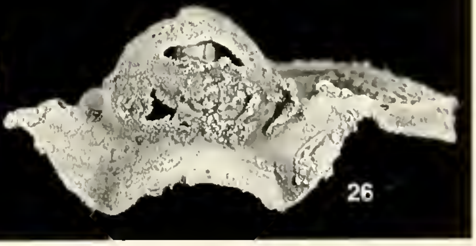
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EXPLANATION OF PLATE 4

Figure Page

1–20, 22, 23. *Idiomesus levisensis* (Rasetti, 1944). 13
1, 5, 8. Cranidium, SUI 99082, dorsal, anterior, and right lateral views, ×15.
2, 6, 9. Cranidium, SUI 99083, dorsal, anterior, and left lateral views, ×15.
3, 7. Cranidium, SUI 99084, dorsal and right lateral views, ×15.
4. Cranidium, SUI 99085, dorsal view, ×15.
10, 14, 18. Cranidium, SUI 99086, dorsal, anterior, and left lateral views, ×15.
11, 15. Cranidium, SUI 99087, dorsal and left lateral views, ×15.
12, 13, 16, 17. Cranidium, SUI 99088, dorsal, left lateral, ventral, and anterior views, ×15.
19. Left librigena, SUI 99089, external view, ×15.
20. Right librigena, SUI 99090, external view, ×15.
22, 23. Left librigena, SUI 99091, external and internal views, ×15.

21, 24–26. *Sunwaptia plutoi* new species. 13
21, 24–26. cranidium, **holotype,** SUI 99092, oblique, dorsal, left lateral, and anterior views, ×7.5.

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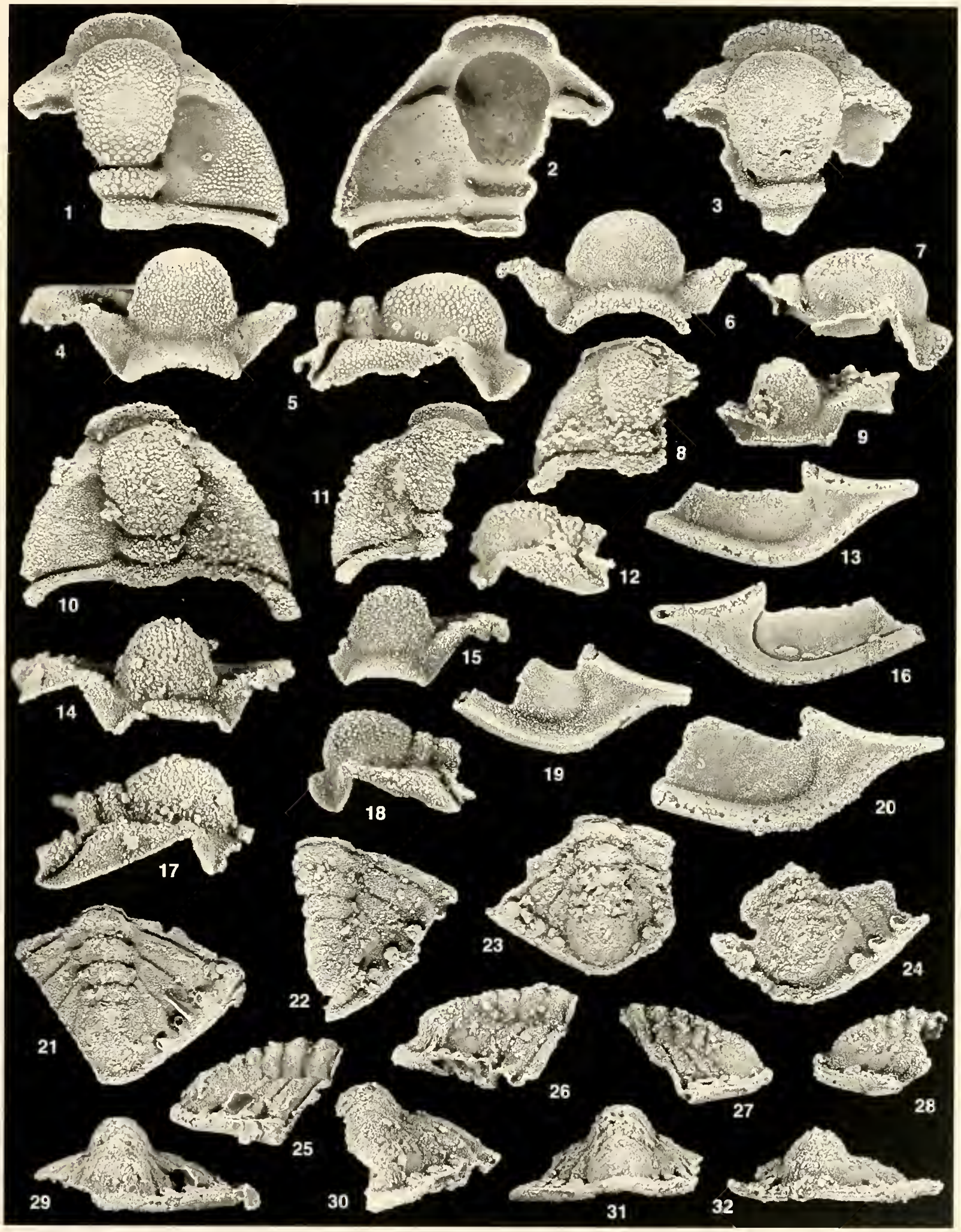
1–32. *Sunwaptia plutoi* new species.	13
1, 2, 4, 5. Cranidium, SUI 99093, dorsal, ventral, anterior, and right lateral views, ×15.	
3, 6, 7. Cranidium, SUI 99094, dorsal, anterior, and right lateral views, ×10.	
8, 9, 12. Cranidium, SUI 99095, dorsal, anterior, and left lateral views, ×20.	
10, 14, 17. Cranidium, SUI 99096, dorsal, anterior, and right lateral views, ×15.	
11, 15, 18. Cranidium, SUI 99097, dorsal, anterior, and left lateral views, ×12.	
13, 16. Left librigena, SUI 99098, external and internal views, ×10.	
19. Left librigena, SUI 99099, external view, ×12.	
20. Left librigena, SUI 99100, external view, ×10.	
21, 25, 29. Pygidium, SUI 99101, dorsal, right lateral, and posterior views, ×10.	
22, 26, 30. Pygidium, SUI 99102, dorsal, right lateral, and posterior views, ×10.	
23, 27, 31. Pygidium, SUI 99103, dorsal, left lateral, and posterior views, ×10.	
24, 28, 32. Pygidium, SUI 99104, dorsal, right lateral, and posterior views, ×12.	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EXPLANATION OF PLATE 6

Figure Page

1–44. *Euptychaspis dougali* new species. 15

1, 5, 11, 12, 22. Cranidium, **holotype,** SUI 99105, dorsal, anterior, oblique, right lateral, and ventral views, ×12.

2, 3, 6, 9. Cranidium, SUI 99106, dorsal, ventral, anterior, and left lateral views, ×12.

4, 7, 10. Cranidium, SUI 99107, dorsal, anterior, and left lateral views, ×12.

8, 14, 16. Cranidium, SUI 99108, dorsal, anterior, and left lateral views, ×10.

13, 17, 18. Cranidium, SUI 99109, dorsal, left lateral and anterior views, ×10.

15, 20, 21. Cranidium, SUI 99110, dorsal, anterior, and right lateral views, ×12.

19. Left librigena, SUI 99111, external view, ×10.

23, 25, 26. Left librigena, SUI 99112, external, ventrolateral, and internal views, ×10.

24. Left librigena, SUI 99113, external view, ×10.

27. Right librigena, SUI 99114, external view, ×10.

28–30. Cranidium, SUI 99115, dorsal, right lateral, and anterior views, ×10.

31. Left librigena, SUI 99116, external view, ×10.

32. Right librigena, SUI 99117, external view, ×10.

33. Left librigena, SUI 99118, external view, ×12.

34–36. Cranidium, SUI 99119, dorsal, anterior, and left lateral views, ×12.

37, 42, 43. Pygidium, SUI 99120, dorsal, left lateral, and posterior views, ×15.

38, 39, 44. Pygidium, SUI 99121, left lateral, dorsal, and posterior views, ×10.

40. Left librigena, SUI 99122, external view, ×10.

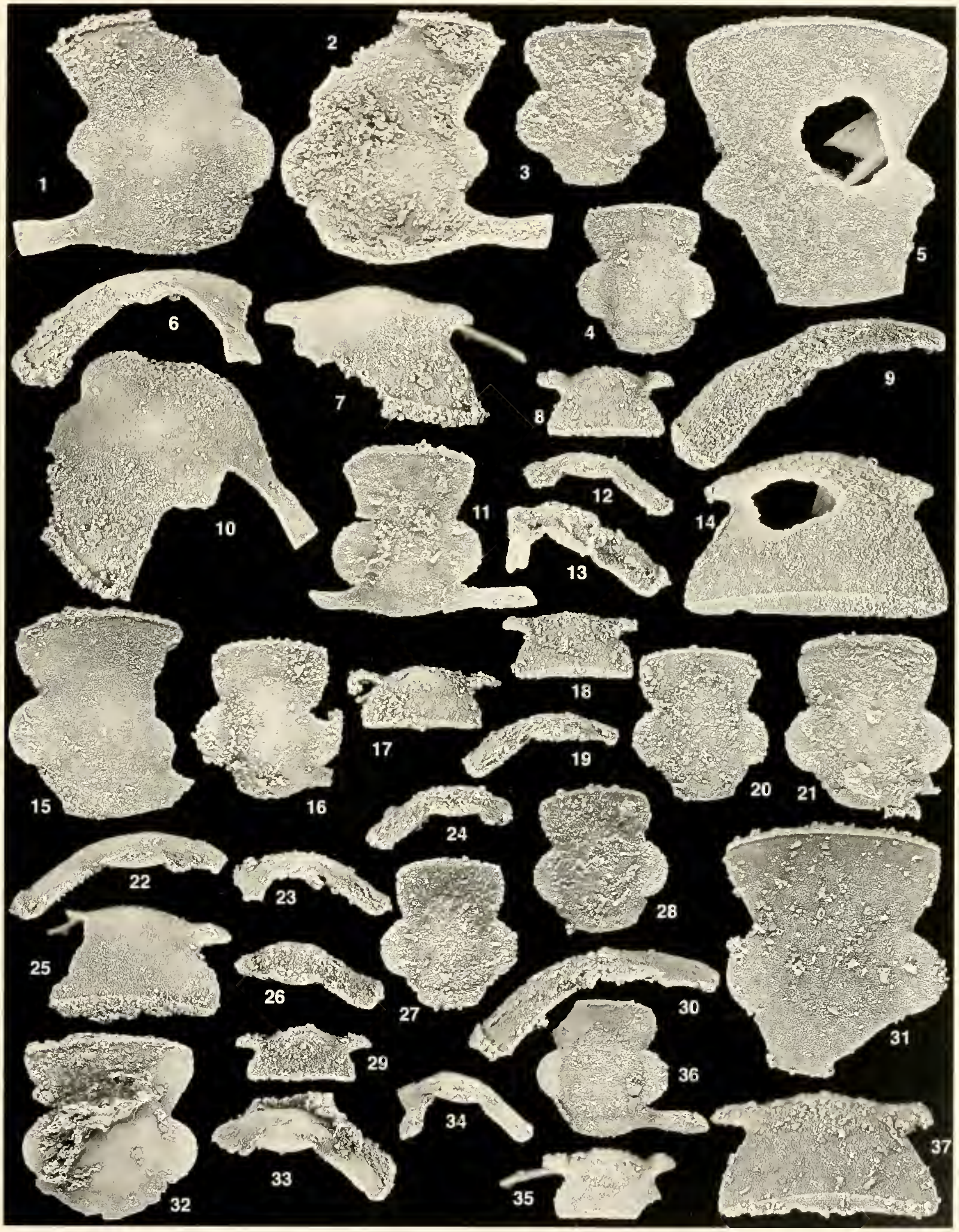
41. Left librigena, SUI 99123, external view, ×20.

EXPLANATION OF PLATE 7

Figure Page

1–37. *Illaenurus montanensis* Kobayashi, 1935. 17

1, 2, 6, 7, 10. Cranidium, SUI 99124, dorsal, ventral, left lateral, anterior, and oblique views, ×7.5.
3. Cranidium, SUI 99125, dorsal view, ×7.5.
4, 8, 12. Cranidium, SUI 99126, dorsal, anterior, and right lateral views, ×10.
5, 9, 14. Cranidium, SUI 99127, dorsal, left lateral, and anterior views, ×4.
11, 13. Cranidium, SUI 99128, dorsal and right lateral views, ×10.
15, 22, 25. Cranidium, SUI 99129, dorsal, left lateral, and anterior views, ×7.5.
16, 17, 23. Cranidium, SUI 99130, dorsal, anterior, and right lateral views, ×10.
18–20. Cranidium, SUI 99131, anterior, left lateral, and dorsal views, ×7.5.
21. Cranidium, SUI 99132, dorsal view, ×7.5.
24, 28. Cranidium, SUI 99133, left lateral and dorsal views, ×10.
26, 27, 29. Cranidium, SUI 99134, right lateral, dorsal, and anterior views, ×10.
30, 31, 37. Cranidium, SUI 99135, left lateral, dorsal, and anterior views, ×7.5.
32, 33. Cranidium, SUI 99136, dorsal and right lateral views, ×7.5.
34–36. Cranidium, SUI 99137, right lateral, anterior, and dorsal views, ×10.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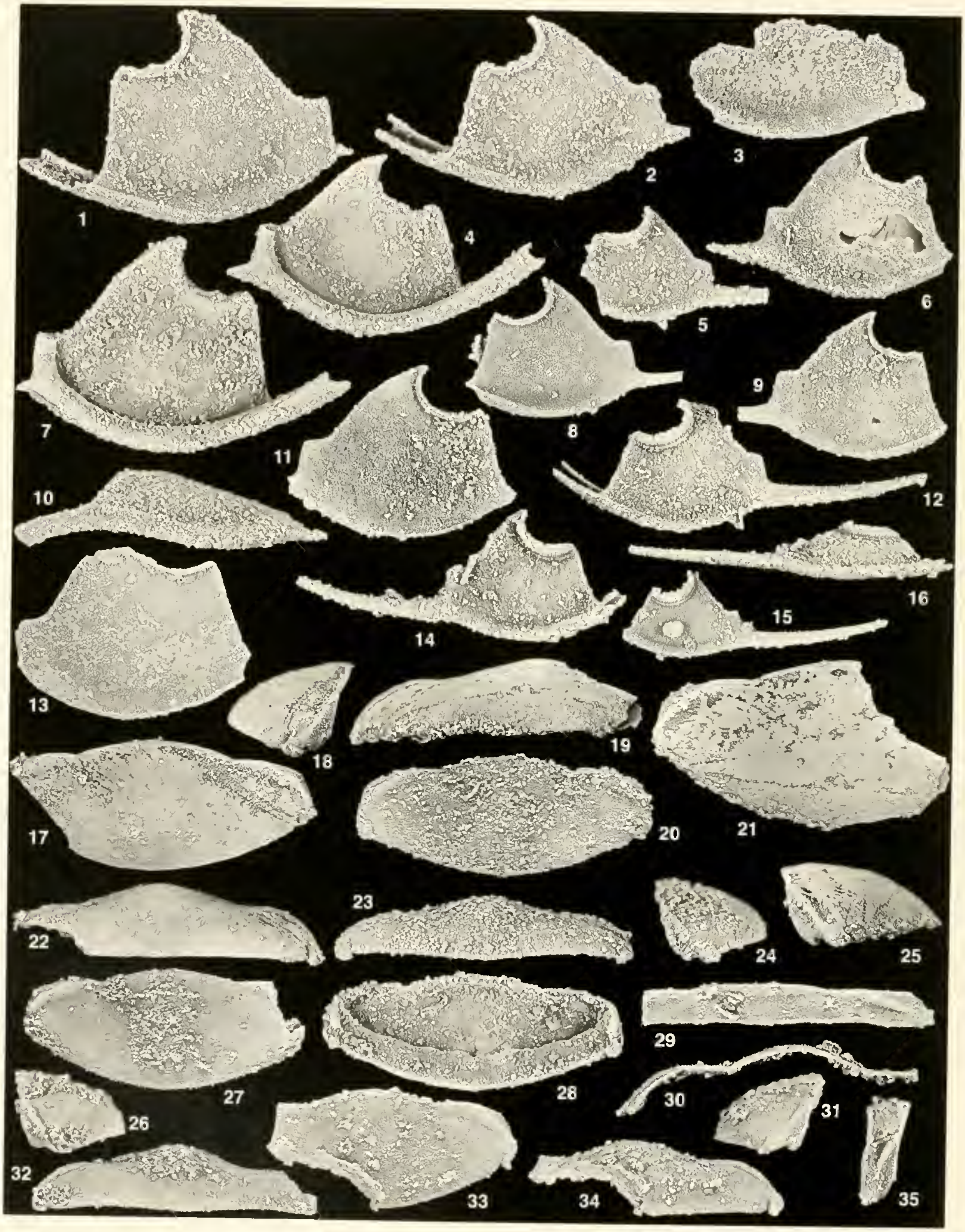
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EXPLANATION OF PLATE 8

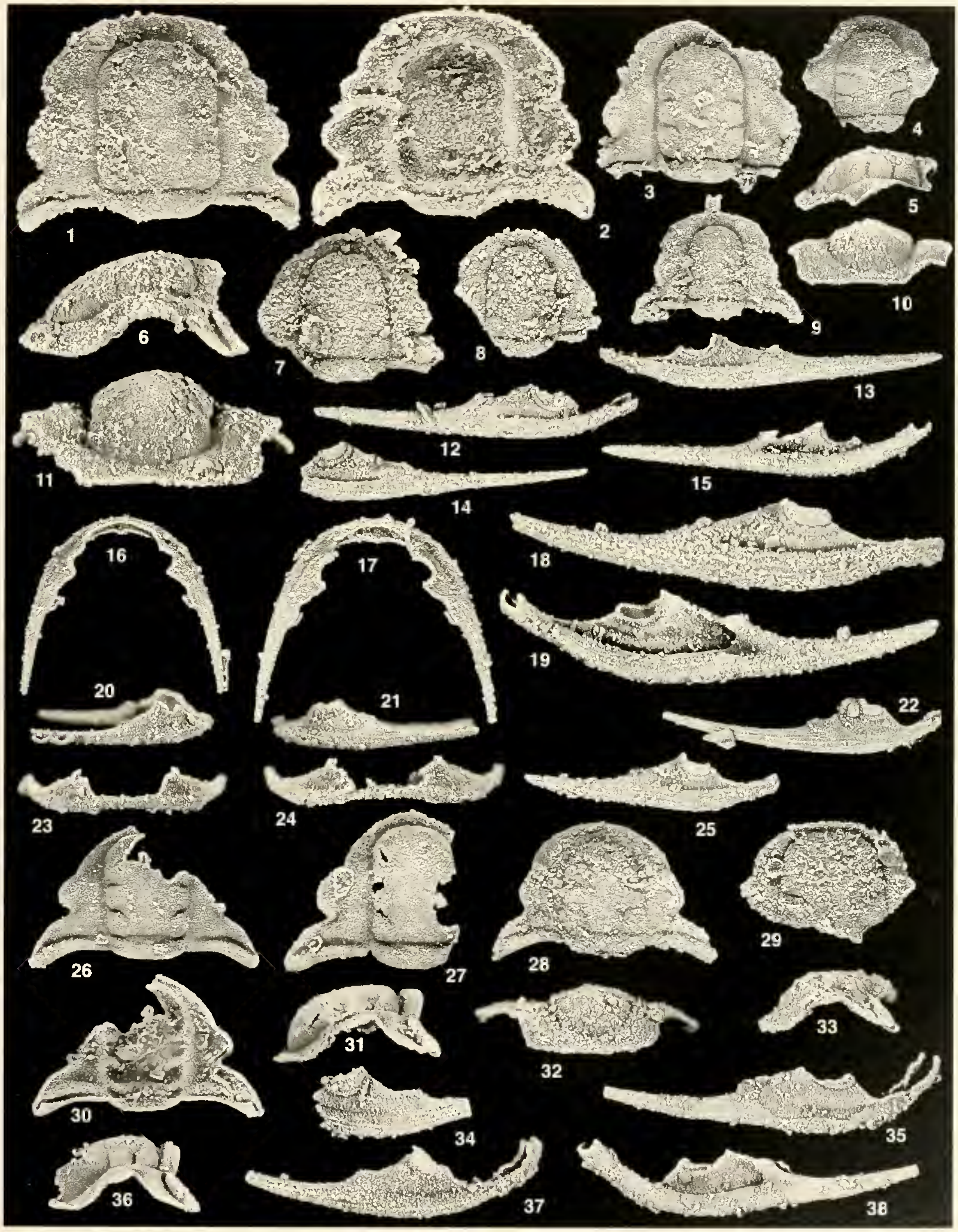
Figure Page

1–35. *Illaenurus montanensis* Kobayashi, 1935. . . 17

1, 7, 10. Left librigena, SUI 99138, external, internal, and ventrolateral views, ×7.5.
2, 4. Left librigena, SUI 99139, external and internal views, ×7.5.
3. Left librigena, SUI 99140, external view, ×10.
5. Left librigena, SUI 99141, external view, ×10.
6. Right librigena, SUI 99142, external view, ×7.5.
8. Left librigena, SUI 99143, external view, ×7.5.
9. Right librigena, SUI 99144, external view, ×7.5.
11. Right librigena, SUI 99145, external view, ×7.5.
12. Left librigena, SUI 99146, external view, ×10.
13. Right librigena, SUI 99147, external view, ×10.
14, 16. Right librigena, SUI 99148, external and ventrolateral views, ×10.
15. Left librigena, SUI 99149, external view, ×10.
17, 18, 22. Pygidium, SUI 99150, dorsal, right lateral, and posterior views, ×6.
19, 21, 25. Pygidium, SUI 99151, posterior, dorsal, and left lateral views, ×5.
20, 23, 24, 28. Pygidium, SUI 99152, dorsal, posterior, left lateral, and ventral views, ×7.5.
26, 27, 32. Pygidium, SUI 99153, left lateral, dorsal, and posterior views, ×7.5.
29, 30, 35. Thoracic segment, SUI 99154, dorsal, anterior, and right lateral views, ×10.
31, 33, 34. Pygidium, SUI 99155, right lateral, dorsal, and posterior views, ×10.

EXPLANATION OF PLATE 9

Figure	Page
1–25, 28, 32, 33. *Triarthropsis limbata* Rasetti, 1959.	18
1, 2, 6, 11. Cranidium, SUI 99156, dorsal, ventral, left lateral, and anterior views, ×10.	
3. Cranidium, SUI 99157, dorsal view, ×10.	
4, 5, 10. Cranidium, SUI 99158, dorsal, left lateral, and anterior views, ×10.	
7. Cranidium, SUI 99159, dorsal view, ×15.	
8. Cranidium, SUI 99160, dorsal view, ×10.	
9. Cranidium, SUI 99161, dorsal view, ×10.	
12. Right librigena, SUI 99162, external view, ×10.	
13, 15. Left librigena, SUI 99163, external and internal views, ×10.	
14. Left librigena, SUI 99164, external view, ×10.	
16, 20, 23. Yoked librigenae, SUI 99165, dorsal, right lateral, and anterior views, ×10.	
17, 21, 24. Yoked librigenae, SUI 99166, dorsal, left lateral, and anterior views, ×10.	
18, 19. Right librigena, SUI 99167, external and internal views, ×10.	
22. Right librigena, SUI 99168, external view, ×10.	
25. Right librigena, SUI 99169, external view, ×10.	
28, 32, 33. Cranidium, SUI 99170, dorsal, anterior, and left lateral views, ×12.	
26, 27, ?29, 30, 31, 34–38. *Triarthropsis* sp. 1	19
26, 30, 36. Cranidium, SUI 99171, dorsal, ventral, and left lateral views, ×10.	
27, 31. Cranidium, SUI 99172, dorsal and left lateral views, ×15.	
29. Cranidium, SUI 99173, dorsal view, ×10.	
34. Left librigena, SUI 99174, external view, ×17.	
35, 38. Right librigena, SUI 99175, external and internal views, ×10.	
37. Right librigena, SUI 99176, external view, ×15.	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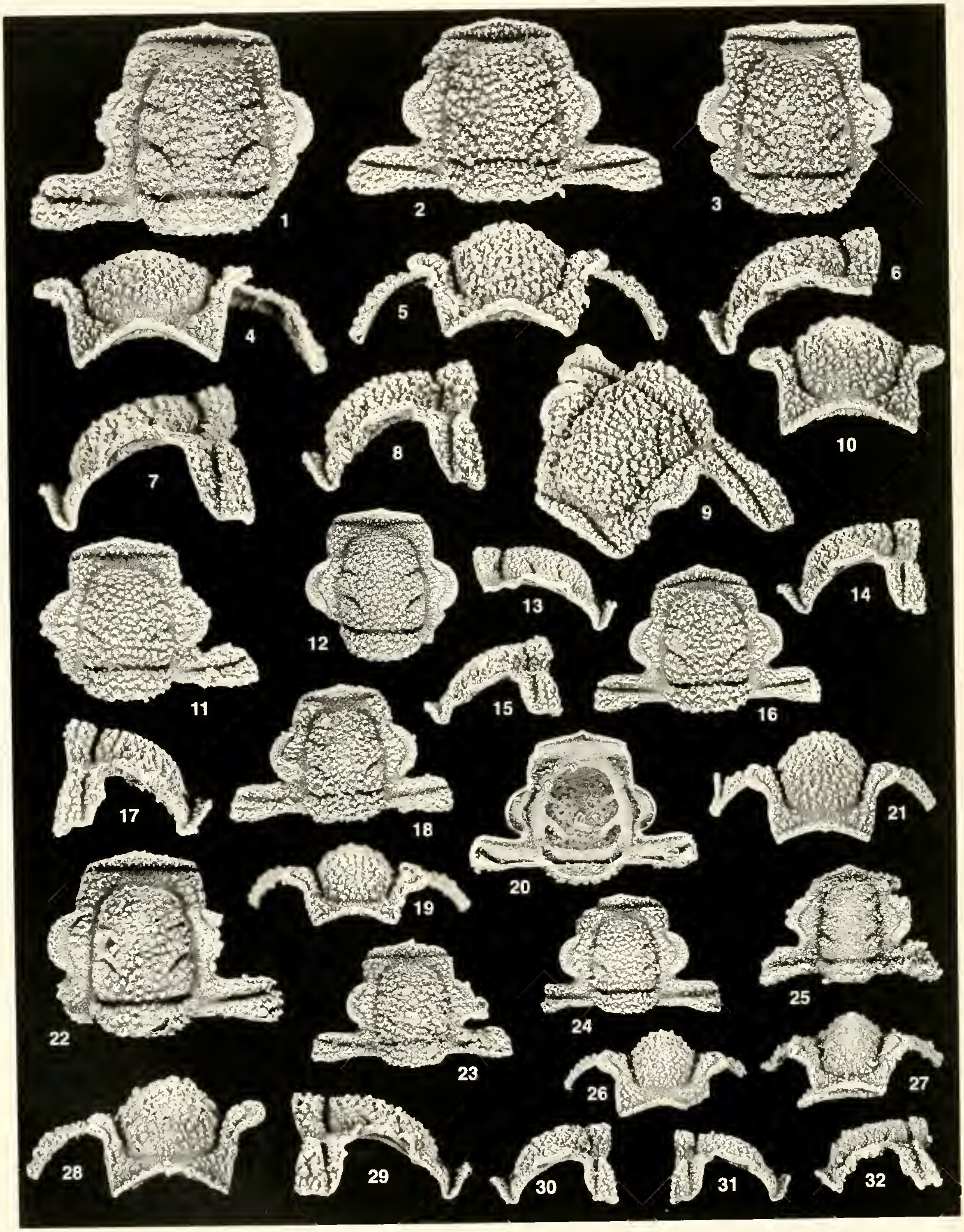
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Explanation of Plate 10

Figure Page

1–32. *Eurekia rintintini* new species 19

1, 4, 7. Cranidium, SUI 99177, dorsal, anterior, and left lateral views, ×7.5.

2, 5, 8, 9. Cranidium, **holotype,** SUI 99178, dorsal, anterior, left lateral, and oblique views, ×7.5.

3, 6, 10. Cranidium, SUI 99179, dorsal, left lateral, and anterior views, ×7.5.

11, 17. Cranidium, SUI 99180, dorsal and right lateral views, ×10.

12, 13. Cranidium, SUI 99181, dorsal and right lateral views, ×7.5.

14, 16, 20, 21. Cranidium, SUI 99182, left lateral, dorsal, ventral, and anterior views, ×7.5.

15, 18, 19. Cranidium, SUI 99183, left lateral, dorsal, and anterior views, ×10.

22, 28, 29. Cranidium, SUI 99184, dorsal, anterior, and right lateral views, ×10.

23, 30. Cranidium, SUI 99185, dorsal and left lateral views, ×7.5.

24, 26, 31. Cranidium, SUI 99186, dorsal, anterior, and right lateral views, ×10.

25, 27, 32. Cranidium, SUI 99187, dorsal, anterior, and left lateral views, ×17.

EXPLANATION OF PLATE 11

Figure Page

1–35. *Eurekia rintintini* new species. 19

1, 6, 7. Hypostome, SUI 99188, ventral, posterior, and left lateral views, ×7.5.

2, 8. Hypostome, SUI 99189, ventral and left lateral views, ×10.

3, 9. Hypostome, SUI 99190, ventral and posterior views, ×5.

4, 10, 14, 15. Hypostome, SUI 99191, ventral, posterior, dorsal, and left lateral views, ×7.5.

5, 11, 16. Hypostome, SUI 99192, ventral, posterior, and left lateral views, ×7.5.

12, 13, 18, 19. Cranidium and thoracic segments, SUI 99193, dorsal view of cranidium, dorsal view of thorax, right lateral, and anterior views, ×15.

17, 24. Left librigena, SUI 99194, external and internal views, ×7.5.

20, 22. Hypostome, SUI 99195, ventral and left lateral views, ×7.5.

21, 23. Hypostome, SUI 99196, ventral and left lateral views, ×10.

25, 26. Right librigena, SUI 99197, internal and external views, ×10.

27. Left librigena, SUI 99198, external view, ×10.

28. Right librigena, SUI 99199, external view, ×10.

29. Left librigena, SUI 99200, external view, ×10.

30–32. Thoracic segment, SUI 99201, left lateral, dorsal, and anterior views, ×7.5.


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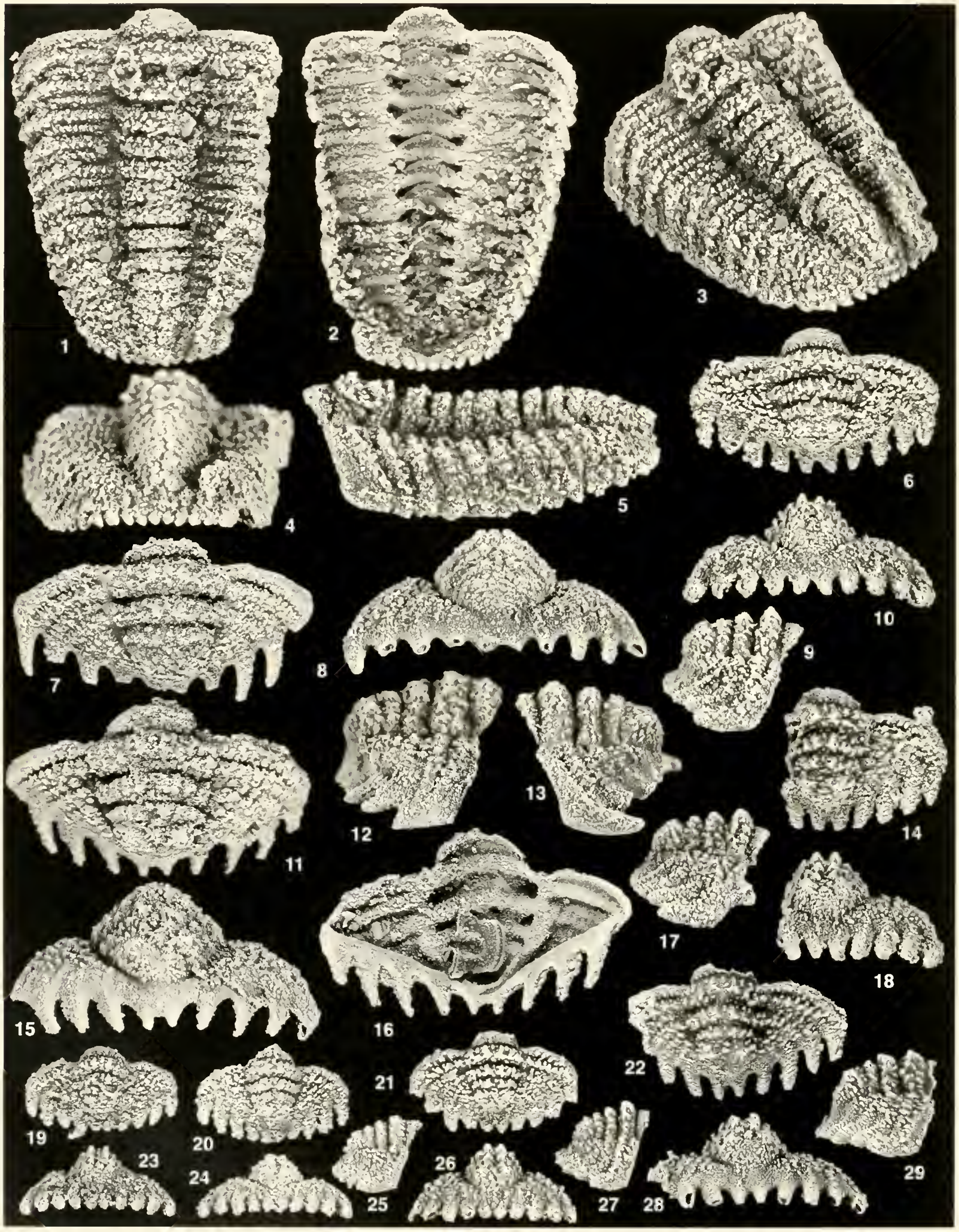
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Explanation of Plate 12

Figure Page

1–29. *Eurekia rintintini* new species. 19

1–5. Thoracopygidium, SUI 99203, dorsal, ventral, oblique, posterior, and left lateral views, ×15.

6, 9, 10. Pygidium, SUI 99204, dorsal, right lateral, and posterior views, ×10.

7, 8, 13. Pygidium, SUI 99205, dorsal, posterior, and left lateral views, ×7.5.

11, 12, 15, 16. Pygidium, SUI 99206, dorsal, right lateral, posterior, and ventral views, ×5 (note inverted cranidum of *Bowmania lassieae* n. sp. visible in fig. 16).

14, 17, 18. Pygidium, SUI 99207, dorsal, right lateral, and posterior views, ×10.

19, 23. Pygidium, SUI 99208, dorsal and posterior views, ×10.

20, 24, 25. Pygidium, SUI 99209, dorsal, posterior, and right lateral views, ×10.

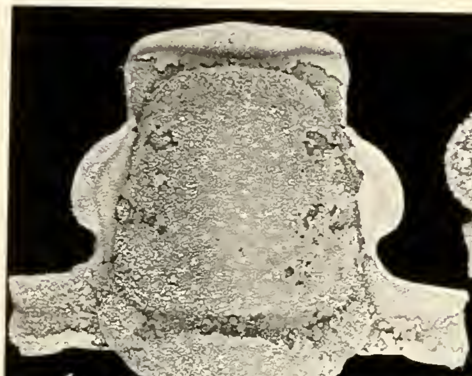
21, 26, 27. Pygidium, SUI 99210, dorsal, posterior, and right lateral views, ×12.

22, 28, 29. Pygidium, SUI 99211, dorsal, posterior, and right lateral views, ×10.

EXPLANATION OF PLATE 13

Figure	Page
1–28. *Corbinia implumis* Winston and Nicholls, 1967	21

1, 11, 12, 14, 15. Cranidium, SUI 99212, dorsal, ventral, right lateral, anterior, and oblique views, ×4.
2, 7, 8, 13. Cranidium, SUI 99213, dorsal, anterior, right lateral, and oblique views, ×10.
3, 5, 9. Cranidium, SUI 99214, dorsal, anterior, and right lateral views, ×10.
4, 6, 10. Cranidium, SUI 99215, dorsal, anterior, and left lateral views, ×10.
16, 20. Right librigena, SUI 99216, external and internal views, ×10.
17, 21, 25. Pygidium, SUI 99217, right lateral, dorsal, and posterior views, ×6.
18, 23, 24, 26, 27. Pygidium, SUI 99218, dorsal, right lateral, oblique, posterior, and ventral views, ×5.
19, 22, 28. Pygidium, SUI 99219, dorsal, left lateral, and posterior views, ×5.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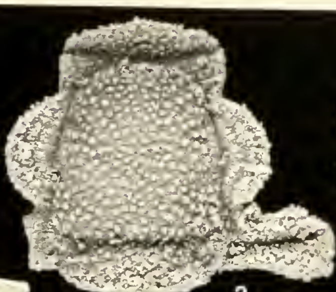
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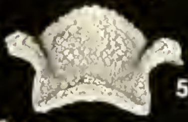
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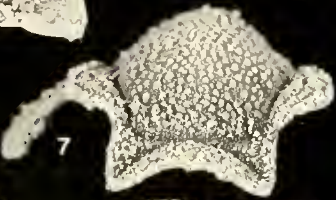
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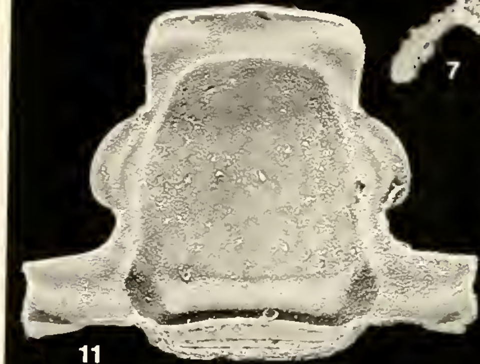
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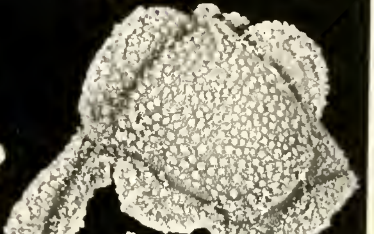
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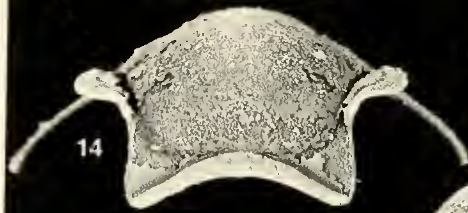
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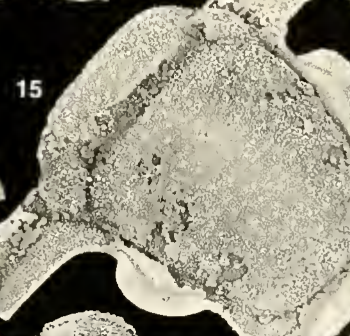
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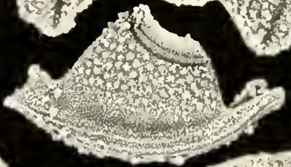
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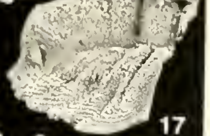
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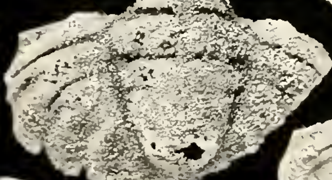
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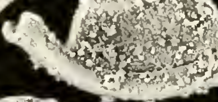
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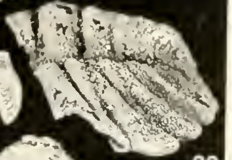
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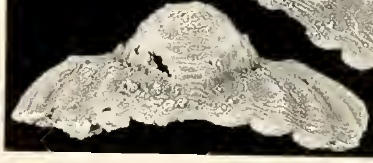
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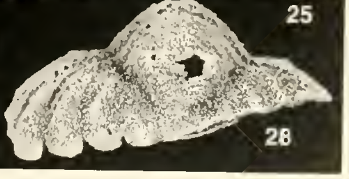
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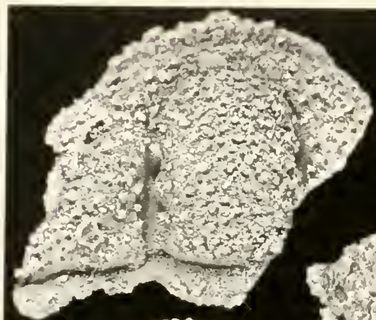
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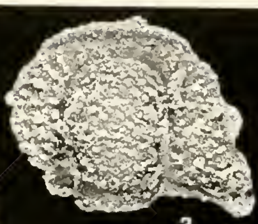
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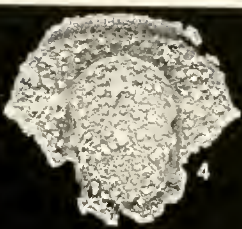
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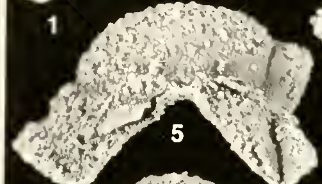
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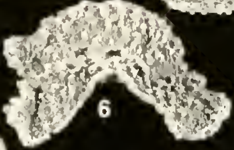
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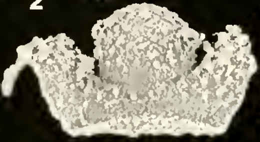
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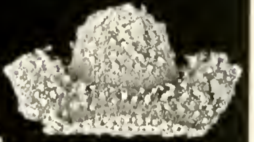
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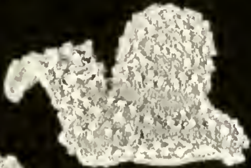
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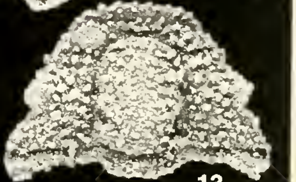
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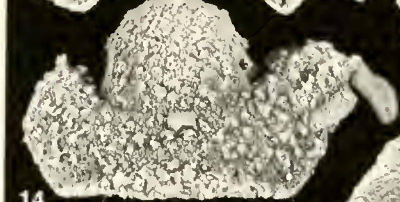
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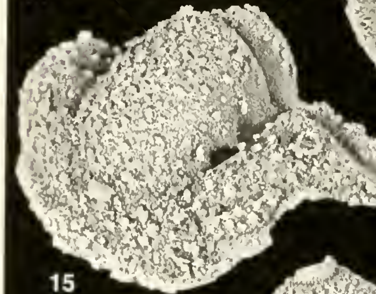
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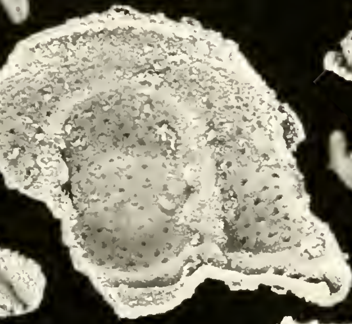
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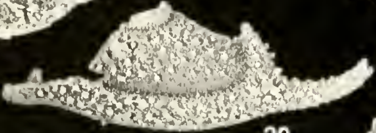
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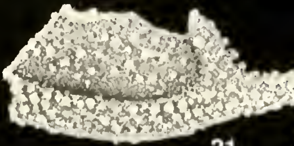
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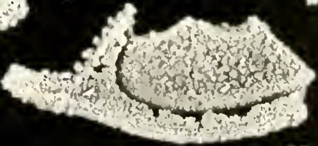
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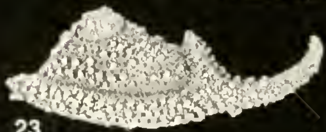
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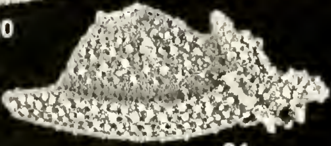
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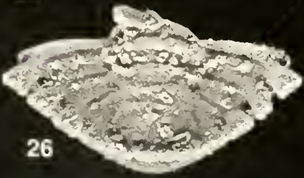
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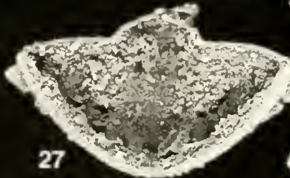
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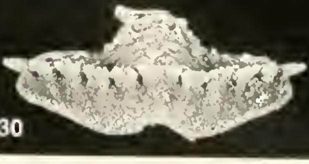
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EXPLANATION OF PLATE 14

Figure	Page
1–33. *Heterocaryon vargum* Westrop, 1986b.	23

1, 5, 14–16. Cranidium, SUI 99220, dorsal, left lateral, anterior, oblique, and ventral views, ×10.
2, 6, 10. Cranidium, SUI 99221, dorsal, right lateral, and anterior views, ×10.
3, 7, 8. Cranidium, SUI 99222, dorsal, anterior, and right lateral views, ×10.
4, 9. Cranidium, SUI 99223, dorsal and anterior views, ×10.
11–13. Cranidium, SUI 99224, anterior, left lateral, and dorsal views, ×12.
17–19. Yoked librigenae, SUI 99225, anterior, right lateral, and dorsal views, ×12.
20. Left librigena, SUI 99226, external view, ×15.
21, 22. Left librigena, SUI 99227, external and internal views, ×15.
23. Left librigena, SUI 99228, external view, ×12.
24. Left librigena, SUI 99229, external view, ×10.
25. Right librigena, SUI 99230, external view, ×10.
26, 27, 30–32. Pygidium, SUI 99231, dorsal, ventral, posterior, right lateral, and anterodorsal views, ×10.
28. Left librigena, SUI 99232, external view, ×12.
29, 33. Pygidium, SUI 99233, dorsal and posterior views, ×10.

EXPLANATION OF PLATE 15

Figure Page

1–30. *Bowmania lassieae* new species. 23

1, 4, 7, 12, 13. Cranidium, **holotype,** SUI 99234, dorsal, anterior, ventral, right lateral, and oblique views, ×7.5.

2, 5, 8. Cranidium, SUI 99235, dorsal, anterior, and right lateral views, ×7.5.

3, 6, 10. Cranidium, SUI 99236, dorsal, anterior, and left lateral views, ×7.5.

9, 11. Cranidium, SUI 99237, dorsal and right lateral views, ×7.5.

14, 19, 20. Cranidium, SUI 99238, dorsal, anterior, and left lateral views, ×10.

15. Cranidium, SUI 99239, dorsal view, ×7.5.

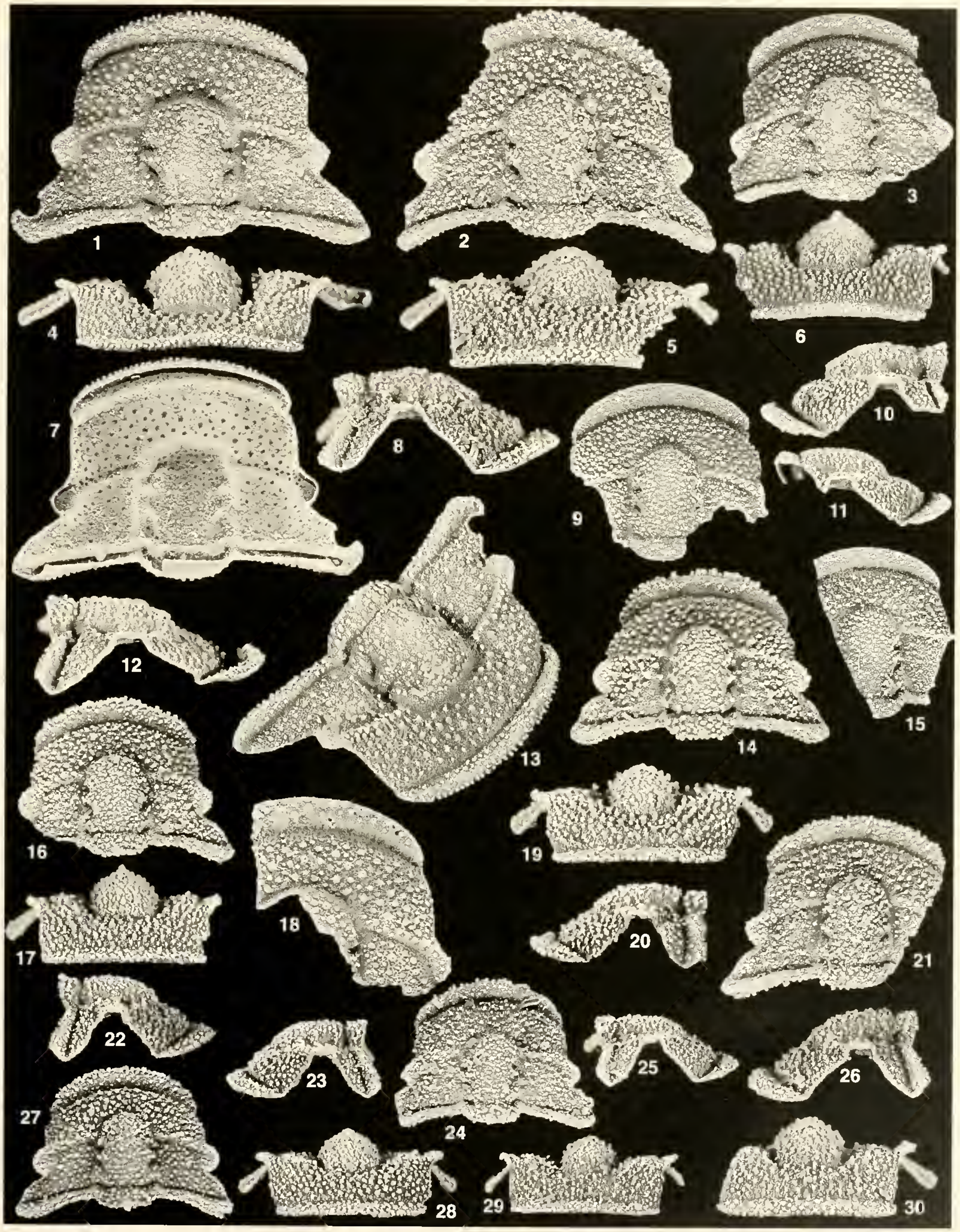
16, 17, 22. Cranidium, SUI 99240, dorsal, anterior, and right lateral views, ×7.5.

18. Cranidium, SUI 99241, dorsal view, ×7.5.

21, 26, 30. Cranidium, SUI 99242, dorsal, left lateral, and anterior views, ×7.5.

23, 27, 28. Cranidium, SUI 99243, left lateral, dorsal, and anterior views, ×7.5.

24, 25, 29. Cranidium, SUI 99244, dorsal, right lateral, and anterior views, ×7.5.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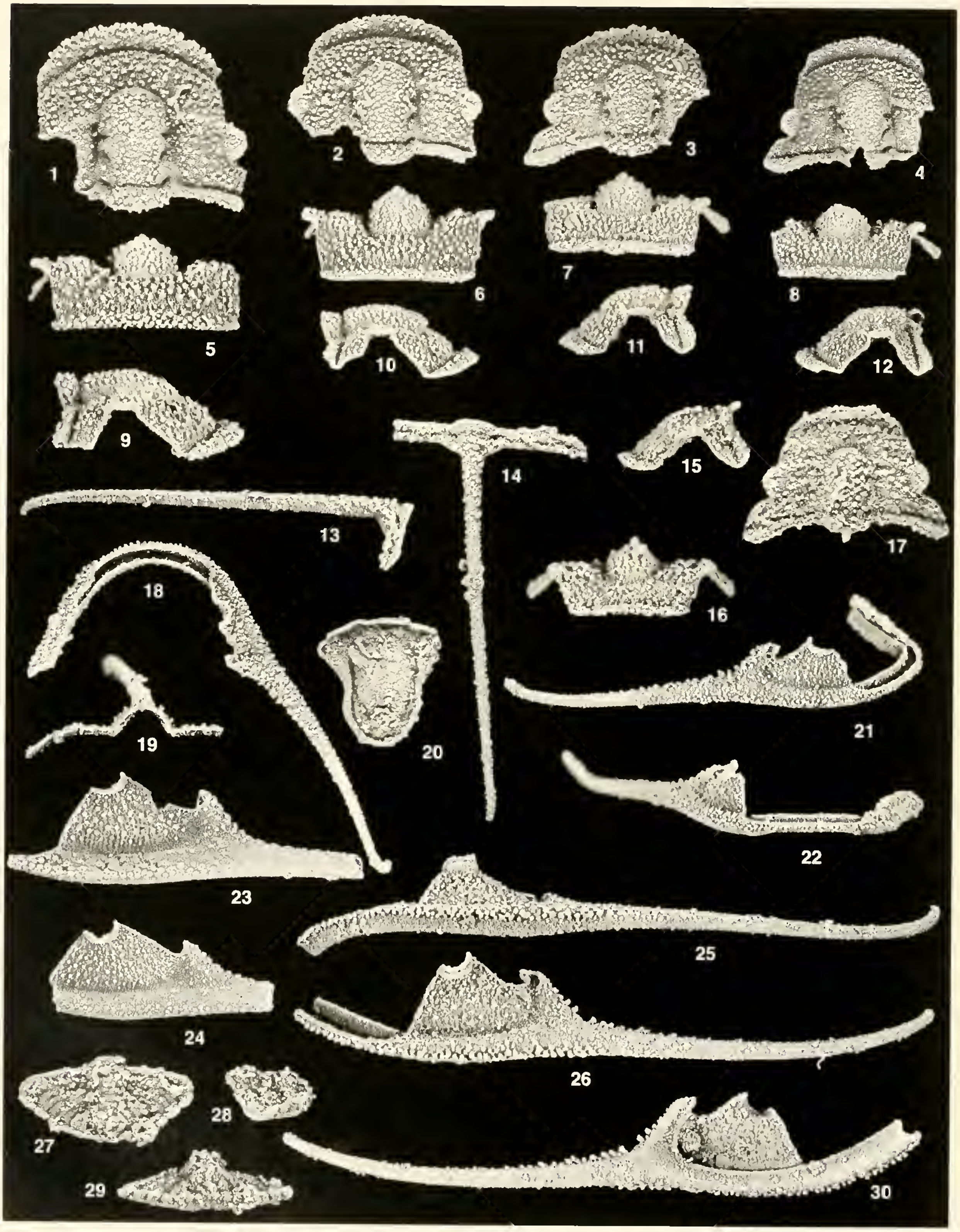
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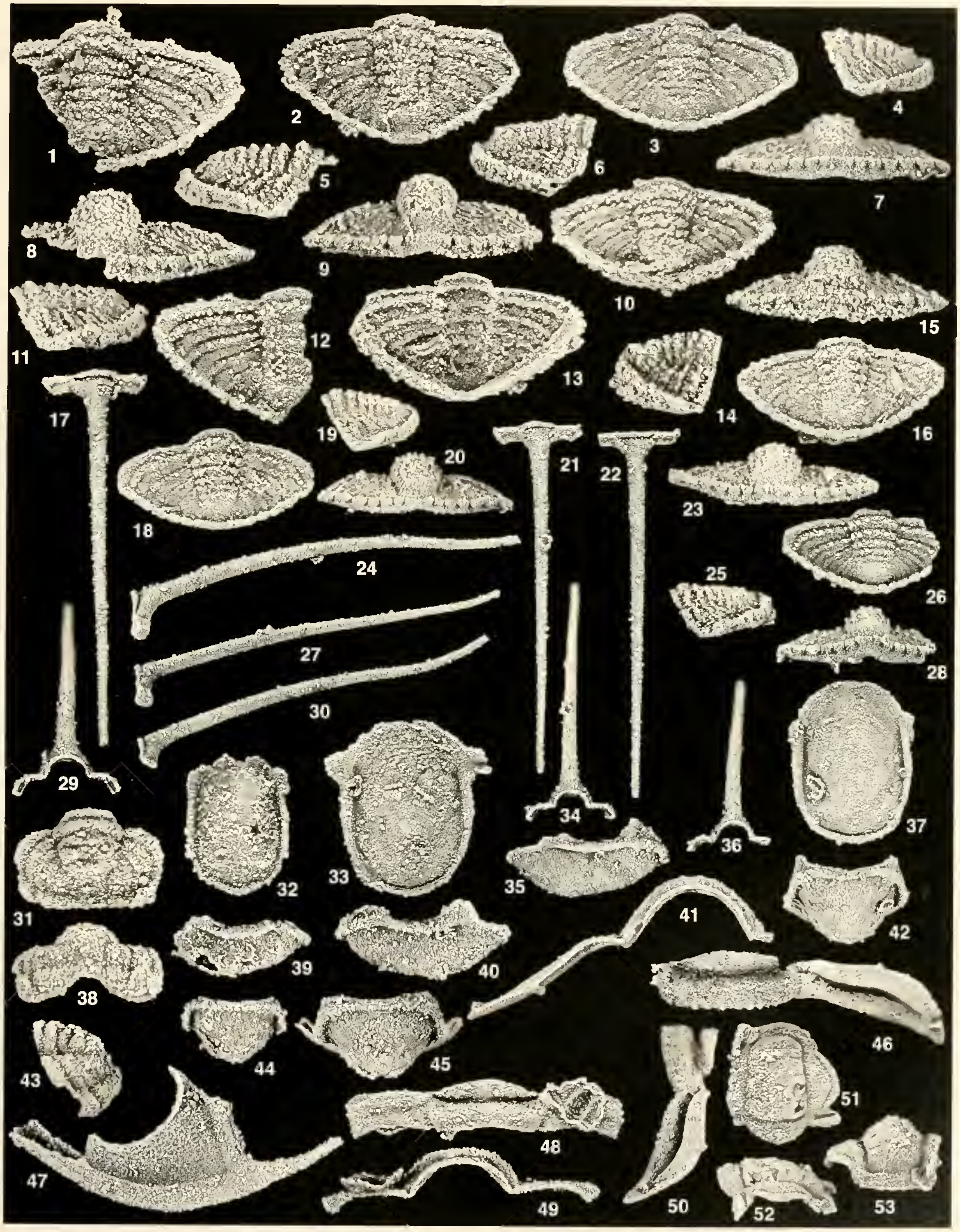
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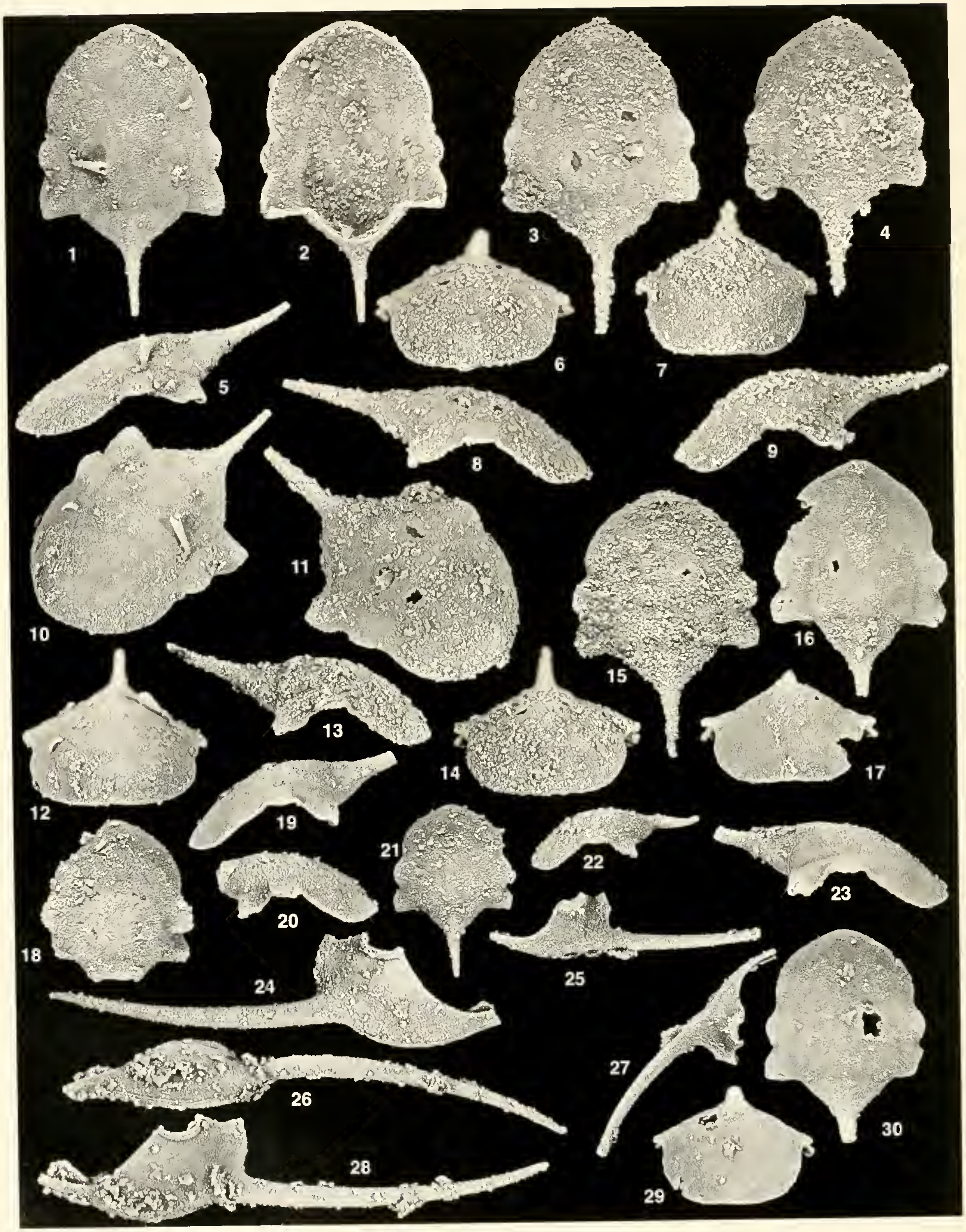
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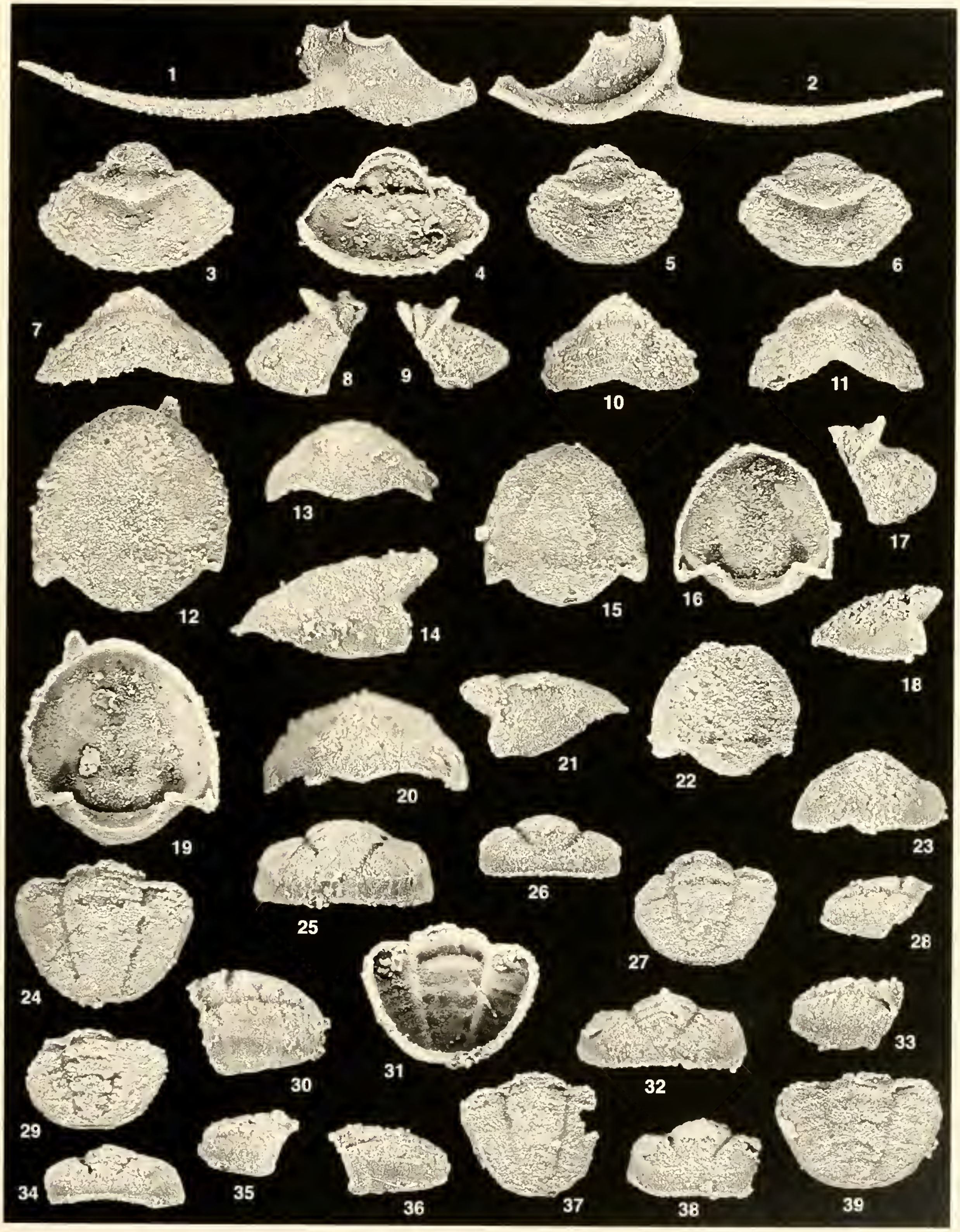
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PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

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The Genus *Lepicythara* (Gastropoda: Turridae) from the Neogene and Pleistocene of Tropical America

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Systematic Paleontology

THE GENUS *LEPICYTHARA* (GASTROPODA: TURRIDAE) FROM THE NEOGENE AND PLEISTOCENE OF TROPICAL AMERICA

Peter Jung

Natural History Musuem Basel, Augustinergasse 2, CH-4001 Basel, Switzerland

ABSTRACT

The shallow to moderately deep water turrid genus *Lepicythara* is restricted to the Neogene and Pleistocene of tropical America including Florida. So far the genus consists of 22 species, twelve of which are specifically identified, five are identified by means of open nomenclature, and five are characterized by letters. Four species are described as new: *L. higensis* from the Pleistocene of Pacific Costa Rica, *L. lopenzana* from the late Early to Middle Miocene Baitoa Formation of the northern Dominican Republic, *L. paradisclusa* from the Early Pliocene Springvale Formation of the Central Range of Trinidad, and *L. toroensis* from the Early Pliocene Shark Hole Point Formation of the Valiente Peninsula, Province of Bocas del Toro, Panama.

The geographic distribution of the species is irregular. Of the 13 areas of occurrence six are situated in Panama and Costa Rica. The amount of material assigned to individual species is also most irregular: only one species (*L. polygona*) is very well represented, two species (*L. costaricensis* and *L. terminula*) are well represented, but all the other species have to be called rare or extremely rare. The species diversity through time is fluctuating. After a period of low diversity during the late Early and Middle Miocene the diversity reached a maximum during Late Miocene times. In the Early Pliocene it was still fairly high, but during Middle and Late Pliocene times there was a steady decrease in diversity, the genus *Lepicythara* seemingly became extinct toward the end of the Pleistocene.

RESUMEN

El genero marino *Lepicythara* (Turridae) vivia en agues de poca hasta mediana profundidad y su distribution se limitaba al Neogeno y Pleistoceno de la America tropical, includido la Florida. Hasta ahora, el genero se compone de 22 especies, de las cuales 12 son identificadas especificaments, 5 se caraterizan por la monemclatura abierta, y las otras 5 por letras. Cuatro especies son nuevas. *L. higensis* del Pleistoceno de la parte pacifica de Costa Rica, *L. lopenzana* de la formacio Baitoa (ultima parte del periodo temprano del Mioceno, hasta lost principios del periodo medio de dicha epoca) de la Republica Dominicana del norte, *L. paradisclusa* de la formacio Springvale (Plioceno temprano) de la Central Range de Trinidad, y *L. toroensis* de la formacion Shark Hole Point (Plioceno temprano) do la peninsula Valiente, Provincia de Bocas del Toro, Panama.

La distribucion geografica de las especies es irregular. De las 13 regiones, en las cuales se conoce *Lepicythara*, seis se encuentran en Panama y Costa Rica. Respecto a la frecuencia de los especimenes, solo una especie (*L. polygona*) es muy bien representada, dos especies (*L. costaricensis* y *L. terminula*) son bien representadas, y las otras especies son raras hasta muy raras. Principiando en el Mioceno tardio inferior, la diversidad de las especies llego a su maximo durante el Mioceno superior. En el Plioceno temprano, la diversidd todavia era relaiveamente considerable, per durante la epoca del Plioceno medio y tardio ocurrio una disminucion, u el genero *Lepicythara* evidentemente resulto extinto a finales del Pleistoceno.

INTRODUCTION

The turrid genus *Lepicythara* Olsson is by no means common where it occurs. A total of only 176 lots have been available for this study (Table 1). This material can be subdivided into three categories:

1) borrowed from other institutions (60 lots)
2) collections in the Naturhistorisches Museum Basel, Switzerland (NMB) (70 lots)
3) collections of the Panama Paleontology Project (PPP) (46 lots)

The NMB material contains 47 lots from the Dominican Republic, 12 from Trinidad, 5 from Costa Rica, 3 from Ecuador, and 3 from Florida. The PPP material contains 24 lots from Panama, 19 from Costa Rica, and 3 from Ecuador.

Not only is the material of *Lepicythara* rather scarce, but the species diversity is not great either. Out of the 22 species discussed in this report only three are represented by a reasonable amount of material; all the others are rare or extremely rare. Table 1 lists these species, and the number of the available lots and specimens is indicated for each.

By far best represented is *L. polygona*; it is followed by *L. costaricensis* and *L. terminula*. After these three species the number of available specimens drops drastically. Twelve species are positively identified, five are identified by means of open nomenclature, and five are characterized by a letter. Four species are described as new. They are: *L. higensis*, *L. lopezana*, *L. paradisclusa*, and *L. toroensis*. For details of lithostratigraphy, exact geographic location of occurrences, and precise stratigraphic position of localities reference is made to Coates (1999a–c).

Table 1 — Total number of lots and specimens of species of *Lepicythara* discussed in this paper.

Species	Number of lots	Number of specimens
basilissa	5	11
camaronensis	7	18
costaricensis	35	138
cf. *costaricensis*	1	1
disclusa	8	29
heptagona	10	16
cf. *heptagona*	1	2
aff. *heptagona*	1	5
higensis	5	15
lopezana	4	6
cf. *lopezana*	2	5
paradisclusa	5	26
polygona	40	1184
terminula	29	136
toroensis	3	7
turrita	8	34
aff. *turrita*	3	4
sp. A	3	3
sp. B	1	4
sp. C	3	3
sp. D	1	1
sp. E	1	1
Total	176	1649

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DISTRIBUTION THROUGH TIME AND SPACE

The genus *Lepicythara* is known only from the Western Hemisphere. Its rather spotty occurrences in tropical America and Florida are shown in Text-figure 1. Below follows a list of the species discussed in this paper arranged by countries:

Southern Florida, U. S. A.

- *L. basilissa*
- *L. terminula*
- *L. turrita*

Eastern Haiti

- *L.* cf. *lopezana*

Northern Dominican Republic

- *L. heptagona*
- *L. lopezana*
- *L. polygona*

Trinidad

- *L. disclusa*
- *L. paradisclusa*

Northern Colombia

- *L.* cf. *Heptagona*

Northwestern Ecuador

- *L. camaronensis*
- *L.* sp. E

Panama

- *L. costaricensis*
- *L.* cf. *costaricensis*
- *L. toroensis*
- *L.* aff. *turrita*
- *L.* sp. A
- *L.* sp. B
- *L.* sp. C

Costa Rica

- *L. costaricensis*
- *L. higensis*
- *L.* sp. D

Southern Mexico

- *L.* aff. *heptagona*

The greatest diversity (seven species) occurs in Panama. On the other hand only one species each is recorded from eastern Haiti, northern Colombia, and southern Mexico. Two species each are recorded from Trinidad and northwestern Ecuador, and three each from Florida, the northern Dominican Republic, and Costa Rica. Thus, the distribution and diversity are rather uneven. The species of *Lepicythara* are part of shallow to moderately deep water assemblages (Jack-

Text-figure 1.—Map showing areas of occurrence of species of *Lepicythara*. 1, northern Florida; 2, southern Florida; 3, eastern Haiti; 4, northern Dominican Republic; 5, Trinidad; 6, northern Colombia; 7, Esmeraldas area, northwestern Ecuador; 8, Darien, eastern Panama; 9, Canal area, Panama; 10, Bocas del Toro Province, northwestern Panama; 11, Limon Basin, Caribbean Costa Rica; 12, Golfo Dulce, Pacific Costa Rica; 13, Puntarenas Province, Pacific Costa Rica; 14, Santa Rosa, Veracruz, Mexico.

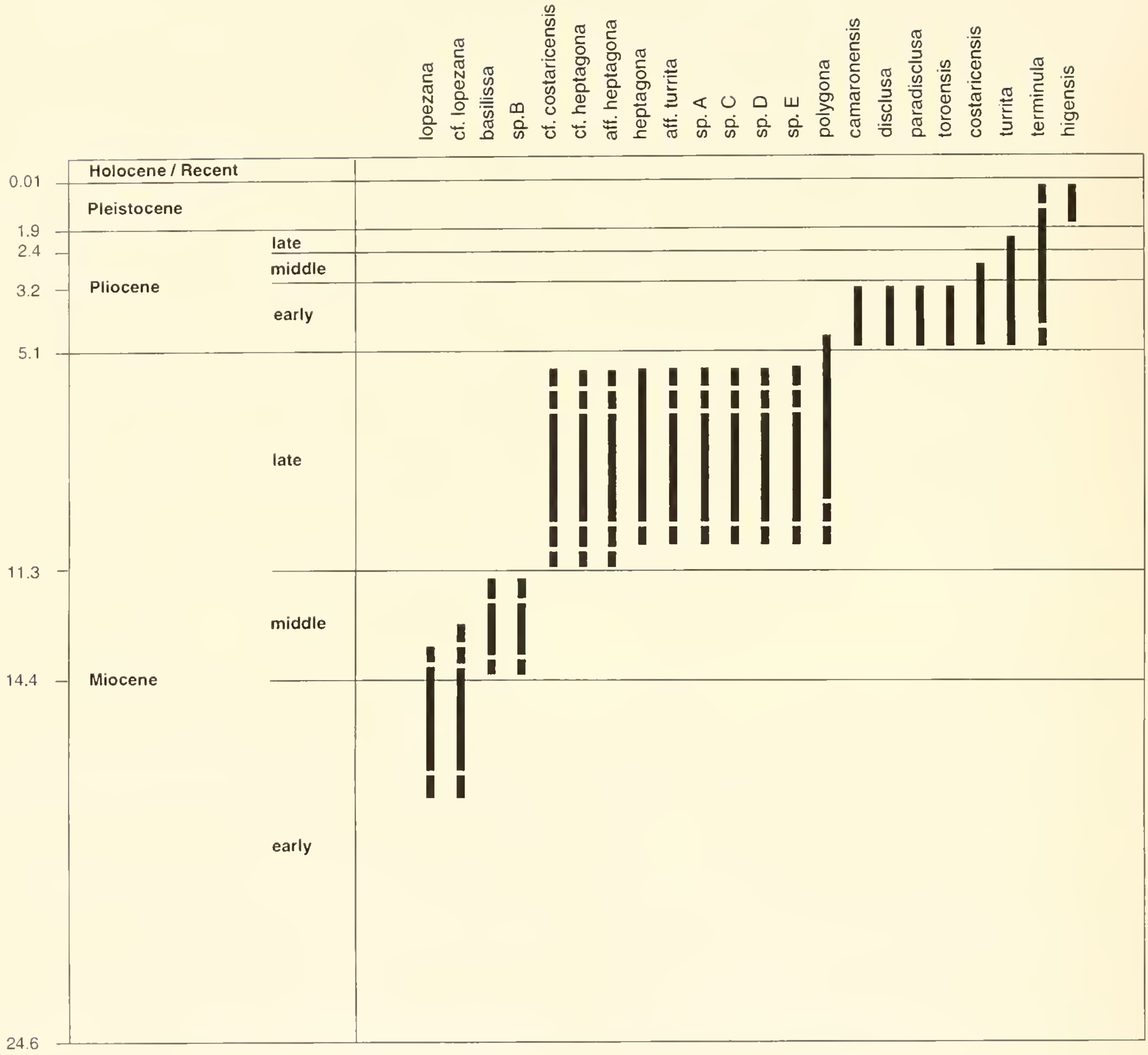
son *et al.*, 1999, table 3, p. 204, appendix 1, pp. 212–213; for details see Appendix II).

The stratigraphic ranges of the species are shown in Text-figure 2. The species diversity through time is visualized in Text-figure 3: after a hesitant beginning in Late Early and Middle Miocene times, the diversity increases rapidly to its maximum during Late Miocene times. During the Early Pliocene the diversity is still quite large, but after that there is a steady decrease until the genus disappears toward the end of the Pleistocene.

Text-figure 3 resembles the analogous representations for genera of the *Strombina*-group (Jung, 1989, fig. 28), and it is especially similar to the genus *Sincola*. There are, however, two basic differences: first the genus *Lepicythara* did not survive the Pleistocene, and second there is not a "bottleneck" during Middle and Late Pliocene times in *Lepicythara*, whereas the genera of the *Strombina*-group all show it. In *Lepicythara* there is a gradual decrease from the Middle Pliocene to the Pleistocene.

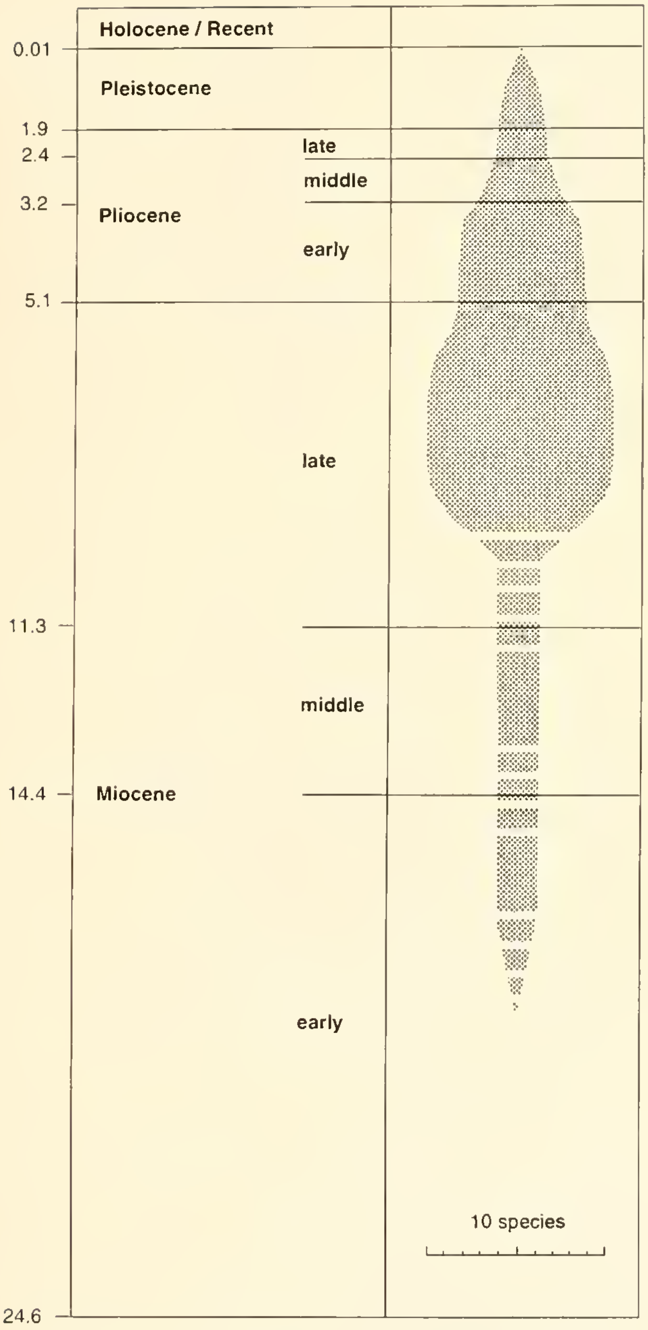
The following list is a summary of the distribution of the 22 discussed species through time and space:

1. *L. basilissa*: Shoal River Formation (Middle Miocene), northern Florida
2. *L. camaronensis*: Onzole Formation (Early Pliocene), northwestern Ecuador
3. *L. costaricensis*: Rio Banano, Cayo Agua, and Shark Hole Point formations (all Pliocene), Caribbean Costa Rica and Province of Bocas del Toro, Panama
4. *L.* cf. *costaricensis*: Nancy Point Formation (Late Miocene), Province of Bocas del Toro, Panama
5. *L. disclusa*: Melajo Clay Member of Springvale Formation (Early Pliocene), Trinidad
6. *L. heptagona*: Cercado and Gurabo Formations (Late Miocene), Dominican Republic
7. *L.* cf. *heptagona*: Late Miocene, northern Colombia
8. *L.* aff. *heptagona*: beds of Late Miocene age, Veracruz, Mexico



Text-figure 2.—Stratigraphic ranges of the species of *Lepicythara*.

9. *L. higensis*: Pleistocene, Pacific coast of Costa Rica
10. *L. lopezana*: Baitoa Formation (late Early to early Middle Miocene), Dominican Republic.
11. *L.* cf. *lopezana*: Thomonde Formation (late Early to early Middle Miocene), Haiti
12. *L. paradisclusa*: Springvale Formation (Early Pliocene), Trinidad
13. *L. polygona*: Cercado and Gurabo Formations (Late Miocene to Early Pliocene), Dominican Republic
14. *L. terminula*: Pliocene to Pleistocene, southern Florida
15. *L. toroensis*: Shark Hole Point Formation (Early Pliocene), Province of Bocas del Toro, Panama
16. *L. turrita*: Jackson Bluff Formation and Pinecrest beds (Pliocene), Florida
17. *L.* aff. *turrita*: Nancy Point Formation (Late Miocene), Province of Bocas del Toro, Panama
18. *L.* sp. A: Gatun Formation (Late Miocene), central Panama
19. *L.* sp. B: Tuira Formation (Middle Miocene), Darien, Panama
20. *L.* sp. C: Nancy Point Formation (Late Miocene), Province of Bocas del Toro, Panama



Text-figure 3.—Species diversity of *Lepicythara* through time. The radiometric ages (in millions of years) on the left margin are taken from Bolli and Saunders (1985, p. 159, text-fig. 3).

21. *L.* sp. D: Late Miocene (?), Punta Judas, Pacific coast of Costa Rica
22. *L.* sp. E: Angostura Formation (Late Miocene), northwestern Ecuador

ARE THERE NO LIVING SPECIES?

Lepicythara ranges from late Early Miocene to Pleistocene. It seems strange that no living species has ever been recorded. In the Gibson-Smith collection of the NMB, there are two small, Recent specimens from two different localities, which are close to *Lepicythara*, but they cannot definitely be assigned to that genus. The larger specimen (restored height 6.2 mm, width 2.8 mm, ratio 2.21: Text-fig. 4) is well preserved. Its protoconch is not quite complete but has 2.5 volutions. There are a little more than four teleoconch whorls. This specimen (NMB H 18118) has been collected at NMB locality 17666: Adicora, east coast of the Paraguana Peninsula, Venezuela. The smaller specimen (restored height 4.9 mm, width 2.1 mm, ratio 2.33: Text-fig. 5) is not well preserved, and the number of volutions of its protoconch cannot be determined. There are 3.25 teleoconch whorls. The specimen (NMB H 18119) has been collected at NMB locality 17671: Tucacas, Falcón, Venezuela.

The two specimens probably do not represent the same species. The larger specimen has twelve axial ribs on its last whorl, the smaller only nine. On the other hand both show many characteristics including the spiral sculpture typical for *Lepicythara*. There is, however, one constant difference: the angulation of the profile of the teleoconch whorls continues to the last whorl, whereas in species of *Lepicythara* it is restricted to the early teleoconch whorls.

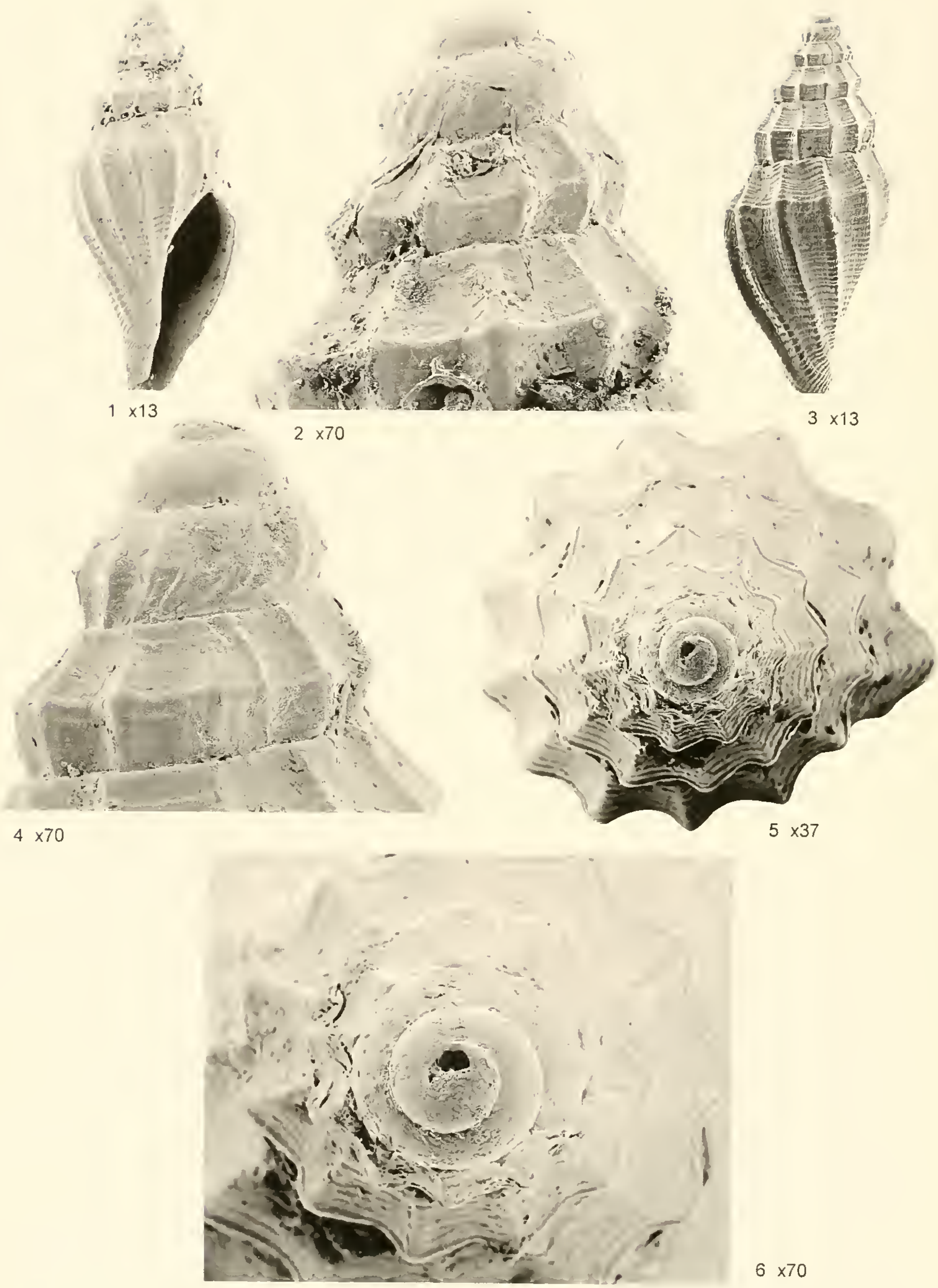
SYSTEMATIC PALEONTOLOGY

INTRODUCTION

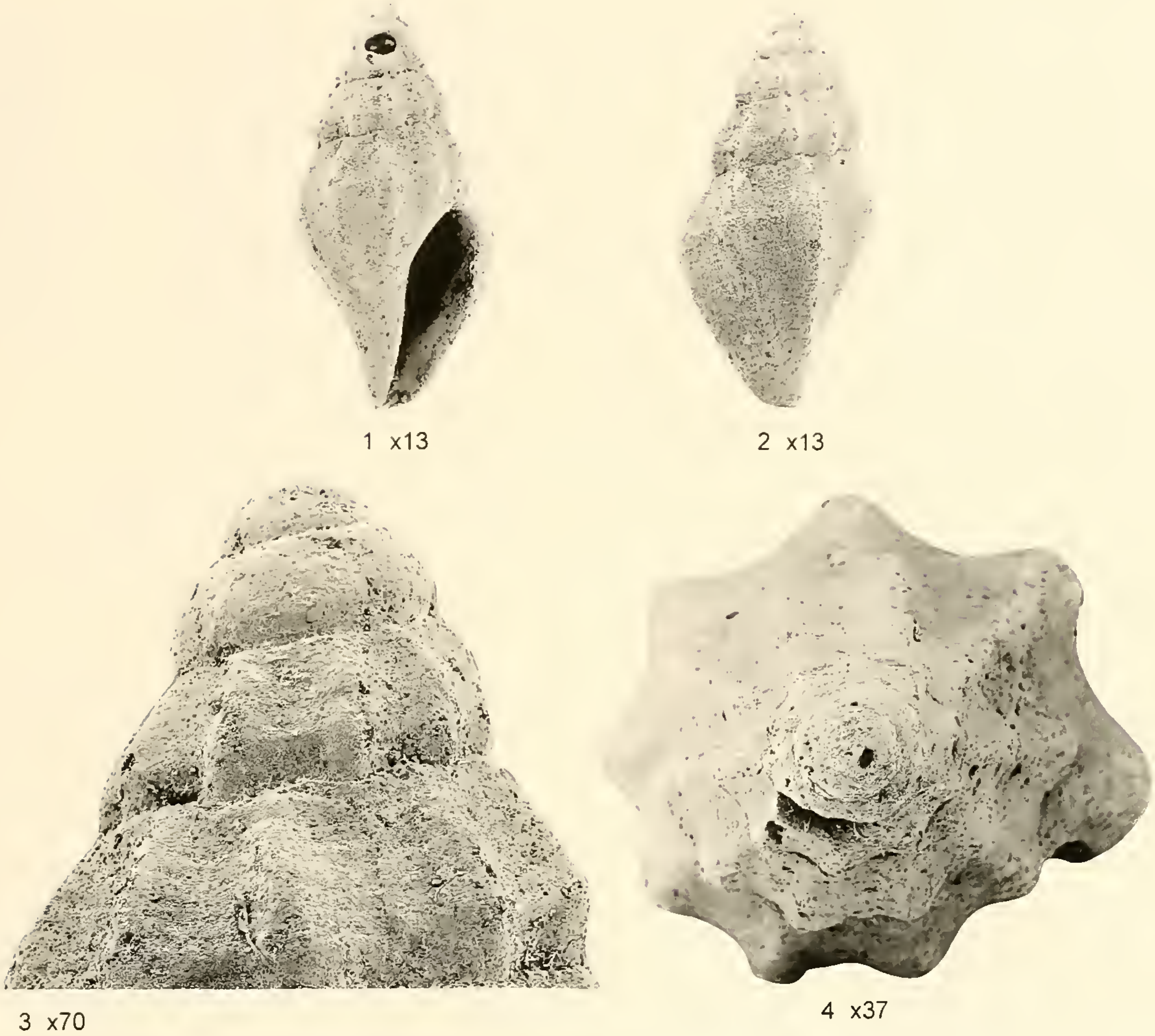
The organization and conventions of the systematic part are basically the same as those followed by Jung (1989, p. 35). In the following descriptions references to the size of a species is made by means of the words small, medium and large. These are defined as: "small": height 10.5 mm or less; "medium": height between 10.6 and 13.00 mm; "large": height 13.1 mm or more.

ABBREVIATIONS

ANSP	Academy of Natural Sciences, Philadelphia, PA, U. S. A.
CR	Costa Rica
DR	Dominican Republic
NMB	Naturhistorisches Museum Basel, Switzerland (the letter H after NMB stands for gastropods)
PPP	Panama Paleontology Project
PRI	Paleontological Research Institution, Ithaca, NY, U. S. A.
UF	Florida Museum of Natural History, University of Florida, Gainesville, FL, U. S. A.
USGS	United States Geological Survey
USNM	United States National Museum of Natural



Text-figure 4.– *Lepicythara*? sp. 1. NMB H 181118. Recent specimen from NMB locality 17666: Adicora, east coast of the Paraguana Peninsula, Falcon, Venezuela. Height 6.2 mm, width 2.8 mm. 1, front view; 2, enlargement of apical area; 3, rear view; 4, enlargement of apical area; 5, apical view; 6, enlargement of apical view.



Text-figure 5.—*Lepicythara*? sp 2. NMB H 18119. Recent specimen from NMB locality 17671: Tucacas, Falcón, Venezuela. Height 4.9 mm, width 2.1 mm. 1, front view; 2, rear view; 3, enlargement of apical area; 4, apical view.

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DIAGNOSTIC FEATURES

The most important morphological characteristics of the species discussed in this paper are summarized in Table 2. They include the general habitus, the range of the restored heights, the number of volutions of the protoconch, the profiles of the early and late whorls, and the number of axial ribs on the body whorl on one hand and early whorls on the other hand.

The species of *Lepicythara* can also be subdivided into groups of species based on the number of axial ribs per whorl. A first group with more or less the same number of axial ribs on early whorls and on the body whorl includes: *L. basilissa*, *L. camaronensis*, *L. costaricensis*, *L.* cf. *heptagona*, *L. lopezana*, *L.* cf. *lopezana*, *L. paradischusa*, *L. terminula*, *L.* sp. A, *L.* sp. B, and *L.* sp. D.

A second group of species having more axial ribs on the body whorl than on early whorls includes: *L.* cf. *costaricensis*, *L. dischusa*, *L. heptagona*, *L.* aff. *heptagona*, *L. higensis*, *L. polygona*, *L. toroensis*, *L.* sp. C, and *L.* sp. E.

A third group of species with more axial ribs on early whorls than on the body whorl includes only: *L. turrita* and *L.* aff. *turrita*.

Family Turridae Adams and Adams, 1853

Genus **LEPICYTHARA** Olsson, 1964

Lepicythara Olsson 1964, p. 110.

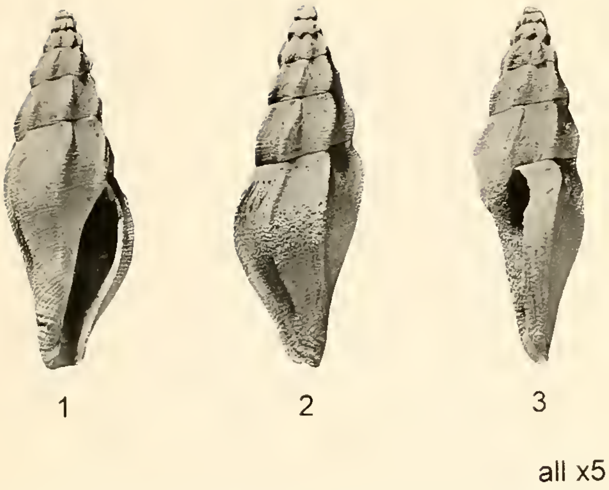
Type species (by original designation).—*Cythara*

Table 2.—Summary of the most important morphological characters discussed in the text.

Species	General habitus	Range of (restored) height (in mm)	Volutions protoconch	Profile early whorls	Profile late whorls	Axial ribs on body whorl	Axial ribs on early whorls
basilissa	small slender	3.7–10.1	3.25	slightly convex	slightly convex	7–8	7–9
camaronensis	medium-large biconic stout	12.4–19.7	3.0	straight ?	slightly convex	8–9	8–9
costaricensis	medium-large moderately slender	9.5–16.1	2.5–2.75	straight angulated	slightly convex	8–10	7–9
cf. *costaricensis*	small biconic	10.5	2.5+	straight angulated	slightly convex	10	9
disclusa	large, biconic moderately stout	13.1–16.9	2.75–3.0	straight angulated	slightly convex	9–10	8–9
heptagona	medium-large biconic, moderately slender	11.3–17.0	2.25	straight angulated	slightly convex	8–9	7–8
cf. *heptagona*	small-large moderately slender	10.4–13.6	2.75–3.0	straight angulated	slightly convex	8–9	8
aff. *heptagona*	large moderately slender	13.7	3.25	straight angulated	slightly convex	9	7
higensis	medium-large slender	12.2–16.7	2.5	straight angulated	slightly convex	10–11	7–9
lopezana	medium-large moderately slender	11.5–14.0	2.75	slightly convex	convex	7–8	7–8
cf. *lopezana*	small-medium slender	7.1–11.0	2.75	slightly convex	convex	8–9	8
paradisclusa	small-medium biconic stout	7.6–12.5	2.75	straight angulated	straight	8–9	8–9
polygona	small-medium slender	6.4–12.1	2.25–2.75	straight to convex	slightly convex	12–28	8–13
terminula	medium-large moderately slender	10.6–19.4	2.5	straight angulated	slightly convex	7–10	7–10
toroensis	large biconic stout	19.3–19.6	2.5	straight angulated	slightly convex	12–13	8–9
turrita	small-large biconic, moderately stout	8.9–14.9	2.75–3.0	straight angulated	convex	8–9	9–10
aff. *turrita*	large, moderately slender	14.8–17.7	2.75+	straight angulated	slightly convex	7	8–9
sp. A	medium slender	12.6–12.8	3.25	straight angulated	slightly convex	8–9	7–8
sp. B	large slender	14.0	3+	straight	slightly convex	6–7	7
sp. C	large, moderately slender	15.1	2.5	straight angulated	slightly convex	12	9
sp. D	large stout	14.1	?	straight ?	straight to slightly convex	8	?
sp. E	medium slender	12.5	?	straight	slightly convex	9	7

terminula Dall (1890, p. 38, pl. 2.5). Pliocene and Pleistocene of southern Florida.

Diagnosis.—Shells of small to large size (total range of height: 10.1–19.7 mm), general shape ranging from stout to slender, protoconch with 2.25 to 3.25 volutions, about its first two volutions are smooth, the remainder sculptured by a varying number of opisthocline to opisthocyrt axial riblets. Outer lip of protoconch opisthocline to opisthocyrt. The number of teleoconch whorls usually lies between 4.5 to 5.5, and in rare cases there are more than six whorls. Profile of early teleoconch whorls rarely slightly convex, usually straight and frequently with a carination or angulation near the abapical suture. Profile of late teleoconch whorls usually slightly convex, rarely convex, and even more rarely straight. Axial sculpture consists of a varying number per whorl of basically orthocline ribs, which may become somewhat sigmoid on the body whorl. Axial ribs usually narrow adapically and wider abapically. Spiral sculpture consists of narrow grooves or incised lines, which increase in number towards late whorls. Secondary spiral grooves are rare on early whorls, but more frequent on late whorls and the body whorl. All spiral grooves cross the sometimes fairly sharp ridges of the axial ribs. Suture not deep. Aperture narrow. Outer lip thickened. Sinus adjoining suture shallow to moderately deep. Inner surface of outer lip smooth, with or without a ridge parallel to



Text-figure 6.—*Lepicythara basilissa* (Gardner). USNM 351224. Holotype. USGS Station 3742. Shell Bluff, Shoal River, Walton County, Florida, Shoal River Formation. Height 9.8 mm, width 3.8 mm. 1, front view; 2, rear view; 3, from right side.

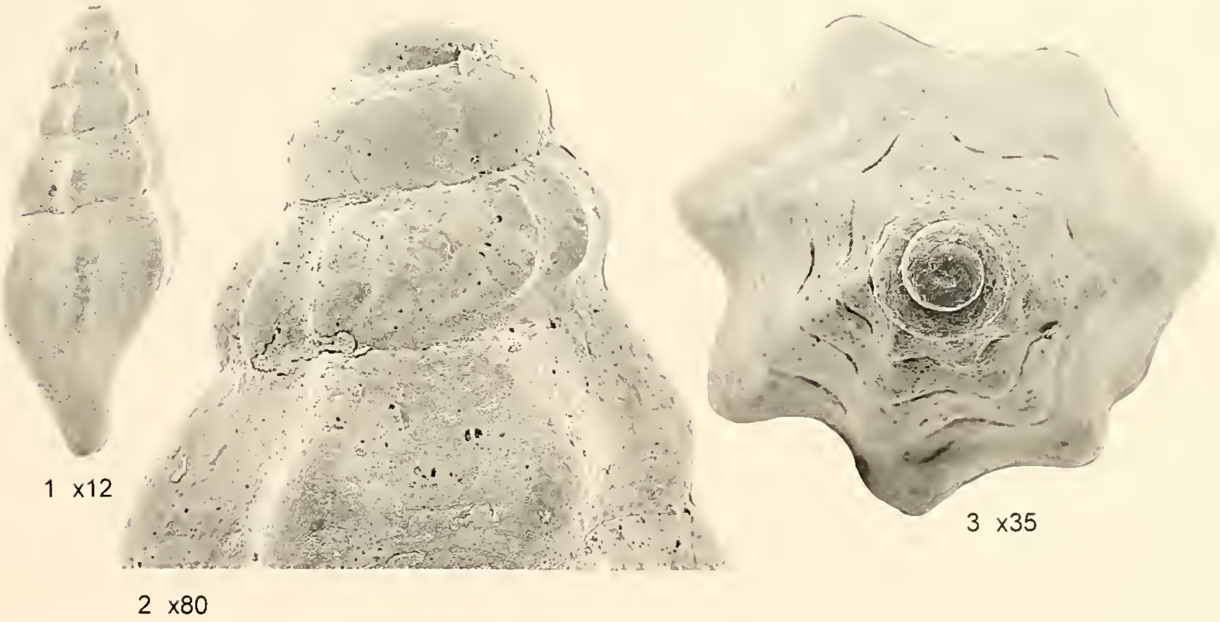
the sharp edge of the outer lip. Columellar callus thin to moderately prominent. Parietal callus usually inconspicuous, rarely thickened near sinus. Anterior canal straight or slightly twisted to the left, usually narrow, and short to moderately long.

Remarks.—As now known the genus *Lepicythara* consists of 22 species, ten of which are not named or are identified by means of open nomenclature only. Its occurrence is restricted to tropical America and Florida and its total stratigraphic range is late Early Miocene to Pleistocene.

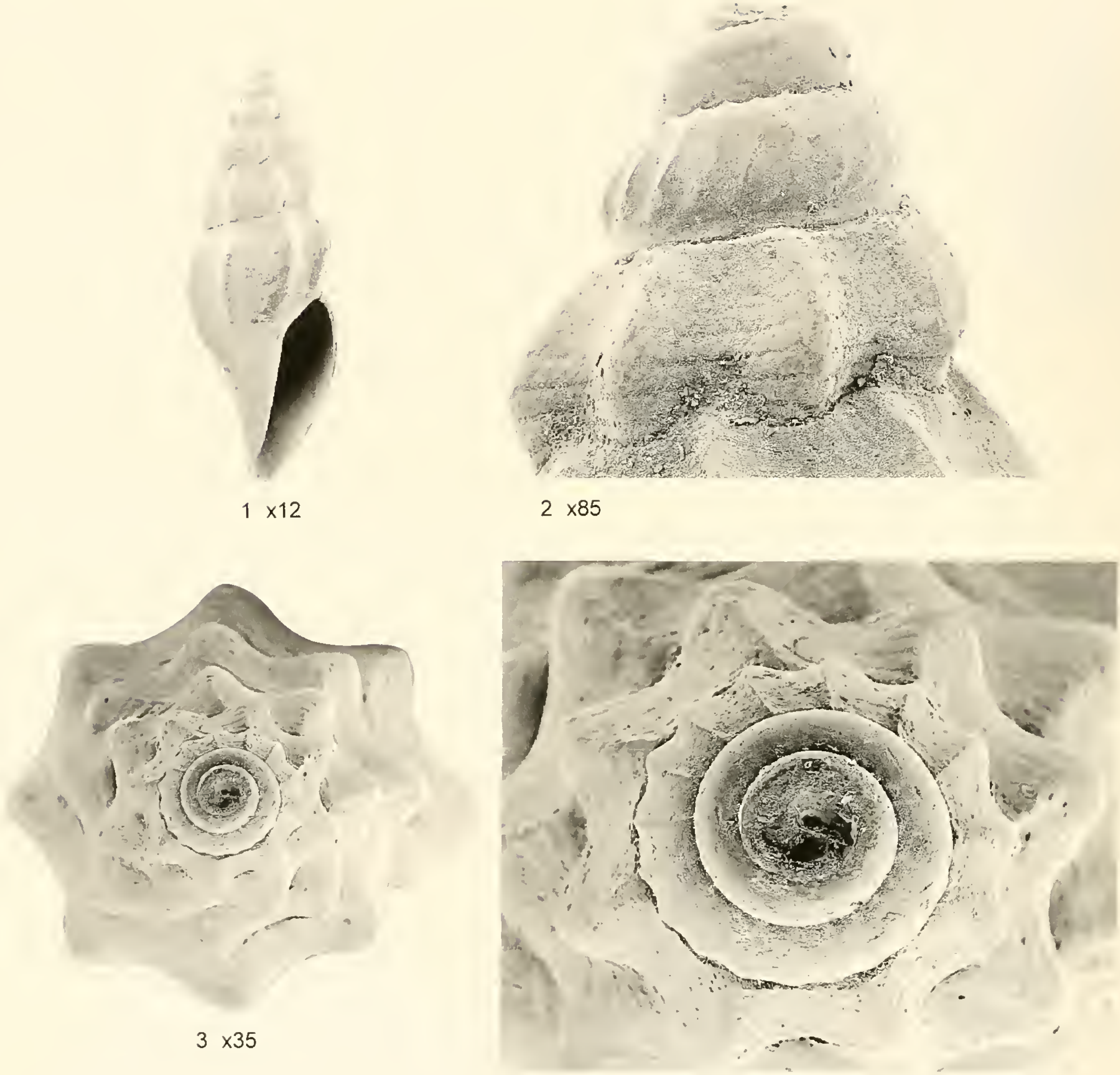
Lepicythara basilissa (Gardner, 1937)
Text-figures 6–9

"*Cythara*" *basilissa* Gardner, 1937, p. 344, pl. 42, f. 23–24.

Description.—Of small size, slender. Protoconch consists of 3.25 volutions; surface of its first 2.5 volutions smooth, the remainder sculptured by up to 15 opisthocyrt axial riblets. Number of teleoconch whorls up to 4.5, their profile slightly convex on early whorls as well as on late whorls. Teleoconch whorls sculptured by opisthocline to slightly sigmoid axial ribs; their number per whorl is seven to eight on early whorls and seven to nine on late whorls. Interspaces of axial ribs slightly concave, smooth except for sigmoid growth lines or weakly sculptured by incised spiral lines on the abapical part of the whorl. The crests of the axial ribs on spire whorls are crossed by a gradually increasing number of incised spiral lines. On the body whorl these incised spiral lines are present on the whole surface including the interspaces of the axial ribs but excluding a narrow zone on the interspaces, which adjoins the suture. Suture not deep. Aperature narrow. Outer lip thickened. Sinus adjoining suture rather shallow. Inner surface of outer lip smooth, without a ridge parallel to the sharp edge of the outer kip. Columellar and parietal calluses not conspicuous. Anterior canal straight, moderately long.



Text-figure 7.—*Lepicythara basilissa* (Gardner). USNM 509803. USGS Station 23979; Shoal River, Walton County, Florida, Shoal River Formation. Height 5.8 mm, width 2.2 mm. 1, rear view; 2, enlargement of apical area; 3, apical view.



1 x12

2 x85

3 x35

4 x90

Text-figure 8.—*Lepicythara basilissa* (Gardner). UF 102877. Shell Bluff, Shoal River, Walton County, Florida. Shoal River Formation. Height 6.0 mm, width 2.3 mm. 1, front view; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

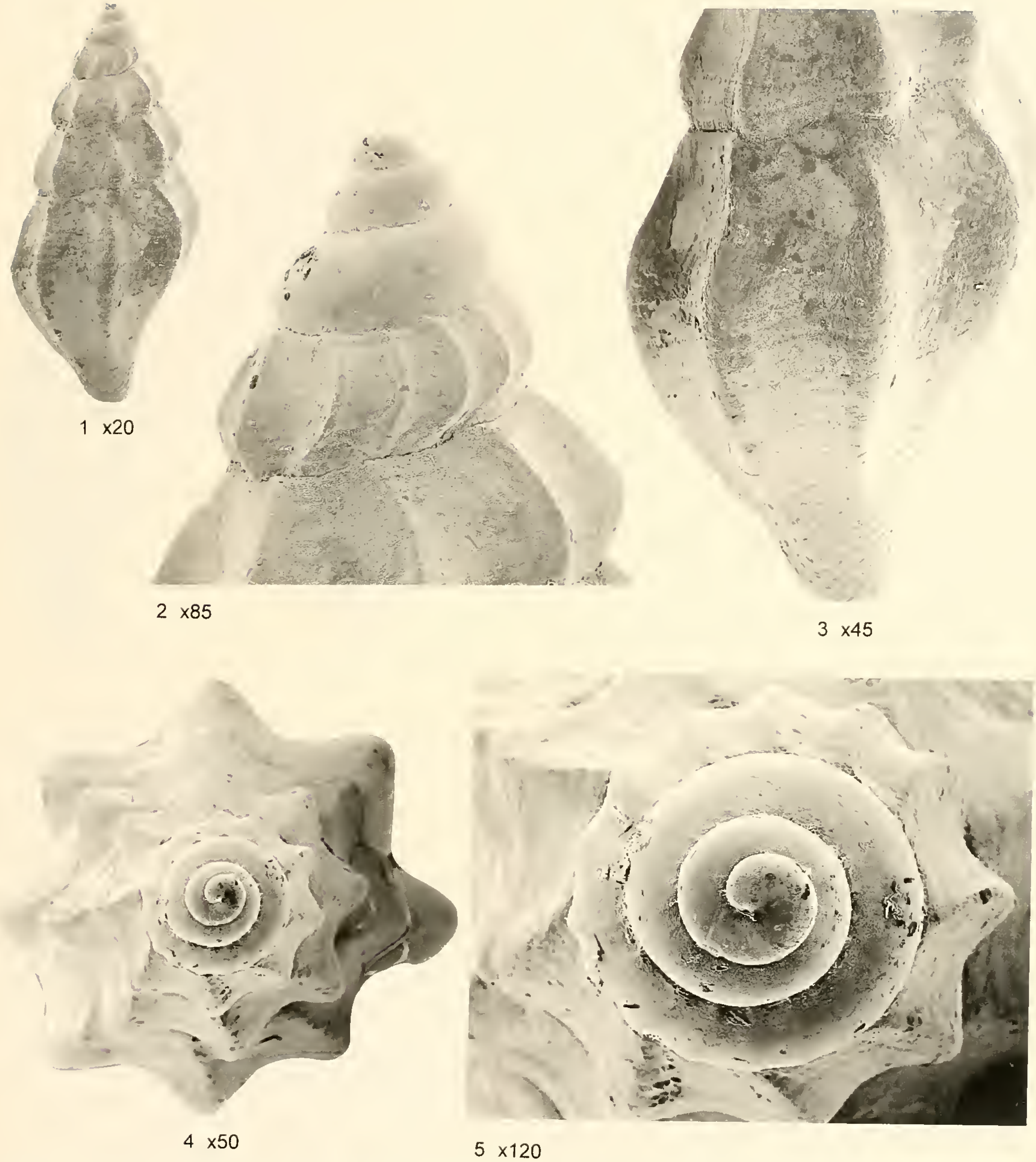
Holotype.—USNM 351224 (Text-fig. 6).

Dimensions of holotype.—Height 9.8 mm, width 3.8 mm.

Type locality.—USGS Station 3742: Shell Bluff, Shoal River, Walton County, Florida. Shoal River Formation (Middle Miocene).

Remarks.—*L. basilissa* is a rare species as only 11 specimens from three different localities are available. Although the holotype—probably the only specimen Gardner (1937, p. 344) had at hand—has an incompletely preserved protoconch, Gardner stated that it must consist of more than three volutions. This statement now proves to be correct as shown by the single specimen with a complete protoconch consisting of 3.25 volutions (Text-fig. 9.5).

Comparisons.—*L. basilissa* is the smallest of the species described in this report and cannot be compared meaningfully with any of them. It is more slen-



Text-figure 9.—*Lepicythara basilissa* (Gardner). UF 102878. Shell Bluff, Shoal River, Walton County, Florida, Shoal River Formation. Height 3.7 mm, width 1.7 m. 1, rear view; 2, enlargement of apical area; 3, enlargement of body whorl; 4, apical view; 5, enlargement of apical view.

Table 3.—Measurements (in mm) of *Lepicythara basilissa* (Gardner, 1937).

Specimen	Restored height	Width	Height/width ratio
USNM 351224 (holotype)	10.1	3.8	2.66
USGS locality 23979	5.8	2.2	2.64
UF 66069	9.4	3.6	2.61
UF 88143	6.2	2.6	2.38
	5.6	2.2	2.55
UF 89592	6.0	2.3	2.61
	3.7	1.7	2.18

der, *i.e.*, it has a smaller apical angle than other species. The only species with which Gardner (1937, p. 344) compared her *L. basilissa* is the living *Mangilia* (*Cythara*) *cymella* Dall (1886:101, pl. 12, f. 4). The present writer received the following material of *M. cymella* on loan from the USNM: two syntypes from Barbados (USNM 87419), one specimen from near Miami, Florida (USNM 410336), three specimens from off Ajax Reef, Florida (USNM 410348), and two specimens from the Campeche Bank off Yucatan, Mexico (USNM 667918). This material clearly shows that *Mangilia cymella* is not a species of *Lepicythara* but belongs to some other, possibly undescribed turrid genus.

A few specimens of the available material of *M. cymella* show faint traces of spiral sculpture on late whorls, but all of the other specimens have no spiral sculpture. In this respect the original figure is misleading.

Another problem of the material of *M. cymella* concerns dimensions. In the original description Dall (1889, p. 102) indicated a maximum height of the shell of 12.5 mm. In the explanation of figure 4 on his Plate 12, Dall gave a height of 13.0 mm. None of the eight specimens cited above exceeds a height of 9 mm. It is therefore evident that a measuring error has occurred.

Material.—Five lots with a total of eleven specimens as listed below:

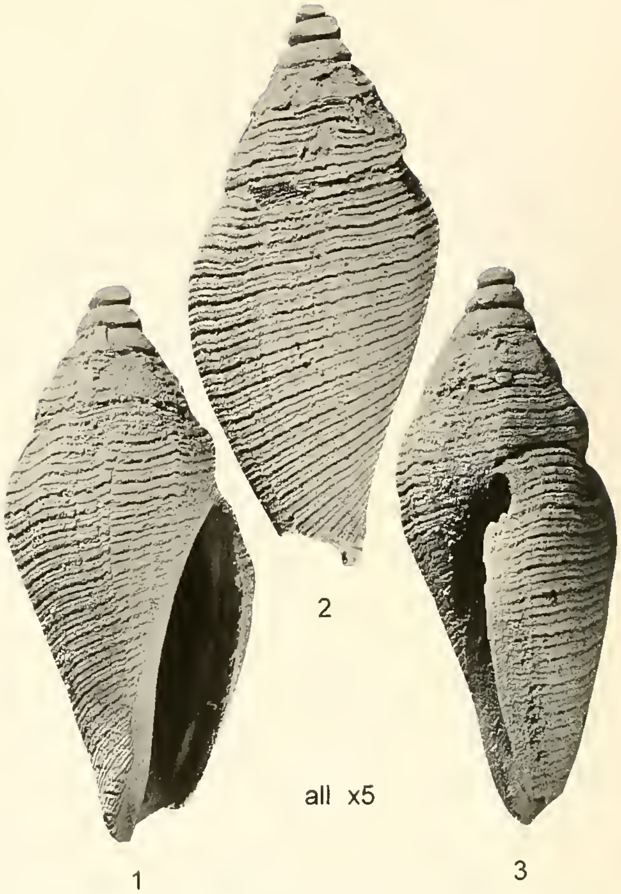
1 spec., USNM 351224: holotype. USGS Station 3642: Shell Bluff, Shoal River, Walton County, Florida. Shoal River Formation (Middle Miocene).

1 spec., USGS locality 23979: Shoal River, Walton County, Florida (no additional details). Shoal River Formation (Middle Miocene).

1 spec., UF 66069: Shoal River Grotto (WL004), Walton County, Florida. Shoal River Formation (Middle Miocene).

2 spec., UF 88143: Shoal River Grotto (WL004), Walton County, Florida. Shoal River Formation (Middle Miocene).

6 spec., UF 89592: Shell Bluff (type locality) (WL002), Walton County, Florida. Shoal River Formation (Middle Miocene).



Text-figure 10.—*Lepicythara camaronensis* Olsson. USNM 644221. Holotype. USGS Station 23480: Quebrada Camarones, Esmeraldas Province, Ecuador. Onzoloe Formation. Height 16.5 mm, width 7.7 mm. 1, front view; 2, rear view; 3, from right side.

Measurements.—(see Table 3).

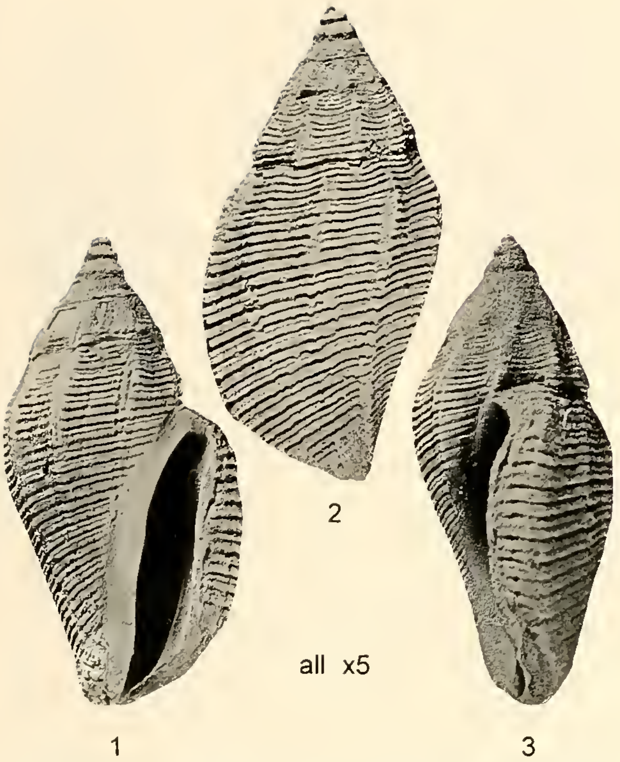
Occurrence.—This species is recorded from the following areas within Walton County, Florida (all Shoal River Formation): Shell Bluff, Shoal River: USGS 3742, UF 89592: Shoal River USGS 23979: Shoal River Grotto: UF 66069, UF 88143.

Distribution.—Not known outside Walton County, Florida.

Lepicythara camaronensis Olsson, 1964
Text-figures 10–13

Lepicythara camaronensis Olsson, 1964, p. 110, pl. 20, fig. 3, 3a.

Description.—Of medium to large size, biconic, rather stout. Protoconch consists of about three volutions. Apex hardly pointed. Number of teleoconch whorls up to five, their profile straight to slightly convex. Teleoconch whorls sculptured by eight to nine



Text-figure 11.—*Lepicythara camaronensis* Olsson. NMB H 18113. NMB locality 128222: km 493.050 of Trans Ecuadorian Pipeline System (TEPS), Esmeraldas Province, Ecuador. Onzole Formation. Height 14.0 mm, width 7.3 mm. 1, front view; 2, rear view; 3, from right side.

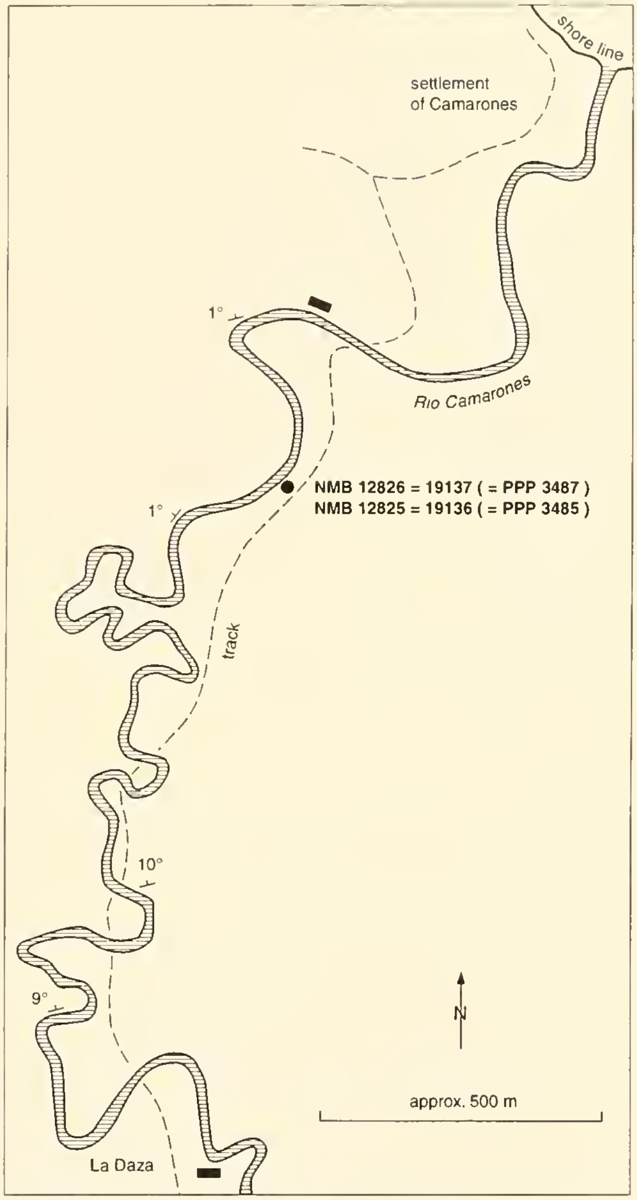
orthocline to slightly opisthocline axial ribs per whorl. Axial ribs more or less alined on successive whorls. Interspaces of axial ribs slightly concave, sculptured by three to seven flat topped spiral riblets on spire whorls, which usually are subdivided centrally by an incised line. The spiral sculpture is crossing the axial ribs not only on the body whorl but also on the spire whorls. Suture not deep. Aperture moderately narrow. Outer lip thickened. Sinus adjoining suture moderately deep. Inner surface of outer lip smooth, but with a ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Columellar and parietal calluses moderately prominent. Anterior canal almost straight and short.

Holotype.—USNM 644221 (Text-fig. 10).

Dimensions of holotype.—Height 16.5 mm, width 7.7 mm.

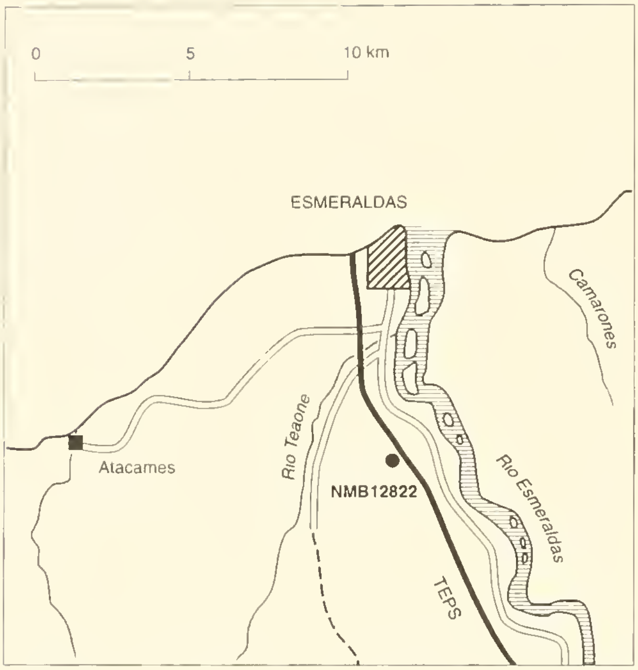
Type locality.—UGSG locality 23480 Quebrada Camarones, Esmeraldas Province, Ecuador. Onzole Formation (Early Pliocene) (Whittaker, 1988, fig. 2 and p. 11).

Remarks.—The protoconch of the holotype is not preserved, and the first 2.5 teleoconch whorls are preserved as an internal mold. The figured paratype (USNM 645311) has a strongly worn protoconch that consists of about three volutions. The specimen is incomplete and has about four teleoconch whorls. Olsson's figure (1964, pl. 20, fig. 3a) is a misleading reconstruction. All the other specimens at hand are not well preserved and partly fragmentary. Sculptural details can hardly be recognized. The early teleoconch whorls are not preserved well enough to determine whether they are somewhat angulated near the periphery.



Text-figure 12.—Sketch map of the lower course of the Rio Camarones, about 10 km east of the town of Esmeraldas, Ecuador, showing NMB localities that have yielded *L. camaronensis.*

Comparisons.—*L. camaronensis* may be compared with *L. disclusa* from the Early Pliocene Melajo Clay



Text-figure 13.—Sketch map of the Esmeraldas area showing NMB locality 12822, that has yielded *L. camaronensis*.

Table 4.—Measurements (in mm) of *Lepicythara camaronensis* Olsson, 1964.

Specimen	Restored height	Width	Height/ width ratio
USNM 644221 (holotype)	16.9	7.7	2.19
	14.6	7.3	2.00
	14.5	6.1	2.38
NMB locality 12826	19.7	—	—
	12.4	5.4	2.23
NMB locality 19136	16.9	6.7	2.52
	16.1	6.9	2.33
NMB locality 19137	14.8	6.6	2.24

Member of the Springvale Formation of Trinidad. *L. camaronensis* is somewhat stouter, its axial ribs are less prominent, and their number per whorl is higher in *L. disclusa*.

Material.—Seven lots with a total of 18 specimens as listed below (see Text-figs. 12, 13):

1 spec., USNM 64421: holotype. USGS locality 23480: Quebrada Camerones, Esmeraldas Province, Ecuador. Onzole Formation (Early Pliocene).
1 spec., USNM 645311: figured paratype. USGS locality 23480: as above.
2 spec., NMB locality 12822: km 493.050 of Trans Ecuadorian Pipeline System (TEPS), Esmeraldas Province, Ecuador. Onzole Formation; *Globorotalia margaritae* Zone (Early Pliocene).
1 spec., NMB locality 12825: Quebrada Camarones, about 10 km east of Esmeraldas, Ecuador. Onzole Formation; Globorotalia margaritae Zone (Early Pliocene).
2 spec., NMB locality 12826: Quebrada Camarones, as above.
4 spec., NMB locality 19136: Quebrada Camarones, as above.
5 spec., NMB locality 19137: Quebrada Camarones, as above.

Measurements.—(see Table 4.)

Occurrence.—This species is recorded from the following NMB localities: 12822, 12825, 12826, 19136, 19137 (all Early Pliocene Onzole Formation, northwestern Ecuador).

Distribution.—So far this species is not known from outside northwestern Ecuador.

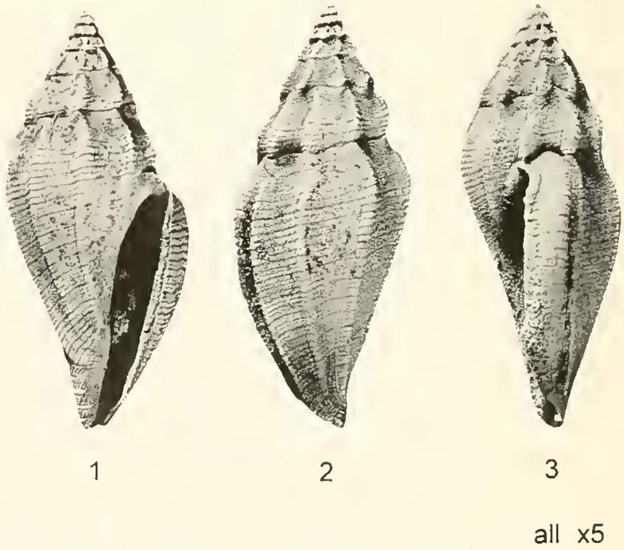
Lepicythara costaricensis (Olsson, 1922)

Text-figures 14–21

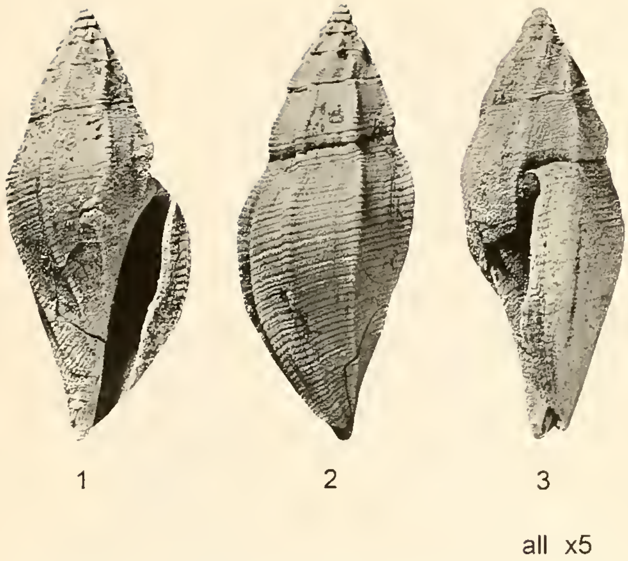
Cythara terminula costaricensis Olsson, 1922, p. 77, pl. 5, figs. 21, 22.

Non Cythara terminula costaricensis Olsson. Woodring, 1970, p. 390.

Description.—Of medium to large size, biconic, moderately slender. Protoconch consists of 2.5 to 2.75 volutions. Surface of the first 1.5 volutions smooth, remainder of the protoconch sculptured by up to 22 opisthocyrt axial riblets. Apex not pointed or only slightly pointed. Number of teleoconch whorls up to



Text-figure 14.—*Lepicythara costaricensis* (Olsson). PRI 20951. Lectotype. Hill 1a, Banana River, Limon Basin, Costa Rica. Rio Banano Formation. Height 12.3 mm, width 5.5 mm. 1, front view; 2, rear view; 3, from right side.



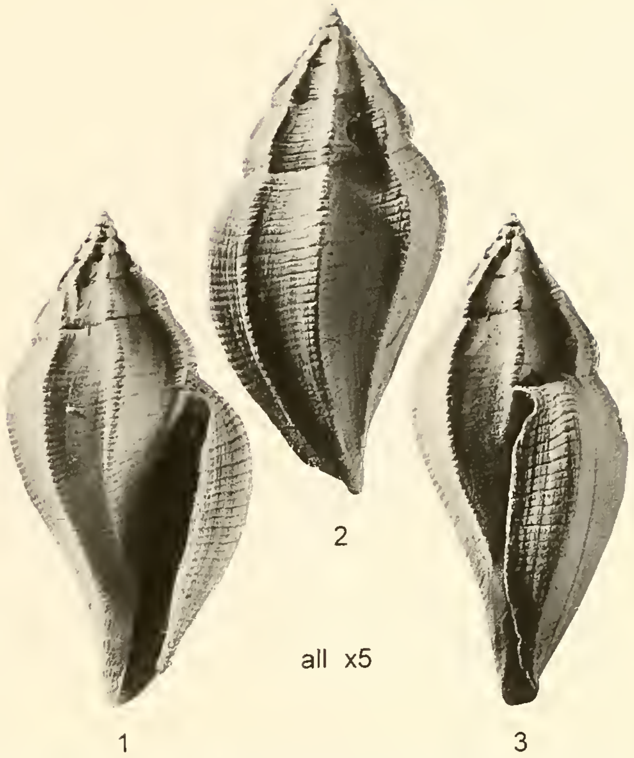
Text-figure 15.—*Lepicythara costaricensis* (Olsson). PRI 42106. Paralectotype. Hill 1a. Banana River, Limon Basin, Costa Rica. Rio Banano Formation. Height 13.0 mm, width 5.7 mm. 1, front view; 2, rear view; 3, from right side.

5.25, their profile straight on early spire whorls, slightly convex on later spire whorls. The first two teleoconch whorls are angulated near the adapical suture and thus overhanging it. Teleoconch whorls sculptured by orthocline to slightly opisthocline axial ribs. Their number per whorl is seven to nine on early whorls and eight to ten on the body whorl. The axial ribs are therefore alined or not quite alined on successive whorls. They usually are narrow adapically and somewhat wider abapically. Interspaces of axial ribs concave, sculptured by four to six incised, spiral lines on spire whorls. On later spire whorls some secondary incised, spiral lines are introduced. All spiral lines cross the axial ribs. Suture not deep. Aperature moderately narrow. Outer lip thickened. Sinus adjoining suture moderately deep. Inner surface of outer lip smooth, with or without a ridge parallel to the sharp edge of the other lip. If present, this ridge extends from the sinus to the beginning of the anterior canal. Columellar and parietal calluses thin. Anterior canal straight or slightly twisted to the left, narrow, and moderately long.

Lectotype.—(selected herein) PRI 20951 (Text-fig. 14).

Dimensions of lectotype.—Height 12.3 mm, width 5.5 mm.

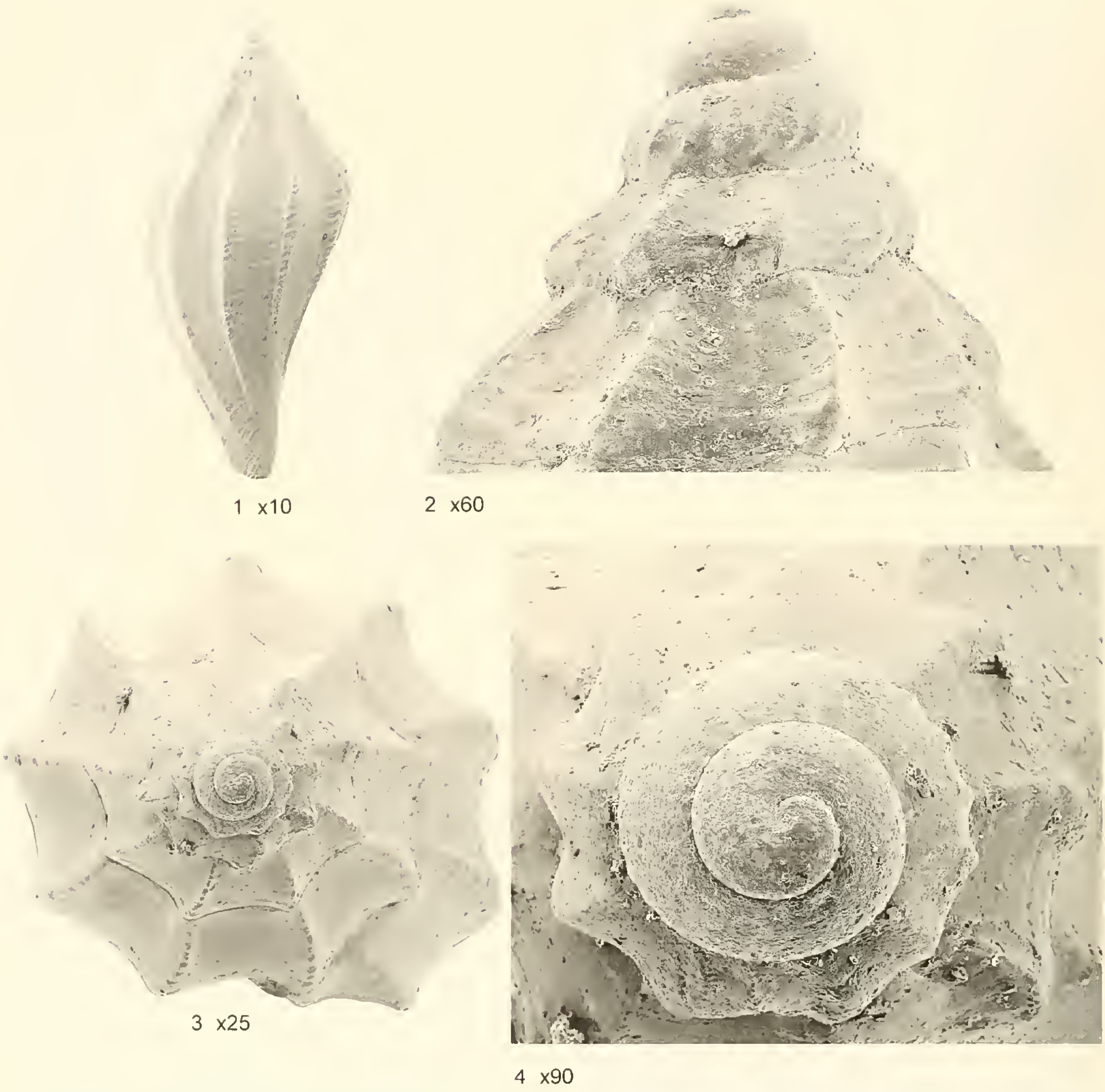
Type locality.—"Hill 1a, Banana River; Gatun Stage". This indication probably refers to outcrops in the vicinity of La Bomba on Rio Banano, Limon Province, Costa Rica (see Jung, 1989, figs. 15–18). Rio Banano Formation (Pliocene).



Text-figure 16.—*Lepicythara costaricensis* (Olsson). NMB H 18148. NMB locality 18721 (=PPP 2224): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cao Agua Formation. Height 14.4 mm, width 6.9 mm. 1, front view; 2, rear view; 3, from right side.

Remarks.—Brann and Kent (1960, p. 309) considered specimen PRI 20951 as the holotype of *L. costaricensis* citing both figures given by Olsson (Olsson, 1922, pl. 5, figs. 21–22). These two figures, however, represent two different specimens, which were united under PRI 20951. A lectotype selection becomes necessary, the lectotype being PRI 29051 (Text-fig. 14), and the paralectotype is renumbered PRI 42106 (Text-fig. 15). Olsson unfortunately gave the same height (13 mm) for both specimens, but they actually differ in height (see legend of the respective figures). As stated in the above description there are seven to nine axial ribs per whorl on early whorls and eight to ten on the body whorl. There is a remarkable exception: two specimens from Cayo Agua (NMB locality 18405) have more axial ribs per whorl: 9–10 on early whorls and 11 to 15 on the body whorl. Specimens of *L. costaricensis* from outside the Limon Basin of Costa Rica, *i.e.*, from the Province of Bocas del Toro, Panama, seem to have a somewhat larger apical angle, and the axial ribs seem to be more regularly aligned on successive whorls (Text-fig. 16). There is, however, here is a variability in those two features as can be seen in the list of height/width ratio values.

Comparisons.—*L. costaricensis* is similar to *L. heptagona* (Gabb). There is one constant difference, the



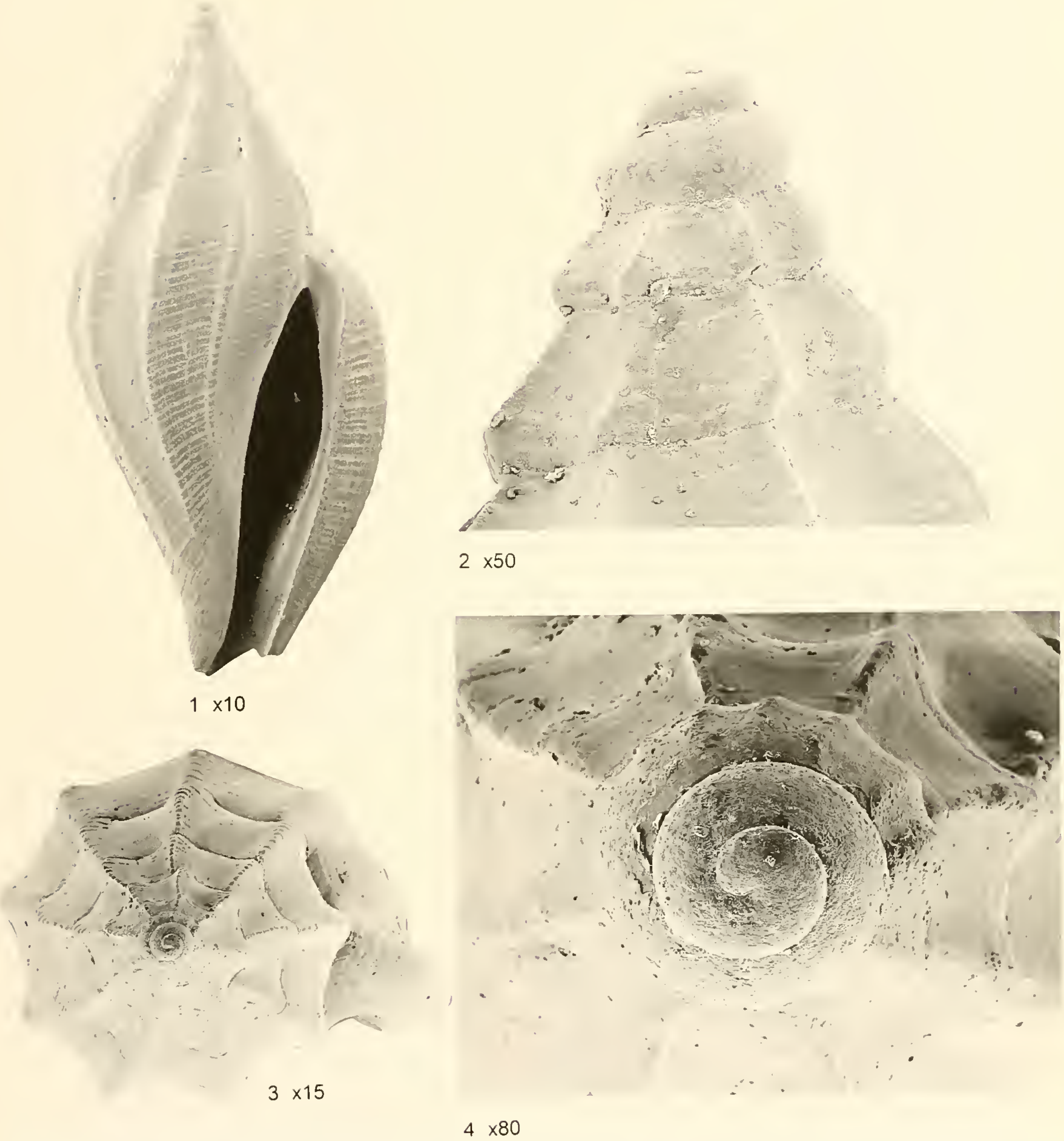
Text-figure 17.—*Lepicythara costaricensis* (Olsson). NMB H 18140. NMB locality 17775 (= PPP 452): La Bomba, Rio Banano, Limon Province, Costa Rica. Rio Banano Formation. Height 7.7 mm, width 3.6 mm. 1, rear view; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

protoconch of *L. heptagona* consists of 2.25 volutions, whereas that of *L. costaricensis* has 2.5 to 2.75. In addition, the number of axial ribs tends to be higher in *L. costaricensis*.

Material.—36 lots with a total of 139 specimens as listed below (for exact locations see Coates, 1999b–c).

1 spec., PRI 20951: lectotype figured by Olsson (1922, pl. 5, p. 21); Hill 1a, Rio Banano, Limon Province, CR; Rio Banano Formation (Pliocene).

1 spec., PRI 42106: paralectotype figured by Olsson (1922, pl. 5, p. 22); Hill 1a, Rio Banano, Limon Province, CR; Rio Banano Formation (Pliocene).

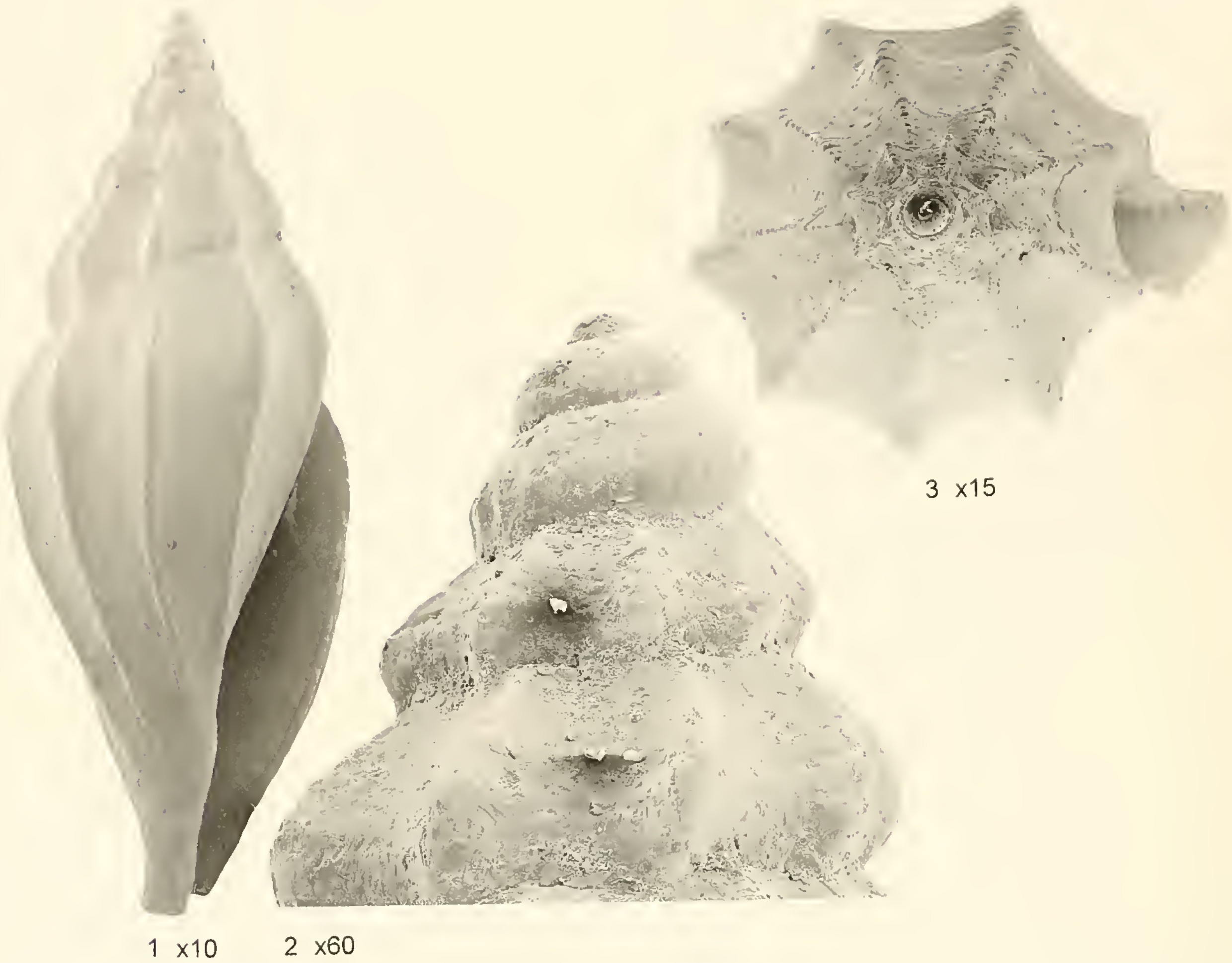


Text-figure 18.—*Lepicythara costaricensis* (Olsson). NMB H 18141. NMB locality 17775 (=PPP 452): La Bomba, Rio Banano, Limon Province, Costa Rica. Rio Banano Formation. Height 12.0 mm, width 5.8 mm. 1, front view; 2, enlargement of apical view; 3, apical view; 4, enlargement of apical view.

10 spec., NMB locality 17445 (=PPP1726): La Bomba, Rio Banano, Limon Province, CR. Left Bank, 700 m southwest of railroad bridge. Type section of Rio Banano Formation (Pliocene).

9 spec., NMB locality 17446 (=PPP 1727): directly overlying NMB locality 17445. Type section of Rio Banano Formation (Pliocene).

4 spec., NMB locality 17447 (=PPP 1728): directly overlying NMB locality 17446. Type section of Rio Banano Formation (Pliocene).



Text-figure 19.—*Lepicythara costaricensis* (Olsson). NMB H 18142. NMB locality 17772 (=PPP 449): Quitaria, Rio Banano, Limon Province, Costa Rica, Rio Banano Formation. Height 12.5 mm, width 5.6 mm. 1, oblique front view; 2, enlargement of apical view; 3, apical view.

13 spec., NMB locality 17451 (=PPP 1732): La Bomba, Rio Banano, Limon Province, CR. Right bank, about 500 m southwest of railroad bridge. Rio Banano Formation (Pliocene).

13 spec., NMB locality 17775 (=PPP 452): La Bomba, Rio Banano, Limon Province, CR. Right bank, 600 m southwest of railroad bridge. Rio Banano Formation (Pliocene).

6 spec., NMB locality 17783 (=PPP 460): La Bomba, Rio Banano, Limon Province, CR. Left bank, 700 m southwest of railroad bridge. Type section of Rio Banano Formation (Pliocene).

1 spec., NMB locality 18091 (=PPP 1983): La Bomba, Rio Banano, Limon Province, CR. Right bank, about 500 m southwest of railroad bridge. Rio Banano Formation (Pliocene).

14 spec., NMB locality 18095 (=PPP1984): La Bomba, Rio Banano, Limon Province, CR. Right bank, about 500 m southwest of railroad bridge. Rio Banano Formation (Pliocene).

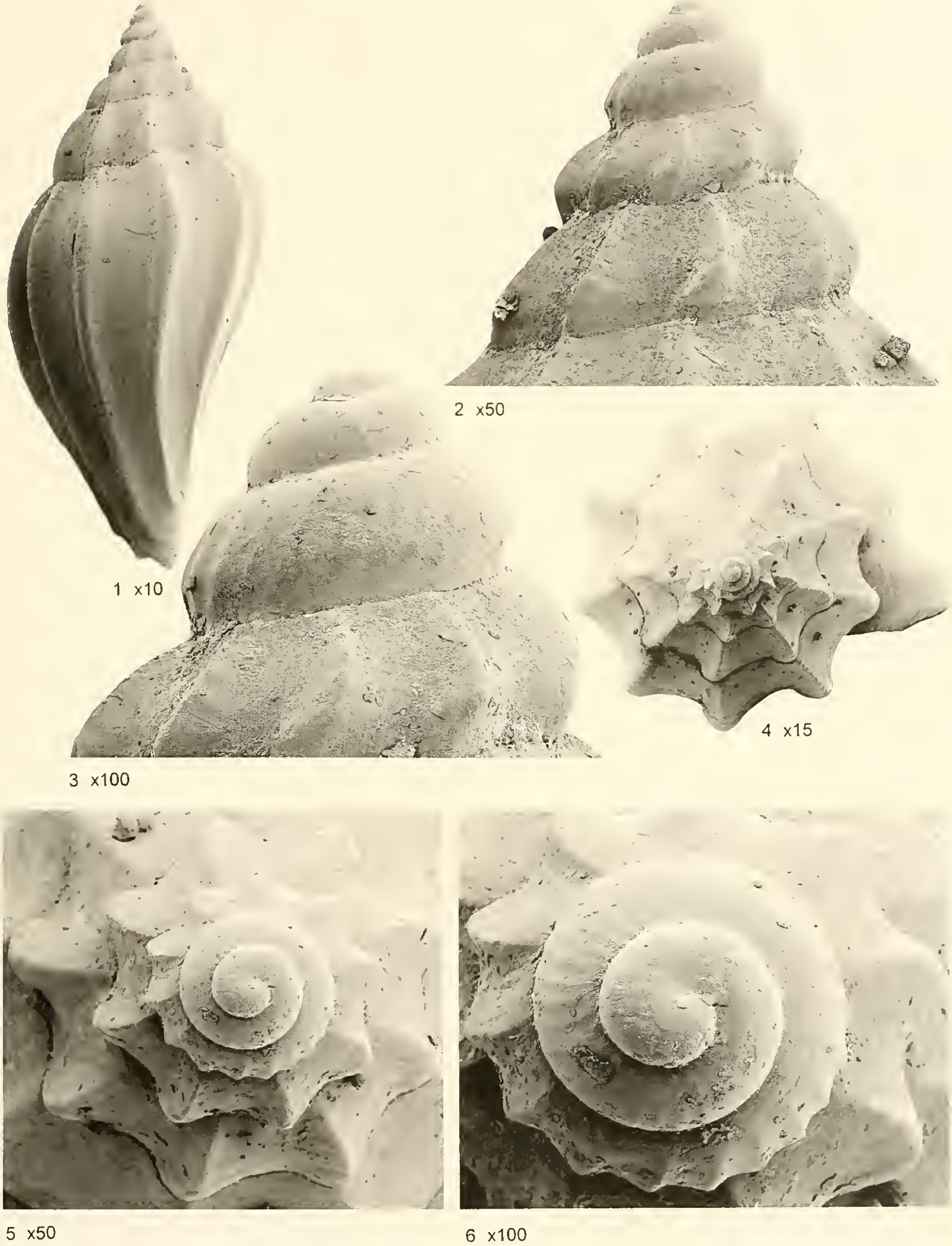
2 spec., NMB locality 18099 (=PPP 686): La Bomba, Rio Banano, Limon Province, CR. Left bank, 700 m southwest of railroad bridge. Type section of Rio Banano Formation (Pliocene).

2 spec., NMB locality 18100 (=PPP 1986): La Bomba, Rio Banano, Limon Province, CR. Left bank, 700 m southwest of railroad bridge. Type section of Rio Banano Formation (Pliocene).

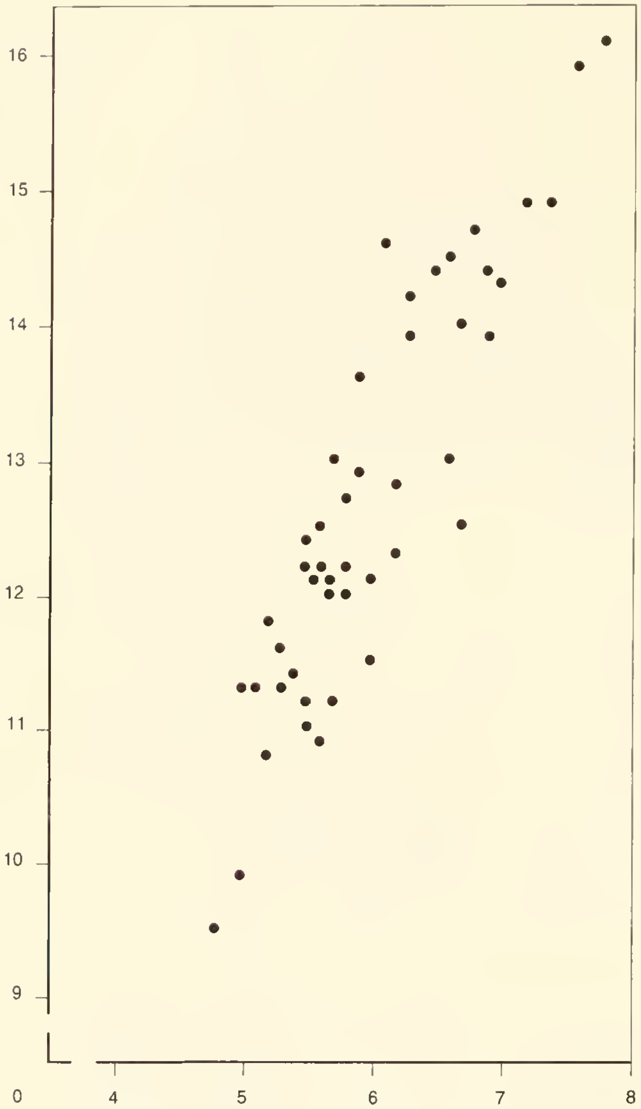
4 spec., NMB locality 18101 (=PPP 691): La Bomba, Rio Banano, Limon Province, CR. Left bank, 700 m southwest of railroad bridge. Type section of Rio Banano Formation (Pliocene).

4 spec., NMB locality 17454 (=PPP 1734): Quitaria, Rio Banano, Limon Province, CR. Rio Banano Formation (Pliocene).

3 spec., NMB locality 17772 (=PPP 449): Quitaria,



Text-figure 20.—*Lepicythara costaricensis* (Olsson). NMB H 18149. NMB locality 18733 a(=PPP 2236): 1 km southeast of Punta de Tiburon, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation. Height 11.1 mm, width 5.0 mm. 1, rear view; 2, enlargement of apical area; 3, further enlargement of apical area; 4, apical view; 5, enlargement of apical view; 6, further enlargement of apical view.



Text-figure 21.—(Restored) height/width diagram of *L. costaricensis.*

Rio Banano, Limon Province, CR. Rio Banano Formation (Pliocene).

1 spec., NMB locality 17773 (=PPP 450): Quitaria, Rio Banano, Limon Province, CR. Rio Banano Formation (Pliocene).

11 spec., NMB locality 18096 (=PPP 679): Quitaria, Rio Banano, Limon Province, CR. Rio Banano Formation (Pliocene).

3 spec., NMB locality 18097 (=PPP 1985): Quitaria, Rio Banano, Limon Province, CR. Rio Banano Formation (Pliocene).

1 spec., NMB locality 18270 (=PPP 1990): Rio Bananito, road cut near Finca Banaga, Limon Province, CR. Rio Banano Formation (Pliocene).

5 spec., NMB locality 18266 (=PPP 932): Rio Vizcaya, 3.5 km south-southwest of Quitaria, Limon Province, CR. Rio Banano Formation (Pliocene).

1 spec., NMB locality 18267 (=PPP 933): Rio Vizcaya, about 3.5 km south-southeast of Quitaria, Limon Province, CR. Rio Banano Formation (Pliocene).

1 spec., NMB locality 18268 (=PPP 935): Rio Vizcaya, 3.5 km south-southeast of Quitaria, Limon Province, CR. Rio Banano Formation (Pliocene).

1 spec., NMB locality 17635 (=PPP 201): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

1 spec., NMB locality 17808 (=PPP 475): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

2 spec., NMB locality 17811 (=PPP 296): west of Punta de Tiburon, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

4 spec., NMB locality 17822 (=PPP 326): west of Punta de Nispero, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

2 spec., NMB locality 18374 (=PPP 1203): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

2 spec., NMB locality 18405 (=PPP 67): south of Punta de Nispero, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

1 spec., NMB locality 18719 (=PPP 2222): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

1 spec., NMB locality 18720 (=PPP 2223): 22 m south-southeast of Punta Norte, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

5 spec., NMB locality 18721 (=PPP 2224): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

3 spec., NMB locality 18722 (=PPP 2225): northeast coast of Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

1 spec., NMB locality 18733 (=PPP 2236): 1 km southeast of Punta de Tiburon, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

3 spec., NMB locality 17864 (=PPP 426): northeast coast of Isla Popa, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

2 spec., NMB locality 18602 (=PPP 423): northeast coast of Isla Popa, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene).

1 spec., NMB locality 18716 (=PPP 2217): Playa Lorenzo, 5 k southeast of Cayo Patterson, south coast of Valiente Peninsula, Bocas del Toro, Panama. Shark Hole Point Formation (Pliocene).

Table 5.—Measurements (in mm) of *Lepicythara costaricensis* (Olsson, 1922).

Specimen	Restored height	Width	Height/ width ratio
PRI 20951: lectotype	12.4	5.5	2.25
PRI 42106: paralectotype	13.0	5.7	2.28
NMB locality 17445	14.4	6.5	2.22
	14.2	6.3	2.25
	13.9	6.3	2.21
	10.8	5.2	2.08
NMB locality 17447	11.8	5.2	2.27
NMB locality 17451	9.9	5.0	1.98
	11.2	5.3	2.11
	13.4	—	—
	9.5	4.8	1.98
NMB locality 17775	12.0	5.8	2.07
	12.7	5.8	2.19
NMB locality 17783	14.5	6.6	2.20
	14.6	6.2	2.35
	11.6	5.3	2.19
NMB locality 18095	12.0	5.7	2.11
	14.4	6.9	2.09
	11.2	5.7	1.96
NMB locality 18099	12.3	6.2	1.98
NMB locality 18101	11.3	5.1	2.22
	12.1	5.6	2.16
	12.2	5.5	2.22
	13.2	—	—
NMB locality 17454	14.7	6.8	2.16
NMB locality 17772	12.5	5.6	2.23
	13.6	5.9	2.30
NMB locality 17808	15.9	7.6	2.09
NMB locality 17811	11.4	5.4	2.11
	11.3	5.0	2.26
NMB locality 17822	10.9	5.6	1.95
	9.9	5.0	1.98
	11.5	6.0	1.92
NMB locality 18374	10.9	—	—
	14.9	7.4	2.01
NMB locality 18405	12.1	6.0	2.02
	16.1	7.8	2.06
NMB locality 18719	12.9	5.9	2.19
NMB locality 18720	13.0	6.6	1.97
NMB locality 18721	14.3	7.0	2.04
	14.9	7.2	2.07
	12.5	6.7	1.87
	13.9	6.8	2.04
NMB locality 18722	12.8	6.2	2.06
	12.2	5.8	2.10
	14.0	6.7	2.09
NMB locality 18733	11.2	5.5	2.04
NMB locality 17864	11.0	5.5	2.00
	12.2	5.6	2.18
NMB locality 18602	12.1	5.7	2.12
NMB locality 18716	12.2	6.5	1.88

Measurements.—(See Table 5, Text-fig. 21.)

Occurrence.—This species is recorded from the following areas:

Rio Banano, Rio Bananito, Rio Vizcaya, and Limon Province, Costa Rica. Rio Banano Formation (Pliocene): NMB localities: 17445–71447, 17451, 17454, 17772, 17773, 17775, 17783, 18091, 18095–18097, 18099–18101, 18266–18268, 18270.

Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene): NMB localities: 17635, 17808, 17811, 17822, 18374, 18405, 18719–18733.

Isla Popas, Bocas del Toro, Panama. Cayo Agua Formation (Pliocene): NMB localities 17864, 18602.

South coast of Valiente Peninsula, Bocas del Toro, Panama. Shark Hole Point Formation (Pliocene): NMB locality 18716.

Distribution.—Rio Banano Formation (Pliocene), Limon Province, Costa Rica. Cayo Agua Formation (Pliocene), Cayo Agua and Isla Popa, Bocas del Toro, Panama. Shark Hole Point Formation (Pliocene), Valiente Peninsula, Bocas del Toro, Panama.

Lepicythara cf. costaricensis (Olsson, 1922)

Text-figure 22

Remarks.—A single, not quite complete specimen from the Late Miocene Nancy Point Formation of NMB locality 18705 (=PPP 2206) is available. This locality is situated in the westernmost part of the south coast of the Valiente Peninsula, Province of Bocas del Toro, Panama (see Coates, 1999b, map 5, inset C, p. 291; 1999c, section 15, p. 322).

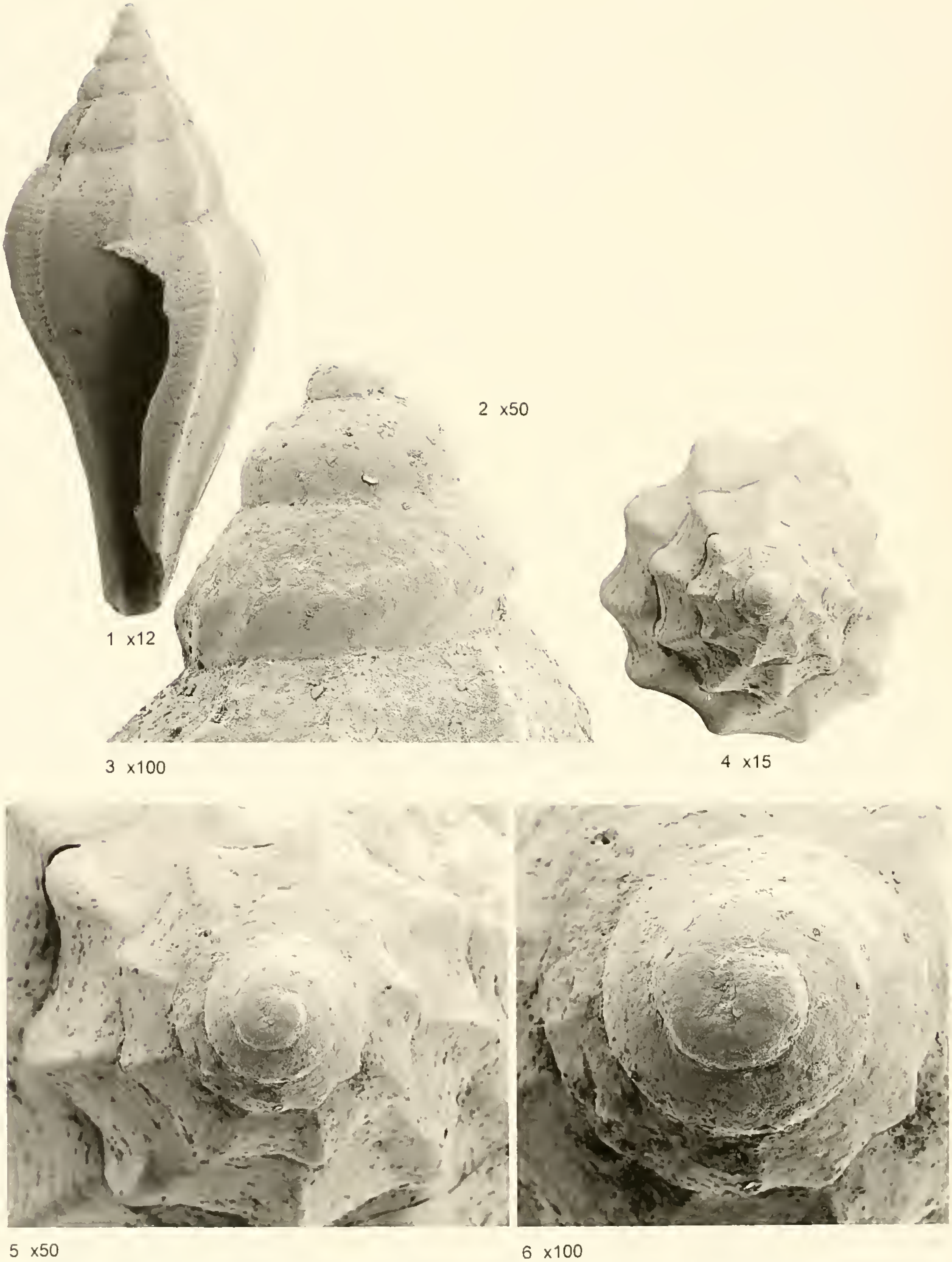
The specimen is small (restored height 10.5 mm, width 4.8 mm, ratio 2.19) and does not have a perfectly preserved protoconch, but is seen to consist of a little more than 2.5 volutions. The last part of the protoconch is sculptured by nine opisthocline to opisthocyrt axial riblets. The number of preserved teleoconch whorls is 4.5. The profile of the early teleoconch whorls is straight, that of the late teleoconch whorls slightly convex. The first two teleoconch whorls ar angulated near the adapical suture. The number of axial ribs per whorl is nine on early whorls and ten on the body whorl. The spiral sculpture is the same as that of *L. costaricensis*. The specimen of *L.* cf. *costaricensis* is smaller than *L. costaricensis* and seems to have more axial ribs per whorl.

Lepicythara disclusa Jung, 1969

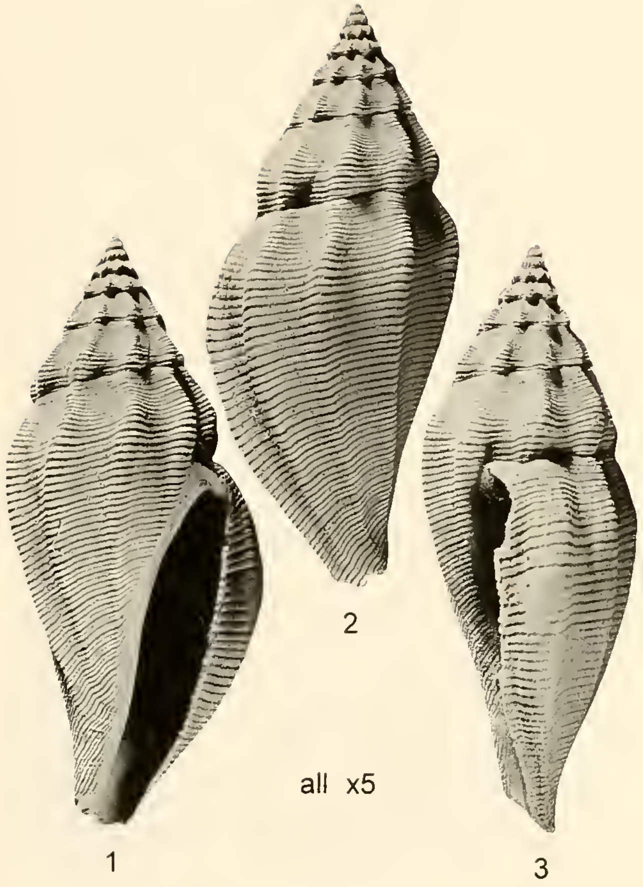
Text-figures 23–25

Lepicythara disclusa Jung, 1969, p. 551, pl. 59, figs. 7–10 (in part).

Description.—Of large size, biconic, moderately stout. Protoconch consists of 2.75 to three volutions. A little less than the first two volutions are smooth, the remainder of the protoconch sculptured by 17 to



Text-figure 22. —*Lepicythara* cf. *costaricensis* (Olsson). NMB H 181150. NMB locality 18705 (= PPP 2206): westernmost of the south coast of the Valiente Peninsula, Province of Bocas del Toro, Panama. Nancy Point Formation. Height 10.4 mm, width 4.7 mm. 1, view from right side; 2, enlargement of apical area; 3, further enlargement of apicalarea; 4, apical view; 5, enlargement of apical view; 6, further enlargement of apical view.



Text-figure 23.—*Lepicythara disclusa* Jung. NMB H 15291 Holotype NMB locality 18574: Melajo River, soiuth slope of the eastern part of the Northern Range, Trinidad. Melajo aClay Member of Springvale Formation. Height 16.0 mm, width 7.1 mm. 1, front view; 2, rear view; 3, from right side.

22 opisthocline to strongly opisthocyrt axial riblets. Apex a little pointed. Number of teleoconch whorls up to five, their profile straight on early teleoconch whorls and slightly convex on late whorls. The axial ribs of the first two teleoconch whorls are somewhat pointed at the periphery thus projecting a little over the abapical suture. Teleoconch whorls sculptured by eight to ten orthocline to slightly opisthocline axial ribs per whorl. The axial ribs may be alined on successive whorls and those on the body whorl may be somewhat sigmoid. Interspaces of axial ribs concave, sculptured by four incised, spiral lines on the first teleoconch whorl. Their number increases to twelve on the penultimate whorl. There are few secondary incised, spiral lines. All spiral lines cross the axial ribs. Suture shallow. Aperature narrow. Outer lip thickened. Sinus adjoining suture moderately shallow. Inner surface of outer lip smooth, in rare cases with an inconspicuous ridge parallel to the slightly crenulated, sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Columellar and parietal calluses weakly developed. Anterior canal straight, fairly long.

Holotype.—NMB H 15291 (Text-fig. 23).

Dimensions of holotype.—Height 16.0 mm, width 7.1 mm.

Type locality.—NMB locality 18574 (=PJ 285): Melajo River on the south slope of the eastern part of the Northern Range, Trinidad (Jung, 1969, p. 296, text-fig. 2). Melajo Clay Member of Springvale Formation (Early Pliocene).

Remarks.—When I originally described *L. disclusa*, the material from the Savaneta Glauconitic Sandstone Member of the Springvale Formation of the Central Range of Trinidad was erroneously included in it (Jung, 1969, p. 552). The material from the Central Range is quite a different species; it is considerably smaller, has a larger apical angle, and is described herein under the name of *L. paradisclusa*.

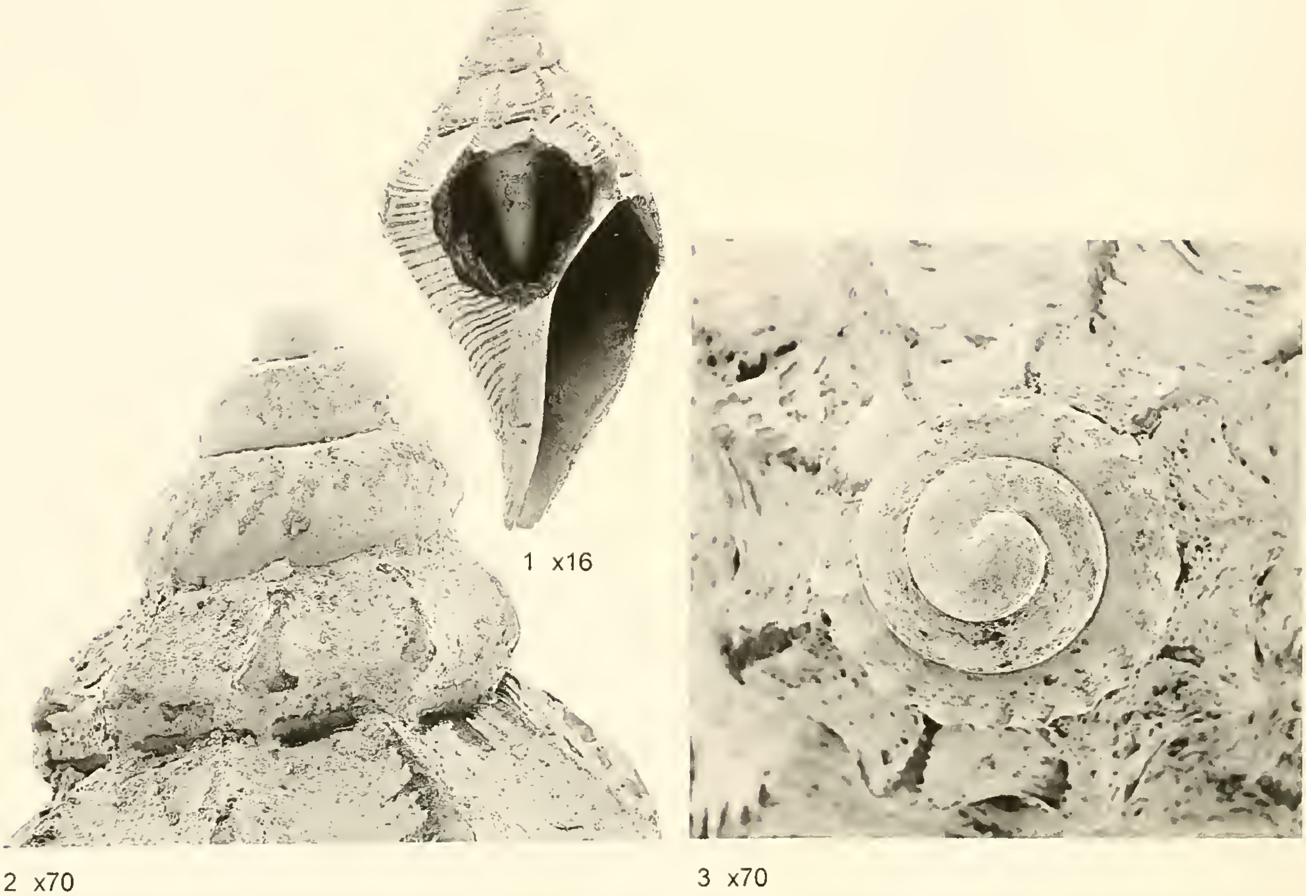
The above description states that the spiral sculpture includes a few secondary incised lines. As a matter of fact, the number of these secondary lines is quite variable. On the penultimate whorl they are present but on the lower part of the body whorl, they are frequently missing.

Comparisons.—The differences between *L. disclusa* and *L. paradisclusa* have been mentioned briefly. *L. toroensis* is larger than *L. disclusa* and has a larger apical angle. Its protoconch consists of 2.5 volutions as compared to 2.75 to 3 in *L. disclusa*. *L. disclusa* has many more opisthocline to opisthocyrt axial, riblets on the late part of the protoconch. In addition the number of axial ribs in *L. toroensis* is eight to nine on early teleoconch whorls, but 12–13 on the body whorl. The corresponding figures in *L. disclusa* are also eight to nine on early whorls, but only 9–10 on the body whorl. The size of *L. disclusa* is similar to that of *L. heptagona*. The protoconch of *L. heptagona* has only 2.25 volutions, whereas that of *L. disclusa* has 2.75 to 3. In addition the number of axial ribs per whorl is smaller in *L. heptagona* on both the early teleoconch whorls and the body whorl.

Material.—Eight lots with a total of 29 specimens as listed below. All the specimens come from the Melajo River, south slope of the Northern Range, northeastern Trinidad, and have been collected fro the Melajo Clay Member of the Springvale Formation (Early Pliocene, *Globorotalia margaritae* Zone). (See Jung, 1969, p. 296, text-fig. 2.)

1 spec., NMB H 15291: holotype. NMB locality 18574 (=PJ 285).

1 spec., NMB H 15292: figured paratype. NMB locality 18574 (=PJ 285).



Text-figure 24.—*Lepicythara disclusa* Jung. NMB H 18114. Paratype. NMB locality 18574: Melajo River, south slope of the eastern part of the Northern Range, Trinidad. Melajo Clay Member of Springvale Formation. Height 5.2 mm, width 2.6 m. 1, front view; 2, enlargement of apical area; 3, enlargement of apical view.

1 spec., NMB H 15293: figured paratype. NMB locality 18574 (=PJ 285).
14 specs., NMB H 15290: paratypes. NMB locality 18574 (=PJ 285).
6 specs., NMB H 15286: paratypes. NMB locality 18923 (=Hutch 47).
2 specs., NMB H 15287: paratypes. NMB locality 18925 (=Hutch 51).
2 specs., NMB H 15288: paratypes. NMB locality 18571 (=KR 11862).
2 specs., NMB H 15289: paratypes. NMB locality 18922 (=RR 293).

Measurements.—(See Table 6.)

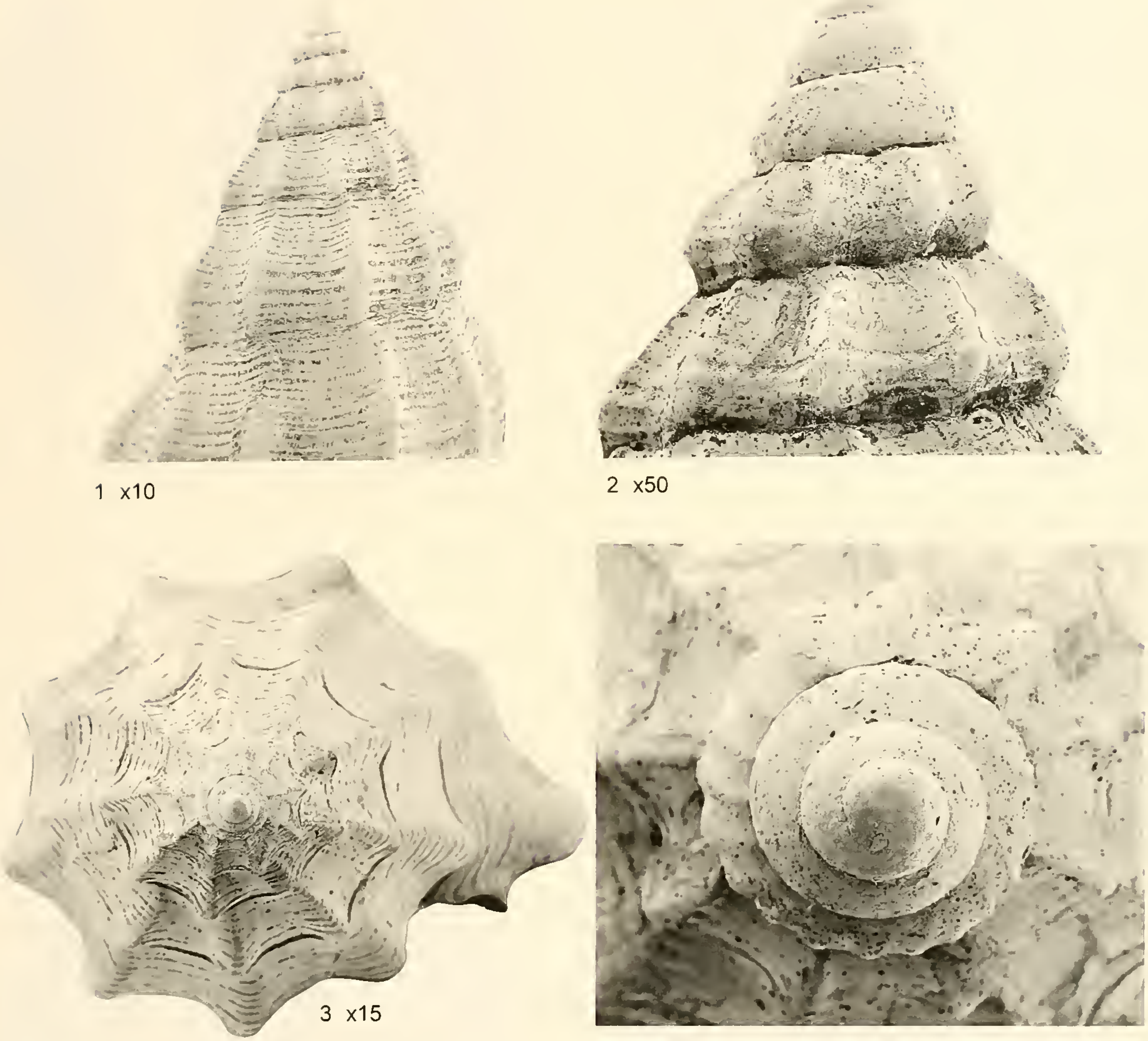
Occurrence.—This species occurs only along the Melajo River on the south slope of the Northern Range of northeastern Trinidad. It has been found at the following NMB localities: 18571, 18574, 18922, 18923 and 18925. All these localities are part of the Melajo Clay Member of the Springvale Formation (Early Pliocene, *Globorotalia margaritae* Zone).

Distribution.—So far *L. disclusa* is not known from outside Trinidad.

Lepicythara heptagona (Gabb, 1873)
Text-figures 26–31

Mangelia heptagona Gabb, 1873, p. 211.
Cythara cercadica Maury, 1917, p. 61, pl. 9, fig. 15.
Cythara heptagona (Gabb). Pilsbry, 1922, p. 322, pl. 17, fig. 9 (in part). *Non* Brown and Pilsbry, 1911, p. 345; see under *L.* sp. A. *Non* Weisbord, p. 55, pl. 5:13–14; see under *L.* cf. *heptagona.*
Non Lepicythara heptagona (Gabb). Woodring, 1970, p. 390, pl. 60: 4, pl. 64:11; see under *L.* sp. A. *Non* Perrilliat, 1973, p. 57, pl. 28, figs. 9–12; see under *L.* aff. *heptagona.*

Description.—Of medium to large size, biconic, rather slender to moderately stout. Protoconch consists of 2.25 volutions. Surface of protoconch smooth except for its last part which is sculptured by up to nine opisthocyrt axial riblets. Apex not pointed. Number of teleoconch whorls up to 5.5, their profile straight on early spire whorls, slightly convex on late spire whorls. The first two teleoconch whorls are somewhat



Text-figure 25.—*Lepicythara disclusa* Jung. NMB H 18115. Paratype. NMB locality 18574: Melajo River, south slope of the eastern part of the Northern Range, Trinidad. Melajo Clay Member of Springvale Formation. Height 15.8 mm, width 6.6 mm. 1, spire whorls; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

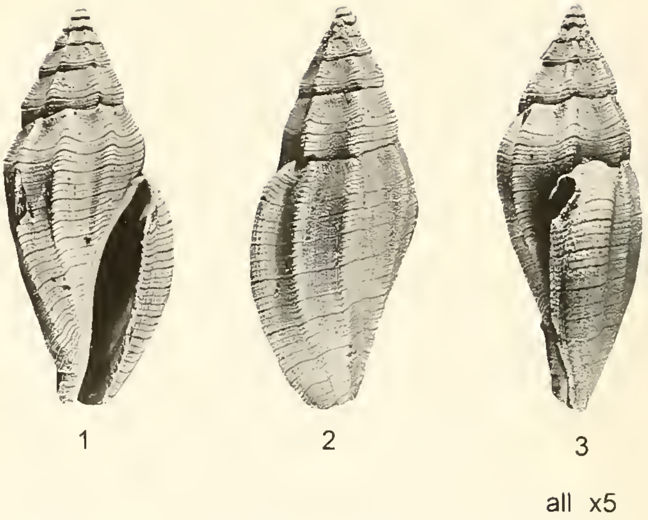
carinated near the abapical suture thus overhanging it a little. Early teleoconch whorls sculptured by seven, rarely eight practically orthocline axial ribs, late whorls usually by nine, sometimes by eight. On the body whorl the axial ribs may be somewhat sigmoid. On the spire whorls the axial ribs are narrow adapically but wider abapically. Interspaces of axial ribs concave, sculptured by four to seven incised spiral lines on spire whorls. On late spire whorls secondary incised spiral lines are introduced. All spiral lines cross the axial ribs. Suture not deep. Aperature narrow. Outer lip thickened. Sinus adjoining suture shallow to moderately deep. Inner surface of outer lip smooth, with a more or less well developed ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Columellar and parietal calluses moderately prominent. Anterior canal straight to slightly twisted to the left, narrow and short.

Dimensions of lectotype.—(of *heptagona*): Height 15.0 mm, width 6.5 mm.

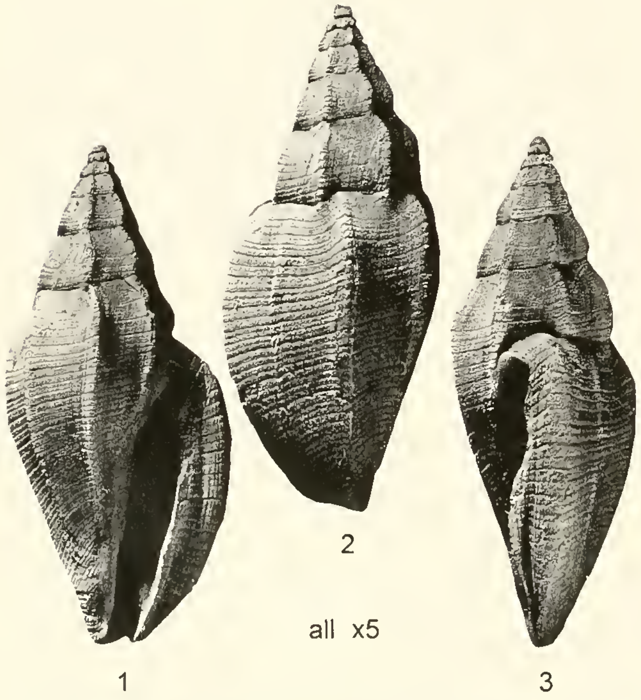
Table 6.—Measurements (in mm) of *Lepicythara disclusa* Jung, 1969.

Specimen	Restored height	Width	Height/ width ratio
NMB H 15291	16.0	7.1	2.25
NMB H 15292	15.6	6.8	2.29
NMB H 15293	13.3	6.7	1.98
	15.8	*7.3*	*2.16*
NMB H 15290	15.8	6.6	2.39
	13.7	6.6	2.07
	15.1	7.2	2.09
	13.8	6.6	2.09
	15.2	7.1	2.14
	14.9	6.6	2.26
	13.9	6.3	2.21
NMB H 15286	15.2	7.4	2.05
	15.3	7.4	2.07
	13.6	6.5	2.09
NMB H 15287	13.2	6.9	1.91
	13.1	—	—
NMB H 15288	15.2	6.5	2.34
	15.0	7.0	2.14
NMB H 15289	16.9	7.4	2.28

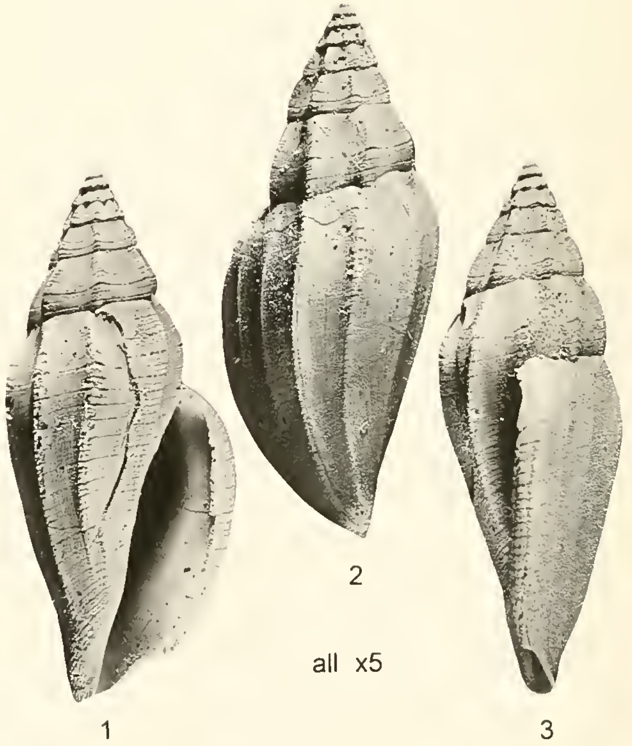
Type locality.—(of *heptagona*) According to Pilsbry (1922, p. 307) the exact locality and the age of the lectotype of *L. heptagona* are not known. For this reason the type locality is here restricted to NMB locality 16932, where 4 of the 16 known specimens have been



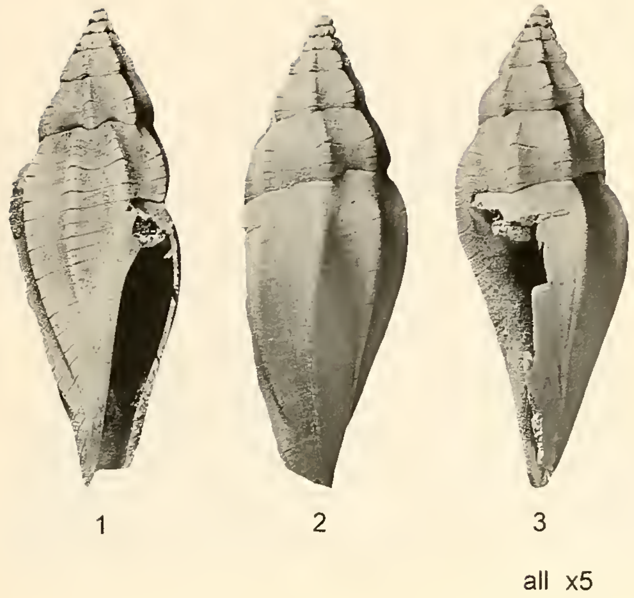
Text-figure 27.—*Lepicythara heptagona* (Gabb). NMB H 18122. NMB locality 16842. Rio Cana, Dominican Republic. Cercado Formation. Height 11.9 mm, width 5.0 mm. (Same specimen as Text-fig. 30.) 1, front view; 2, rear view; 3, front right side.



Text-figure 26.—*Lepicythara heptagona* (Gabb). ANSP 2915. Lectotype. Cibao Region, Dominican Republic. Height 15.0 mm, width 6.5 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 28.—*Lepicythara heptagona* (Gabb). NMB H 18123. NMB locality 16914: Rio Mao, Dominican Republic. Cercado Formation. Height 15.6 mm, width 7.0 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 29.—*Lepicythara heptagona* (Gabb). PRI 28656. Holotype of *Cythara cercadica* Maury. Rio Mao, Bluff 1 f Maury, Dominican Republic. Gurabo Formation. Height 14.6 mm, width 5.4 mm. 1, front view: 2, rear view; 3, from right side.

collected: Rio Mao, Bluff 2 of Maury, Dominican Republic. Cercado Formation (Late Miocene). For exact location see Saunders *et al.* (1986, text-figs. 29–31).

Holotype.—(of *cercadica*) PRI 28656 (Text-fig. 29).

Dimensions of holotype.—(of *cercadica*) Height 14.6 mm, width 5.4 mm.

Type locality.—(of *cercadica*) Rio Mao, Bluff 1 of Maury, Dominican Republic. Gurabo Formation (Late Miocene).

Remarks.—Pilsbry (1922, p. 322) mentioned the type (lectotype) and another specimen. This specimen is the only paralectotype (ANSP 79153). Its protoconch is incomplete, but its last volution is sculptured by nine opisthocline to slightly opisthocyrt axial riblets. The number of its teleoconch whorls is 4.5; these are sculptured by seven axial ribs, which are alined on successive whorls. *L. heptagona* is not a common species at all. As interpreted here it occurs only in the Late Miocene of the Dominican Republic.

Comparisons.—*L. heptagona* may be compared with *L. costaricensis*, but there are some clear differences mentioned under the latter species. *L. lopezana* from the late Early to early Middle Miocene Baitoa Formation of the Dominican Republic has more protoconch volutions, is smaller than *L. heptagona*, and its parietal callus is more strongly developed.

Material.—Ten lots (all from the Dominican Republic) with a total of only 16 specimens as listed below:

1 spec., ANSP 2915 (lectotype), Ciboa Region. Exact locality and age not known.
1 spec., ANSP 79135 (paralectotype), Cibao Region. Exact locality and age not known.
1 spec., PRI 28656 (holotype of *Cythara cercadica* Maury): Rio Mao, Bluff 1 of Maury. Gurabo Formation (Late Miocene).
1 spec., NMB locality 15871: Rio Gurabo. Gurabo Formation (Late Miocene).
1 spec., NMB locality 16821: Rio Cana. Gurabo Formation (Latest Miocene).
1 spec., NMB locality 16842: Rio Cana. Cercado Formation (Late Miocene).
3 spec., NMB locality 16910: Rio Mao. Bluff 1 of Maury. Gurabo Formation (Late Miocene).
1 spec., NMB locality 16912: Rio Mao. Bluff 3 of Maury. Cercado Formation (Late Miocene).
2 spec., NMB locality 16914: Rio Mao. Bluff 2 of Maury. Cercado Formation (Late Miocene).
4 spec., NMB locality 16832: Rio Mao. Bluff 2 of Maury. Cercado Formation (Late Miocene).

Measurements.—(See Table 7.)

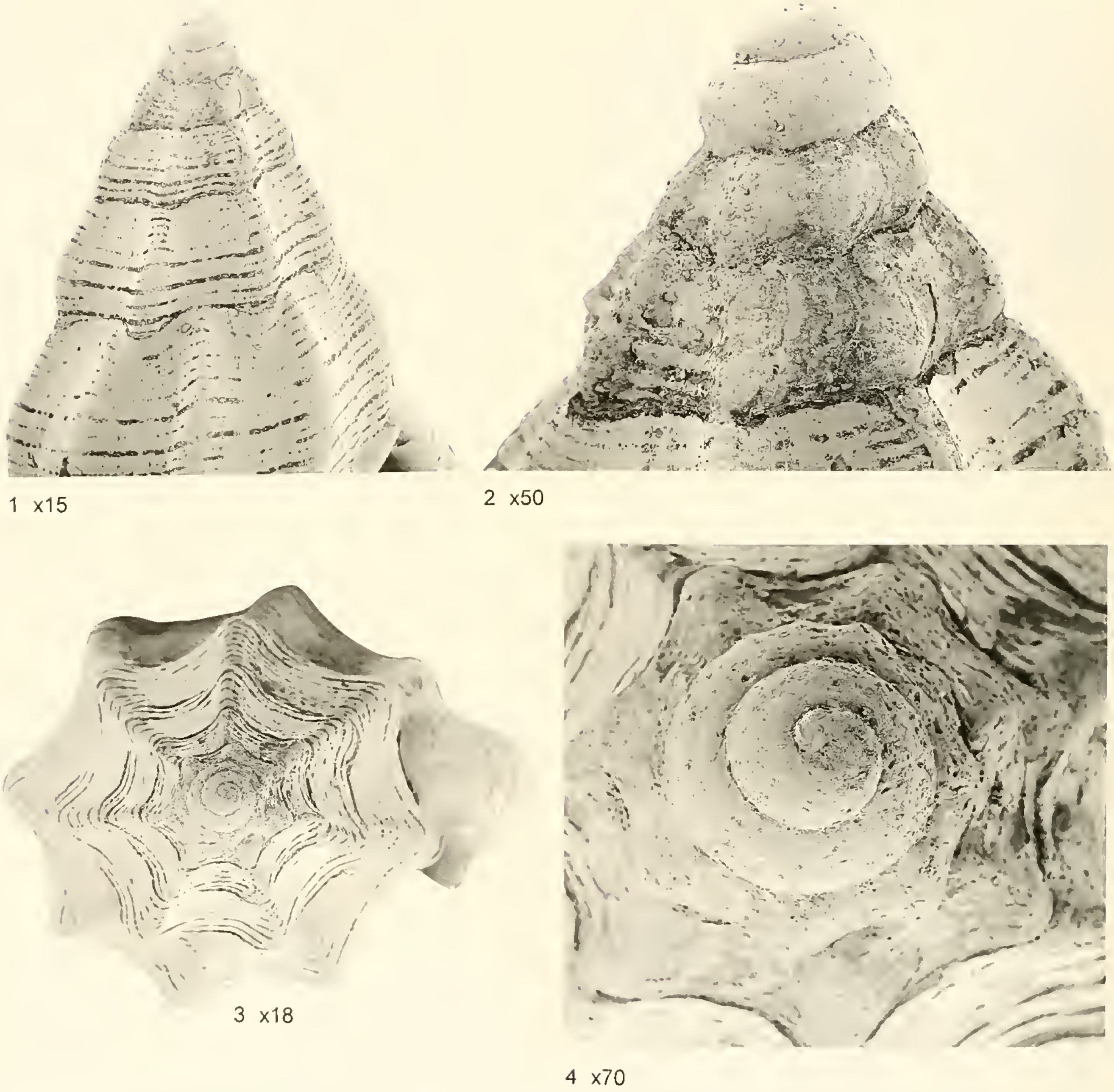
Occurrences.—This species is recorded from the following sections in the Dominican Republic (for location see Saunders *et al.*, 1986). Rio Gurabo: NMB locality 15871: Gurabo Formation (Late Miocene). Rio Cana: NMB localities 16821: Gurabo Formation (Latest Miocene) and 16842: Cercado Formation (Late Miocene). Rio Mao: NMB localities 16910: Gurabo Formation (Late Miocene) and 16912, 16914, and 16932: all Cercado Formation (Late Miocene).

Distribution.—So far this species is not known from outside the Dominican Republic.

Lepicythara cf. heptagona (Gabb, 1873)

Text-figure 32

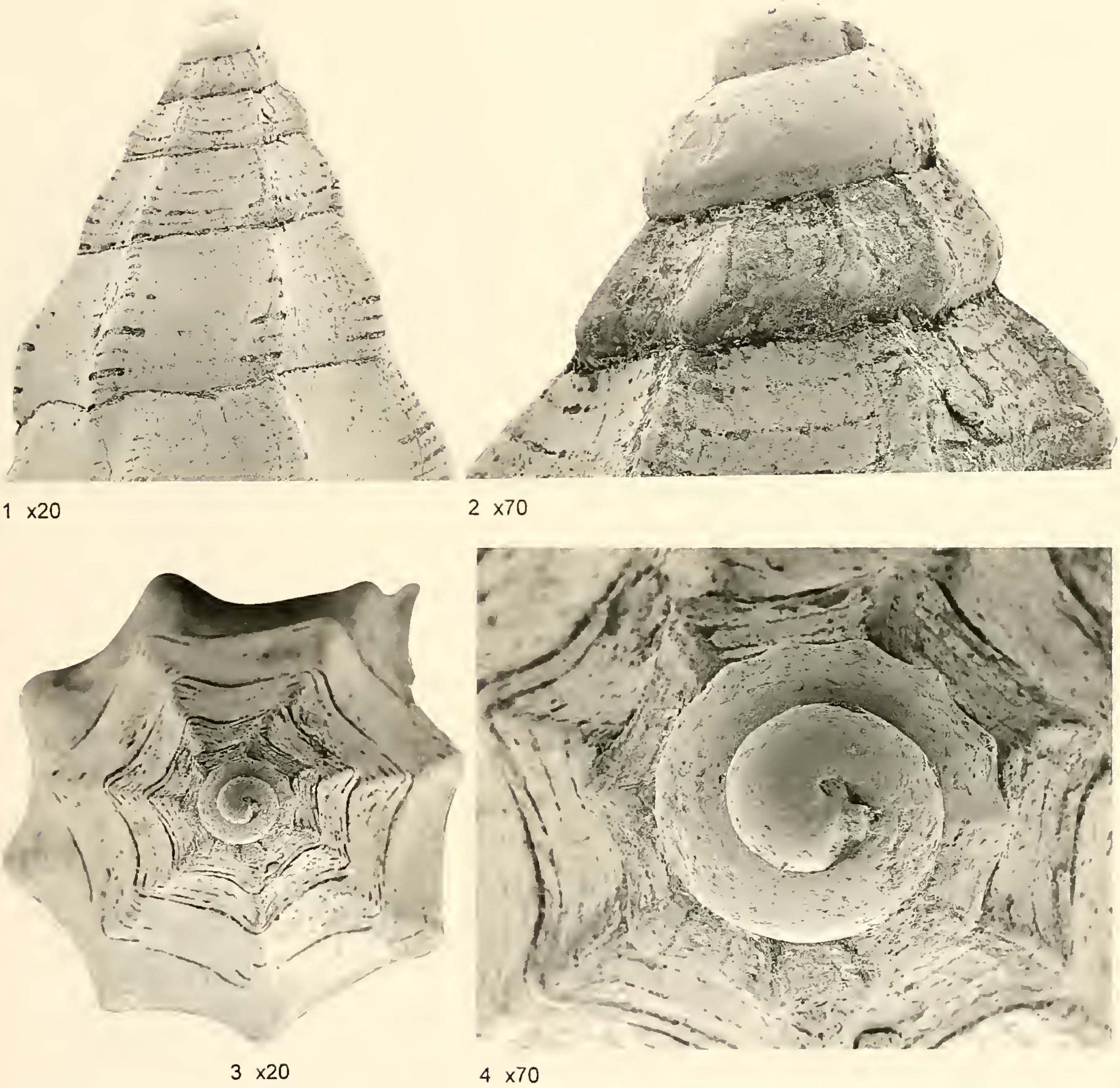
Remarks.—The two specimens from Colombia mentioned by Woodring (1970, p. 391) under his *Lepicythara heptagona* are at hand. They were collected from a horizon assigned by Woodring to the Middle Miocene (probably rather Late Miocene), about half a kilometer east of Usiacuri, northern Columbia (USGS Station 7873). The larger specimen (restored height 13. mm, width 6.5 mm, ratio 2.09) has a protoconch with a little less than three volutions carrying nine slightly opisthocyrt axial riblets on its last portion. It has a little more than 4.5 teleoconch whorls carrying eight axial ribs per whorl on early whorls as well as on the body whorl. The profile of the teleoconch whorls is straight on the early whorls with an angulation near the abapical suture, but slightly convex on late whorls. The protoconch of the smaller specimen (restored height 10.4 mm, width 4.8 mm, ration 2.17) is not completely preserved, but carries ten opisthocyrt axial riblets on its last portion. The number of teleoconch whorls is 4.25. They



Text-figure 30.—*Lepicythara heptagona* (Gabb). NMB H 18122. NMB locality 16842: Rio Cana, Dominican Republic, Cercado Formation. Height 11.9 mm, width 5.0 mm. (Same specimen as Text-fig. 27.) 1, front view of spire whorls; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

are sculptured by eight axial ribs per whorl on early whorls, but by nine on the body whorl. The profile of the teleoconch whorls is the same as in the larger specimen. Both specimens from USGS Station 7873 are biconic and moderately slender. Their spiral sculpture consists of fine, incised lines which cross the axial ribs.

Specimen PRI 22939 is the specimen described and figured by Weisbord (1929, p. 55, pl. 5, figs. 13–14) as *Cythara heptagona*? (Gabb), which was been collected from an unspecified locality and horizon in Colombia. It is re-figured here under this heading because it is only the third specimen of *Lepicythara* recorded from Colombia, if Oinomikado's (1939, p. 624) undocumented record of *Cythara* cf. *cercadica* Maury from southwestern Colombia is not taken into consideration. The protoconch of this weathered specimen is not preserved. The early teleoconch whorls carry seven axial ribs per whorl, the body whorl nine. Its anterior canal is broken.



Text-figure 31.—*Lepicythara heptagona* (Gabb). NMB H 18124. NMB locality 16932: Rio Mao, Bluff 2 of Maury, Dominican Republic, Cercado Formation. Height 12.3 mm, width 4.5 mm. 1, spire whorls; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

Due to its rather poor preservation the present writer is not able to determine whether specimen PRI 22939 is conspecific with the two specimens from USGS Station 7873. On the other hand he is confident that they do not belong to *L. heptagona* (Gabb). Their protoconch has a little less than three volutions, whereas specimens of *L. heptagona* from the Dominican Republic never have more than 2.25 volutions.

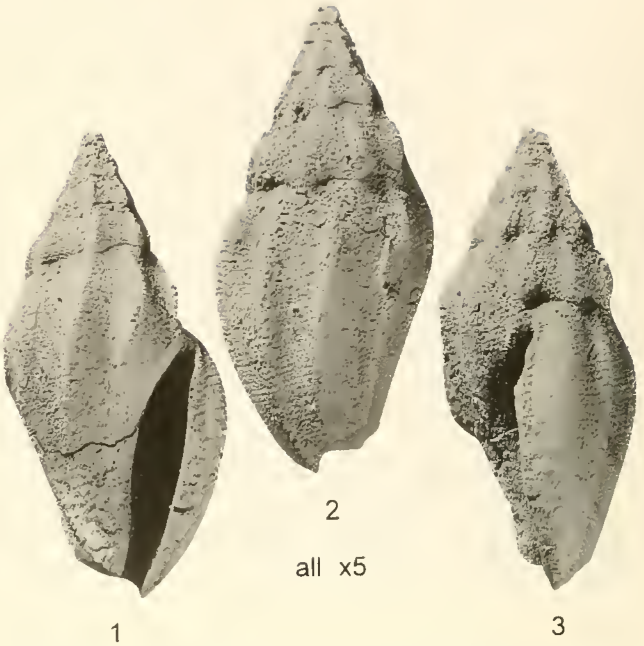
Lepicythara aff. heptagona (Gabb, 1873)
Text-figure 33

Lepicythara heptagona (Gabb). Perrilliat, 1973, p. 57, pl. 28, figs. 9–12.

Remarks.—Under the name of *L. heptagona* Perrilliat (1973, p. 57) recorded specimens from Santa Rosa, Veracruz, Mexico. The location of this locality

Table 7.—Measurements (in mm) of *Lepicythara heptagona* (Gabb, 1873).

Specimen	Restored height	Width	Height/ width ratio
ANSP 2915	15.2	6.5	2.34
ANSP 79153	11.3	5.0	2.26
PRI 28656	14.6	5.4	2.70
NMB locality 16821	13.2	5.7	2.32
NMB locality 16842	12.0	5.0	2.40
NMB locality 16910	14.9	7.5	1.99
	14.2	6.8	2.09
NMB locality 16912	15.9	6.9	2.30
NMB locality 16914	15.6	7.0	2.23
NMB locality 16932	14.6	6.4	2.29
	17.0	7.0	2.43



Text-figure 32.—*Lepicythara cf. heptagona* (Gabb). PRI 22939. Specimen from an unspecified locality and horizon in northern Colombia figured by Weisbord (1929, pl. 5:13–14) under the name of *Cythara heptagona*? (Gabb). Height 13.7 mm, width 6.8 mm. 1, front view; 2, rear view; 3, from right side.

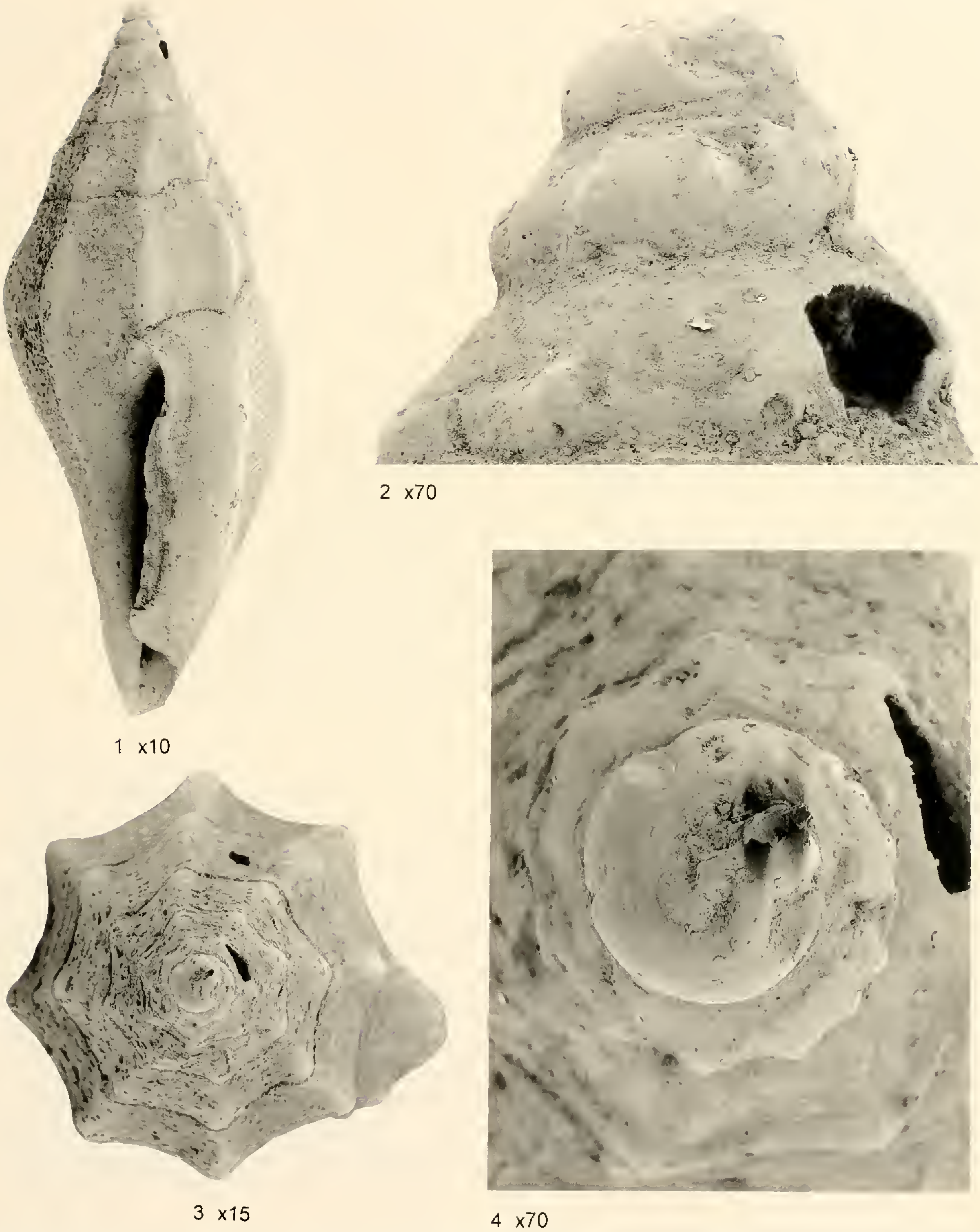
is given by Perrilliat (1972, p. 11, fig. 1). Akers (1972, p. 30) assigned those beds to the Agueguexquite Formation, which he dated as Middle to Late Pliocene. Later Akers (1979, p. 497) introduced the name "Medias Aguas Formation" stating that it "will be designated in a subsequent report (Tulane Studies in Geology and Paleontology) for unnamed beds of upper Miocene age (Zone N17)". This promised paper, however, never appeared, and the Medias Aguas Formation is therefore a *nomen nudum*. For further discussion of the Santa Rosa beds reference is made to Vokes (1994, p. 138) and Vermeij and Vokes (1997, p. 84).

Perrilliat had six specimens from the same locality (USGS 23737) at hand, when she described her *L. heptagona*. The present writer has seen five of them. The sixth specimen was not available; it has been figured by Perrilliat (1973, pl. 28, figs. 11–12) carrying the number IGM2415, and is deposited in the Instituto de Geologia of the Universidad Nacional Autonoma de Mexico. The dimensions given by Perrilliat show that this is a *Lepicythara* of large size like *L. heptagona* from the Dominican Republic. The number of axial ribs per whorl ranges from seven on early whorls to nine on late whorls like in *L. heptagona* from the Dominican Republic.

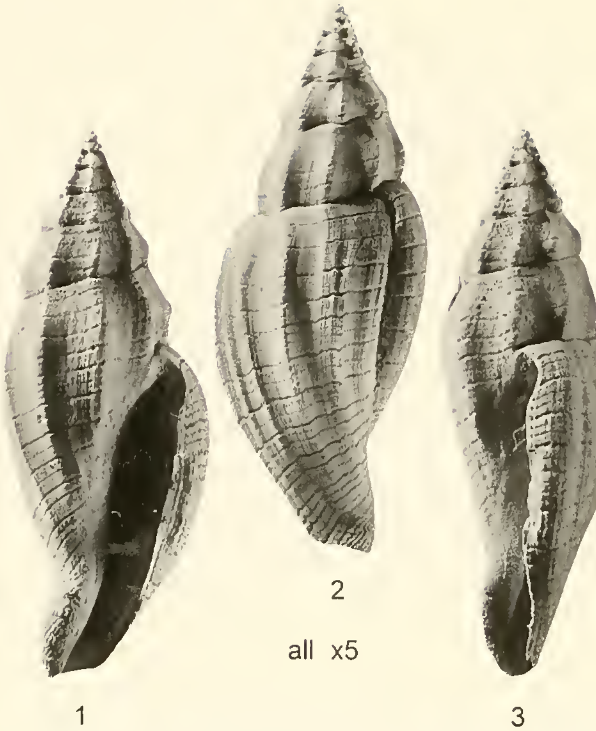
The specimen figured here (Text-fig. 33) has an incomplete protoconch, but its last part shows eleven opisthocline to slightly opisthocyrt axial riblets. The number of its teleoconch whorls is 4.25. The first teleoconch whorl is sculptured by seven, later whorls by eight to nine axial ribs. Specimen USNM 647171 has been figured by Perrilliat (1973, pl. 28, figs. 9–10). Its protoconch is not quite complete, but it is seen to consist of probably 3.25 volutions. This is a clear difference to the protoconch of *L. heptagona* from the Dominican Republic, which consists of only 2.25 volutions. The material from Santa Rosa is therefore not identified as *L. heptagona*, and it is insufficient to serve as type material for the formal description of a new species.

Lepicythara higensis, new species
Text-figures 34–36

Description.—Of medium to large size, slender. Protoconch consists of 2.5 volutions. The surface of a little less than the first two volutions is smooth. The remainder of the protoconch is sculptured by up to 14 opisthocline to opisthocyrt axial riblets. Apex not pointed. Number of teleoconch whorls up to 6.75; their profile straight on early spire whorls, slightly convex on late spire whorls. The first two to three teleoconch whorls are somewhat carinated near the abapical suture thus overhanging it a little. Early teleoconch whorls sculptured by seven to nine orthocline to slightly opisthocline axial ribs, late whorls by ten to eleven. Interspaces of axial ribs concave, sculptured by three incised, spiral lines on early teleoconch whorls, by five on the penultimate whorl. There are a few secondary incised, spiral lines. All spiral lines cross the axial ribs. Suture shallow. Aperture narrow. Outer lip thickened. Sinus adjoining suture shallow. Inner surface of outer lip smooth, without a ridge parallel to the sharp edge of the outer lip, but with a small thickening just below the sinus adjoining the suture. Parietal callus slightly thickened near sinus, columellar callus inconspicuous.



Text-figure 33.—*Lepicythara* aff. *heptagona* (Gabb). USNM 495825. USGS Station 23737: Santa Rosa, Veracruz, Mexico. Beds of Late Miocene age. Height 13.7 mm, width 6.0 mm. 1, from right side; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.



Text-figure 34.—*Lepicythara higensis* n. sp. NMB H 18146. Holotype. NMB locality 17736: southern end of Golfo Dulce, Pacific side of Costa Rica: Quebrada El Higo, about 5 km northeat of Punta Banco; at bridge across Quebrada. Pleistocene. Height 16.1 mm, width 6.4 mm. 1, front view; 2, rear view; 3, from right side.

Anterior canal twisted to the left, rather narrow, and moderately long.

Holotype.—NMB H 18146 (Text-fig. 34).

Dimensions of holotype.—Height 16.1 mm, width 6.4 mm.

Type locality.—NMB locality 17736 (=PPP 237): southern end of Golfo Dulce, Pacific side of Costa Rica, Quebrada El Higo, about 5 km northeast of Punta Banco; at bridge across Quebrada. Pleistocene. See Text-figure 36.

Remarks.—The largest lot of *L. higensis* consists of nine specimens, which are part of a float collection. The specimens are rolled and sculptural details are not preserved. With the exception of the protoconch most of them are complete specimens. The protoconch of the figured paratype is complete but a little weathered.

Comparisons.—Specimens of *L. polygona* from the Cercado and Gurabo Formations (Late Miocene to Early Pliocene) of the Dominican Republic are smaller than *L. higensis* and have many more axial ribs per whorl. Specimens of *L. toroensis* from the Early Pliocene Shark Hole Point Formation of the Valiente Peninsula, Panama, have the same number of volutions of the protoconch, but *L. toroensis* is a larger and stouter species with more axial ribs per whorl.

Material.—Five lots with a total of 15 specimens as listed below (all of the localities are situated in the Quebrada El Higo, about 5 km northeast of Punta Banco, southern end of Golfo Dulce, Pacific side of Costa Rica): (see Text-fig. 36).

1 spec., NMB locality 17736 (=PPP 237): at bridge across Quebrada El Higo. Pleistocene. Holotype.
9 spec., NMB locality 17745 (=PPP 436): Quebrada El Higo. Float collected over an air distance of 550 m, *i.e.*, from near mouth of Quebrada to contact with basalt. Pleistocene. Paratypes.
1 spec., NMB locality 17746 (=PPP 273): Quebrada El Higo. Float collected over an air distance of 1.5 km above waterfall (basalt). Pleistocene. Paratype.
3 spec., NMB locality 17752 (=PPP 262): Quebrada El Higo, about 550 m air distance downstream from contact with basalt. Pleistocene. Paratypes.
1 spec., NMB locality 17793 (=PPP 268): Quebrada El Higo, above waterfall. Pleistocene. Paratype.

Measurements.—(See Table 8.)

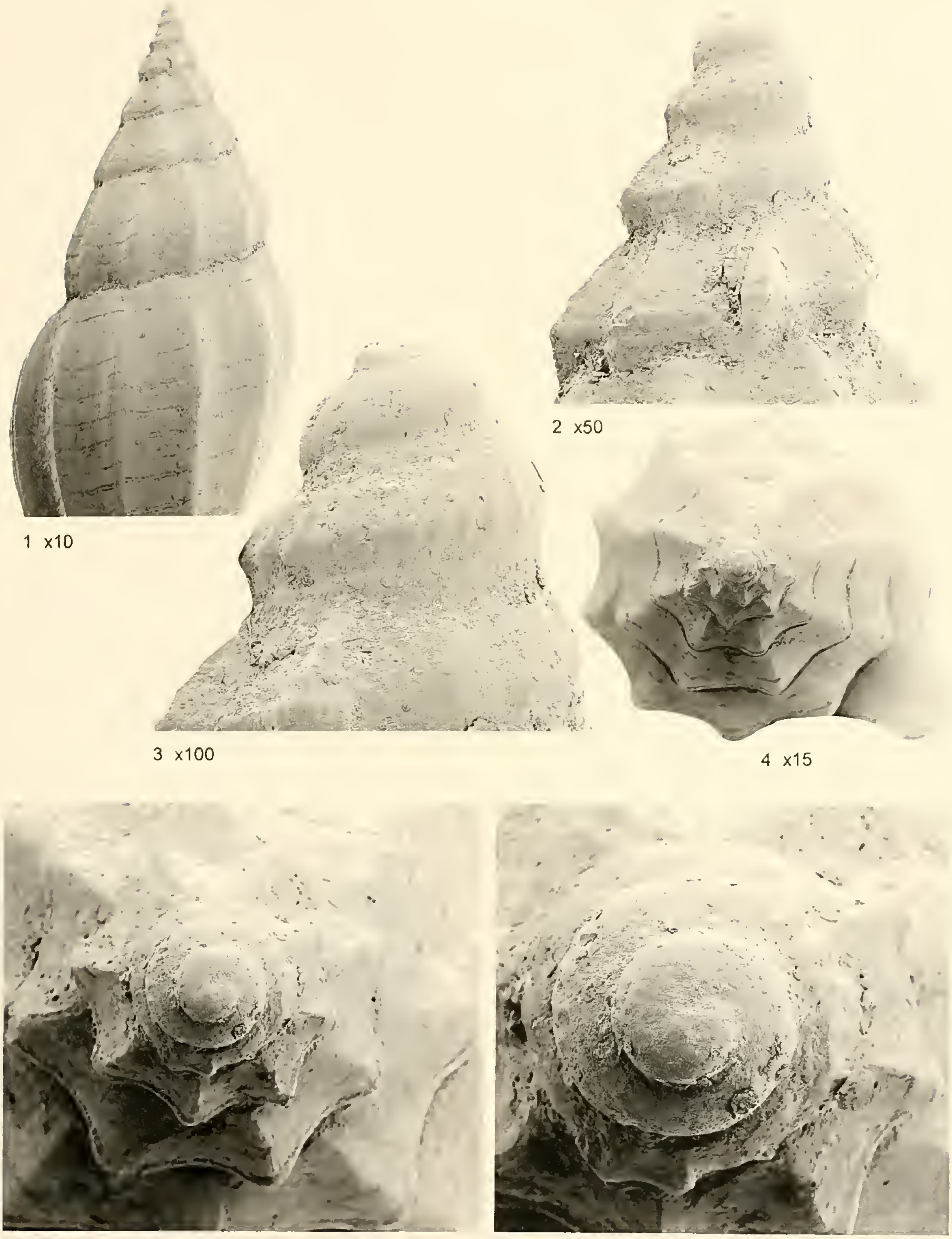
Occurrence.—This species is recorded from the following NMB localities, which are all situated in the Quebrada El Higo, Pacific side of Costa Rica (Text-fig. 36): 17736, 17745, 17746, 17752, 17793 (Pleistocene).

Distribution.—So far this species is not known outside the type area.

Etymology.—Refers to the geographic name of Quebrada El Higo, Province of Puntarenas, Costa Rica.

Lepicythara lopezana, new species
Text-figures 37–38

Description.—Of medium to large size, moderately slender. Protoconch consists of 2.75 volutions. The surface of the first two and a little more volutions is smooth, the remainder of the protoconch sculptured by up to eight opisthocline to opisthocyrt axial riblets. Apex slightly pointed. Number of teleoconch whorls up to 5.25; their profile is slightly convex on early whorls and convex on later whorls. Early teleoconch whorls sculptured by seven to eight orthocline to slightly opisthocline axial ribs, concave, sculptured by four incised spiral lines on the first teleoconch whorl and increasing in number to eight on the penultimate whorl There are a few secondary incised, spiral lines. All spiral lines cross the axial ribs. Suture moderately deep. Aperature narrow. Outer lip thickened. Sinus adjoining suture rather deep. Inner surface of outer lip smooth, with a prominent ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Parietal callus thickened near sinus, columellar callus moderately promi-



1 x10

2 x50

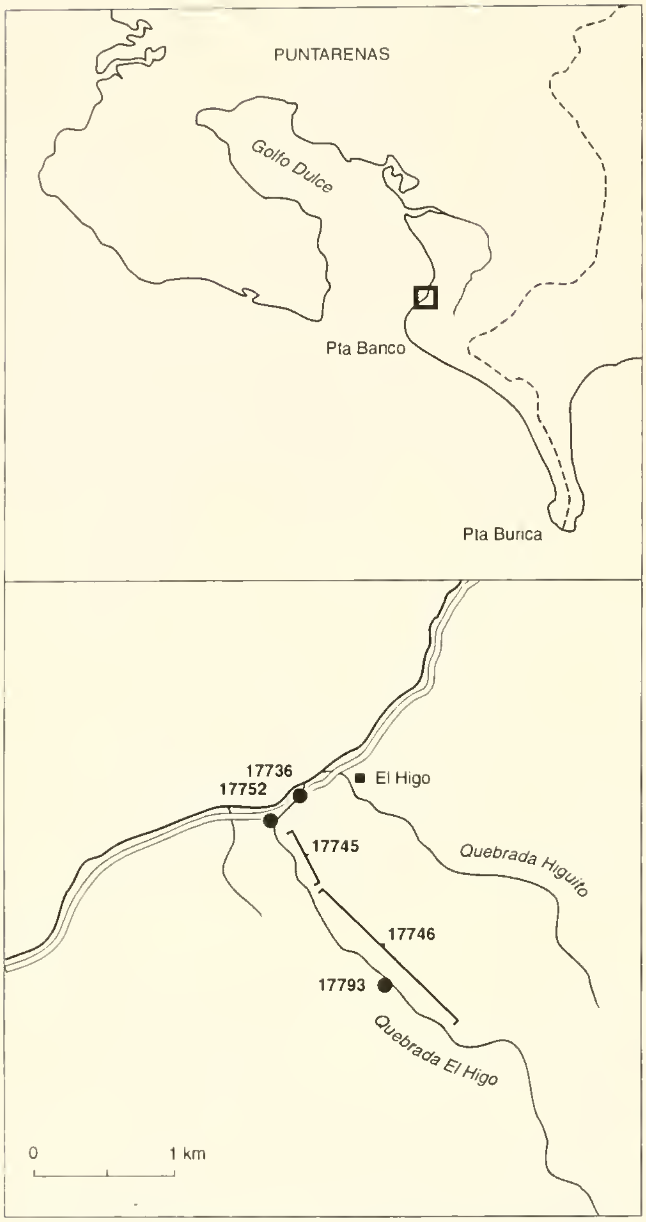
3 x100

4 x15

5 x50

6 x100

Text-figure 35.—*Lepicythara higensis* n. sp. NMB H 18147. Paratype. NMB locality 17752: Quebrada El Higo, about 5 km northeast of Punta BAnco, southern end of Golfo Dulce, Pacific side of Costa Rica, about 550 m air distance downstream from contact with basalt. Pleistocene. Height 14.6 mm, width 5.6 mm. 1, rear view; 2, enlargement of apical area; 3, further enlargement of apical area; 4, apical view; 5, enlargement of apical view; 6, further enlargement of apical view.



Text-figure 36.—Sketch map of Quebrada El Higo, Costa Rica, showing position of NMB localitites that have yielded *L. higensis*.

Table 8.—Measurements (in mm) of *Lepicythara higensis* new species.

Specimen	Restored height	Width	Height/ width ratio
NMB locality 17736	16.2	6.4	2.53
NMB locality 17745	16.7	6.0	2.78
	13.9	5.4	2.57
	13.2	5.0	2.64
	13.0	5.3	2.45
	14.8	5.6	2.64
	14.3	5.8	2.47
NMB locality 17746	12.2	4.8	2.54
NMB locality 17752	14.6	5.6	2.60
	13.3	5.2	2.56
NMB locality 17793	12.9	5.3	2.43

nent. Anterior canal slightly twisted to the left and short.

Holotype.—NMB H 18126 (Text-fig. 37).

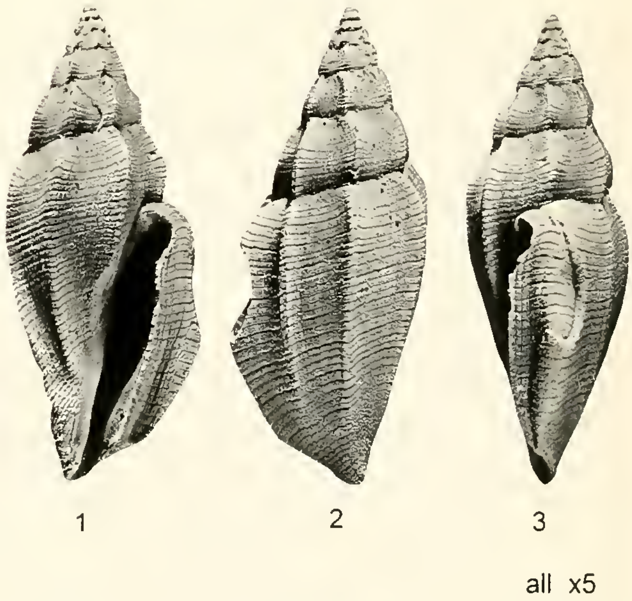
Dimensions of holotype.—Height 13.9 mm, width 6.0 mm.

Type locality.—NMB locality 17288: Lopez section on Rio Yaque del Norte, Dominican Republic. Baitoa Formation (Late Early to Early Middle Miocene). For location and stratigraphic position see Saunders *et al.* (1986, text-fig. 21, 25, pl. 9).

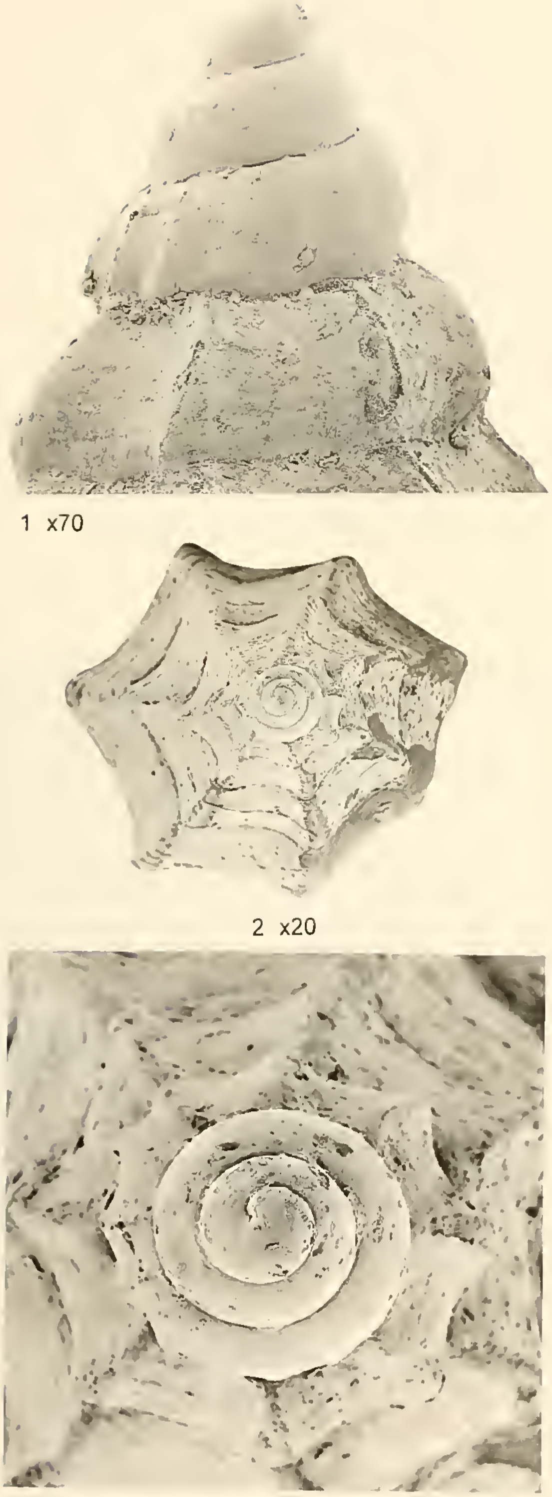
Remarks.—This species is based on six specimens only. The holotype and two paratypes from NMB locality 17289 are the only adult and more or less complete specimens. One of the paratypes is immature and the remaining two are fragmentary. However, one of the fragmentary paratypes has a complete protoconch (see Text-fig. 38.3).

Comparisons.—*L. lopezana* is very similar to *L. heptagona* (Gabb) from the Cercado and Gurabo Formations (Late Miocene) of the Dominican Republic. On an average *L. heptagona* is somewhat larger than *L. lopezana*. The main differences, however, is seen in the protoconch: that of *L. heptagona* has 2.25 volutions, that of *L. lopezana* 2.75. In addition the parietal callus of *L. lopezana* is more strongly developed.

Material.—Four lots with a total of only six speci-



Text-figure 37.—*Lepicythara lopezana* n. sp. NMB H 18126. Holotype. NMB locality 17288: Lopez section on Rio Yaque del Norte, Dominican Republic. Baitoa Formation. Height 13.9 mm, width 6. mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 38.—*Lepicythara lopezana* n. sp. NMB H 18125. Paratype. NMB locality 17287. Lopez section on Rio Yaque del Norte, Dominican Republic. Baitoa Formation. Height 6.4 mm, width 3.0 mm. 1, enlargement of apical area; 2, apcal view; 3, enlargement of apical view.

Table 9.—Measurements (in mm) of *Lepicythara lopezana* new species.

Specimen	Restored height	Width	Height/ width ratio
NMB locality 17288	14.0	6.0	2.33
NMB locality 17289	12.4	5.7	2.17
	11.5	5.0	2.30

mens are listed below. All the lots come from the Lopez section on Rio Yaque del Norte, Dominican Republic. Baitoa Formation (late Early to early Middle Miocene):

1 spec., NMB locality 17286. Paratype.
2 specs., NMB locality 17287. Paratypes.
1 spec., NMB locality 17288. Holotype.
2 specs., NMB locality 17289 Paratypes.

Measurements.—(See Table 9.)

Occurrence.—This species occurs only in the Lopez section on Rio Yaque del Norte, Dominican Republic. It has been found at the following NMB localities: 17286–17289. All these localities are situated in the Baitoa Formation (late Early to early Middle Miocene) (Saunders *et al.*, 1986, text-figs. 21, 25, pl. 9).

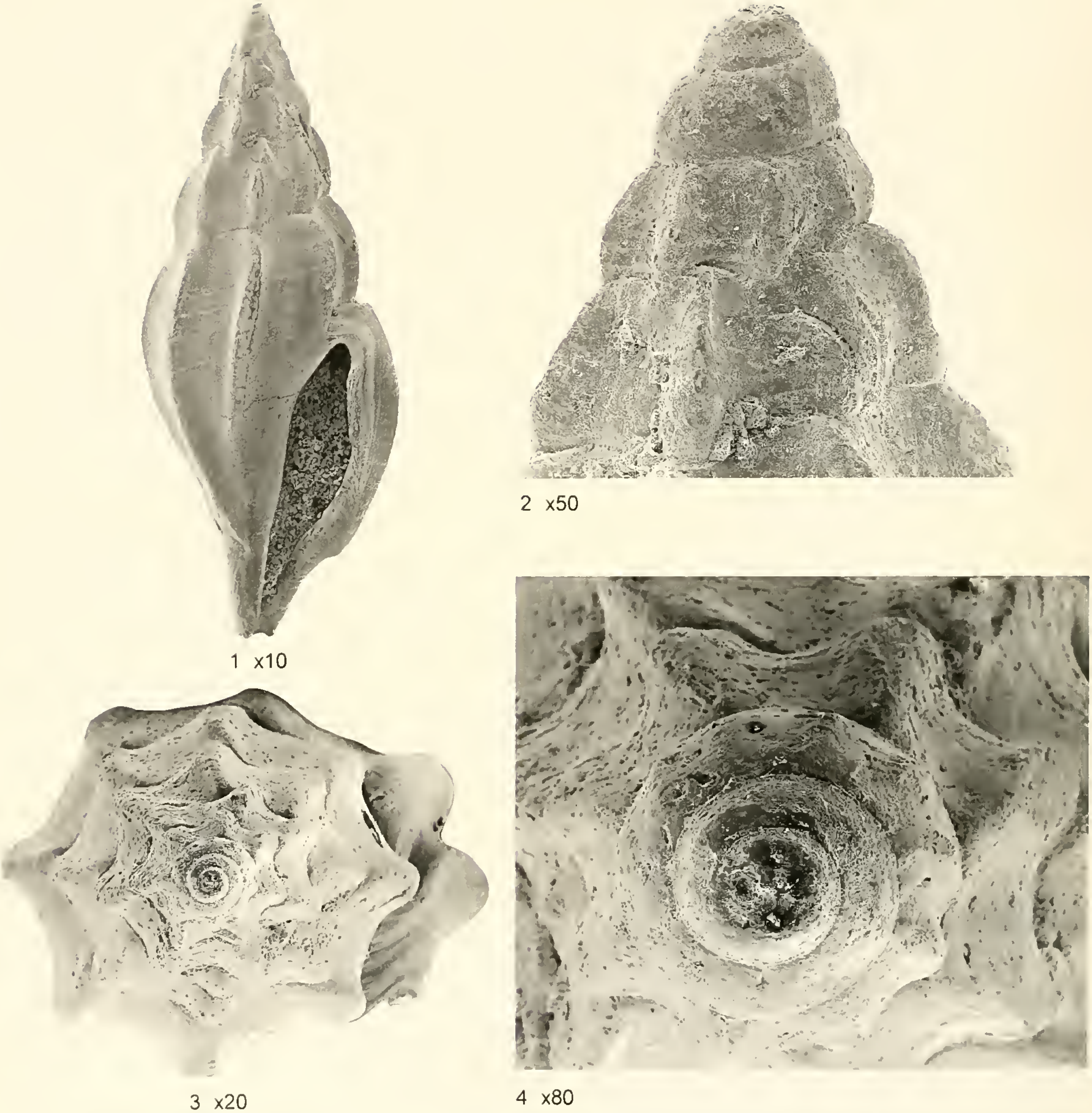
Distribution.—So far *L. lopezana* is not known from outside the type area.

Etymology.—Refers to the Lopez section on Rio Yaque del Norte, Dominican Republic.

Lepicythara cf. lopezana, new species

Text-figure 39

Remarks.—At first the present writer was tempted to include in *L. lopezana*, five specimens from the Thomonde Formation of Haiti, which are of about the same age as *L. lopezana* from the Lopez section. Three of these specimens (USNM 482429) are from USGS locality 9945: trail from Hinche to Thomassique, at a crossing of Riviere Roche Salee, left bank, Departement del l'Artibonite. The remaining two specimens (USNM 482596) are from USGS locality 9946, which is almost the same locality, but on the right bank of the river and stratigraphically 1 m above USGS locality 9945. The specimens from Haiti have a protoconch like that of *L. lopezana* consisting of 2.75 volutions. The figured protoconch (see Text-fig. 39.4) is not preserved well enough to see this, but a specimen from USGS locality 9945 has a protoconch consisting of 2.75 volutions, but other features are incomplete. The Haitian specimens are smaller and a little more slender than those from the Lopez section, *i.e.*, their apical angle is somewhat smaller. There are eight axial ribs per whorl on early teleoconch whorls, but eight to nine



Text-figure 39.—*Lepicythara* cf. *lopezana* n. sp. USNM 482596. USGS Station 9946: trail fro Hinche to Thomassique at crossing of Riviere Roche Salee, right bank, Department de l'Artibonite, Haiti. Thomonde Formation. Height 11.0 mm, width 4.4 mm. 1, front view; 2, enlargement of apical area; 3, apical area; 4, enlargement of apical view.

on the body whorl, which is slightly more than in *L. lopezana*. In addition the spiral sculpture of the Haitian specimens is not well developed. Because of these differences and in view of the scarcity of material the specimens from Haiti are not considered conspecific with *L. lopezana*.

Measurements.—(See Table 10.)

Lepicythara paradisclusa, new species
Text-figures 40–42

"*Cythara*" (*Brachicythara*?) cf. *terminula* Dall. Rutsch, 1942, p. 169, pl. 3, figs. 10–11.

Table 10.—Measurements (in mm) of *Lepicythara* cf. *lopezana* new species.

Specimen	Restored height	Width	Height/ width ratio
USNM 482429	9.8	3.9	2.51
	7.1	3.2	2.22
USNM 482596	11.0	4.4	2.50

Lepicythara disclusa Jung, 1969, p. 551, in part (not pl. 59, figs. 7–10).

Description.—Of small to medium size, strongly biconic and stout. Protoconch consists of 2.75 volutions. The surface of the first two volutions is smooth, the remainder of the protoconch is sculptured by about 12 opisthocline to opisthocyrt axial riblets. Apex hardly pointed. Number of teleoconch whorls 4.5, their profile practically straight. Teleoconch whorls sculptured by eight, rarely nine, orthocline to slightly opisthocline axial ribs per whorl thus being alined on successive whorls. The axial ribs of the first two teleoconch whorls are somewhat pointed at the periphery thus projecting a little over the abapical suture. Interspaces of axial ribs a little concave, sculptured by four incised, spiral lines on the first teleoconch whorl and increasing in number to ten on the penultimate whorl There are few secondary incised, spiral lines. All spiral lines cross the axial ribs. Suture shallow. Aperture narrow. Outer lip thickened. Sinus adjoining suture shallow. Inner surface of outer lip smooth, in rare cases with an inconspicuous ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Columellar and parietal calluses weakly developed. Anterior canal slightly twisted to the left, rather short.

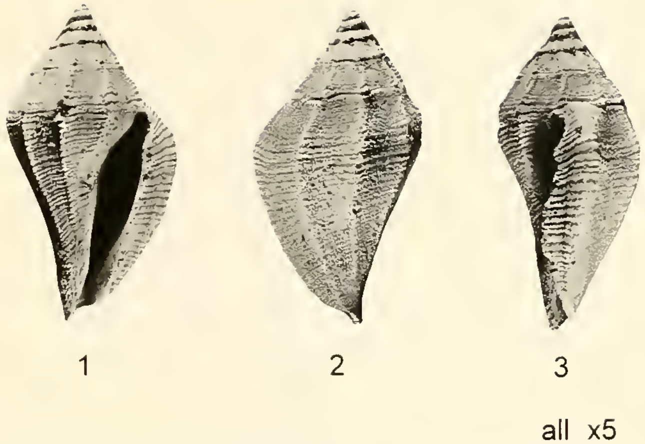
Holotype.—NMB H 18120 (Text-fig. 40).

Dimensions of holotype.—Height 8.6 mm, width 4.7 mm.

Type locality.—NHB locality 13720: Central Range, Trinidad; 1700 feet southwest of Philippine Estate. Savaneta Glauconitic Sandstone Member of Springvale Formation (Early Pliocene, *Globorotalia margaritae* Zone) (Jung, 1989, p. 13, fig. 13).

Remarks.—Many of the available specimens are incomplete. There is not a single perfectly preserved protoconch.

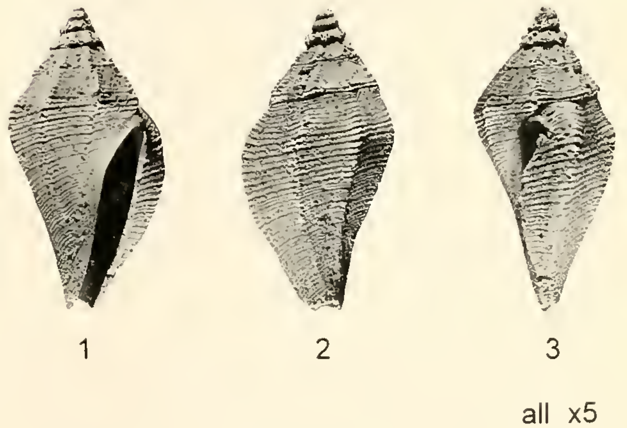
Comparisons.—*L. paradisclusa* cannot be compared with any of the species described herein. It is the only species with a straight profile on its late teleoconch whorls. In addition its apical angle is larger than in other species.



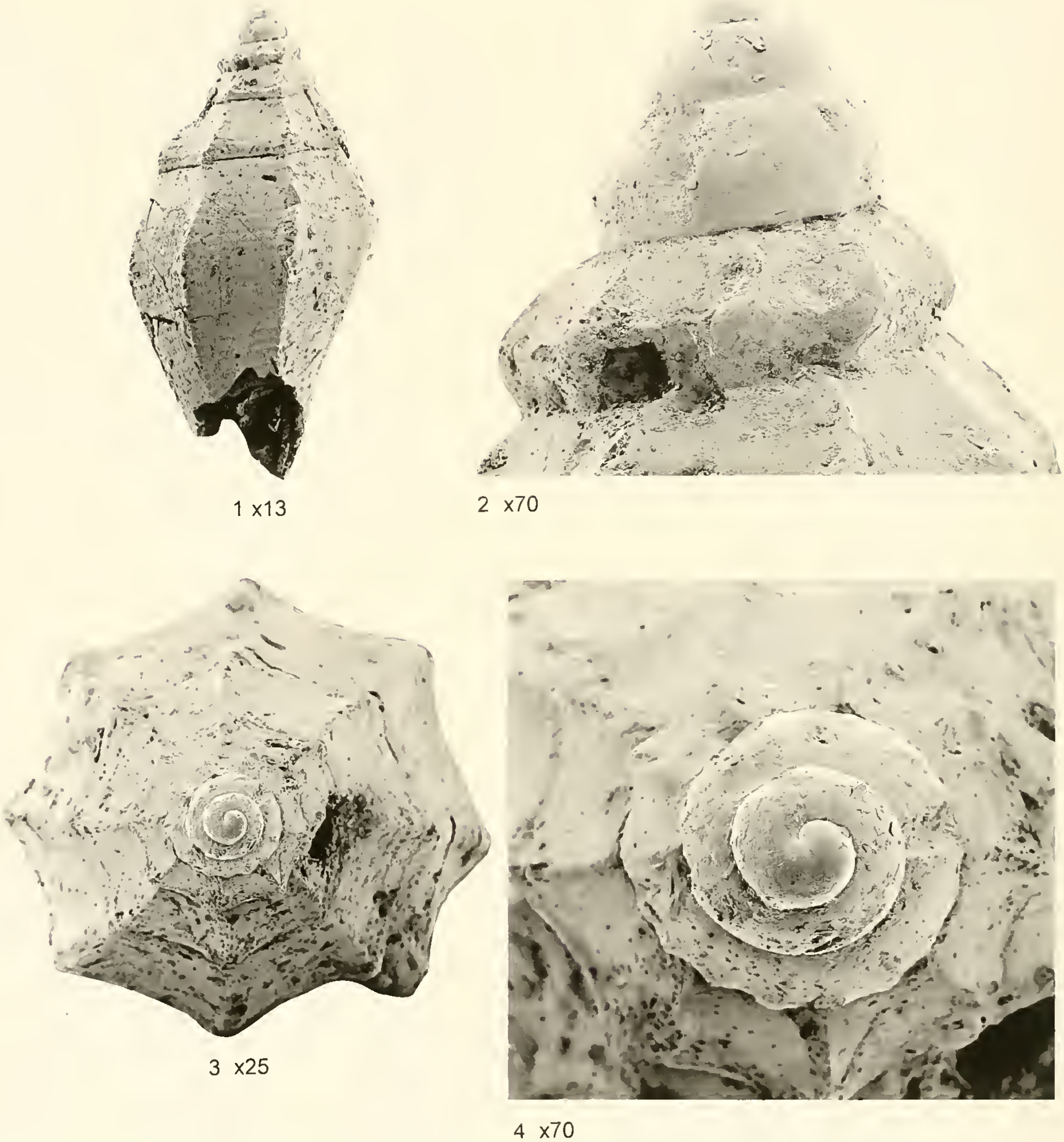
Text-figure 40.—*Lepicythara paradisclusa* n. sp. NMB H 18120. Holotype. NMB locality 13720: 1700 feet southwest of Philippine Estate, Central Range, Trinidad. Savaneta Glauconitic Sandstone Member of Springvale Formation. Height 8.6 mm, width 4.7 mm. 1, front view; 2, rear view; 3, from right side.

Material.—Five lots with a total of 26 specimens as listed below:

- 19 specs., NMB locality 13720 (holotype and paratypes): 1700 feet southwest of Philippine Estate, Central Range, Trinidad. Savaneta Glauconitic Sandstone Member of Springvale Formation (Early Pliocene, *Globorotalia margaritae* Zone).
- 2 specs., NMB locality 10490 (paratypes): same locality as lot 1.
- 1 spec., NMB H 6250 (paratype; figured by Rutsch, 1942, pl. 3, fig. 10) NMB locality 10515: Brechin Castle Estate, Central Range, Trinidad. Savaneta



Text-figure 41.—*Lepicythara paradisclusa* n. sp. NMB H 18121. Paratype. NMB locality 13720: 1700 feet southwest of Philippine Estate, Central Range, Trinidad. Savaneta Glauconitic Sandstone Member of Springvale Formation. Height 8.1 mm, width 4.3 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 42.—*Lepicythara paradisclusa* n. sp. NMB H 18116. Paratype. NMB locality 13720: 1700 feet southwest of Philippine Estate, Central Range, Trinidad, Savaneta Glauconitic Sandstone Member of Springvale Formation. Height 6.4 mm, width 3.3 mm. 1, rear view; 2, enlargement of apica area; 3, apical area; 4, enlargement of apical view.

Glauconitic Sandstone Member of Springvale Formation (Early Pliocene, *G. margaritae* Zone).

1 spec., NMB H 6251 (paratype; figured by Rutsch, 1942, pl. 3, fig. 11). NMB locality 10515: same as lot 3.

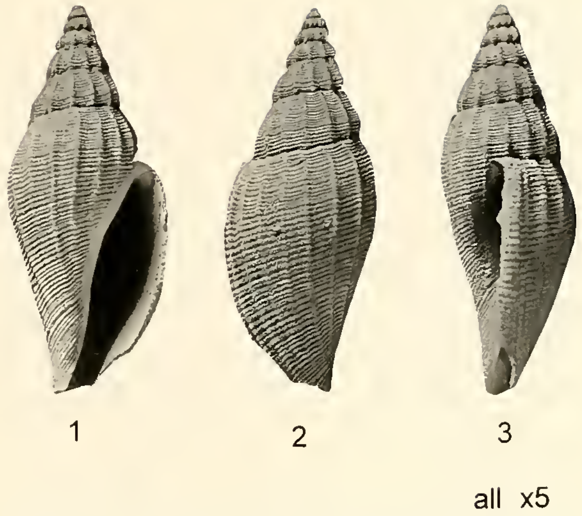
3 spec., NMB H 6288 (paratypes; mentioned by Rutsch, 1942, p. 170). NMB locality 10512: Rio Dulce, Central Range, Trinidad, Gransaull Clay Member of Springvale Formation (Early Pliocene, *G. margaritae* Zone).

Measurements.—(See Table 11.)

Occurrences.—This species is recorded from the following NMB localities, which are all situated in the Early Pliocene Springvale Formation of the Central Range of Trinidad: 10490, 10512, 10515, 13720.

Table 11.—Measurements (in mm) of *Lepicythara paradisclusa* new species.

Specimen	Restored height	Width	Height/ width ratio
NMB locality 13720	8.6	4.7	1.82
	8.2	4.3	1.91
	12.5	5.8	2.16
	9.7	4.9	1.98
	7.6	4.1	1.85
	9.3	5.0	1.86
	10.1	4.8	2.10
	11.0	5.2	2.12
	9.0	4.6	1.96
NMB H 6250	10.5	4.9	2.14
NMB H 6251	12.3	6.2	1.98
HMB H 6288	10.5	5.6	1.87



Text-figure 44.—*Lepicythara polygona* (Gabb). PRI 28654. Specimen figured by Maury (1917, pl. 9, p. 130). Rio Mao, Bluff 3 of Maury, Dominican Republic. Cercado Formation. Height 10.7 mm, width 4.6 mm. 1, front view; 2, rear view; 3, from right side.

Distribution.—So far this species is not known from outside the Central Range of Trinidad.

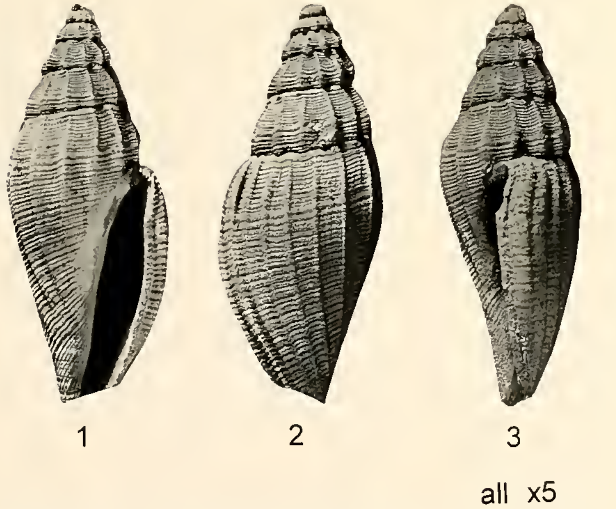
Etymology.—Greek *para* (= next to, beside); referring to the fact that geographically and stratigraphically this species is close to *L. disclusa.*

Lepicythara polygona (Gabb, 1873)

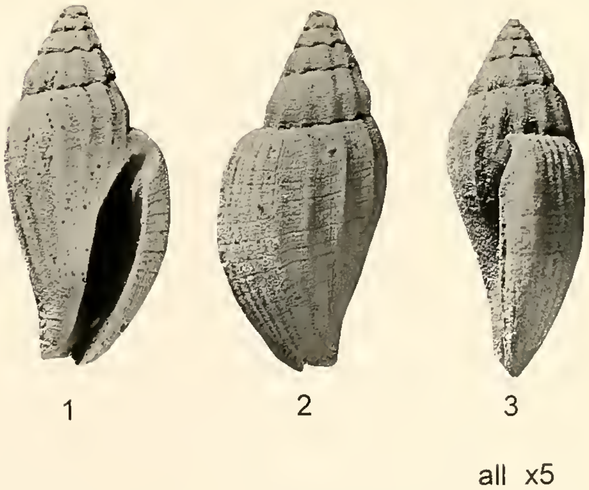
Text-figures 43–56

Mangelia polygona Gabb, 1873, p. 211.
Cythara polygona (Gabb). Pilsbry, 1922, p. 322, pl. 17, fig. 10.
Cythara polygona Gabb. Maury, 1917, p. 60, pl. 9, fig. 13.
Cythara caimitica Maury, 1917, p. 60, pl. 9, fig. 14.

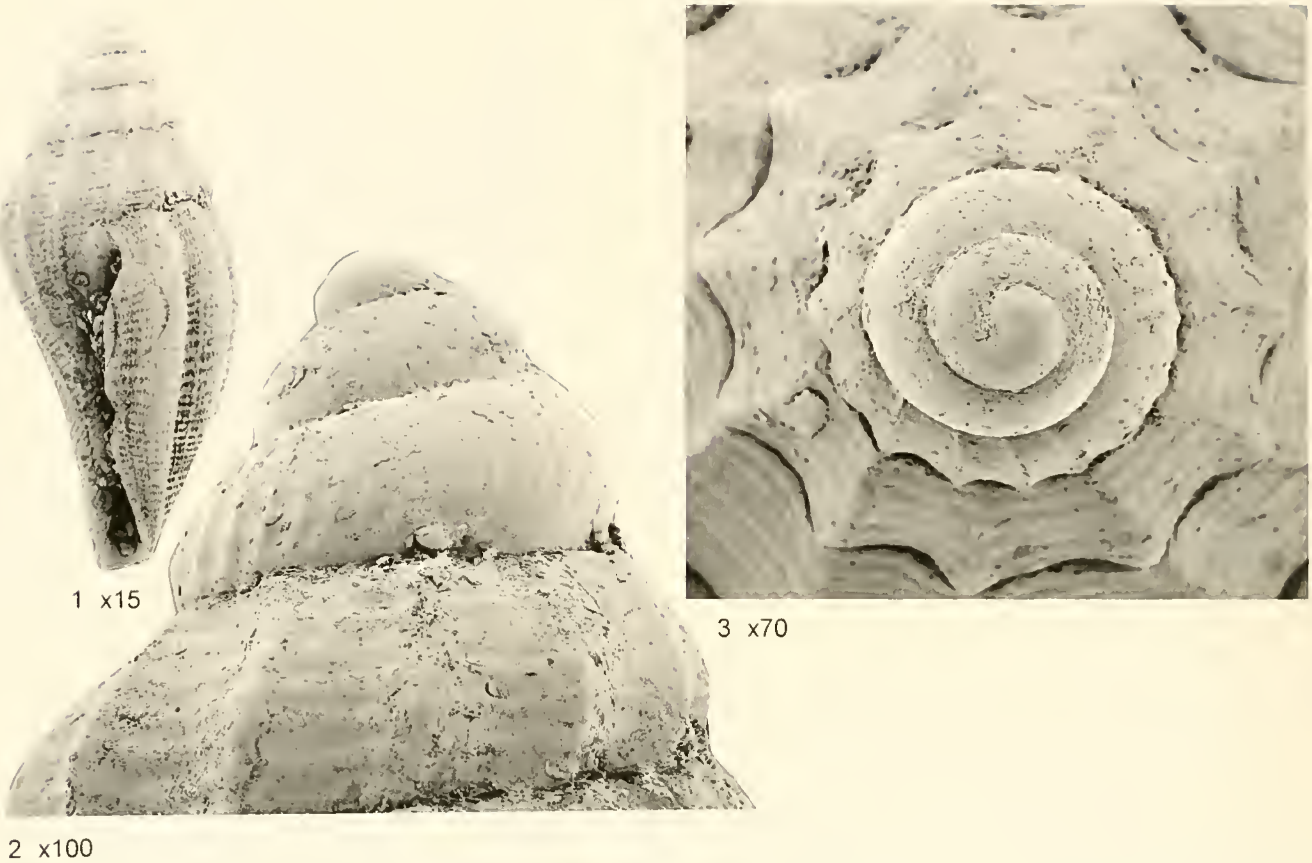
Description.—Of small to medium size, slender to moderately slender. Protoconch consists of 2.25 to 2.75 volutions. Surface of protoconch smooth except for its last part, which is sculptured by up to 20 axial riblets. The first riblets are faint, but gradually become more conspicuous. At the same time their shape is changing from opisthocyrt in the beginning to opisthocline toward the end of the protoconch. In the interspaces of the last axial riblets there are four (rarely five) equally spaced flat, spiral ridges, which do not cross the axial riblets. Apex not pointed. Number of teleoconch whorls up to five, their profile almost straight to convex on early spire whorls, slightly convex on late spire whorls. The first one to two teleoconch whorls may be somewhat carinated near the ab-



Text-figure 43.—*Lepicythara polygona* (Gabb). ANSP 2916. Lectotype. Cibao Region, Dominican Republic. Exact locality and age unknown. Height 10.9 mm, width 4.6 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 45.—*Lepicythara polygona* (Gabb). PRI 28655. Holotype of Cythara caimitica Maury (1917, p. 60, pl. 7, fig. 14). Rio Cana near Caimito, Dominican Republic. Cercado Formation. Height 9.8 mm, width 4.9 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 46.—*Lepicythara polygona* (Gabb). ANSP 79154. Paralectotype (with 13 axial ribs on body whorl). Cibao Region, Dominican Republic. Exact locality and age unknown. Height 5.8 mm, width 2.7 mm. 1, from right side; 2, enlargement of apical area; 3, enlargement of apical view.

apical suture. Early teleoconch whorls sculptured by eight to thirteen practically orthocline axial ribs, late whorls by 12 to 28. On the body whorl the axial ribs may be slightly sigmoid. On the spire whorls the axial ribs have practically the same width from suture to suture. Interspaces of axial ribs concave. On the first teleoconch whorl these interspaces are sculptured by five or six spiral threads with interspaces of varying width. On later whorls these spiral threads become flat-topped and their interspaces narrower. On late whorls these flat-topped and wide spirals may be subdivided by a median, incised line. All spiral threads of the teleoconch cross the axial ribs. Suture not deep. Aperture narrow. Outer lip thickened. Sinus adjoining suture shallow to moderately deep. Inner surface of outer lip smooth, with a more or less well-developed ridge parallel to the sharp edge of the outer lip. This ridge extends from the sinus to the beginning of the anterior canal or only part of this distance. Columellar and parietal calluses moderately prominent. Anterior canal slightly twisted to the left, narrow, and short.

Lectotype.—(of polygona) ANSP 2916 (Text-fig. 43).

Dimensions of lectotype.—(of polygona) Height 10.9 mm, width 4.6 mm.

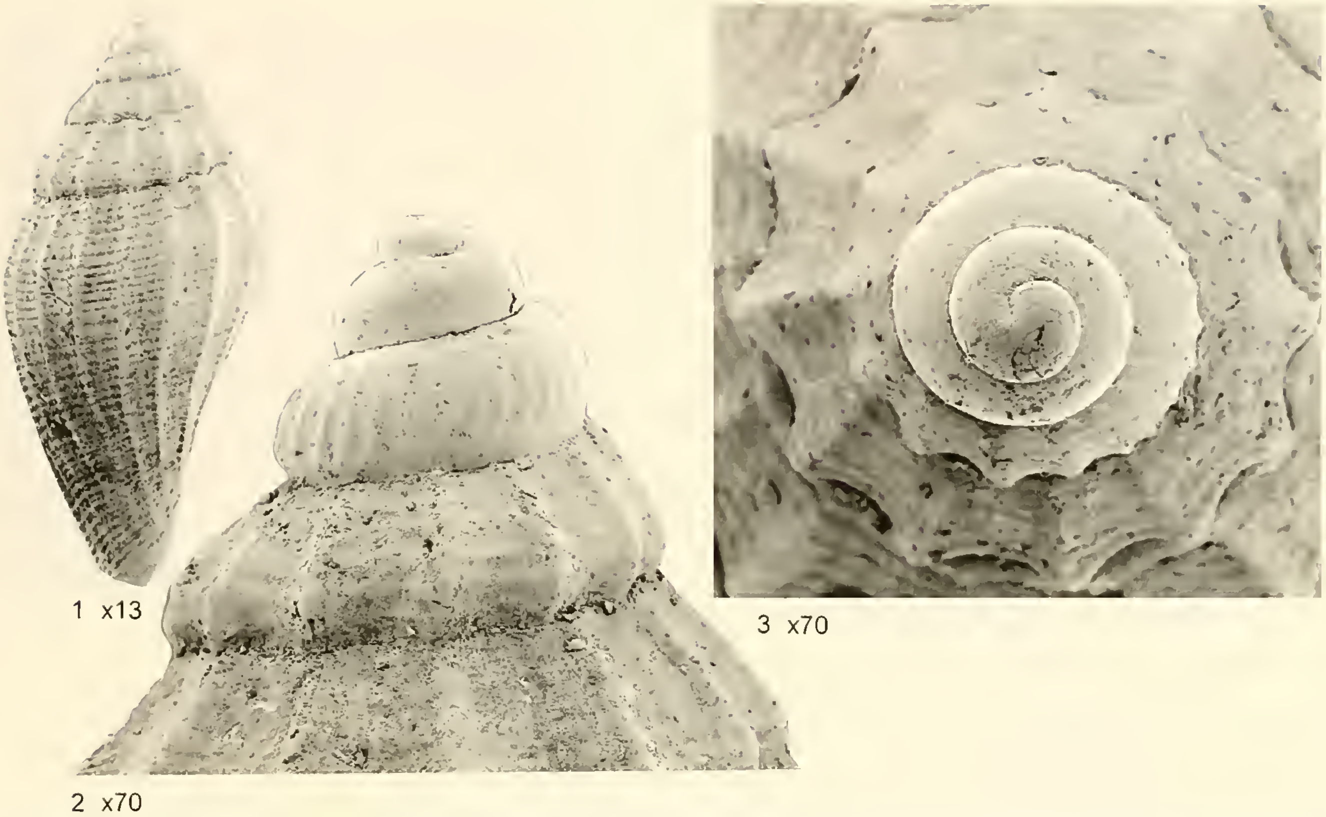
Type locality.—(of *polygona*) According to Pilsbry (1922, p. 307), the exact locality and age of the lectotype of *L. polygona* are not known. For this reason the type locality is here restricted to NMB locality 16923 (from where 83 specimens are available): Rio Mao, mouth of Arroyo Bajon, Dominican Republic. Cercado Formation (Late Miocene). For exact location and stratigraphic position, see Saunders *et al.* (1986, text-figs. 29–30, 32).

Holotype.—(of *caimitica*) PRI 28655 (Text-fig. 45).

Dimensions of holotype.—(of *caimitica*) Height 9.8 mm, width 4.9 mm.

Type locality.—(of *caimitica*) Rio Cana near Caimito, Dominican Republic. Cercado Formation (Late Miocene).

Remarks.—*L. polygona* is represented by a total of 1184 specimens from 40 different localities from the sections of Rio Mao, Rio Cana, and Rio Gurabo. The provenance of the material is not even: there are 526 specimens from 18 localities along Rio Mao, 23 spec-



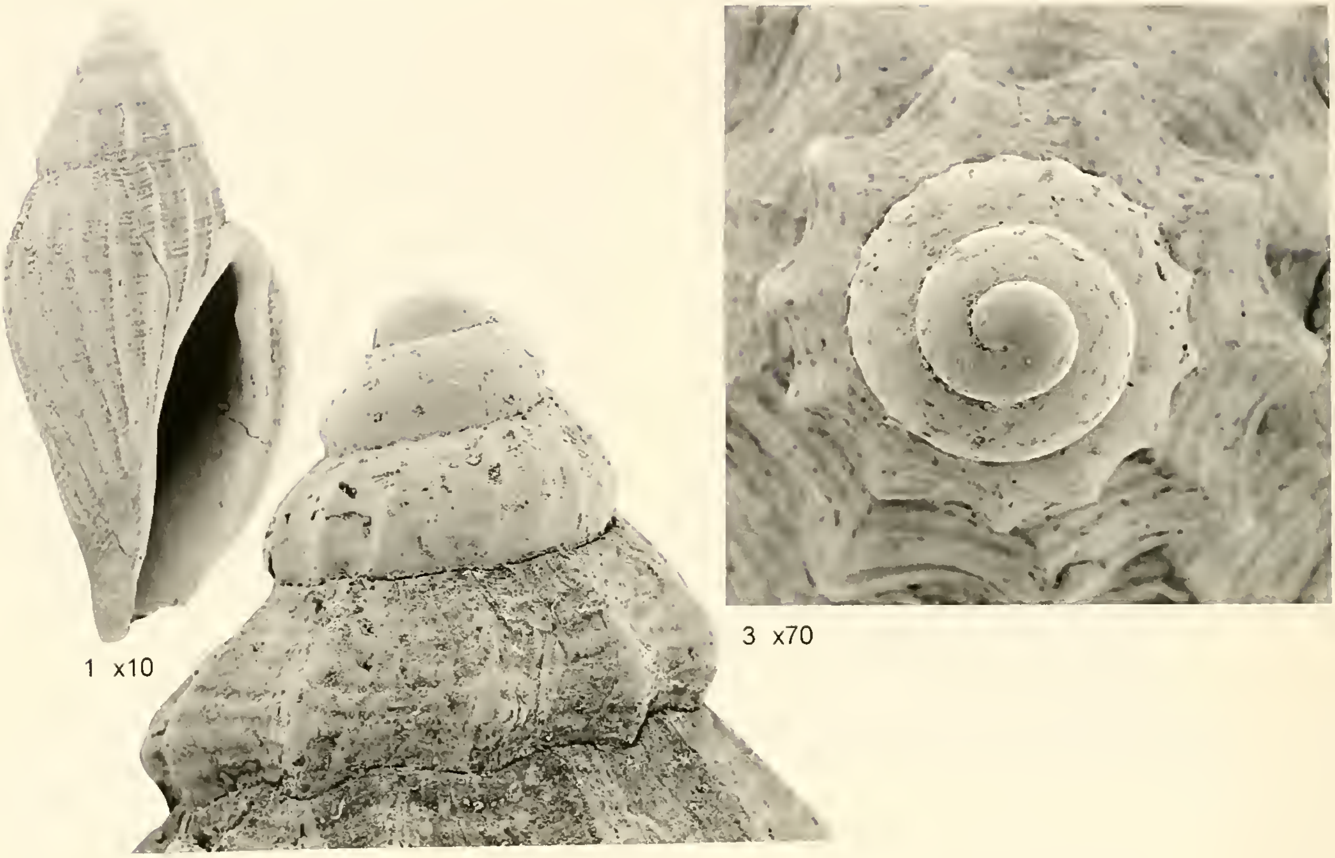
Text-figure 47.—*Lepicythara polygona* (Gabb). ANSP 79514. Paralectotype (with 17 axial ribs on body whorl). Cibao Region, Dominican Republic. Exact locality and age unknown. Height 7.0 mm, width 3.4 mm. 1, from left side; 2, enlargement of apical area; 3, enlargement of apical view.

imens from nine localities along Rio Cana, and 635 specimens from 13 localities along Rio Gurabo.

It is not surprising that this large amount of material shows some variability in several respects. As indicated in the description the number of axial ribs on teleoconch whorls varies greatly but differently from river to river. The number of axial ribs on early teleoconch whorls varies from ten to thirteen on Rio Mao, from eight to eleven on Rio Cana, and from ten to thirteen again on Rio Gurabo. The corresponding number on the body whorl varies from 14 to 23 on Rio Mao, from 12 to 18 on Rio Cana, and from 13 to 28 on Rio Gurabo.

The protoconch is said to vary from 2.25 to 2.75 volutions in the above description. As a matter of fact, it varies from 2.5 to 2.74 volutions in the material from Rio Mao, but from 2.25 to 2.5 in the material from Rio Cana and Rio Gurabo. In addition the initial volution in the material from Rio Mao is very slightly smaller than that in the material from Rio Cana and Rio Gurabo. Whether this has to be interpreted as a geographic variation remains undetermined for the time being. Stratigraphically, the material from Rio Mao occurs between Bluff 2 and 3 of Maury, which corresponds to about 45 m of section within the Cercado Formation. In Rio Cana, *L. polygona* occurs from 170 to 230 m in the section, *i.e.*, over a thickness of 60 m in the upper part of the Cercado Formation, and in the Rio Gurabo from 80 to 140 m in the section, *i.e.*, also over a thickness of 60 m in the upper part of the Cercado Formation. Thus, *L. polygona* lived at about the same time in all three river sections. There is one stratigraphic exception in the Rio Cana section: NMB locality 16817 has yielded a single specimen of *L. polygona*, which belongs to the Early Pliocene part of the Gurabo Formation (stratigraphic distribution according to Saunders *et al.*, 1986).

As listed under material, there are nine paralectotypes of *L. polygona* (ANSP 79154). Three of them are figured (see Text-fig. 46). Two of them have a protoconch with 2.5 volutions, the third with 2.75 volutions. The surface of the first two volutions is smooth. The remainder of the protoconch is sculptured by about twelve axial riblets. The first of these riblets are faint, but gradually become more conspicuous. At the same time, their shape is changing from opisthocyrt in the beginning to opisthocline toward the end of the protoconch. In the interspaces of the last few axial



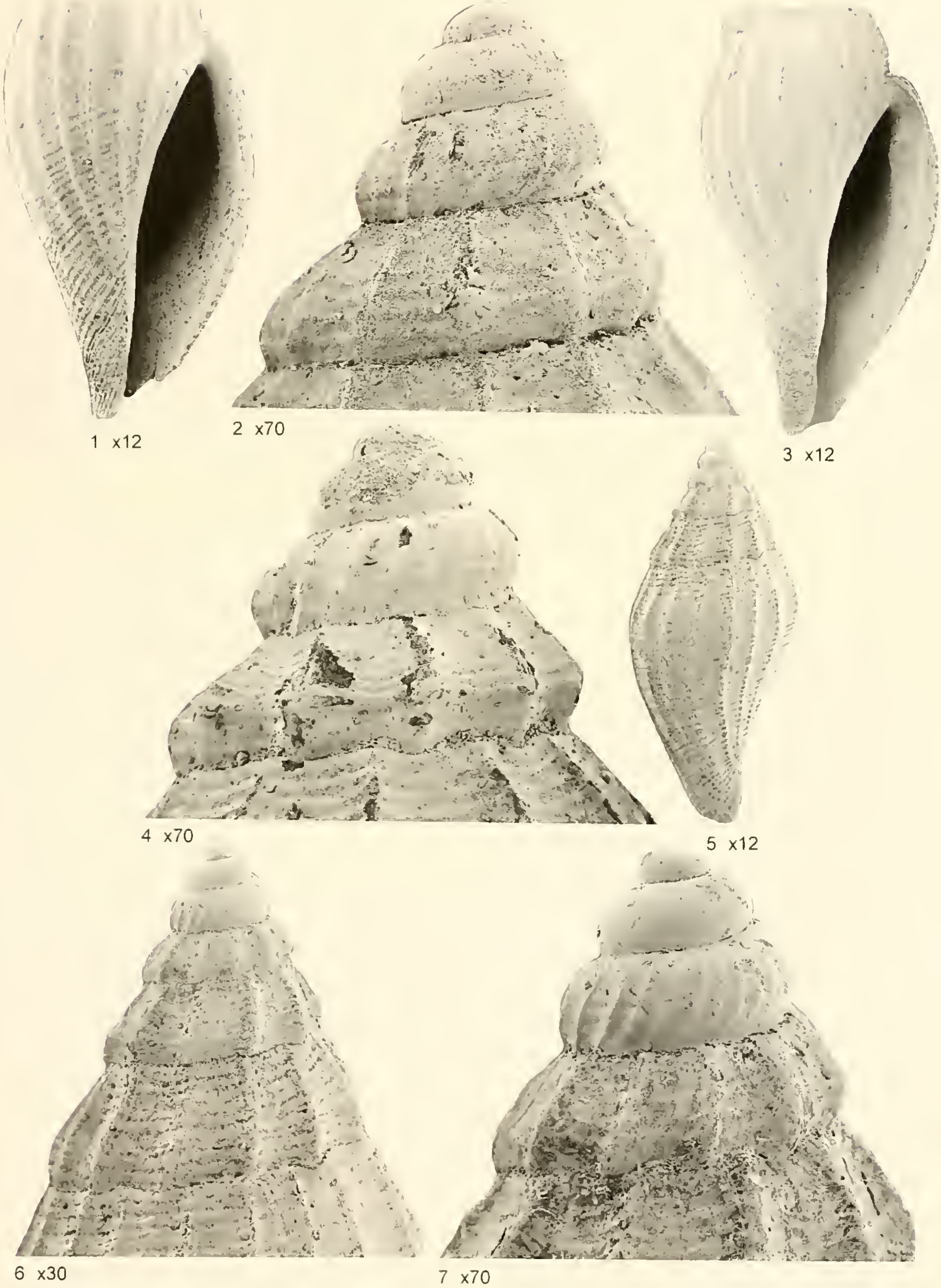
Text-figure 48.—*Lepicythara polygona* (Gabb). ANSP 79154. Paralectotype (with 19 axial ribs on body whorl) Cibao Region. Dominican Republic. Exact locality and age unknown. Height 9.7 mm, width 4.0 mm. 1, front view; 2, enlargement of apical area; 3, enlargement of apical view.

riblets, there are four equally spaced spiral threads, which however, do not cross the axial riblets. Furthermore, their initial volution is slightly smaller than that of protoconchs from the sections of Rio Cana and Rio Gurabo (see above). Comparison with a protoconch from NMB locality 16915 on Rio Mao (Text-fig. 50.4) shows that they are practically identical These features make it highly probable that the type lot of *L. polygona* had been collected from the Rio Mao section.

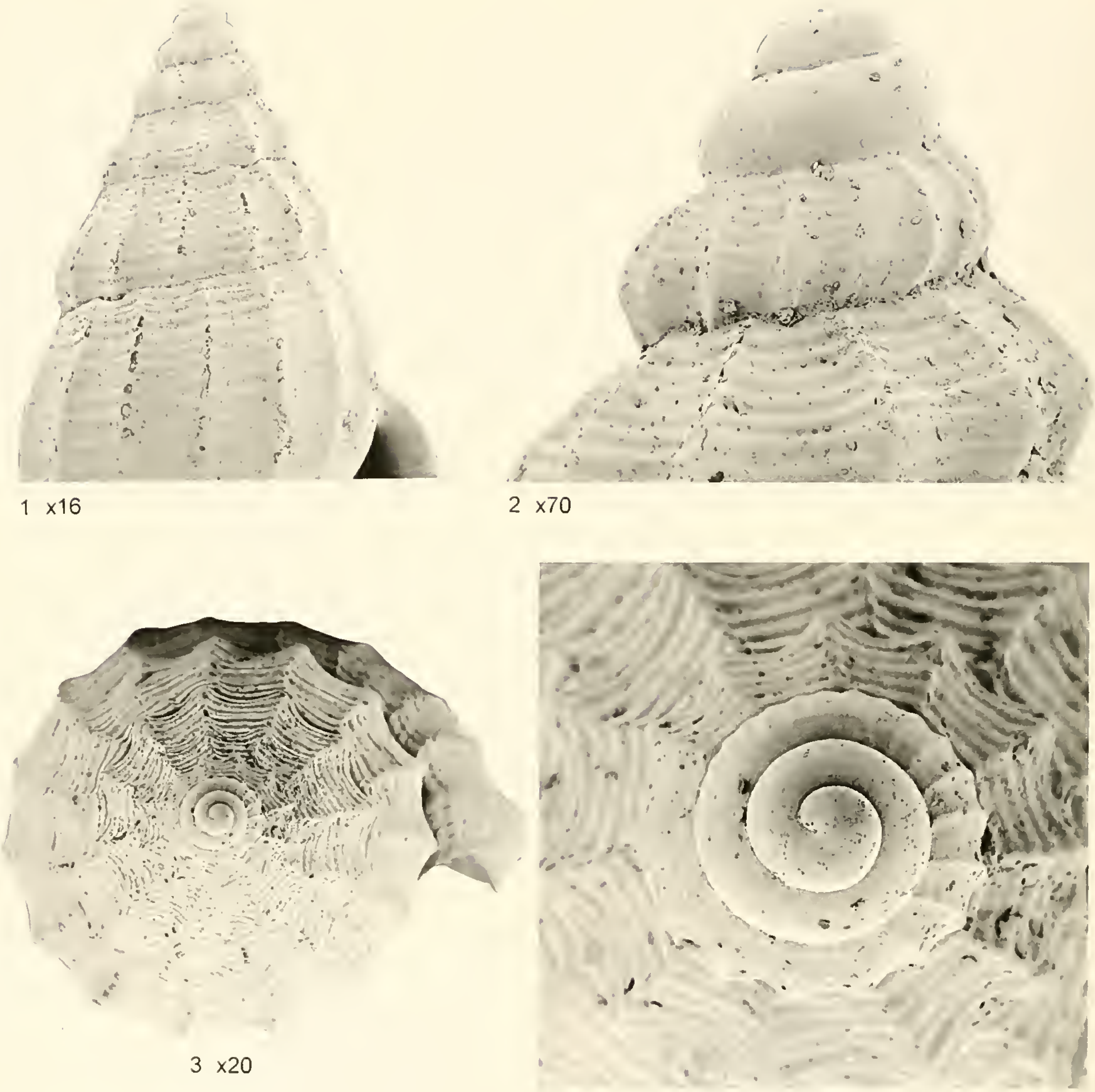
Comparisons.—*L. polygona* cannot meaningfully be compared with any of the species described herein. It has many more axial ribs on the teleoconch whorls than any other species.

Material.—The NMB localities cited are all from the Late Miocene Cercado Formation of the Dominican Republic except as noted (NMB locality 16817: Rio Cana, Early Pliocene part of Gurabo Formation, and NMB locality 15878: Rio Gurabo, Late Miocene part of Gurabo Formation). There are 40 lots with a total of 1184 specimens as listed below:

1 spec., ANSP 2916 (lectotype): Cibao Region. Exact locality and age unknown.
9 spec., ANSP 79154 (paralectotypes): Cibao Region. Exact locality and age unknown.
1 spec., PRI 28654 (figured by Maury 1917, pl. 9, fig. 13): Rio Mao, Bluff 3 of Maury.
1 spec., PRI 28655: holotype of *L. caimitica*; Rio Cana near Caimito.
18 spec., NMB locality 16912: Rio Mao, Bluff 3 of Maury.
79 spec., NMB 16913: Rio Mao, Bluff 3 of Maury.
1 spec., NMB 16914: Rio Mao, Bluff 2 of Maury.
37 spec., NMB 16915: Rio Mao, Arroyo Bajon.
7 spec., NMB 16917: Rio Mao, Arroyo Bajon.
32 spec., NMB 16917: Rio Mao, Arroyo Bajon.
42 spec., NMB 16918: Rio Mao, Arroyo Bajon.
11 spec., NMB 16922: Rio Mao, Arroyo Bajon.
83 spec., NMB 16923: Rio Mao, Arroyo Bajon.
42 spec., NMB 16924: Rio Mao, Arroyo Bajon.
74 spec., NMB 16926: Rio Mao, Arroyo Bajon.
63 spec., NMB 16927: Rio Mao, Arroyo Bajon.

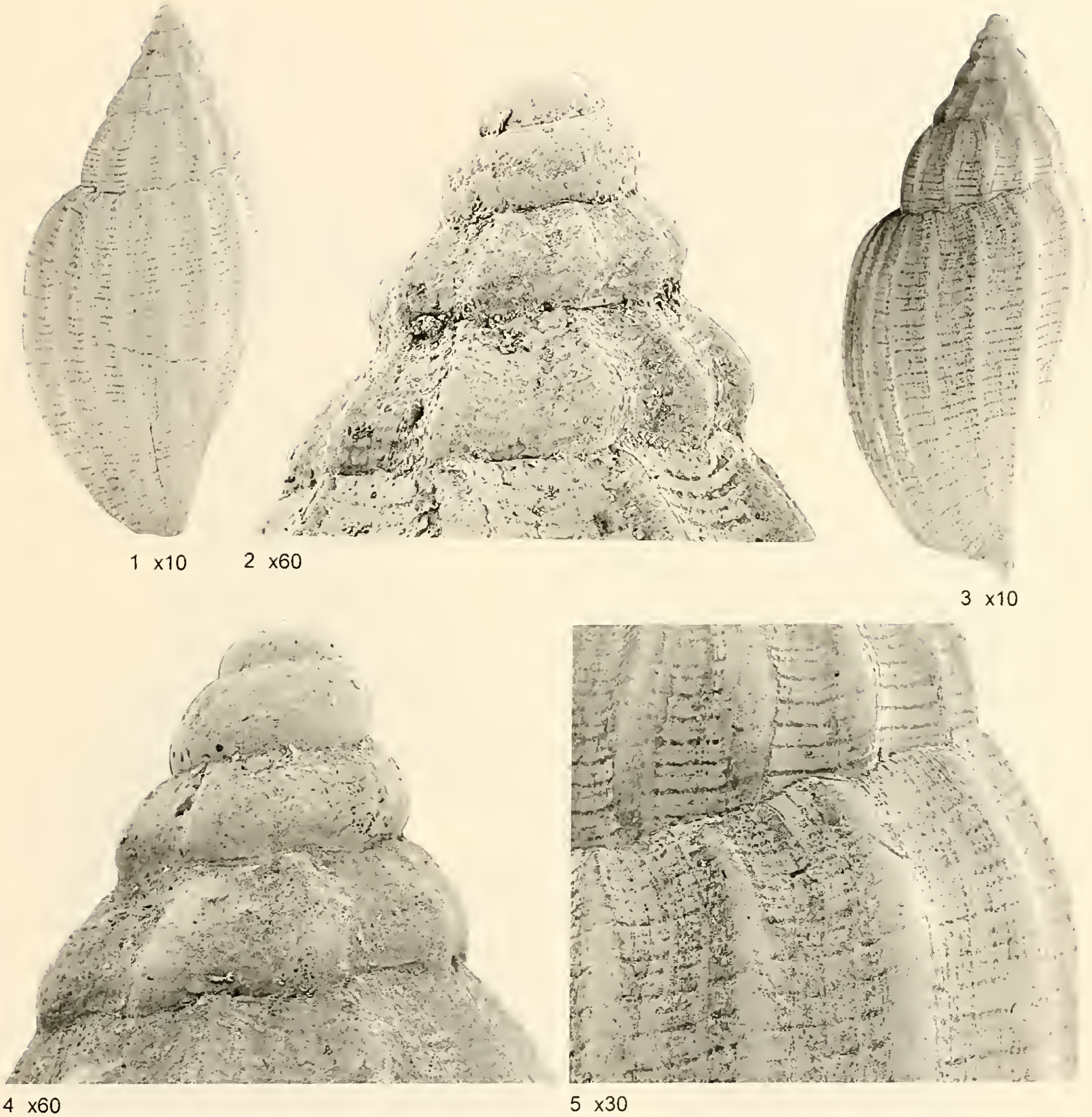


Text-figure 49.—*Lepicythara polygona* (Gabb). NMB locality 16913: Rio Mao, Bluff 3 of Maury, Dominican Republic, Cercado Formation. 1–2, NMB H 18127. Height 9.9 mm, width 3.6 mm. 1, front view of aperture; 2, enlargement of apical area. 3–4, NMB H 18128. Height 8.6 mm, width 3.6 mm. 3, front view of aperature; note inner surface of outer lip with a ridge parallel to the sharp edge of the outer lip; 4, enlargement of apical area. 5–7, NMB 18129. Height 6.5 mm, width 2.7 mm. 5, rear view; 6, enlargement of apical area; 7, further enlargement of apical area.



Text-figure 50.—*Lepicythara polygona* (Gabb). NMB H 18139. NMB locality 16915: Rio Mao, Arroyo Bajon, Dominican Republic. Cercado Formation. Height 10.6 mm, width 4.4 mm. 1, front view of spire whorls; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

20 spec., NMB 16928: Rio Mao, Arroyo Bajon.
4 spec., NMB 16929: Rio Mao, 130 m below Arroyo Bajon.
2 spec., NMB 17269: Rio Mao, Bluff 3 of Maury.
1 spec., NMB 16817: Rio Cana, Canada de Zamba. Gurabo Formation (Early Pliocene).
5 spec., NMB 16838: Rio Cana.
1 spec., NMB 16844: Rio Cana.
1 spec., NMB 16854: Rio Cana.
5 spec., NMB 16855: Rio Cana.
3 spec., NMB 16856: Rio Cana.
3 spec., NMB 16986: Rio Cana.
3 spec., NMB 17003: Rio Cana.
8 spec., NMB 15878: Rio Gurabo. Gurabo Formation (Late Miocene).
14 spec., NMB 15900: Rio Gurabo.
180 spec., NMB 15903: Rio Gurabo.
78 spec., NMB 15904: Rio Gurabo.

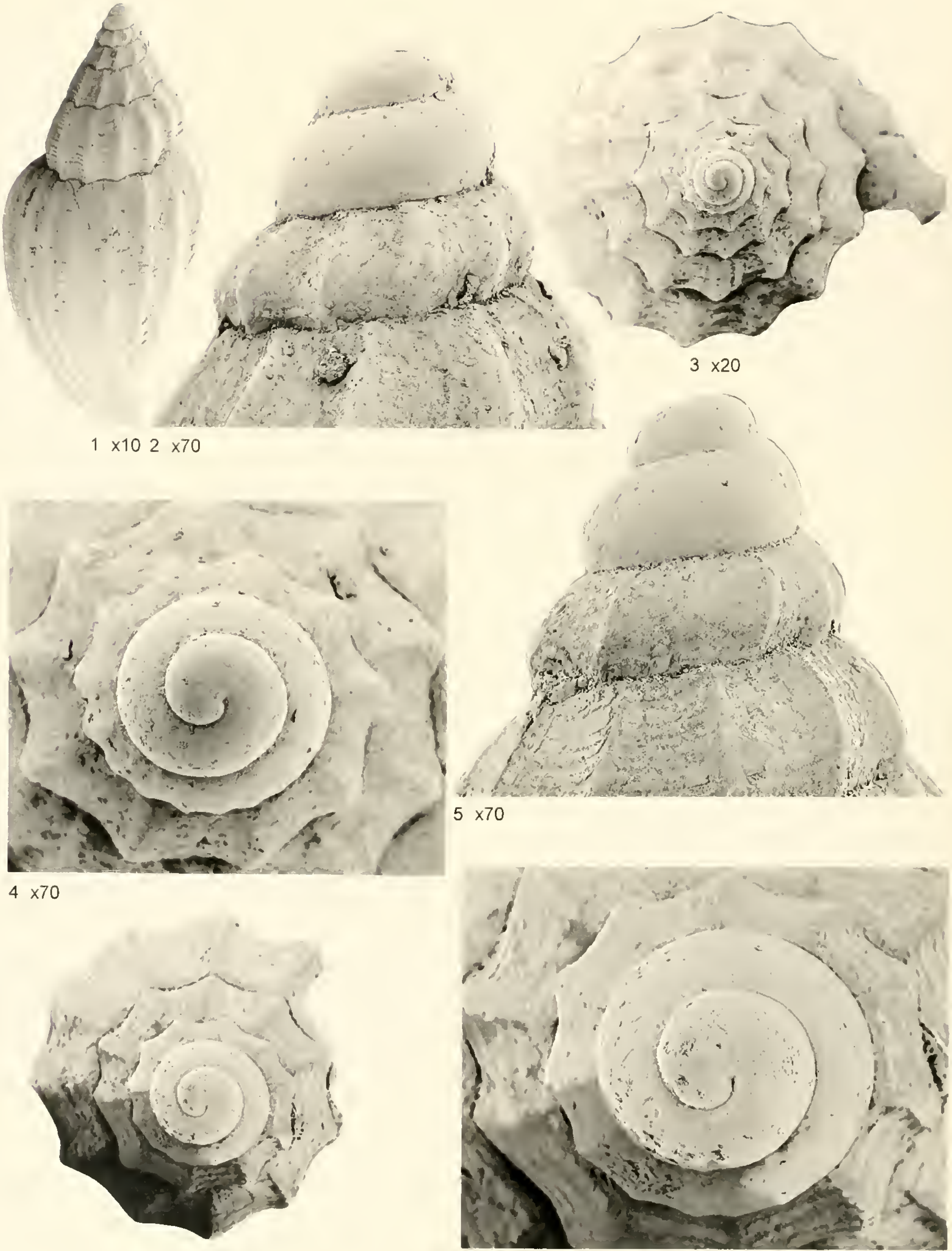


Text-figure 51.—*Lepicythara polygona* (Gabb). 1–2, NMB H 18130, NMB locality 16844, Rio Cana, Dominican Republic. Cercado Formation. Height 9.0 mm, width 4.3 mm. 1, rear view; 2, enlargement of apical area. 3–5, NMB H 18131, NMB locality 16844, Rio Cana, Dominican Republic. Cercado Formation. Height 9.0 mm, width 4.3 mm. 3, rear view; 4, enlargement of apica area; 5, enlargement to show spiral sculpture.

113 spec., NMB 15906: Rio Gurabo.
65 spec., NMB 15907: Rio Gurabo.
55 spec., NMB 15910: Rio Gurabo.
32 spec., NMB 15911: Rio Gurabo.
31 spec., NMB 15912: Rio Gurabo.
3 spec., NMB 15913: Rio Gurabo.
15 spec., NMB 15914: Rio Gurabo.
27 spec., NMB 15915: Rio Gurabo.
14 spec., NMB 15916: Rio Gurabo.

Measurements.—(See Table 12 and Text-figure 56.)

Occurrence.—This species is recorded from the fol-



1 x10 2 x70

3 x20

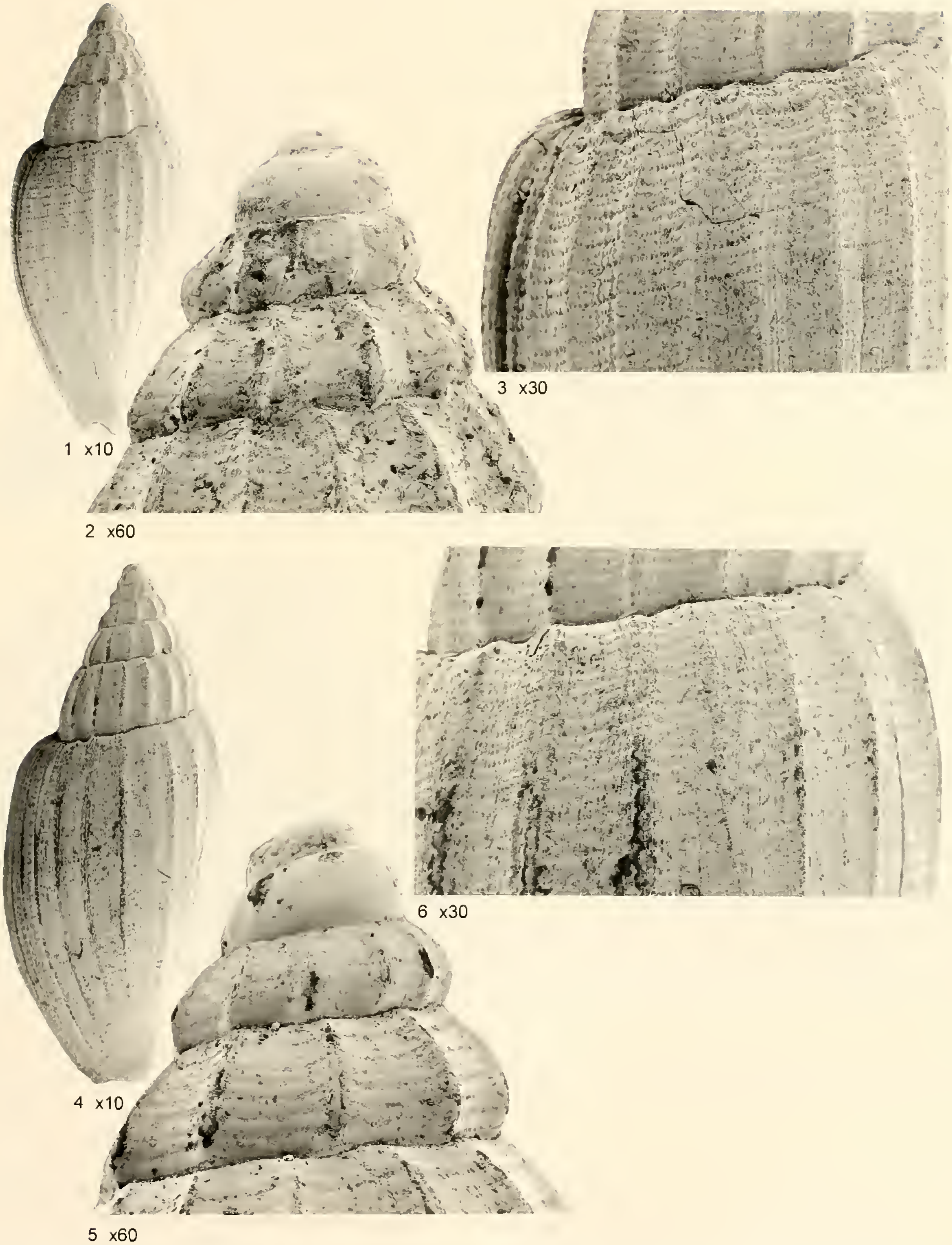
4 x70

5 x70

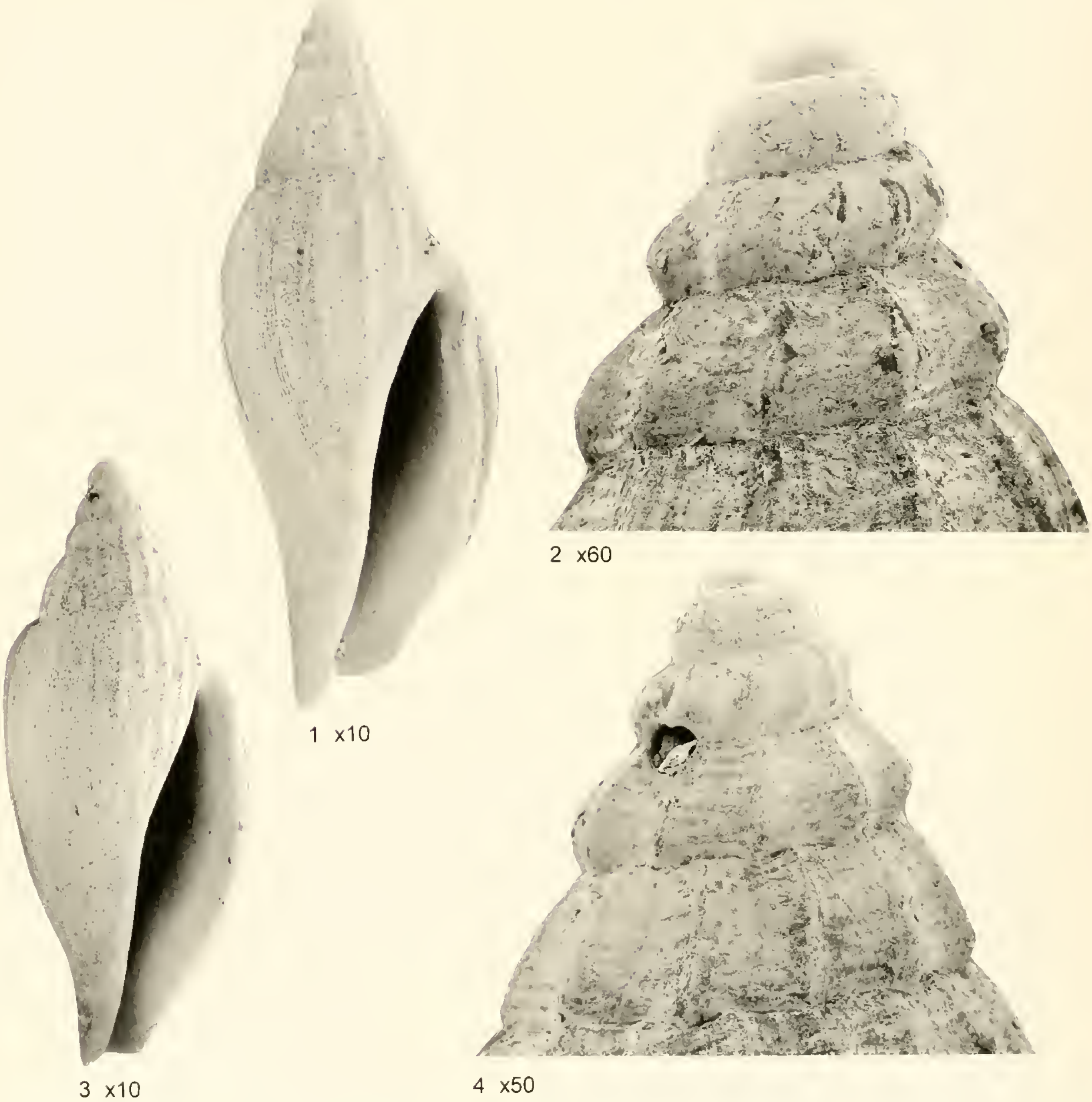
6 x40

7 x90

Text-figure 52.— *Lepicythara polygona* (Gabb). 1–4, NMB H 18137, NMB locality 16856: Rio Cana, Dominican Republic, Cercado Formation. Height 9.5 mm, width 4.0 mm. 1, rear view; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view. 5–7, NMB H 18138, NMB locality 17003: Rio Cana, Dominican Republic, Cercado Formation. Height 5.2 mm, width 2.6 mm. 5, enlargement of apiclarea; 6, apical view; 7, enlargement of apical view.



Text-figure 53.—*Lepicythara polygona* (Gabb). NMB locality 15906: Rio Gurabo, Dominican Republic, Cercado Formation. 1–3, NMB H 18132. Height 8.6 mm, width 3.33 mm. 1, rear view; 2, enalrgement of apical area; 3, enlargement to show spiral sculpture. 4–6, NMB H 18133. Height 10.2 mm, width 4.9 mm. 4, rear view; 5, enlargement of apical area; 6, enlargement to show spiral sculpture.



Text-figure 54.—*Lepicythara polygona* (Gabb). NMB locality 15906: Rio Gurabo, Dominican Republic, Cercado Formation. 1–2, NMB H 18134. Height 11.4 mm, width 4.4 mm. 1, front view; 2, enlargement of apical area. 3–4, NMB H 18135. Height 10.0 mm, width 4.1 mm. 3, front view; 4, enlargement of apical area.

lowing NMB localities and section in the Dominican Republic:

Rio Mao: 16912–16918, 16922–16924, 16926–16929, 17269: all Cercado Formation (Late Miocene).

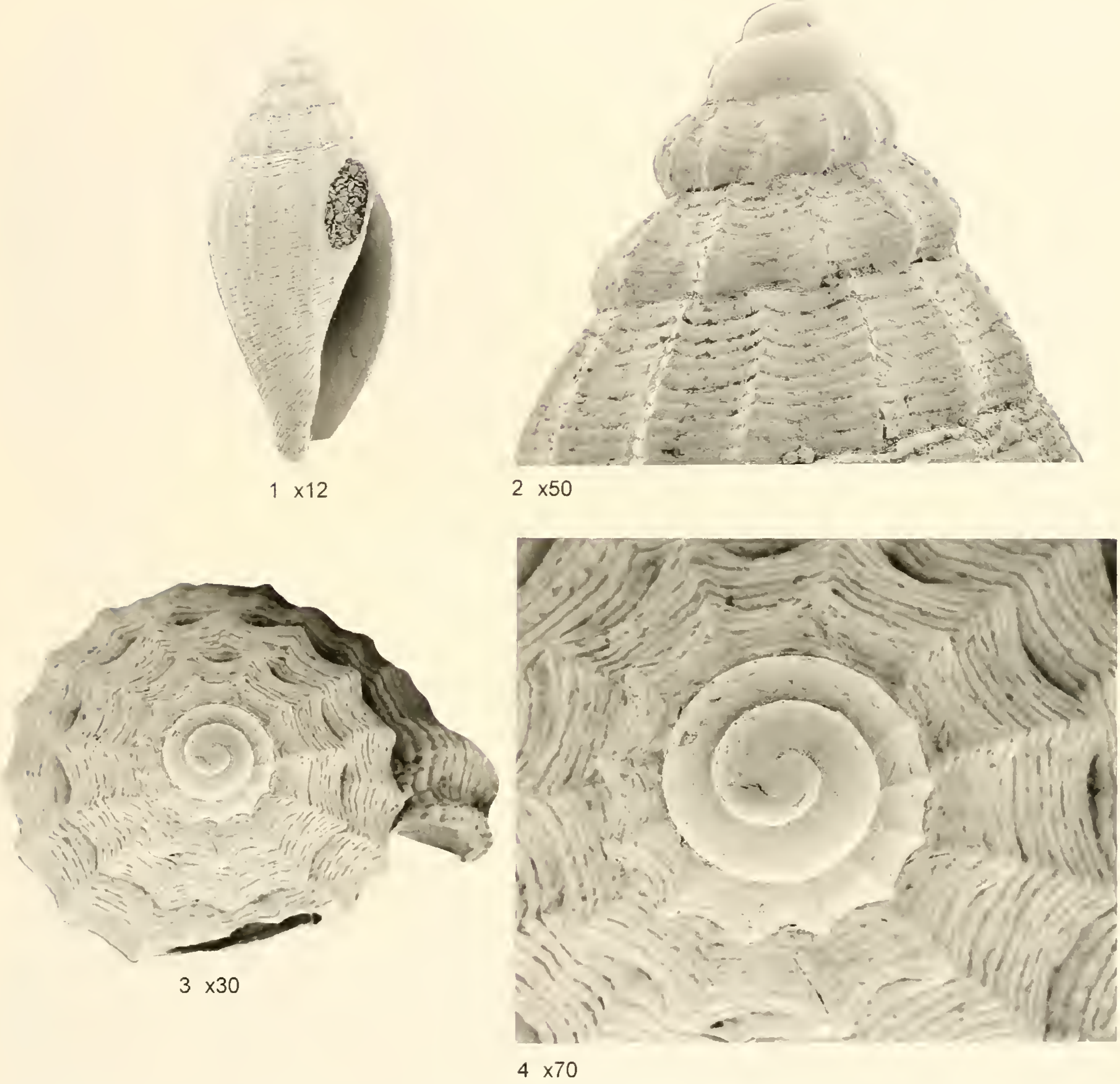
Rio Cana: 16838, 16844, 16854–16856, 16986, 17003: all Cercado Formation (Late Miocene); 16817: Gurabo Formation (Early Pliocene).

Rio Gurabo: 15900, 15903, 15904, 15906, 15907, 15910–15916: all Cercado Formation (Late Miocene); 15878: Gurabo Formation (Late Miocene).

Distribution.—So far this species is not known from outside the Dominican Republic.

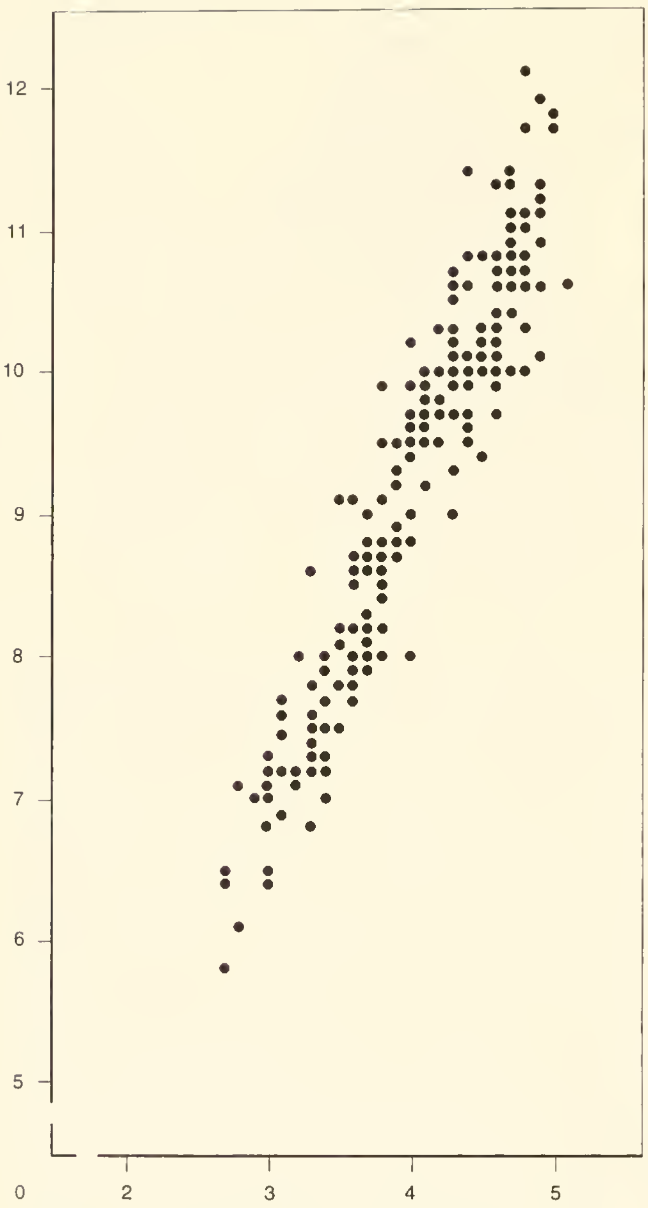
Lepicythara terminula (Dall, 1890)
Text-figures 57–64

Mangilia (Cythara) terminula Dall, 1890, p. 38, pl. 2, fig. 5.
Lepicythara terminula Dall. Olsson, 1964, p. 111.



Text-figure 55.—*Lepicythara polygona* (Gabb). NMB H 18136. NMB locality 15903: Rio Gurabo, Dominican Republic, Cercado Formation. Height 6.1 mm, width 2.8 mm. 1, oblique front view; 2, enlargement of apical area; 3, apical area; 4, enlargement of apical view.

Description.—Of medium to large size, biconic, moderately slender. Protoconch consists of 2.5 volutions. The surface of the first one and a half volutions is smooth, the remainder of the protoconch sculptured by up to 17 slightly opisthocline axial riblets. Apex not pointed. Number of teleoconch whorls up to 5.75, their profile straight on early spire whorls, slightly convex on later spire whorls. The first two teleoconch whorls are somewhat carinated near the abapical suture and thus overhanging it. Teleoconch whorls sculptured by orthocline to slightly opisthocline axial ribs. Their number per whorl is usually eight or nine, rarely seven, or up to ten. The axial ribs may or may not be alined on successive whorls. They are narrow adapically and wider abapically. Interspaces of axial ribs concave, sculptured by three to seven incised, spiral lines on spire whorls. On later spire whorls some secondary incised, spiral lines are introduced. All spiral lines cross the axial ribs. Suture not deep. Aperture narrow. Outer lip thickened. Sinus adjoining suture

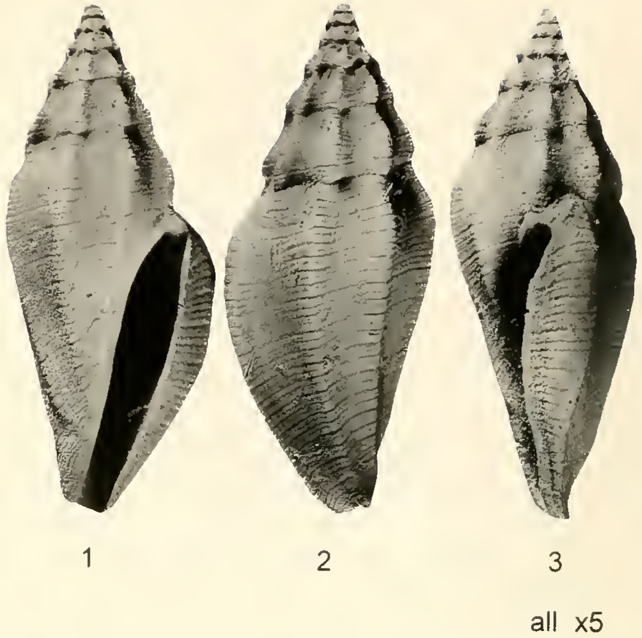


Text-figure 56.—(Restored) height/width diagram of *L. polygona.*

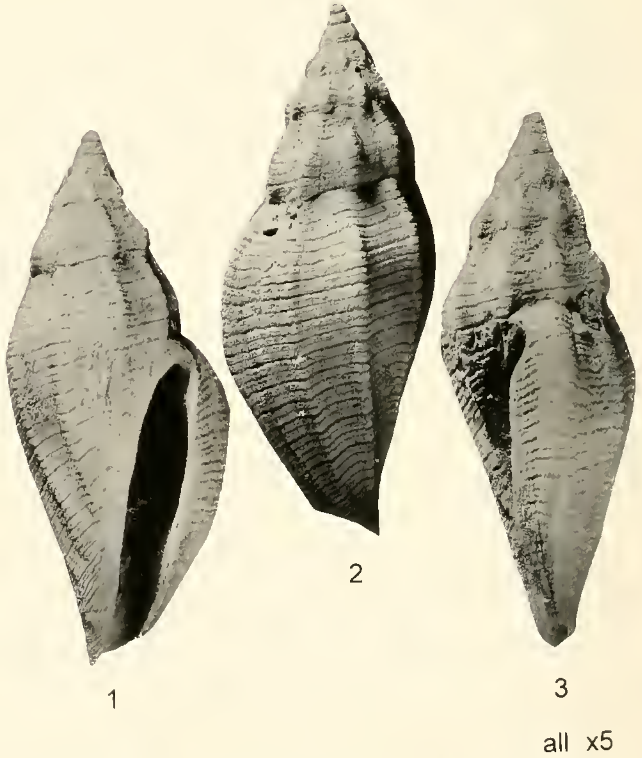
moderately deep. Inner surface of outer lip smooth, with a slight indication of a ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal Columellar and parietal

Table 12.—Measurements (in mm) of *Lepicythara polygona* (Gabb, 1873).

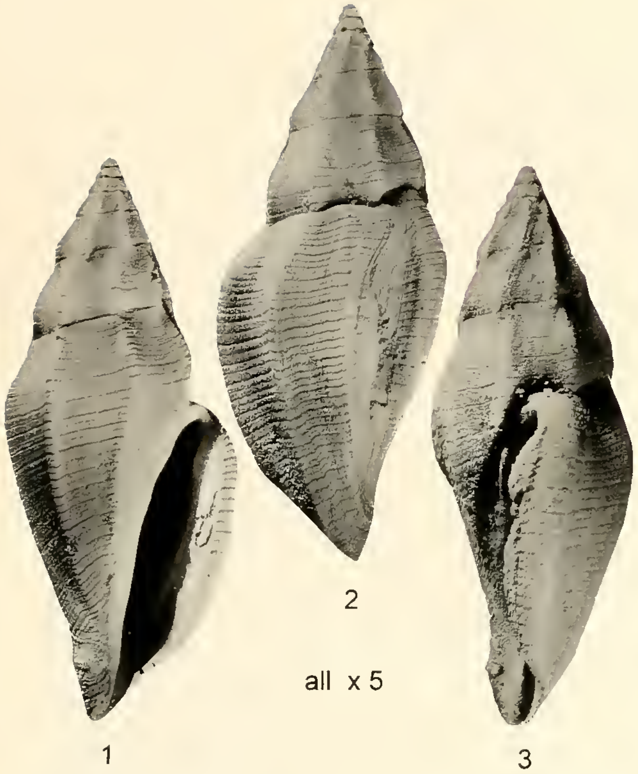
Specimen	Restored height	Width	Height/ width ratio
PRI 28654	10.7	4.6	2.32
ANSP 2916	11.3	4.6	2.46
ANSP 79154	9.1	3.6	2.53



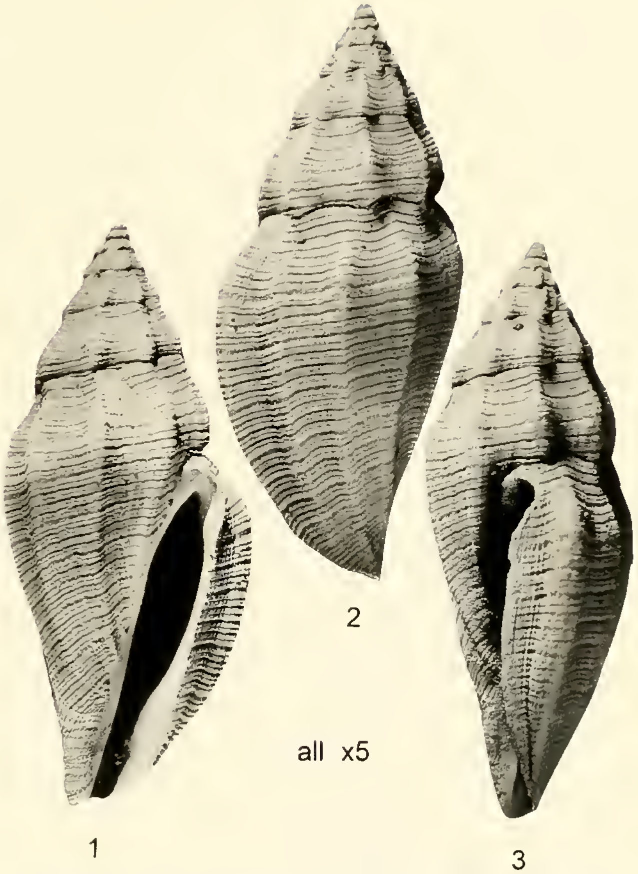
Text-figure 57.—*Lepicythara terminula* (Dall). USNM 97338. Lectotype. Caloosahatchee River, Florida. Caloosahatchee Formation. Height 14.4 mm, width 6.2 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 58.—*Lepicythara terminula* (Dall). USNM 647034. Paralectotype. Caloosahatchee River, Florida. Caloosahatchee Formation. Height 15.7 mm, width 6.6 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 59.—*Lepicythara terminula* (Dall). USNM 495823 (ex 163902). USGS Station 3300. Shell Creek, De Soto County, Florida. Caloosahatchee Formation. Height 16.4 mm, width 7.0 mm. 1, front view; 2, rear view; 3, from right side.



Text-figure 60.—*Lepicythara terminula* (Dall). NMB H 18117. NMB locality 18960: Shell Pit south of Arcadia, De Soto County, Florida. Caloosahatchee Formation. Height 16.6 mm, width 7.2 mm. 1, front view; 2, rear view; 3, from right side.

calluses thin. Anterior canal straight or slightly twisted to the left, narrow, and moderately long.

Lectotype.—(selected herein) USNM 97338 (Text-fig. 57).

Dimensions of lectotype.—Height 14.4 mm, width 6.2 mm.

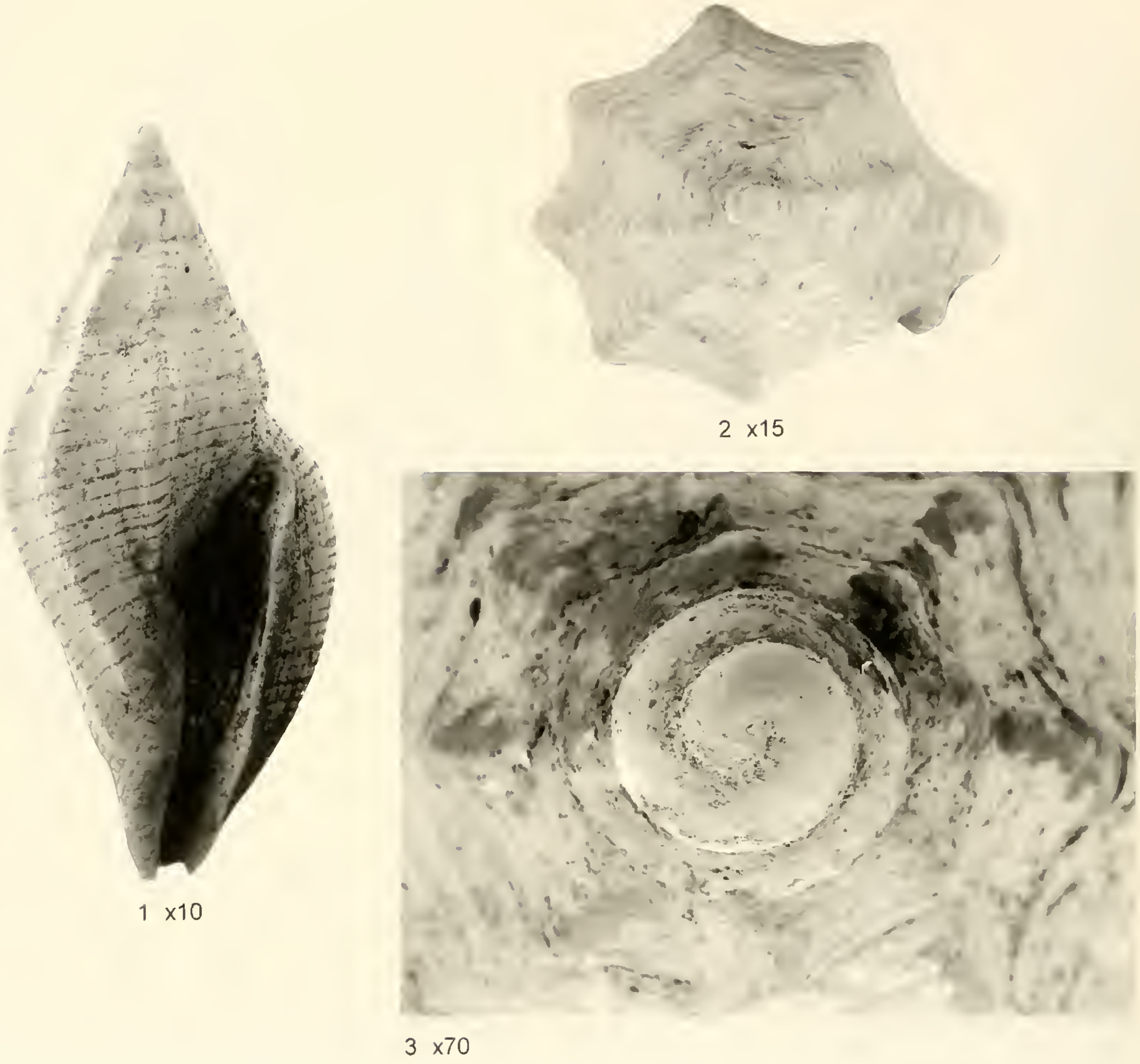
Type locality.—Caloosahatchee River, Florida. Caloosahatchee Formation (Plio-Pleistocene).

Remarks.—Dall (1890, p. 38) apparently had two specimens available when he described *L. terminula.* He commented that the species is rare. On the label accompanying specimen USNM 97338 it says "figured syntype", which is here selected as the lectotype. The label of specimen USNM 647034 says "measured syntype". This specimen is the paralectotype (Text-fig. 58). The present writer was first confused about the identity of these specimens until he found out that Dall had given the (approximate) measurements of the unfigured paralectotype in the original description but not those of the lectotype.

Whenever preserved, the protoconch of this species consists of 2.5 volutions and therefore represents a constant feature. The last volution of the protoconch is sculptured by slightly opisthocline axial riblets. The number of 17 such riblets given in the above description is rarely observable due to imperfect preservation. On the other hand, the number of axial ribs per teleoconch whorl is somewhat variable with the result that these axial ribs may be alined on successive whorls or not.

Comparisons.—*L. toroensis* from the Early Pliocene Shark Hole Point Formation of the Valiente Peninsula of Panama is also a large species. *L. toroensis* and *L. terminula* both have 2.5 protoconch volutions. *L. toroensis* has a larger apical angle, *i.e.,* it is less slender than *L. terminula.* In addition, *L. toroensis* has more axial ribs on the body whorl than on early whorls, whereas *L. terminula* belongs to the group of species having more or less the same number of axial ribs on early whorls and on the body whorl. Almost the same can be said of *L. costaricensis* except that it has 2.5 to 2.75 protoconch volutions.

Material.—29 lots with a total of 136 specimens as listed below:



Text-figure 61.—*Lepicythara terminula* (Dall). USNM 495820 (ex 163902). USGS Station 3300: Shell Creek, De Soto County Florida, Caloosahatchee Formation. Height 11.5 mm, width 5.3 mm. 1, front view; 2, apical view; 3, enlargement of apical view.

1 spec., USNM 97338: lectotype. Caloosahatchee River, Florida. Caloosahatchee Formation (Plio-Pleistocene).

1 spec., USNM 647034: paralectotype. Caloosahatchee River, Florida. Caloosahatchee Formation (Plio-Pleistocene).

35 spec., USNM 163902, USGS Station 3300: Shell Creek, DeSoto County, Florida. Caloosahatchee Formation (Plio-Pleistocene).

3 spec., USNM 113175: Shell Creek, De Soto County, Florida. Caloosahatchee Formation (Plio-Pleistocene).

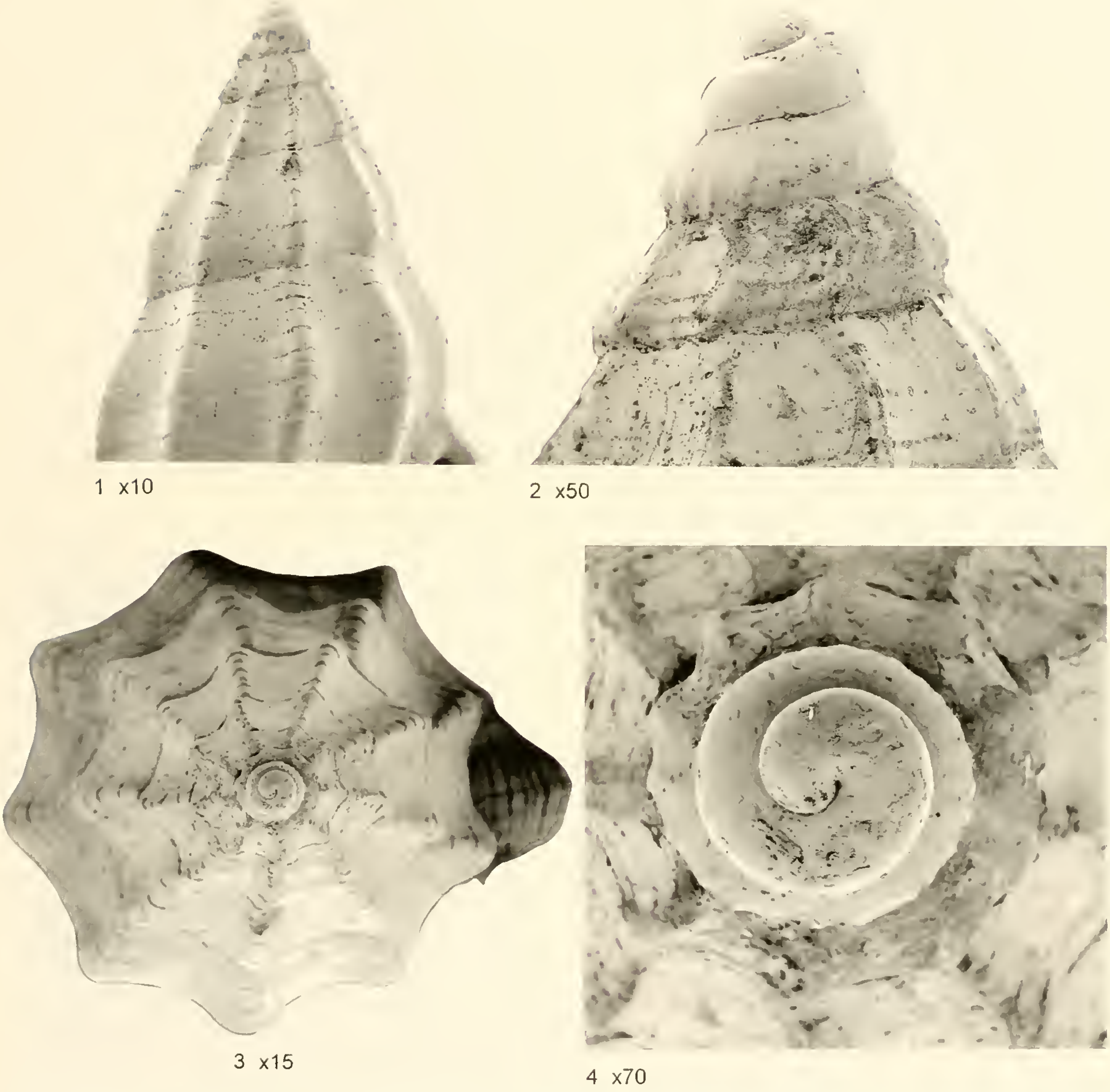
1 spec., NMB locality 11187: Spoil banks, north side of Caloosahatchee River, 5.5 miles west of Ortona Lock, Glades County, Florida. Caloosahatchee Formation and unnamed Caloosahatchee mixed (Plio-Pleistocene).

5 spec., NMB locality 18959: Quality Aggregates Pit, Sarasota County, Florida (27″21′N, 82″26′W). Pinecrest beds (Pliocene).

4 spec., NMB locality 18960: Shell Pit south of Arcadia, DeSoto County, Florida (27″03′00″N, 81″49′30″W). Caloosahatchee Formation (Plio-Pleistocene).

19 spec., UF 47779: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

13 spec., UF 61417: Fort Basinger 02 (OB002), Okeechobee County, Florida. Pinecrest beds (Pliocene).



Text-figure 62.—*Lepicythara terminula* (Dall). USNM 495821 (ex 163902) USGS Station 3300: Shell Creek, De Soto County, Florida, Caloosahatchee Formation. Height 16.5 mm, width 7.3 mm. 1, front view of spire whorls; 2, enlargement of apical area; 3, apical area; 4, enlargement of apical view.

2 spec., UF 49149: Kissimmee River 01 (HG001), Highlands County, Florida. Pinecrest beds/Caloosahatchee Formation (Plio-Pleistocene).

2 spec., UF 42662: Mule Pen (CR004), Collier County, Florida. Pinecrest beds (Pliocene).

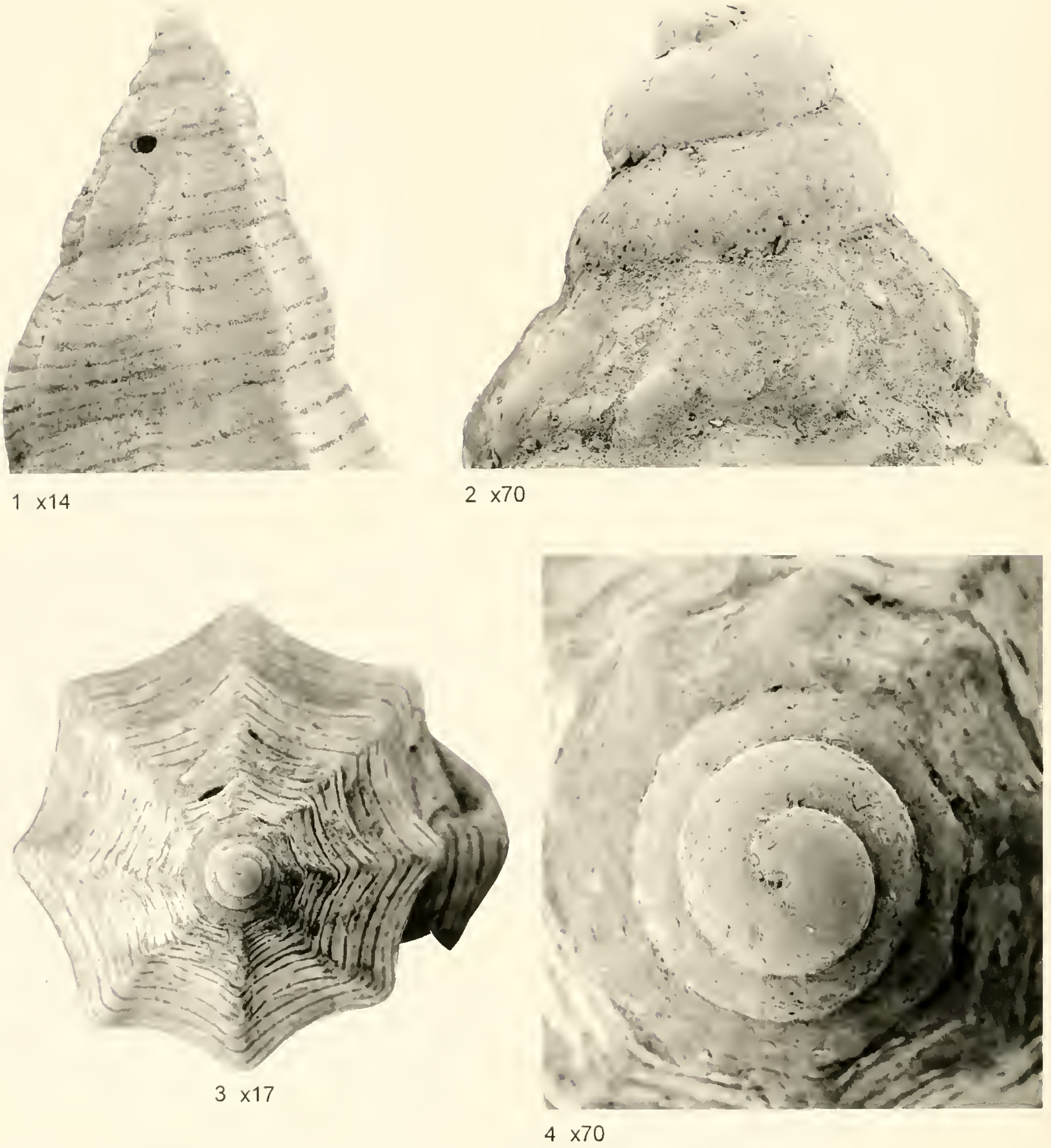
2 spec., UF 61635: Fort Basinger 01 (OB001), Okeechobee County, Florida. Pinecrest beds (Pliocene).

2 spec., UF 11084: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

2 spec., UF 47371: Caloosahatchee Canal 06 (GL025), Glades County, Florida. Pleistocene.

6 spec., UF 59983: Fort Basinger 02 (OB002), Okeechobee County, Florida. Pinecrest beds (Pliocene).

1 spec., UF 62383: Fort Basinger 04 (OB008),



Text-figure 63.—*Lepicythara terminula* (Dall). USNM 495822 (ex 163902). USGS Station 3300: Shell Creek, De Soto County, Florida. Caloosahatchee Formation. Height 14.1 mm, width 5.6 mm. 1, view of spire whorls from left side; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view.

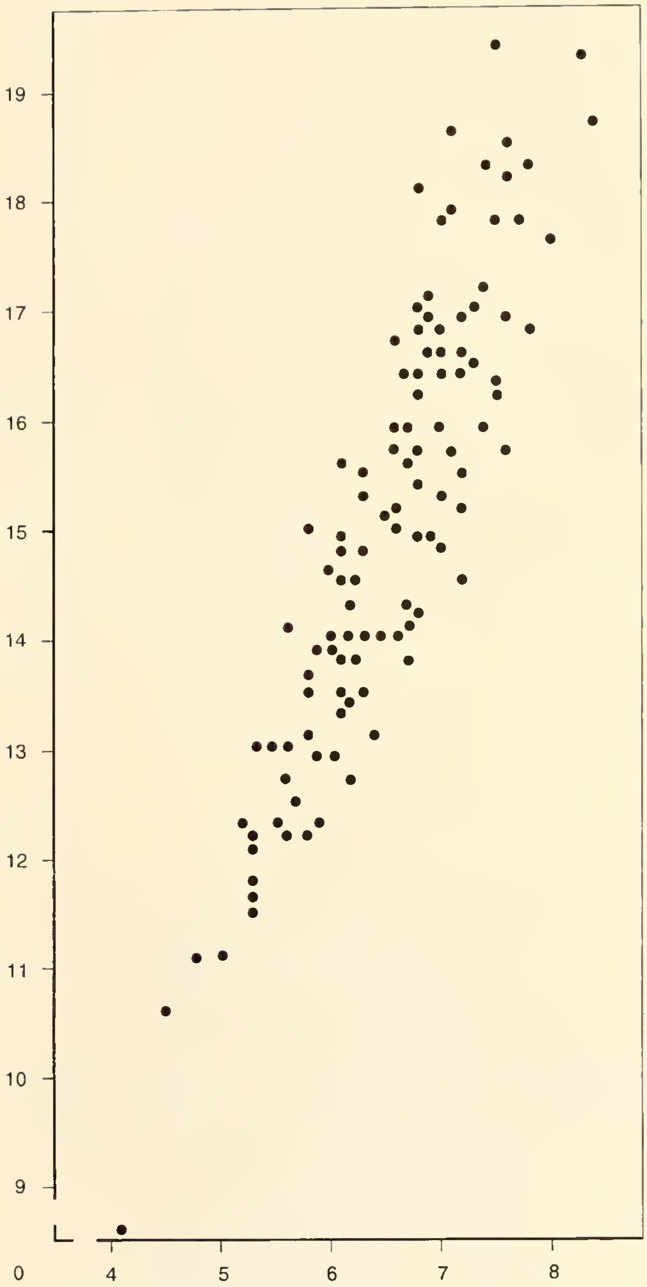
Okeechobee County, Florida. Pinecrest beds (Pliocene).

1 spec., UF 61394: Fort Basinger 02 (OB002), Okeechobee County, Florida. Pinecrest beds (Pliocene).

2 spec., UF 2835: Caloosahatchee River 01 (HN002), Hendry County, Florida. Pinecrest beds (Pliocene).

2 spec., UF 61036: Fort Basinger 01 (OB001), Okeechobee County, Florida. Caloosahatchee Formation (Plio-Pleistocene).

3 spec., UF 46672: Clewiston (HN017), Hendry



Text-figure 64.—(Restored) height/width diagram of *L. terminula.*

County, Florida. Caloosahatchee Formation (Plio-Pleistocene).

4 spec., UF 57865: Caloosahatchee Canal 04 (GL009), Glades County, Florida. Caloosahatchee/Bermont formations (Plio-Pleistocene).

2 spec., UF 31933: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

1 spec., UF 13441: Bird Road (DA001), Dade County, Florida. Pinecrest beds (Pliocene).

6 spec., UF 29119: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

Text-figure 65.—*Lepicythara toroensis* n. sp. NMB H 18143. Holotype. NMB locality 18724; north side of Valiente Peninsula, Province of Bocas del Toro, Panama. Bruno Bluff. Shark Hole Point Formation. Height 19.3 mm, width 9.0 mm. 1, front view; 2, rear view; 3, from right side.

2 spec., UF 50624: Fort Basinger 01 (OB001), Okeechobee County, Florida. Pinecrest beds (Pliocene).

8 spec., UF 47824: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

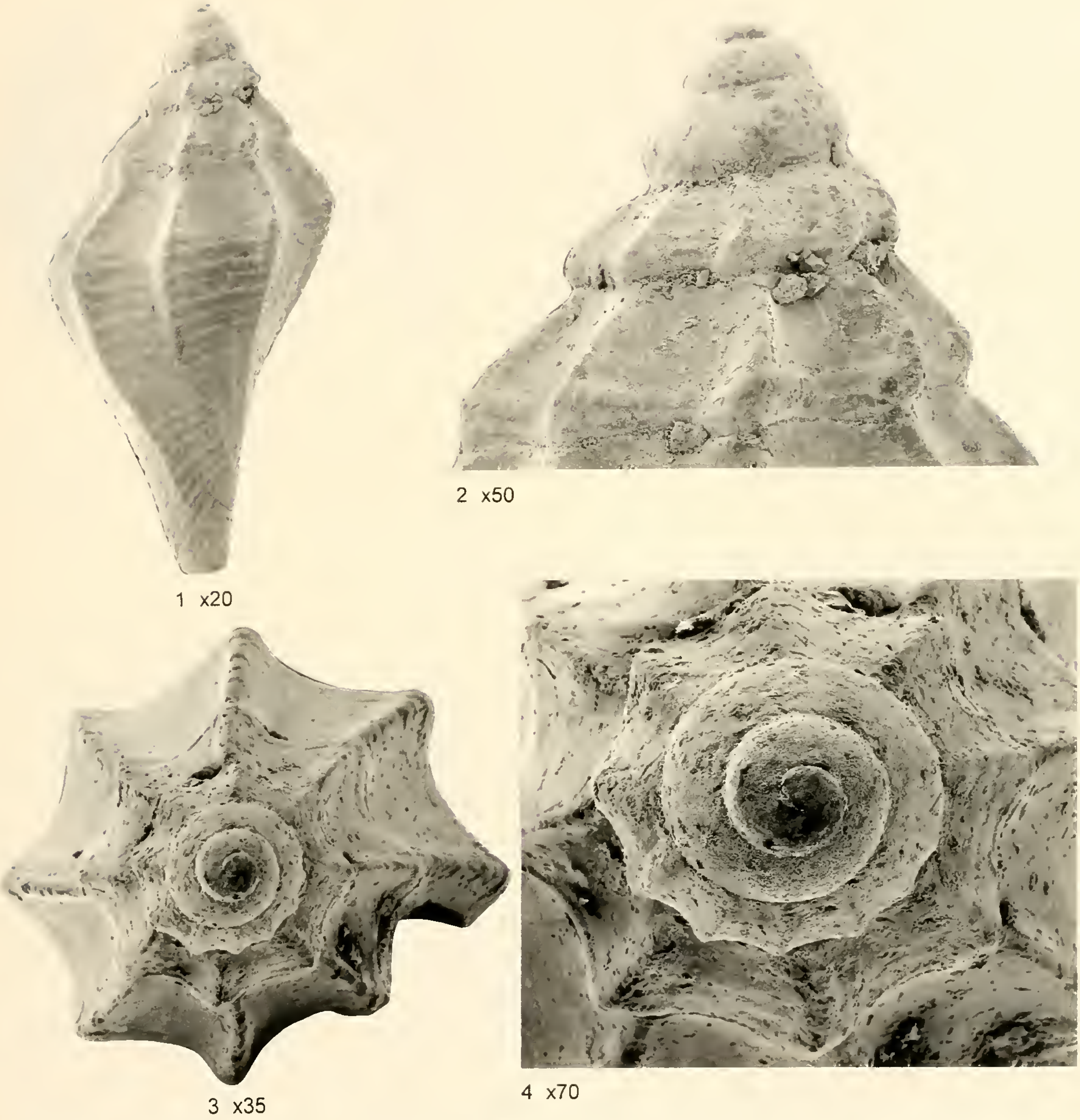
2 spec., UF 42992: Mule Pen (CR004), Collier County, Florida. Pinecrest beds (Pliocene).

1 spec., UF 60107: Cochran Shell Pit (HN004), Hendry County, Florida. Caloosahatchee Formation (Plio-Pleistocene).

4 spec., UF 22190: Macasphalt Shell Pit (SO001), Sarasota County, Florida. Plio-Pleistocene.

Table 13.—Measurements (in mm) of *Lepicythara terminula* (Dall, 1890).

Specimen	Restored height	Width	Height/ width ratio
USNM 97338	14.5	6.2	2.34
USNM 647034	15.9	6.6	2.41
USNM 163902	13.6	5.8	2.34
	11.5	5.3	2.17
	16.5	7.3	2.26
	15.6	6.7	2.33
	17.1	6.9	2.48
	14.1	5.6	2.52
	16.4	7.0	2.34
	14.8	6.3	2.35
	15.2	6.6	2.30
	13.1	5.8	2.26
	15.0	6.6	2.27
	12.2	5.6	2.18
	16.2	6.8	2.38
	18.6	7.1	2.62
	16.8	6.8	2.47
	16.9	7.6	2.22
	13.9	6.0	2.32
	17.9	7.1	2.52
	13.5	6.1	2.21
	14.9	6.1	2.44
	14.6	6.0	2.43
	12.9	5.9	2.19
	15.3	6.3	2.43
	13.0	5.5	2.36
	13.0	5.6	2.32
	14.0	6.2	2.26
	15.7	6.6	2.38
	16.9	6.9	2.45
	16.9	7.2	2.35
	10.6	4.5	2.36
	8.6	4.1	2.10
	12.2	5.3	2.30
	11.1	5.0	2.22
	15.7	7.1	2.21
	16.6	7.2	2.31
	15.9	6.7	2.37
	18.3	7.4	2.47
	17.2	7.4	2.32
	18.5	7.6	2.43
	15.0	5.8	2.59
	14.8	6.1	2.43
	15.2	6.6	2.30
	15.9	7.0	2.27
	16.4	7.2	2.28
	16.4	6.8	2.41
	15.6	6.1	2.56
	15.7	6.8	2.31
	14.3	6.2	2.31
	15.5	6.3	2.46
	13.8	6.2	2.23
	18.1	6.8	2.66
	15.4	6.8	2.26
	16.8	7.0	2.40
	14.0	6.3	2.22
	17.8	7.7	2.31
	13.4	6.2	2.16
	16.2	7.5	2.16
	14.1	6.7	2.10
	12.7	6.2	2.05
	12.3	5.2	2.37
	11.8	5.3	2.23
	17.8	7.0	2.54
	12.7	5.6	2.27
	14.3	6.7	2.13
	14.0	6.4	2.19
	13.0	5.4	2.41
	13.3	6.2	2.15
	17.0	7.3	2.33
	17.8	7.5	2.37
	18.7	8.4	2.23
	15.8	6.9	2.29
	19.3	8.3	2.33
	15.3	7.0	2.19
	13.1	6.4	2.05
	14.0	6.6	2.12
	14.2	6.8	2.09
	14.5	7.2	2.01
	14.9	6.9	2.16
	16.8	7.8	2.15
	14.8	7.0	2.11
	13.8	6.7	2.06
	15.1	6.5	2.32
	16.6	6.9	2.40
	15.2	7.2	2.11
	16.3	7.5	2.17
	13.8	6.1	2.26
	17.0	6.8	2.50
	16.7	6.6	2.53
	16.6	7.0	2.37
	15.9	7.4	2.15
	19.4	7.5	2.59
	15.5	7.2	2.15
	12.5	5.7	2.19
	12.9	6.0	2.15
	13.5	5.8	2.33
	12.3	5.5	2.24
	12.2	5.8	2.10
	12.1	5.3	2.28
	13.5	6.3	2.14
	15.8	7.0	2.26
	14.0	6.0	2.33
	15.7	7.6	2.07
	13.9	5.9	2.36
	16.4	6.7	2.45
	14.9	6.8	2.19
	18.3	7.8	2.35
	14.5	6.1	2.38
	17.6	8.0	2.20
	11.6	5.3	2.19
	12.3	5.9	2.08
	18.2	7.6	2.39



Text-figure 66.—*Lepicythara toroensis* n. sp. NMB H 18144. Paratype. NMB locality 18724: north side of Valiente Peninsula, Province of Bocas del Toro, Panama, Bruno Bluff, Shark Hole Point Formation. Height 5.0 mm, width 2.3 mm. 1, oblique rear view; 2, enlargement of apcal area; 3, apical view; 4, enlargement of apical view.

Measurements.—(See Table 13, Text-fig. 64.)

Occurrence.—This species is recorded from formations of Pliocene and Pleistocene age of southern Florida (for details see under "Material").

Distribution.—So far this species is not known from outside southern Florida.

Lepicythara toroensis, new species
Text-figures 65–66

Description.—Of large size, strongly biconic and stout. Protoconch consists of 2.5 volutions. The surface of the first two and a little more volutions is smooth, the remainder of he protoconch sculptured by four opisthocline to opisthocyrt axial riblets. Apex slightly pointed. Number of teleoconch whorls up to 5.75; their profile is straight on early whorls with an angulation near the abapical suture, but slightly convex on later whorls. Early teleoconch whorls sculptured by eight to nine orthocline to slightly opisthocline axial ribs. The number of axial ribs per whorl gradually increases reaching twelve to thirteen on the body whorl The axial ribs of the first two teleoconch whorls are somewhat pointed at the periphery thus projecting a little over the abapical suture. Interspaces of axial ribs concave, sculptured by four to five incised, spiral lines on the first teleoconch whorl and increasing in number to eleven on the penultimate whorl There are a few secondary incised, spiral lines. All spiral lines cross the axial ribs. Suture shallow. Aperture narrow. Outer lip thickened. Sinus adjoining suture moderately deep. Inner surface of outer lip smooth, with a prominent ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Parietal callus somewhat thickened near sinus, columellar callus moderately prominent. Anterior canal straight and short.

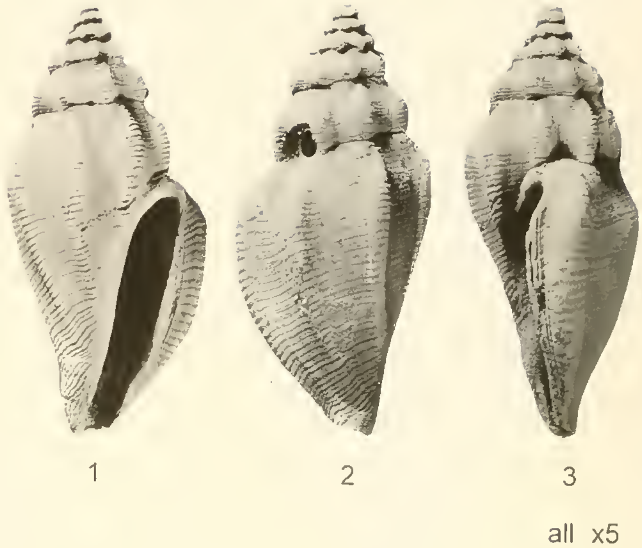
Holotype.—NMB H 18143 (Text-fig. 65).

Dimensions of holotype.—Height 19.3 mm, width 9.0 mm.

Type locality.—NMB locality 18724 (=PPP 2227 north side of Valiente Peninsula, Province of Bocas del Toro, Panama. Bruno Bluff. Shark Hole Point Formation (Early Pliocene). See Coates, 1999b, map 5, p. 290; 1999c, section 12, p. 312.

Remarks.—This species is based on seven specimens only. Three of them are adult, but only one—the holotype—has a moderately well-preserved protoconch. The other four specimens are juveniles. The type lot of *L. toroensis* from NMB locality 18724 was collected in 1995. The lot from NMB locality 17851 (=PPP 379) consisting of three paratypes was collected in 1988. Both localities are exactly the same (Coates, 1999b, map 5, p. 290; 1999c, section 12, p. 312). The fossils from both were collected from a 20 cm thick shell bed with leached mollusks situated about 8 m above sea level and hence were taken from fallen blocks. The third lot consisting of a single paratype from NMB locality 17850 (=PPP 376) was collected about 8 m below the other two localities, *i.e.*, at about sea level (Coates, 1999b, map 5, p. 290; 1999c, section 12, p. 312).

Comparisons.—*L. toroensis* is the largest species described herein and belongs to the group of species having more axial ribs on the body whorl than on early whorls. *L. disclusa* is smaller than *L. toroensis* and has a smaller apical angle, *i.e.*, it is less stout. Its protoconch consists of 2.75 to 3 volutions, whereas that of *L. toroensis* of only 2.5. The number of opisthocline to opisthocyrt axial riblets on the late part of the protoconch is much larger in *L. disclusa.* Finally the number of axial ribs in *L. disclusa* is 8–9 on early teleoconch whorls and 9–10 on the body whorl The corresponding figures in *L. toroensis* are also 8–9 on early whorls, but 12–13 on the body whorl.

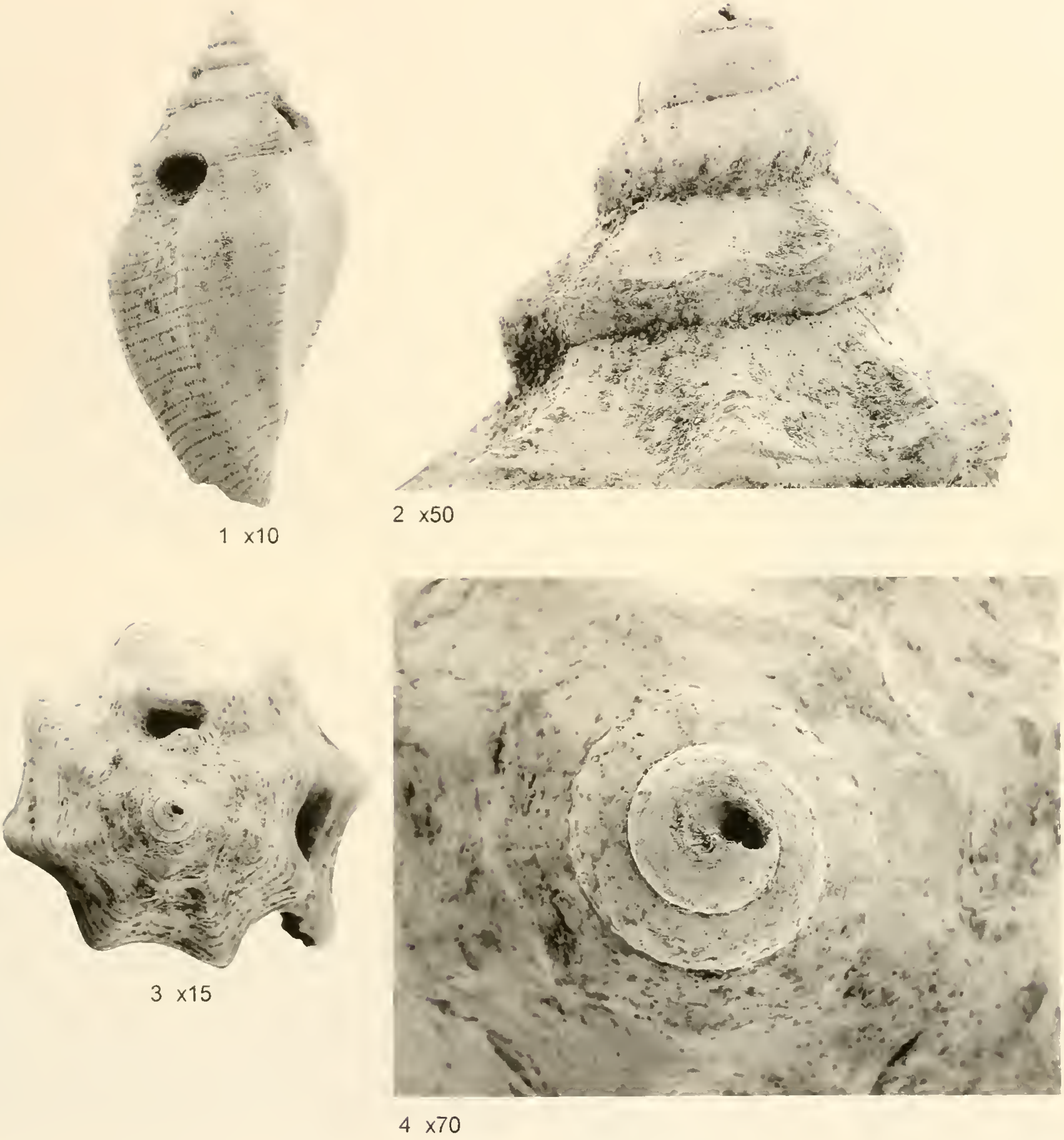


Text-figure 67.—*Lepicythara turrita* (Mansfield). USNM 369984. Holotype. UGSG Station 3671 Hosford, Liberty County, Florida. Jackson Bluff Formation (Choctawhatchee Group). Height 12.2 mm, width 5.6 mm. 1, front view; 2, rear view; 3, from right side.

L. heptagona is also smaller than *L. torensis* and also has a smaller apical angle and therefore is more slender. Its protoconch consists of 2.25 volutions, that of *L. toroensis* of 2.5. the number of opisthocline to opisthocyrt axial riblets on the late part of the protoconch is up to eight in *L. heptagona,* but only up to four in *L. toroensis.* The number of axial ribs in *L. heptagona* is seven to eight on early teleoconch whorls and eight to nine on the body whorl, which is less than the corresponding numbers in *L. toroensis. L. toroensis* may also be compared with *L. terminula* (see p. 55 for more information).

Material.—Three lots with a total of only seven specimens as listed below:

1 spec., NMB locality 17850 (=PPP 376): Bruno Bluff, outer coast of Valiente Peninsula, Bocas del Toro, Panama. Shark Hole Point Formation (Early Pliocene). Paratype.
3 spec., NMB locality 17891 (=PPP 379): Bruno Bluff (as above). Shark Hole Point Formation (Early Pliocene). Paratypes.
3 spec., NMB locality 18724 (=PPP 2227): Bruno


1 x10

2 x50

3 x15

4 x70

Text-figure 68.—*Lepicythara turrita* (Mansfield). USNM 495824 (ex 369986). USGS Station 3421: Harveys Creek, about half a mile above the abandoned mill, Leon County, Florida. Jackson Bluff Formation (Choctawhatchee Group). Height 9.7 mm, width 4.5 mm. 1, rear view; 2, enlargement of apical area; 3, apical area; 4, enlargement of apical view.

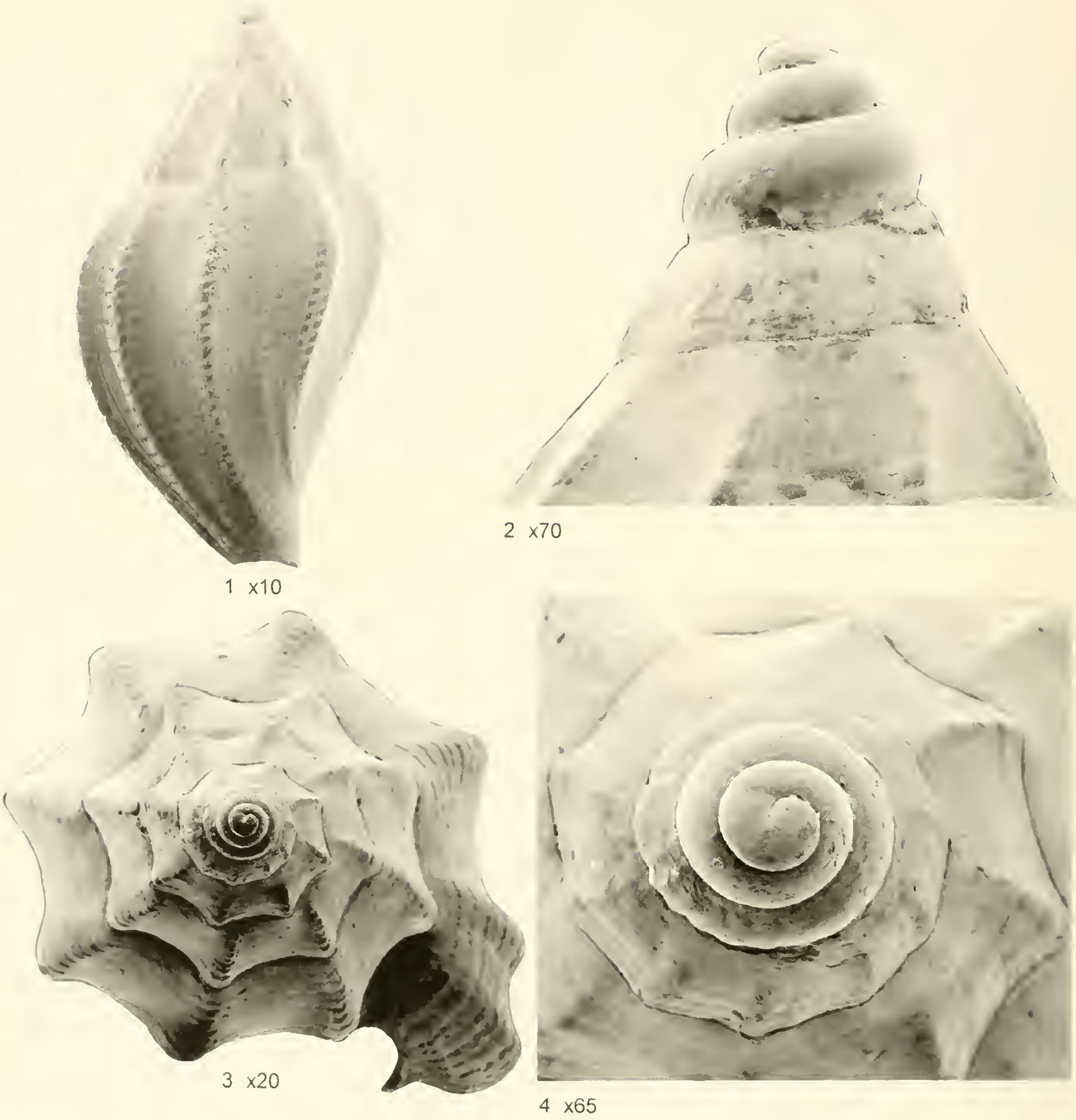
Bluff (as above). Shark Hole Point Formation (Early Pliocene). Holotype and two paratypes.

Measurements.—(See Table 14.)

Occurrence.—This species is recorded from the following NMB localities: 17950, 17851, 18724: all Bruno Bluff, outer coast of the Valiente Peninsula, Province of Bocas del Toro, Panama. Shark Hole Formation (Early Pliocene).

Distribution.—Not known from outside the type area.

Etymology.—Refers to the geographic name of the Province of Bocas del Toro, Panama.



Text-figure 69. —*Lepicythara turrita* (Mansfield). UF 102876 (ex 71582). Alligator Alley (CR007), Collier County, Florida, Pinecrest beds. Height 10.9 mm, width 5.0 mm. 1, rear view; 2, enlargement of apical area; 3, apical area; 4, enlargement of apical view.

Lepicythara turrita (Mansfield, 1930)

Text-figures 67–70

Brachycythara turrita Mansfield, 1930, p. 43, pl. 3, fig. 8.

Description.—Of small to medium size, biconic, rather stout. Protoconch consists of 2.75 to 3 volutions. Surface of the first two volutions smooth, remainder of the protoconch sculptured by thirteen opisthocyrt axial riblets. Number of teleoconch whorls almost five, their profile straight on early spire whorls, convex on late spire whorls. On all spire whorls, there is a slight concavity adjoining the adapical suture. The first two to three teleoconch whorls may be somewhat carinated near the abapical suture thus overhanging it. Early te-

Table 14.—Measurements (in mm) of *Lepicythara toroensis* new species.

Specimen	Restored height	Width	Height/ width ratio
NMB locality 17850	19.6	9.3	2.11
NMB locality 18724	19.5	8.9	2.19
	19.3	9.0	2.14

leoconch whorls sculptured by nine practically orthocline axial ribs, late whorls by eight. The axial ribs are narrow adapically and much wider abapically. Interspaces of axial ribs strongly concave, sculptured by three to seven incised, spiral lines on spire whorls. On late spiral whorls secondary incised, spiral lines are introduced. All spiral lines cross the axial ribs. Suture not deep. Aperture narrow. Outer lip thickened. Sinus adjoining suture moderately deep. Inner surface of outer lip smooth, but with a well-developed ridge parallel to the sharp edge of the outer lip extending from the sinus to the beginning of the anterior canal. Columellar and parietal calluses moderately prominent. Anterior canal straight, moderately narrow, and short.

Holotype.—USNM 369984 (Text-fig. 68).

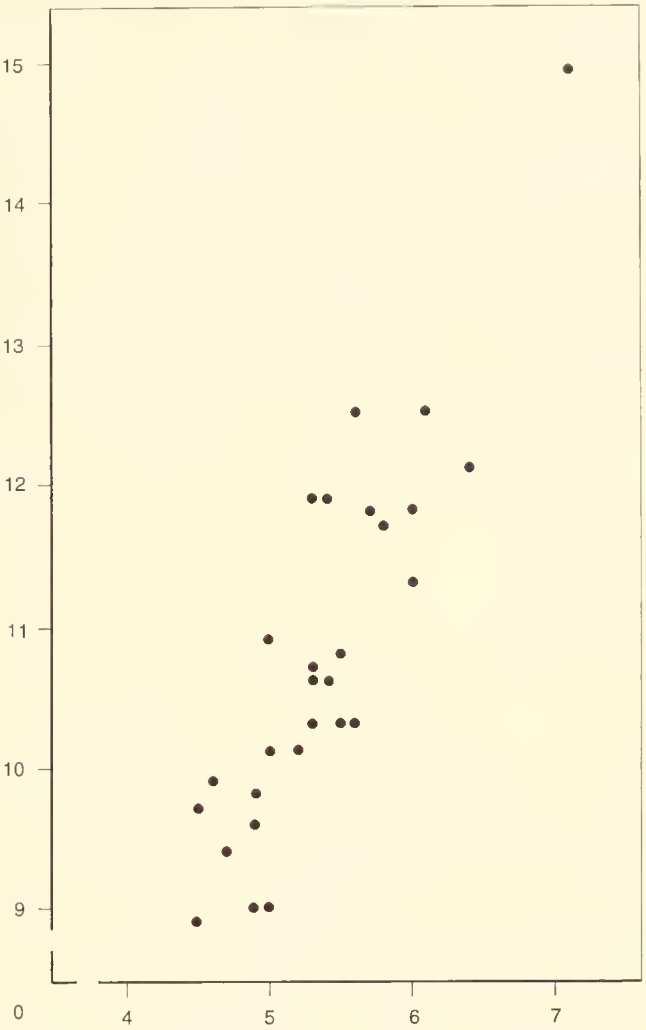
Dimensions of holotype.—Height 12.2 mm, width 5.6 mm.

Type locality.—USGS Station 3671: Hosford, Liberty County, Florida. Jackson Bluff Formation (Pliocene).

Remarks.—This species is described as being of small to medium size. Actually there is a single specimen from the Pliocene Pinecrest beds of Basinger, Okeechobee County (UF 48019), which has a restored height of 14.9 mm, and should therefore be called "large" according to the definition given on page 9. *L. turrita* is being described as having nine axial ribs on early teleoconch whorls and eight axial ribs on late teleoconch whorls. There are, however, a few specimens with ten axial ribs on early, and nine axial ribs on late teleoconch whorls. It is thus practically the only species having more axial ribs on early whorls than on the body whorl.

In the above description, it is stated that the first two to three teleoconch whorls may be somewhat carinated near the abapical suture. One of the figured specimens from the Pliocene Pinecrest beds (Text-fig. 69.2) looks like an exception in having an almost straight profile without carination on early teleoconch whorls. Other Pliocene specimens, however, do have a carination near the abapical suture.

Comparisons.—*L. turrita* and *L.* aff. *turrita* are the only species of the genus having less axial ribs on the body whorl than on early teleoconch whorls. Therefore they cannot really be compared to other species of *Lepicythara*. The two species are compared under *L.* aff. *turrita*.



Text-figure 70.—(Restored) height/width diagram of *L. turrita*.

Material.—Eight lots with a total of 34 specimens as listed below:

1 spec., USNM 369984: holotype: USGS Station 3671: Hosford, Liberty County, Florida. Jackson Bluff Formation (Pliocene).

12 spec., USNM 369985: paratypes; USGS Station 3421: Harveys Creek, about half mile above the abandoned mill, Leon County, Florida. Jackson Bluff Formation (Pliocene).

2 spec., USNM 369986: paratypes; USGS Station 3421: Harveys Creek, approx. one half mile above an abandoned mill, Leon County, Florida. Jackson Bluff Formation (Pliocene).

2 spec., UF 6952: Harveys Creek (LN003), Leon County, Florida. Jackson Bluff Formation (Pliocene).

Table 15.—Measurements (in mm) of *Lepicythara turrita* (Mansfield, 1930).

Specimen	Restored height	Width	Height/ width ratio
USNM 369984	12.5	5.6	2.23
USNM 369985	9.9	4.6	2.15
	9.6	4.9	1.96
	10.1	5.2	1.94
	9.8	4.9	2.00
	10.3	5.5	1.87
	10.3	5.6	1.84
	10.1	5.0	2.02
	10.6	5.3	2.00
	11.9	5.3	2.25
	11.8	5.7	2.07
USNM 369986	11.9	5.4	2.20
	9.7	4.5	2.16
UF 6952	9.4	4.7	2.00
	12.1	6.4	1.89
UF 71582	10.9	5.0	2.18
	11.7	5.8	2.02
UF 69302	8.9	4.5	1.98
	9.0	4.9	1.84
	10.6	5.4	1.96
	10.3	5.3	1.94
	10.7	5.3	2.02
	10.8	5.5	1.96
	10.1	5.0	2.02
	11.8	6.0	1.97
UF 69296	9.0	5.0	1.80
	11.3	6.0	1.88
UF 48019	12.5	6.1	2.05
	14.9	7.1	2.10

2 spec., UF 71582: Alligator Alley (CR007), Collier County, Florida. Pinecrest beds (Pliocene).

10 spec., UF 69302: Jackson Bluff (LN004), Leon County, Florida. Jackson Bluff Formation (Pliocene).

3 spec., UF 69296: Jackson Bluff (LN004), Leon County, Florida. Jackson Bluff Formation (Pliocene).

2 spec., UF 48019: Basinger (2664), Okeechobee County, Florida. Pinecrest beds (Pliocene).

Measurements.—(See Table 15 and Text-figure 70.)

Occurrence.—This species is recorded from the Jackson Bluff Formation and the Pinecrest beds of Florida.

Distribution.—So far this species is not known from outside Florida.

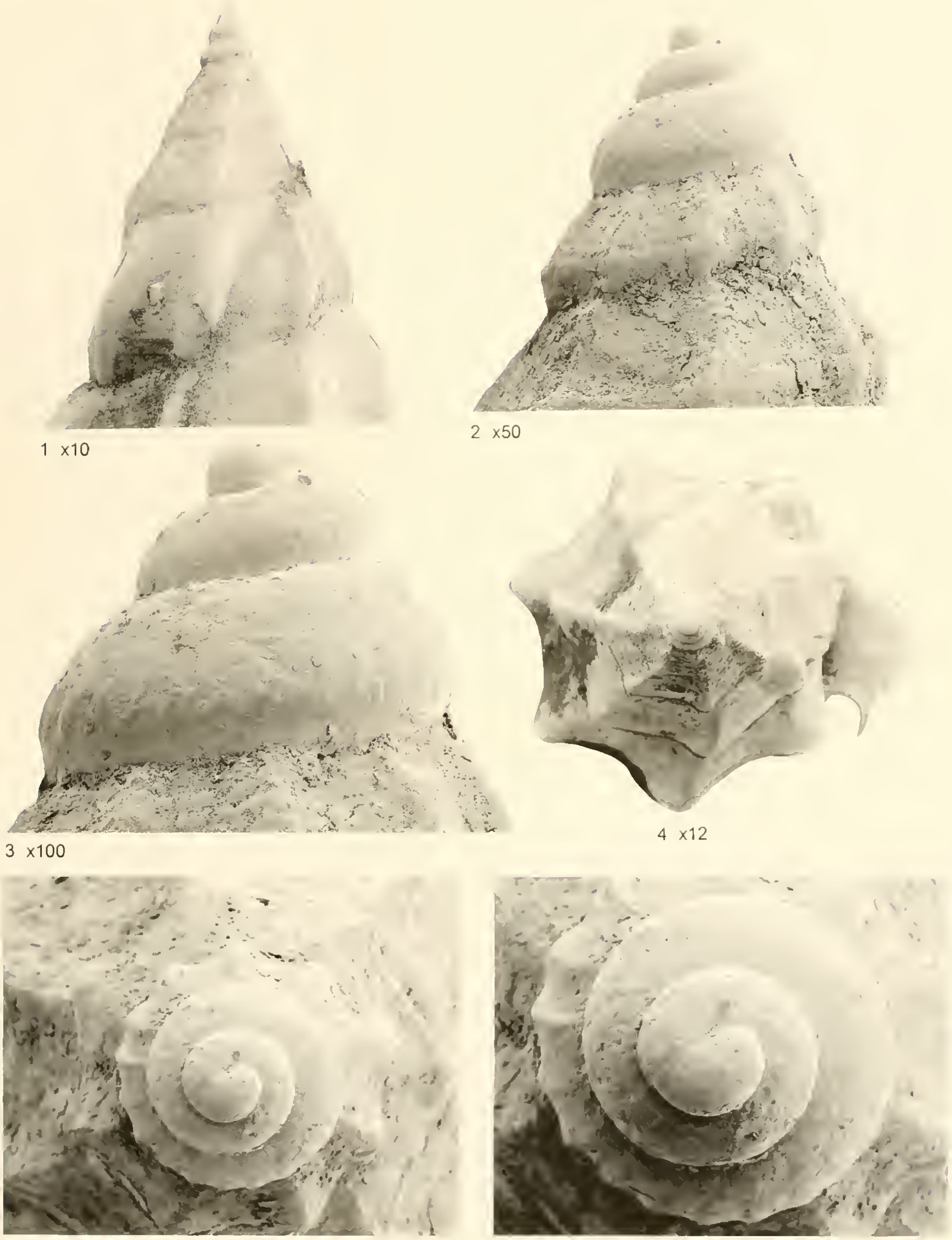
Lepicythara aff. turrita (Mansfield)
Text-figures 71–72

Remarks.—There are four specimens of this species occurring in the Late Miocene Nancy Point Formation. One practically complete specimen has been collected at NMB locality 18705 (=PPP 2206), which is situated in the westernmost part of the south coast of the Valiente Peninsula, Province of Bocas del Toro, Panama. This is the largest of all four specimens (Text-fig. 71).

Text-figure 71.—*Lepicythara* aff. *turrita* (Mansfield). NMB H 18151. NMB locality 18705: westernmost part of the south coast of the Valiente Peninsula, Province of Bocas del Toro, Panama. Nancy Point Formation. Height 17.7 mm, width 7.9 mm. 1, front view; 2, rear view; 3, from right side.

The remaining three specimens are adult and have been collected at two localities on Finger Island, which is situated west of Bluefield Bay, Valiente Peninsula, Bocas del Toro, Panama. One specimen was collected at NMB locality 17824 (=PPP 477), the other two at NMB locality 18375 (=PPP 1996). For the exact location of these localities see Coates (1999b, map 5, insets A and C, p. 291; 1999c, section 14, p. 318; 1999c, section 15, p. 322).

L. aff. *turrita* is a large species of the genus. Its protoconch consists of a little more than 2.75 volutions, the first two of which are smooth and the re-



Text-figure 72.—*Lepicythara* aff. *turrita* (Mansfield). NMB H 18151 (same specimen as Text-fig. 72) NMB locality 18705: westernmost part of the south coast of the Valiente Peninsula, Province of Bocas del Toro, Panama. Nancy Point Formation. Height 17.7 mm, width 7.9 mm. 1, rear view of spire whorls; 2, enlargement of apical area; 3, further enlargement of apical area; 4, apical view; 5, enlargement of apical view; 6, further enlargement of apical view.

Table 16.—Measurements (in mm) of *Lepicythara* aff. *turrita* (in mm).

Specimen	Restored height	Width	Height/ width ratio
NMB locality 18705	17.7	7.9	2.24
NMB locality 17824	14.9	7.0	2.13
NMB locality 18375	14.8	7.0	2.11
	15.8	7.0	2.26

mainder sculptured by up to fourteen opisthocline to opisthocyrt axial riblets. There are up to 5.25 teleoconch whorls. The profile of the early teleoconch whorls is straight, and there is a small angulation near the abapical suture. The profile of the late whorls is slightly convex. There are eight to nine axial ribs on the first teleoconch whorl, but only seven on late whorls. The spiral sculpture of the body whorl consists not only of primary and secondary, but also of some tertiary incised lines. This species is larger than *L. turrita*, and there are no tertiary spiral incised lines on the body whorl of *L. turrita*. The two species, however, have two important features in common; their protoconchs are practically identical, and both have more axial ribs on early whorls than on late whorls. This latter feature is rare in *Lepicythara*, having been observed only in *L. turrita* and *L.* aff. *turrita*.

Measurements.—(See Table 16.)

Lepicythara sp. A
Text-figure 73

?*Cythara heptagona* (Gabb). Brown and Pilsbry, 1911, p. 345.
Lepicythara heptagona (Gabb). Woodring, 1970, p. 390, pl. 60, no. 4, pl. 64, no. 11.

Remarks.—Woodring (1970, p. 390) recorded specimens from a number of localities within the Gatun Formation of Panama under the name of *L. heptagona* (Gabb). The single specimen reported by Brown and Pilsbry (1911, p. 345) under this name probably represents the same species.

Three specimens of Woodring's material from three different localities are at hand. The localities are:

1. USGS 8382: railroad cuts west of Gatun Dam, Canal area,
2. USGS 8383: Caribbean coast, west of Rio San Miguel, Panama,
3. USGS 16926: westernmost cut on Panama Railroad cutoff south of Fort Davis, 1.9 km northeast of Gatun railroad station, Canal area.

The specimen from USGS 8383 is a fragment and therefore does not provide much morphological information. The other two specimens are of medium size, biconic, and slender. *L. heptagona* from the Dominican Republic on the other hand is of large size, also biconic, but rather slender to moderately stout. The number of axial ribs on early whorls is seven to eight, and on the body whorl eight to nine like in *L. heptagona* from the Dominican Republic. The protoconch consists of 3.25 volutions, and its apex is pointed, whereas the protoconch of *L. heptagona* from the Dominican Republic only has 2.25 volutions, and its apex is not pointed. Surprisingly, the large PPP collections have yielded only a single fragmentary specimen from NMB locality 17641 (=PPP 223): Sabanita, Panama; lower Gatun Formation (Coates, 1999b, map 1, inset, p. 287; 1999c, section 1, p. 301). This specimen has an incomplete protoconch, and only a few early teleoconch whorls are preserved. Based on this information is obvious that the *Lepicythara* from the Gatun Formation of Panama cannot be identified as *L. heptagona*, but probably represents some other species. The existing materials, however, are considered insufficient for a formal description.

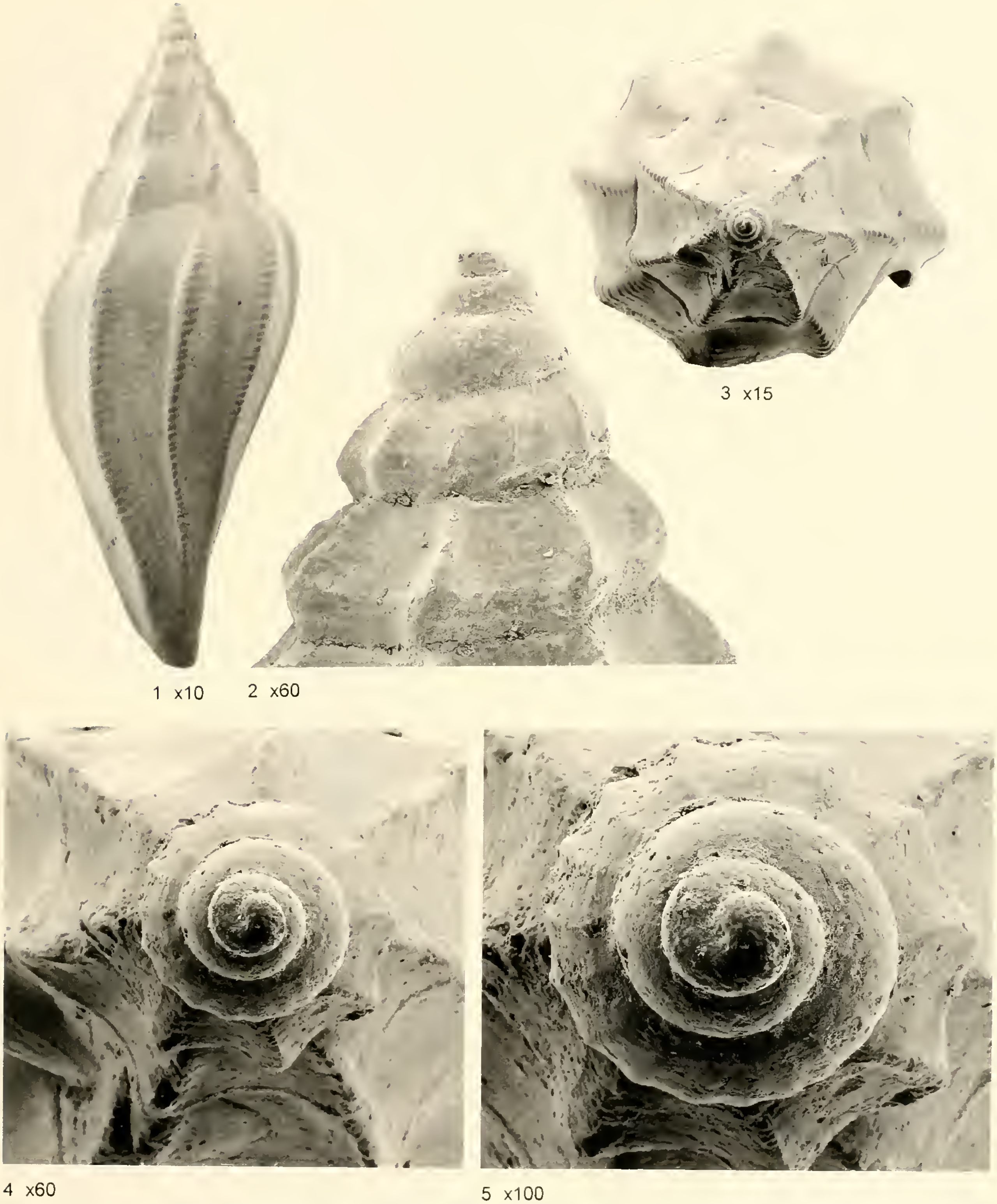
Table 17.—Measurements (in mm) of *Lepicythara* sp. A (in mm).

Specimen	Restored height	Width	Height/ width ratio
USGS 16926	12.8	5.0	2.56
USGS 8382	12.6	5.5	2.29

Measurements.—(See Table 17.)

Lepicythara sp. B

Remarks.—Woodring (1970, p. 391) mentioned a lot from USGS Station 8477 (Rio Tuira between Limones and Rio Cube, Darien, Panama), which he identified as *L. heptagona* (Gabb). This locality is part of the Middle Miocene Tuira Formation. The lot consists of four worn specimens. Three of them are fragmentary, their body whorl not being preserved. The fourth is an adult specimen lacking its protoconch (restored height 14.0 mm, width 5.7 mm, ratio 2.46). They all are not preserved well enough to be illustrated. These specimens cannot be identified as *L. heptagona* (Gabb). Two of the fragments have an apparently complete protoconch which, however, is badly preserved. Although not clearly recognizable, these two protoconchs seem to consist of a little more than three volutions. The protoconch of *L. heptagona* from the Dominican Republic on the other hand has only 2.25 volutions The number of axial ribs on early whorls is seven in the material from Darien and seven to eight in *L. heptagona* from the Dominican Republic. The corresponding number on the body whorl is six to seven in the material from Darien but eight to nine in *L.*



Text-figure 73.—*Lepicythara* sp. A. USNM 509803. USGS Station 16926: westernmost cut on Panama Railroad cutoff south of Fort Davis, 1.9 km northeast of Gatun railroad station. Canal area. Middle part of Gatun Formation. Height 12.8 mm, width 5.0 mm. 1, rear view; 2, enlargement of apical area; 3, apical view; 4, enlargement of apical view; 5, further enlargement of apical view.

heptagona from the Dominican Republic. Due to the lack of more and better preserved material it is not possible to positively identify the *Lepicythara* from Darien. The large PPP collections at the NMB do not contain a single specimen of this species.

Lepicythara sp. C

Remarks.—There are three specimens from the Late Miocene Nancy Point Formation of Finger Island, west of Bluefied Bay, Valiente Peninsula, Province of Bocas del Toro, Panama, which were collected on different occassions and therefore carry different locality numbers: NMB 17629 (=PPP 191), NMB 17824 (=PPP 477), and NMB 18711 (=PPP 2212). For exact location see Coates (1999b, map 5, inset A, p. 291; 1999c, section 14, p. 318).

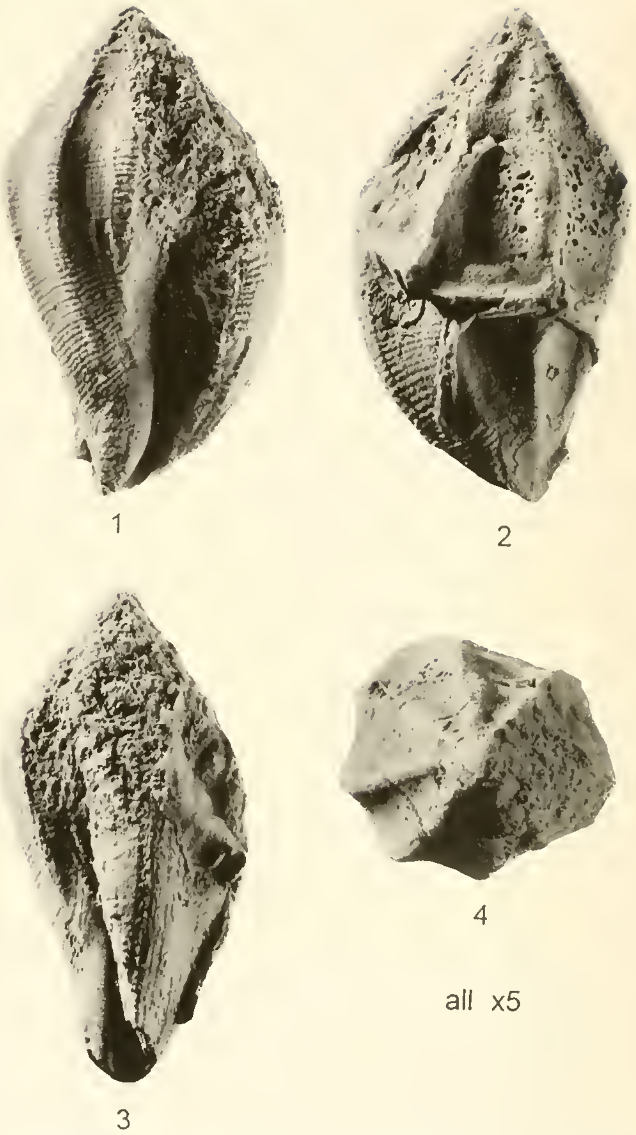
Two of these specimens are incomplete juveniles, and the third is a worn adult lacking its protoconch. One of the juveniles has an incompletely preserved protoconch, which consists of abut 2.5 volutions. On its last part a few opisthocryt axial riblets are recognizable. The adult specimen from NMB locality 17824 is fairly large (restored height 15.1 mm, width 7.2 mm, ratio 2.10). The profile of the early teleoconch whorls is straight, with a slight angulation near the abapical suture, and that of late whorls is slightly convex. The number of axial ribs per whorl is nine on early whorls and 12 on the body whorl. The preservation of this material is insufficient to allow meaningful comparisons with described species.

Lepicythara sp. D
Text-figure 74

Remarks.—A single specimen from NMB locality 17757 (=PPP 275) is available. This locality is situated near Punta Judas on the Pacific coast of the Province of Puntarenas, Costa Rica (for exact location see Jung 1995, p. 44, fig. 1), and the age is probably Late Miocene. The specimen is fairly large (restored height 14.1 mm, width 7.4 mm, ratio 1.91) and stout, *i.e.*, it has a large apical angle. Unfortunately it is worn and partly encrusted, so that some features cannot be observed. The protoconch is not preserved. The profile of the early teleoconch whorls is straight, that of late whorls slightly convex. The number of axial ribs per whorl on early whorls cannot be determined, but is probably eight as on the body whorl. The anterior canal is short and slightly twisted to the left.

Lepicythara sp. E

Remarks.—A single specimen is available from NMB locality 19126 (=PPP 3437): Cueva de Angostura on Rio Santaigo, Borbon, northwestern Ecuador: Angostura Formation (Late Miocene) (Whittaker, 1988, p. 10). The specimen is of medium size (restored height 12.5 mm, width 4.9 mm, ratio 2.55) and slender. It is somewhat deformed, its main axis not being quite straight. Its dorsal side has been exposed to erosion, and the sculpture is therefore not preserved. The tip of the protoconch is missing, and the sculpture on the last volution of the protoconch is hardly recognizable. The number of teleoconch whorls is 5.25, their profile is straight on early whorls and slightly convex on late whorls. The number of axial ribs is seven on early whorls and nine on the body whorl.



Text-figure 74.—*Lepicythara* sp. D. NMB H 18145. NMB locality 17757: near Punta Judas, Pacific coast of the Province of Puntarenas, Costa Rica. Probably Late Miocene. Height 13.6 mm, width 7.4 mm. 1, front view; 2, rear view; 3, from right side; 4, apical view.

REFERENCES CITED

Akers, W.H.

1972. Planktonic Foraminifera and Biostratigraphy of some Neogoen Formations, Northern Florida and Atlantic Coastal plain.—Tulane Studies in Geology and Paleontology, vol. 9, pp. 1–139, pl. 1–60, fig. 1–4, 1 map.

1979. Ancient Environments and Geological Ages in Mexico. *In* Proceedings of the International symposium on Marine biogeography and Evolution in the Southern Hemisphere. Auckland, New Zealand, 17–20 July 1978. New Zealand Department of Scientific and Industrial Research Information Series, vol. 2, pp. 491–499.

Bolli, H.M. and Saunders, J.B.

1985. Oligocene to Holocene low latitude planktic foraminifera. *In* Bolli, H.M., Saunders, J.B., and Perch-Nielson, K., *eds.*, Plankton stratigraphy. Cambridge University Press, Cambridge, pp. 155–262.

Brann, D.C. and Kent, L.S.

1960. Catalogue of type and figured specimens in the Paleontological Research Institution. Bulletins of American Paleontology. vol. 40, no. 184, 995 p.

Brown, A.P. and Pilsbry, H.A.

1911. Fauna of the Gatun Formation, Isthmus of Panama. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 63, pp. 336–373.

Carter, J.G.

1984. Summary of Lithostratigraphy and Biostratography for the Coastal Plain of the South Eastern United States. Biostratigraphy Newsletter No. 2.

Coates, A.G.

1999a. Lithostratigraphy of the Neogene strata of the Caribbean Coast from Limon, Costa Rica, to Colon, Panama. *In* Collins, L.S., and Coates, A.G., *eds.*, A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, no. 357, pp. 17–38.

1999b. Appendix A: maps. *In* Collins, L.S., and Coates, A.G., *eds.*, A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, no. 357, pp. 287–298.

1999c. Appendix B: stratigraphic sections. *In* Collins, L.S., and Coates, A.G., *eds.*, A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, no. 357, pp. 299–348.

Collins, L.S. and Coates, A.G., *eds.*

1999. A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, no. 357.

Dall, W.H.

1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S Coast Survey Steamer "Blake", Lieut. Commander C.D. Sigsbee, U. S. N., and Commander J.R. Bartlett, U. S. N., commanding. XIXX. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology, no. 18, 492 pp.

1890. Contributions to the Tertiary fauna of Florida; with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchee River. Transactions of the Wagner Free Institute of Science, Philadelphia, vol. 3, no. 1, pp. 1–200.

Gabb, W.M.

1873. On the topography and geology of Santo Domingo. Transactions of the American Philosophical Society (n.s.), vol. 15, pp. 49–259.

Gardner, J.

1937. The Molluscan fauna of the Alum Bluff Group of Florida. Part VI. Pteropoda, Opisthobranchia, and Ctenobranchia (in part). U. S. Geological Survey Professional Paper 142-F, pp. 251–435.

Jackson, J.B.C., Todd, J.A., Fortunato, H., and Jung, P.

1999. Diversity and Assemblages of Neogene Caribbean Mollusca of Lower Central America. *In* Collins, L.S., and Coates, A.G., *eds.*, A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. Bulletins of American Paleontology, no. 357, pp. 193–230.

Jung, P.

1969. Miocene and Pliocene mollusks from Trinidad. Bulletins of American Paleontology, vol. 55, no. 247, pp. 289–657.

1989. Revision of the *Strombina*-Group (Gastropoda: Columbellidae), fossil and living. Distribution, biostratigraphy, systematics. Schweizerische Paläontologische Abhandlungen, vol. 111, 298 pp.

1995. *Judaphos*, a new genus of buccinid Gastropod from the Neogene of Costa Rica. The Veliger, vo. 38, no. 1, pp. 43–46.

Mansfield, W.C.

1930. Miocene gastropods and scaphopods of the Choctawhatchee Formation of Florida. Florida Geological Survey Bulletin 3, pp. 1–185.

Maury, C.J.

1917. Santo Domingo type sections and fossils. Pt. 1: Mollusca. Bulletins of American Paleontology, vol. 5, no. 29, pp. 1–251.

Oinoomikado, T.

1939. Miocene Mollusca from the neighbourhood of Cucurrupi, Department of Choco, Colombia. Journal of the Geological Society of Japan, vol. 46, pp. 617–630.

Olsson, A.A.

1922. The Miocene of northern Costa Rica. Bulletins of American Paleontology, vol. 9, no. 39, pp. 1–168.

1964. Neogene mollusks from northwestern Ecuador. Paleontological Research Institution, Ithaca, New York, 256 pp.

Perrilliat, M.C.

1972. Monografia de los moluscos del Mioceno medio de Santa Rosa, Veracruz, Mexico. Parte I. (Gasteropodos: Fiussurellidae a Olividae). Paleontología Mexicana, vol. 32, pp. 1–130.

1973. Monografia de los moluscos del Mioceno medio de Santa Rosa, Veracruz, Mexico. Parte II. (Gasteropodos: Mitridae a Terebridae). Paleontología Mexicana, vol. 35, pp. 1–97.

Pilsbry, H.A.

1922. Revision of W.M. Gabb's Tertiary Mollusca of Santo Domingo. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 73, pp. 305–435.

Rutsch, R.F.

1942. Die Mollusken der Springvale-Schichten (Obermiocaen) von Trinidad (Britisch-West-Indien). Verhandlungen Naturforschende Gesellschaft Basel, vol. 54, pp. 96–182.

Saunders, J.B., Jung, P., and Biju-Duval, B.

1986. Neogene Paleontology in the Northern Dominican Republic. 1. Field Surveys, Lithology, Environment, and Age. Bulletins of American Paleontology, vol. 89, no. 323, pp. 1–79.

Vermeij, G.J. and Vokes, E.H.

1997. Cenozoic Muricidae of the Western Atlantic Region. Part

XII. The Subfamily Ocenebrinae (in part). Tulane Studies in Geology and Paleontology, vol. 29, no. 3, pp. 69–118.

Vokes, E.H.

1994. Cenozoic Muricidae of the Western Atlantic Region. Part X. The Subfamily Muricopsinae. Tulane Studies in Geology and Paleontology, vol. 26, nos. 2–4, pp. 49–160.

Weisbord, N.E.

1929. Miocene Mollusca of northern Colombia. Bulletins of American Paleontology, vol. 14, no. 54, pp. 1–57.

Whittaker, J.E.

1988. Benthic Cenozoic Foraminifera from Ecuador. Taxonomy and Distribution of Smaller Benthic Foraminifera from Coastal Ecuador (Late Oligocene-Late Pliocene). British Museum (Natural History), London, 194 pp.

Woodring, W.P.

1970. Geology and Paleontology of Canal Zone and Adjoining Parts of Panama. Description of Tertiary Mollusks (Gastropods: Eulimidae, Marginellidae to Helminthoglyptidae). U. S. Geological Survey Professional Paper 306-D, pp. 299–452.

APPENDIX I. Species excluded from *Lepicythara.*

Although the species described below does not belong to *Lepicythara,* it is briefly discussed here for the sake of completeness.

Lepicythara veracruzana Perrilliat
Text-figure 75

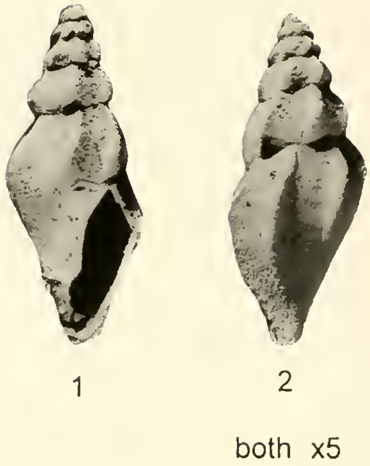
1973 *Lepicythara veracruzana* Perrilliat, Perrilliat, p. 58, pl. 28, pp. 13–14.

Description.—Of small size, not biconic, slender. Protoconch incomplete, without recognizable axial riblets on its last part. Number of teleoconch whorls 4.25, their profile convex. First teleoconch whorl sculptured by eight, subsequent whorls by six opisthocline to opsithocyrt axial ribs. The width of the axial ribs is about the same from suture to suture. Interspaces of axial ribs concave, without spiral sculpture. Suture not deep. Aperture moderately narrow. Shape of outer lip not known. Columellar and parietal calluses not preserved. Anterior canal broken.

Holotype.—USNM 647172 (Text-fig. 75).

Dimensions of holotype.—Height 9.0 mm, width 4.0 mm.

Type locality.—USGS Station 9995: Santa Rosa, Veracruz, Mexico. For location see Perrilliat (1972, p. 11, fig. 1). Beds of late Miocene age. For more information see under *L.* aff. *heptagona,* and Akers (1979, p. 497) and Vokes (1994, p. 138).



Text-figure 75.—*Lepicythara veracruzana* Perrilliat, USNM 647172, Holotype, USGS Station 9995, Santa Rosa, Veracruz, Mexico. Beds of Late Miocene age. Height 9.0 mm, width 4.0 mm. 1, front view; 2, rear view.

Remarks.—*Lepicythara veracruzana* is based on a single, incomplete specimen, the holotype. The above description is therefore not the description of a species but the description of a specimen, which the present writer considers as undesirable to serve as type material. This species lacks several features characterizing other species of the genus *Lepicythara.* It is not biconic in general shape, the last part of its protoconch has no recognizable axial riblets, the teleoconch whorls are not sculptured spirally, and the axial ribs of the teleoconch whorls have about the same width from suture to suture instead of being narrow adapically and wider abapically. Due to the poor quality of preservation, it is not possible to assign it to another turrid genus.

Material.—As mentioned above the holotype is the only available specimen.

Measurements.—Restored height 9.7 mm, width 4.0 mm, ratio 2.42.

Occurrence.—Known only from USGS Station 9995, the type locality: Santa Rosa, Veracruz, Mexico. Beds of Late Miocene age. See also under "type locality", above.

Appendix II.—In the chapter "Distribution through time and space" reference was made to Jackson et al. (1999, table 3, p. 204, appendix 1, pp. 212–213). In order to be more specific, the cited table 3 and appendix 1 are reproduced hereafter.

A. List of 37 faunules (molluscan taxa from a single horizon at a single outcrop or closely grouped outcrops) and descriptive statistics used for the ordination analyses. Taxa are genera or subgenera. Lists of PPP numbers for each faunule are given in Appendix 3. Documentation for ages and depths are given in Appendix 1. Estimated ages and depths placed in brackets. L = Limon Basin, B = Bocas del Toro Basin, NC = North Coast of Panama, C = Panama Canal Basin.

Faunule number	Faunule name	Basin	Section number	Median age	Median depth	Number of collections	Number of specimens	Number of taxa	Fisher's alpha
1	Swan Cay	B	25	1.4	100	1	1,418	135	36.691
2	Cemetery Pueblo Nuevo	L	35	1.6	75	1	452	67	21.744
3	Upper Lomas del Mar east (reef)	L	36	1.6	75	12	5,986	219	44.637
4	Empalme	L	34	1.6	20	5	2,188	143	34.508
5	Cangrejos Creek	L	37	1.6	200	5	828	116	36.734
6	Lower Lomas del Mar east (non-reef)	L	36	1.7	75	10	6,458	304	66.229
7	Northwest Escudo de Veraguas	B	10	2.0	125	4	433	49	14.206
8	Fish Hole	B	22/23	2.6	70	3	331	114	61.516
9	Ground Creek	B		[2.6]	[50]	2	1,723	90	20.283
10	North central Escudo de Veraguas	B	10	2.8	125	8	5,019	227	48.916
11	Rio Limoncito	L		3.0	[30]	1	148	39	17.269
12	Chocolate Buenos Aires	L	33	3.1	[50]	3	1,011	45	9.657
13	Bomba	L	29	3.1	30	34	18,181	285	47.980
14	Agua	L	29	3.3	30	2	841	53	12.565
15	Bruno Bluff	B	12	3.5	175	4	1,310	133	35.822
16	Cayo Agua: west side Punta Norte	B	16	3.5	30	8	2,715	139	31.238
17	Quitaria	L	29	3.5	30	7	12,690	179	29.508
18	Rio Vizcaya	L	39	3.5	25	7	979	47	10.296
19	Santa Rita	L	32	3.5	30	2	497	81	27.462
20	Northeast Escudo de Veraguas	B	10	3.6	125	4	2,588	175	42.847
21	Southeast Escudo de Veraguas	B	11	3.6	125	9	2,215	166	41.888
22	Cayo Agua: Punta Tiberon	B	19	3.6	60	9	4,001	270	65.368
23	Cayo Agua: Punta Nispero west	B	19	3.6	60	6	1,339	122	32.648
24	Cayo Agua: southeast Punta Nispero	B	20	3.6	60	7	3,307	175	39.562
25	Isla Popa	B		[4.3]	[60]	7	2,445	101	22.431
26	Cayo Agua: Punta Norte east	B	19	4.3	60	6	2,185	124	28.663
27	Cayo Agua: Punta Piedra Roja west	B	17	4.3	43	6	6,640	275	57.881
28	Quebrada Brazo Seco	L		4.8	[50]	3	240	57	23.632
29	Shark Hole Point	B	12	5.7	150	7	432	57	17.586
30	Finger Island	B	14	6.9	80	3	1,817	165	44.354
31	Rio Sand Box and Hone Creek	L	27	7.7	175	6	697	65	17.534
32	Rio Tuba	L		[7.7]	[175]	5	91	40	27.279
33	Rio Calzones	NC	9	[8.3]	[25]	2	185	43	18.598
34	Miguel de la Borda	NC	6	[8.3]	25	1	699	97	30.580
35	Isla Payardi	C	1	9.0	28	14	14,627	172	27.376
36	Mattress Factory	C	1	9.0	28	16	11,957	236	41.677
37	Martin Luther King Jr.	C	1	11.6	28	11	9,242	155	26.455

B. Ages and paleobathymetries of faunules

Faunule (with section #)	Age (Ma)	Depth (m)	Abundant diagnostic taxa
1. Swan Cay (#25)	1.6–1.2	80–120[1]	*Amphistegina gibbosa, Cassidulina curvata, Eponides antillarum, Eponides repandus, Pararotalia rosea, Planulina ariminensis* var. *exorna, Quinqueloculina lamarckiana, Siphonina pulchra*
2. Cemetery Pueblo Nuevo (#35)	1.7–1.5	50–100	based on lithostratigraphic relation to faunule #3
3. Upper Lomas del Mar East (reef) (#36)	1.7–1.5	50–100	*C. curvata, Elphidium discoidale, P. ariminensis* var. *exorna, Sigmoilina tenuis, Spirillina vivipara*
4. Empalme (#34)	1.7–1.5	10–30	*E. discoidale, Fursenkoina pontoni, Nonionella atlantica, Pararotalia magdalenensis, Sagrina pulchella*
5. Cangrejos Creek (#37)	1.6–1.5	150–250	*Bulimina aculeata, Bulimina marginata, Cassidulina minuta, Gyroidina regularis, Planulina foveolata, Trifarina eximia*
6. Lomas del Mar East (non-reef) (#36)	1.9–1.5	50–100	based on lithostratigraphic relation to Faunule #3
7. Northwest Escudo de Veraguas (#10)	2.1–1.9	100–150	*Bolivina paula, B. marginata, C. curvata, C. minuta, G. regularis, Hanzawaia concentrica, Melonis barleeanum, Reussella spinulosa, S. tenuis, S. pulchra, Uvigerina laevis, Uvigerina peregrina*
8. Fish Hole (#22/23)	3.0–2.2	75–100 (upper mudstone) 40–100 (lower reef conglomerate)	*B. marginata, E. antillarum, P. ariminensis* var. *exorna, T. eximia, U. peregrina, A. gibbosa, E. discoidale, E. antillarum, Nodobaculariella cassis, P. ariminensis* var. *exorna, Q. lamarckiana, S. pulchra*
9. Ground Creek (no section)	3.5–1.6[3]	<50?	estimate based on sediments and mollusks
10. North-central Escudo de Veraguas (#10)	3.6–1.9	100–150	same as Faunule #7
11. Rio Limoncito (no section)	3.6–2.4	20–40?	based on apparent stratigraphic relationship to Faunule #'s 13 and 17–19
12. Chocolate Buenos Aires (#33)	3.2–3.0	<50?	Based on lithostratigraphic position between reef trends
13. Bomba (#29)	3.2–2.9	20–40	*Ammonia decorata, P. magdalenensis, P. sarmientoi, Rotorbinella umbonata, S. tenuis*
14. Agua (#29)	3.6–2.9	20–40	Based on stratigraphic relations to Faunule #'s 13, 17–19
15. Bruno Bluff (#12)	3.6–3.3	150–200	*B. marginata, C. curvata, C. minuta, C. norcrossi australis, T. eximia, U. peregrina.*
16. Cayo Agua: West side of Punta Norte (#16)	3.5	20–40	*E. discoidale, E. antillarum, F. pontoni, H. concentrica, N. cassis, N. atlantica, Quinqueloculina compta, Q. lamarckiana*
17. Quitéria (#29)	3.6–3.4	20–40	Same as Faunule #'s 13 and 19
18. Rio Vizcaya (#39)	3.5	<25	*Ammonia becarii, A. gibbosa, Buccella hannai, N. atlantica, P. magdalenensis, Trifarina occidentalis*
19. Santa Rita (#32)	3.5	20–40	*A. gibbosa, E. antillarum, Hauerina fragillissima, N. cassis, P. ariminensis* var. *exorna, R. umbonata*
20. Northeast Escudo de Veraguas (#10)	3.6–3.5	100–150	Same as Faunule #7
21. Southeast Escudo de Veraguas (#11)	3.6–3.5	100–150	Same as Faunule #7
22. Cayo Agua: Punta Tiburon (#19)	3.6–3.5	40–80	*Cassidulina subglobosa, E. discoidale, E. antillarum, F. pontoni, H. concentrica, N. atlantica, P. ariminensis, R. spinulosa, S. tenuis*
23. Cayo Agua: Punta Nispero West (#19)	3.6–3.5	40–80	Same as Faunule #22
24. Cayo Agua: Punta Nispero Southeast (#20)	3.6–3.5	40–80	Same as Faunule #22
25. Isla Popa (no section)	5.0–3.5	<50?	Based on apparent stratigraphic equivalence and proximity to older Cayo Agua Fm.
26. Cayo Agua: Punta Norte East (#19)	5.0–3.5	40–80	Same as Faunule #22
27. Cayo Agua: Punta Piedra Roja West (#17)	5.0–3.5	10–75	*A. gibbosa, Cancris sagra, E. discoidale, E. antillarum, Quinqueloculina* spp.

Appendix II—Continued.

28. Quebrada Brazo Seco (no section)	5.2–4.3	<50?	Based on stratigraphic position between reef tracts and Rio Banano Fm.
29. Shark Hole Point and top of Nancy Point (#12)	5.7–5.6	100–200	*Bolivina barbata, Bolivina imporcata, N. atlantica, P. ariminensis, U. peregrina*
30. Finger Island (#14)	8.2–5.6	60–100	*A. gibbosa, B. barbata, C. curvata, E. antillarum, H. concentrica, Hanzawaia isidroensa, Lenticulina calcar, P. ariminensis, Quinqueloculina seminulum, S. pulchra, U. peregrina*
31. Rio Sand Box (#27)	8.7–7.2	150–200	*B. imporcata, Bolivina lowmani, Bolivina mexicana, C. minuta, N. atlantica, P. magdalenensis, R. umbonata*
32. Rio Tuba (no section)	8.2–7.2[4]	150–200	Assumed equivalent to Faunule #31 based on apparent stratigraphic position
33. Rio Calzones (#9)	11.2–5.3[5]	25?	Assumed equivalent to Faunule #34
34. Miguel de la Borda (#6)	11.2–5.3[5]	25?	
35. Isla Payardi (#1)	9.4–8.6	15–40	*A. beccarii, Bolivina merecuani, Bolivina vaughani, B. hannai, P. magdalenensis, R. spinulosa, R. umbonata*
36. Mattress Factory (#1)	9.4–8.6	15–40	same as Faunule #35
37. Martin Luther King (#1)	11.8–11.4[6]	15–40	same as Faunule #35

[1] We used the maximum rather than the median depth because the sediments are a reef talus slump deposit.

[2] Assumed Late Pliocene age based on inferred stratigraphic position.

[3] Assumed equivalent to older Cayo Agua Fm.

[4] Assumed equivalent to nearby Rio Sandbox.

[5] Assumed Late Miocene.

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PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

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EARLY PALEOCENE MOLLUSKS OF ANTARCTICA: SYSTEMATICS, PALEOECOLOGY AND PALEOBIOGEOGRAPHIC SIGNIFICANCE

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ABSTRACT

The Paleocene (Danian) molluscan fauna of the López de Bertodano and Sobral formations of Seymour Island, Antarctic Peninsula, is the only shelf fauna of this age from the continent of Antarctica and provides the critical insight into the emergence of marine faunas of the Southern Hemisphere following the mass extinction at the end of the Cretaceous. The Danian molluscan fauna on Seymour Island consists of 58 species of which 40 are new.

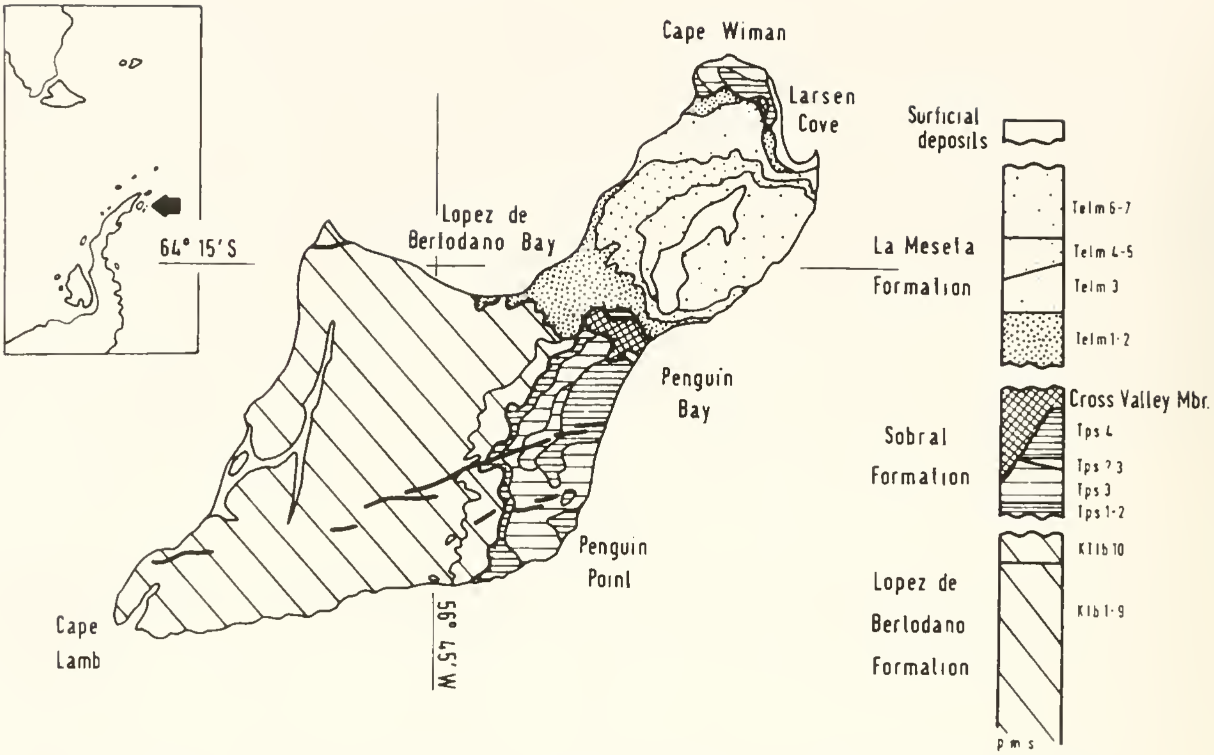
Bivalves are represented by 20 species from the López de Bertodano Formation unit 10 and the Sobral Formation. Newly recognized taxa in the Antarctic Danian include: *Nucula* sp., *Nuculana antarctirostrata* n. sp., *Ledina*? sp., *Jupiteria*? sp., *Saxolucina antarctipleura* n. sp., *Thyasira austrosulca* n. sp. and *Periploma*? sp.

The gastropod component of the Danian molluscan fauna of Antarctica is by far the most diverse, with 37 species recorded, of which the following 30 are newly described: *Conotomaria* sp. A, *Conotomaria* sp. B, *Conotomaria* sp. C, *Acmaea submesidia* n. sp., *Bittium* (*Bittium*?) *paleonotum* n. sp., *Bittium* (*Zebittium*?) *brooksi* n. sp., *Turritella* (*Haustator*?) *parisi* n. sp., *Mesalia virginiae* n. sp., *Struthiochenopus hurleyi* n. sp., *Antarctodarwinella austerocallosa* n. sp., *Amauropsis notoleptos* n. sp., *Euspira antarctidia* n. sp., *Antarctiranella tessela* n. gen. n. sp., *Melanella seymourensis* n. sp., *Heteraterma*? n. sp., *Pyropsis*? *australis* n. sp., *Colus delrioae* n. sp., *Pseudofax*? *paucus* n. sp., *Levifusus woolfei* n. sp., *Probuccinum palaiacostatum* n. sp., *Serrifusus binodosum* n. sp., *Sycostoma pyrinota* n. sp., *Strepsidura*? *polaris* n. sp., *Paleopsephaea*? *nodoprasta* n. sp., *Taioma sobrali* n. sp., *Zygomelon apheles* n. sp., *Mitra* (*Eumitra*?) *antarctmella* n. sp., *Marshallaria variegata* n. sp., *Cosmasyrinx* (*Tholitoma*) *antarctigera* n. sp., and *Cylichnania*? cf. *C. impar* Finlay and Marwick, 1937. These gastropods occupied various niches in temperate shallow shelf environments and are represented by only a few individuals at any given locality. The Danian gastropod fauna of Seymour Island is dominated by carnivores (c. 60%) with epifaunal grazers (c. 17%), deposit feeders (c. 13%), epifaunal browsers (c. 7%), and a single ectoparasite (c. 3%) composing the remainder of the fauna.

The fauna extends the geologic range of many groups with several crossing the K-T boundary extinction event. Species-level survivorship is relatively high at 39%. Five gastropod genera (*Antarctodarwinella*, *Antarctiranella* n. gen., *Probuccinum*, *Seymourosphaera*, and *Struthiochenopus*) are endemic to Seymour Island. All species reported from the Danian of Seymour Island are endemic, pointing to a strong degree of provincialism and isolation of the fauna from coeval forms in the Southern Hemisphere. These new data suggest that the molluscan faunas of Antarctica belonged to a distinct biotic province by Danian time.

INTRODUCTION

Paleocene molluscan faunas are rare in the Southern Hemisphere fossil record, and those from the earliest Paleocene (early Danian) are particularly important, in that they provide data on the early biotic recovery and repopulation phase following the Cretaceous-Tertiary (K-T) boundary extinction event. Paleocene faunas are characterized by complex evolutionary histories following the end-Cretaceous event. The survivors of the K-T event and also the appearance of new groups and migrants in the Danian not only herald the beginnings of the modern biota, but further mark the initial recovery and radiation phase immediately following the extinction interval. Few diverse Paleocene molluscan faunas have been recorded in the Southern Hemisphere, and of these faunas, the shallow-marine succession on Seymour Island, Antarctic Peninsula (Text-fig. 1) represents the only well-preserved molluscan record across the K-T interval and into the early Paleocene (Danian). The Seymour Island sequence preserves an important record of the composition of Danian Mollusca, which is providing exciting new data on the extent of the extinction event in the high southern latitudes and also the complex processes of biotic recovery. These records document changing environmental conditions relating to the final breakup of Gondwana, lowering sea-surface temperatures, the K/T extinction event, and the refilling of vacant ecospace with opportunistic and migrant groups of mol-



Text-figure 1.—Index map showing Seymour Island located on the northeast tip of the Antarctic Peninsula.

lusks following the impact event at the end of the Cretaceous.

Most previous work on Antarctic Paleogene mollusks has focused on the highly diverse Eocene assemblages of the La Meseta Formation of Seymour and Cockburn islands (see Wilckens, 1911; Zinsmeister, 1984; Stilwell and Zinsmeister, 1992; Stilwell and Gaździcki, 1998; Stilwell, 2003a) and those taxa recovered from Eocene erratics of the McMurdo Sound region of East Antarctica (Stilwell, 2000; Stilwell and Zinsmeister, 2000). Stilwell and Zinsmeister (1992) recognized 170 species of Eocene Antarctic mollusks, collected from a spectrum of environmental settings spanning barrier islands to nearshore tidal and wave-dominated environments. At least 10 species remain undescribed (JDS, personal observation). Stilwell (2000) recently described 65 species from McMurdo Sound glacial deposits in nearshore shelf settings and facies. Of these, at least 22 species of mollusks, a single brachiopod, and a shark were found to be common to both the Antarctic Peninsula and East Antarctica. The discovery of a significant number of taxa common to both regions indicates unequivocal marine links during the Eocene and circum-Antarctic circulation (Stilwell and Zinsmeister, 2000). These authors concluded that the East Antarctic sea-surface temperatures during the Eocene may have been temperate, based on the composition of characteristic warmer water taxa and the marked percentages of characteristic Indo-Pacific/Tethyan and cosmopolitan genera and subgenera in the fauna. Further, approximately 11% of the 136 mollusk genera and subgenera and all of the species recorded from the Eocene of Antarctica are endemic, indicating that the continent belonged to a distinct biotic province by this time. The strong endemicity of the fauna suggests that the isolation of Antarctica commenced by the early Paleocene.

To date four taxonomic papers have been published on Antarctic Paleocene mollusks; these include a scaphopod *Eodentalium grandis* Medina and del Valle, 1985, from the Sobral Formation; bivalves from the López de Bertodano and Sobral formations (Zinsmeister and Macellari, 1988); one species of aporrhaid gastropod, *Struthiochenopus hurleyi* n. sp. (= *S. nordenskjoldi* (Wilckens, 1910)), originally thought to be restricted to the latest Cretaceous but now known to span the K-T boundary into the Danian interval on Seymour Island (Zinsmeister and Griffin, 1995); and a new genus of probable pseudolivine gastropod, *Seymourosphaera*, represented by four species (Oleinik and Zinsmeister, 1996) in the Danian. These studies reveal that a rich, shallow-marine fauna existed during the early Paleocene along the Antarctic Peninsula. This research not only provides additional insight into the immediate post K-T boundary radiation of marine mollusks in Antarctica and globally, but further, yields exceptional new data on the patterns of biotic recovery of post K-T extinction faunas in the high southern latitudes.

PALEOCENE STRATIGRAPHY

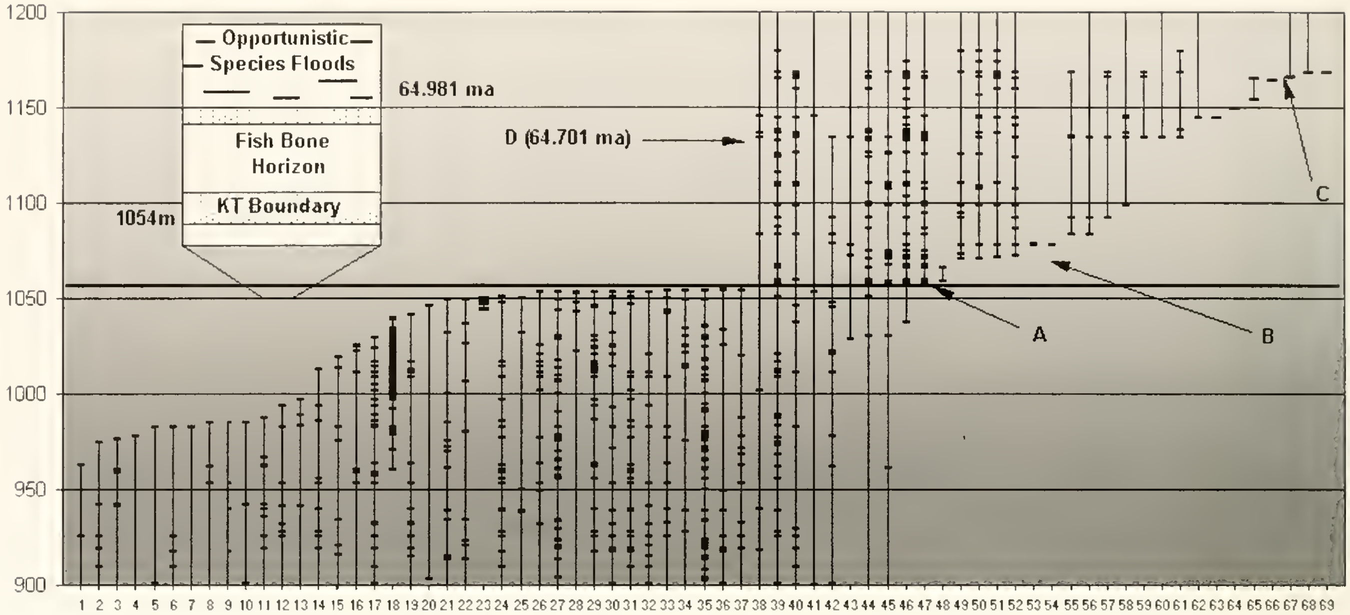
Seymour Island contains the most complete, well-exposed section of Upper Cretaceous to lower Tertiary rocks in the Southern Hemisphere and is composed of highly fossiliferous marine sandstones and siltstones reflecting a spectrum of environments along the shallow- to mid-shelf. The sequence is exposed over the southern two-thirds of the island, an area of approximately 70 km^2. The extensive exposures of these rocks include one of the best K-T boundary sections in the world, which is providing an important opportunity to examine in detail the events at the close of the Cretaceous, not only in a temporal context, but spatially as well (see Zinsmeister, 1998a).

Upper Cretaceous and lower Paleocene strata on Seymour Island consist of approximately 1600 m of homoclinal, gently eastward-dipping, mid-shelf clastic to inner shelf concretionary siltstones and silty sandstones, comprising strata of gray to tan fine-grained sandstone and sandy siltstone of the López de Bertodano and Sobral formations (Zinsmeister, 1998a). The López de Bertodano Formation ranges in age from late Maastrichtian to Danian, and the Sobral Formation is of Danian age. Faunal diversity is relatively high with an admirable record of mollusks, corals, brachiopods, annelids, decapods, echinoderms, and marine reptiles. Substantial tree fragments up to 1 m in diameter are abundant at various levels in the succession. Sedimentological evidence, such as extensive bioturbation in the strata and the absence of primary sedimentological structures, suggests that deposition was, in all likelihood, mid-shelf below effective wave base (Macellari and Zinsmeister, 1983; Macellari, 1988; Oleinik and Zinsmeister, 1996).

The K-T boundary interval is located at the base of a glauconitic unit referred to as the "K-T Glauconite" and crops out in a snake-like pattern along strike for approximately 7 km forming a belt about 2 km wide. No K-T boundary section in the Northern or elsewhere in the Southern Hemisphere has aerial exposures that approach those on Seymour Island. The K-T Glauconite consists of three lithologic units: Lower Glauconite with iridium anomaly (0–1.5 m), Fish Bone Layer (2–3 m), and Upper Glauconite (0–0.1 m) (Zinsmeister, 1998a). Precise dating of events through the extinction-survival-recovery interval on Seymour Island is limited by the absence of calcareous nannoplankton and planktic foraminifera in some horizons.

Work by Huber (1988) suggested that the last Cretaceous planktic foraminifera are recovered from an interval 1 to 4 m below the glauconite bed and that the first Danian species of planktic forms are recognized 1 m below the contact between the López de Bertodano and Sobral formations approximately 45 m above the K-T boundary. This places the contact between these formations with the AP1 Foraminiferal Zone. Huber (1988) referred to this gap in the presence of planktic microfossils as the "dissolution" zone resulting from the perturbation of the sea chemistry following the K-T boundary event. The ubiquitous presence of well-preserved macrofossil assemblages throughout the K-T boundary section indicates that whatever processes dictated the presence or preservation of calcareous plankton did not affect calcareous macrofossils such as mollusks. The K-T boundary is pinned to the Lower Glauconite based on the presence of the iridium anomaly at the base of the "K-T Glauconite" (Elliot *et al.*, 1994). The extinction-survival-recovery phases succeeding the boundary event on Seymour Island span the approximately 90-m interval of Unit 10 of the López de Bertodano Formation and the lower two units of the Sobral Formation (see Text-fig. 3).

Analysis of the geological range data of species recovered from the K-T boundary interval on Seymour Island (Text-fig. 2) reveals that at least 20 species (55%) disappeared through a 16-m interval below the K-T boundary (Zinsmeister, 1998a). Two extinction steps occur 1.5 m and 1 m below the Lower Glauconite. Two species (6%) last occur in the "K-T Glauconite" and 14 (39%) Maastrichtian species pass through the boundary event into the Danian. The Lower Glauconite is interpreted to represent the boundary event with the extinction interval commencing 1 m below, following the study by Kauffman and Harries (1996) on biotic recovery. The survival interval is represented in the Fish Bone Layer and the recovery interval occurs in the Upper Glauconite. Some 11 species of mollusks are present in the "K-T Glauconite," 6 species in the Lower Glauconite, 6 in the Fish Layer and 8 in the Upper Glauconite (WJZ and JDS). Only two species, bivalves *Panopea clausa* and *Seymourtula antarctica*, become extinct within this interval. These bivalves were probably suspension feeders, which were especially hard hit during the K-T boundary event with the significant reduction in primary production at the boundary (Rhodes and Thayer, 1991; Hansen *et al.*, 1993; Sheehan *et al.*, 1996). The Fish Bone Layer (see Zinsmeister, 1998a) is believed to represent the "crisis zone" immediately following the boundary event. The significant occurrence of fish debris over an interval of ~2 to 3 m indicates multiple local kill events, which suggests that the Fish Bone Layer represents an interval of unstable conditions following the extinction event.

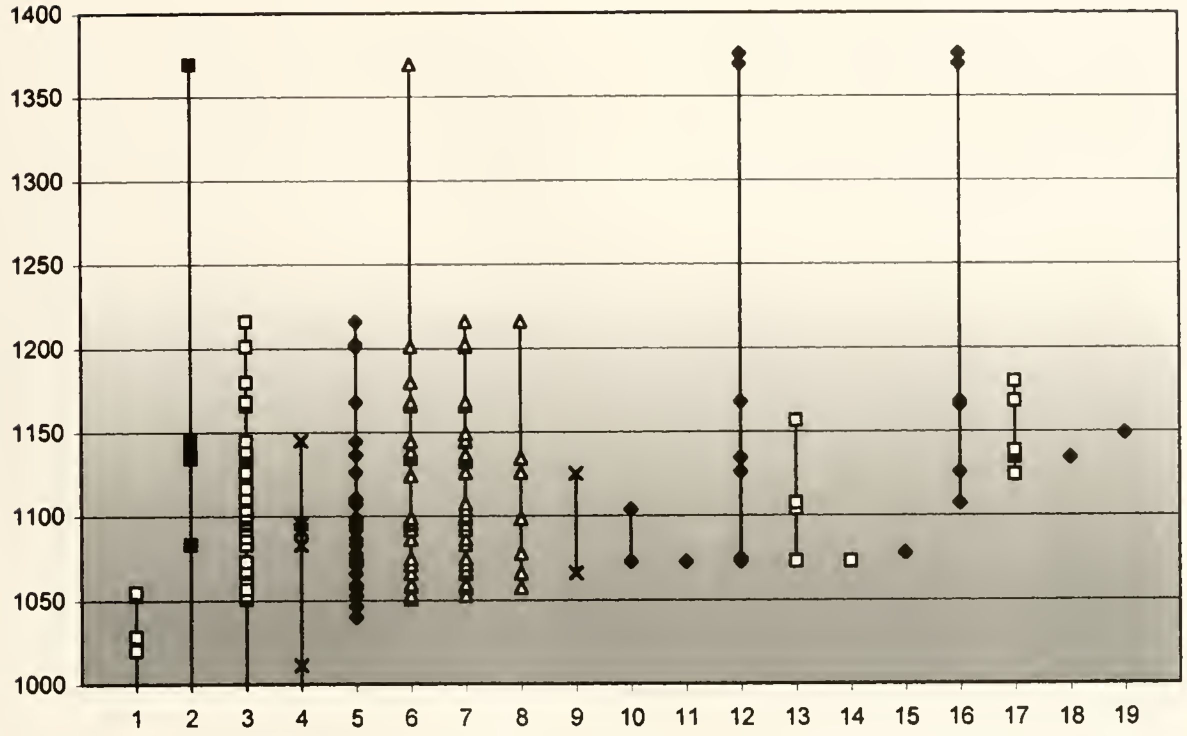


Text-figure 2.—Distribution of latest Maastrichtian and Danian mollusks between 900 m and 1200 m of the López de Bertodano and Sobral formations. Data obtained from 327 localities from ~70 km^2 on the southern two thirds of the island in addition to 25 limited measured sections (see Zinsmeister (1998a) for discussion of data from these limited measured sections). Stratigraphic occurrence of each taxon was determined using Stratigraphic Plane analysis (Zinsmeister, 2001). Dates highlighted in figure were determined by McArthur *et al.* (1998). The expanded box shows the K/T boundary (1054 m); Fish Bone Layer; first appearance of opportunistic *Lahillia larseni* and *Struthiochenopus hurleyi* floods (64.981 ma); A, first appearance of crisis progenitor species *Struthiochenopus hurleyi*; B, first appearance of northern refugia species (*Seymourosphaera* spp.) from Southern South America and cosmopolitan immigrants; C, first occurrence of western refugia immigrant species (*Antarctodarwinella austerocallosa* n. sp.); and D, diversity of Danian molluscan assemblage reaches pre-extinction diversity (64.701 ma). Ages of opportunistic floods and diversity based on strontium isotope profile (McArthur *et al.*, 1998). Taxa in figure—1. *Entolium seymourensis*; 2. *Nekewis* n. sp.; 3. *Nordenskjoldea nordenskjoldi*; 4. *Austrocucullaea oliveroi*; 5. *Pulvinites antarcticus*; 6. *Dozyia drygalskiana*; 7. "*Buccinum*" n. sp. A; 8. *Modiolus pontotocensis*; 9. *Thyasira towsendi*; 10. *Lucina scotti* 11. *Solemya rossiana*; 12. *Seymourtula antarctica*; 13. *Vanikoropsis* n. sp.; 14. *Buccinum* n. sp. B; 15. *Pycnodonte seymourensis*; 16. *Anagaudryceras seymourensis*; 17. *Perotrochus larseniana*; 18. "*Fusus*" *philippiana*; 19. *Pachydiscus ultimus*; 20. *Eselaevitrigonia regina*; 21. *Amauropsis* n. sp.; 22. *Pseudophyllites loryi*; 23. *Zelandites varuna*; 24. *Diplomoceras maximum*; 25. *Austroaporrhais larseni*; 26. *Kitchinites laurae*; 27. *Taioma charcotianus*; 28. *Grossouverites gemmatus*; 29. *Goniomya hyriiformis*; 30. *Pycnodonte vesiculosa*; 31. *Cucullaea antarctica*; 32. *Amberleya spinigera*; 33. "*Cassidaria*" *mirabilis*; 34. *Oistotrigonia pygocelium*; 35. *Cimomia* sp.; 36. *Maorites densicostatus*; 37. *Cyclorisma chaneyi*; 38. *Panopea clausa*; 39. *Pinna freneixae*; 40. *Lahillia larseni*; 41. *Vanikoropsis arktowskiana*; 42. *Mesalia virginiae* n. sp.; 43. *Acesta webbi*; 44. *Cosmasyrinx* (*Tholitoma*) *antarctigera* n. sp.; 45. *Cucullaea ellioti*; 46. *Nucula* (*Leionucula*) *suboblonga*; 47. *Marwickia woodburnei*; 48. *Struthiochenopus hurleyi*; 49. *Ostrea* sp.; 50. *Seymourosphaera elevata*; 51. *Seymourosphaera bulloides*; 52. *Seymourosphaera subglobosa*; 53. *Euspira antarctidia* n. sp.; 54. *Acmaea submesidia* n. sp.; 55. *Bittium* (*Bittium*?) *paleonotum* n. sp.; 56. *Australoneilo casei*; 57. *Conotomaria* sp A.; 58. *Conotomaria* sp. B; 59. *Conotomaria* sp. C; 60. *Saxolucina antarctipleura* n. sp.; 61. *Antarctodarwinella austerocallosa* n. sp.; 62. *Periploma*? sp.; 63. *Seymourosphaera depressa*; 64. *Levifusus woolfei* n. sp.; 65. *Pseudofax*? *paucus* n. sp.; 66. *Colus delrioae* n. sp.; 67. *Sycostoma pyrinota* n. sp.; 68. *Thyasira austrosulca* n. sp.; 69. *Nuculana antarctirostrata* n. sp. Stratigraphic ranges based on regional dip of 7.4°.

The contact between the López de Bertodano unit 10 and the Sobral Formation is marked by a discontinuity. The relief along the discontinuity may be as much as 50 m. Phosphatic nodules, many with fossil cores and corroded concretions, occur along the discontinuity. The discontinuity appears to represent a short period of scouring along storm weather wave base which may have been associated with the first drop in sea level during the earliest Danian. The absence of any significant changes in the composition in the benthic fauna suggests that the disconformity does not represent a significant gap in time within the sequence.

PALEOECOLOGY

Little has been published on the paleoecology of Tertiary Antarctic bivalves, apart from a few works dealing with life habits and environmental settings of Eocene mollusks of the La Meseta Formation of Seymour and Cockburn islands, Antarctic Peninsula, and McMurdo Sound, East Antarctica (Stilwell and Zinsmeister, 1992; Stilwell, 2000); and also Pliocene deposits (Jonkers, 1998a, b, 1999). These assemblages of mollusks were derived from a spectrum of environments along the upper shelf ranging from beach to tidal-dominated nearshore facies. Paleocene mollusks of Antarctica lived in temperate sandy, shallow- to middle-shelf environ-

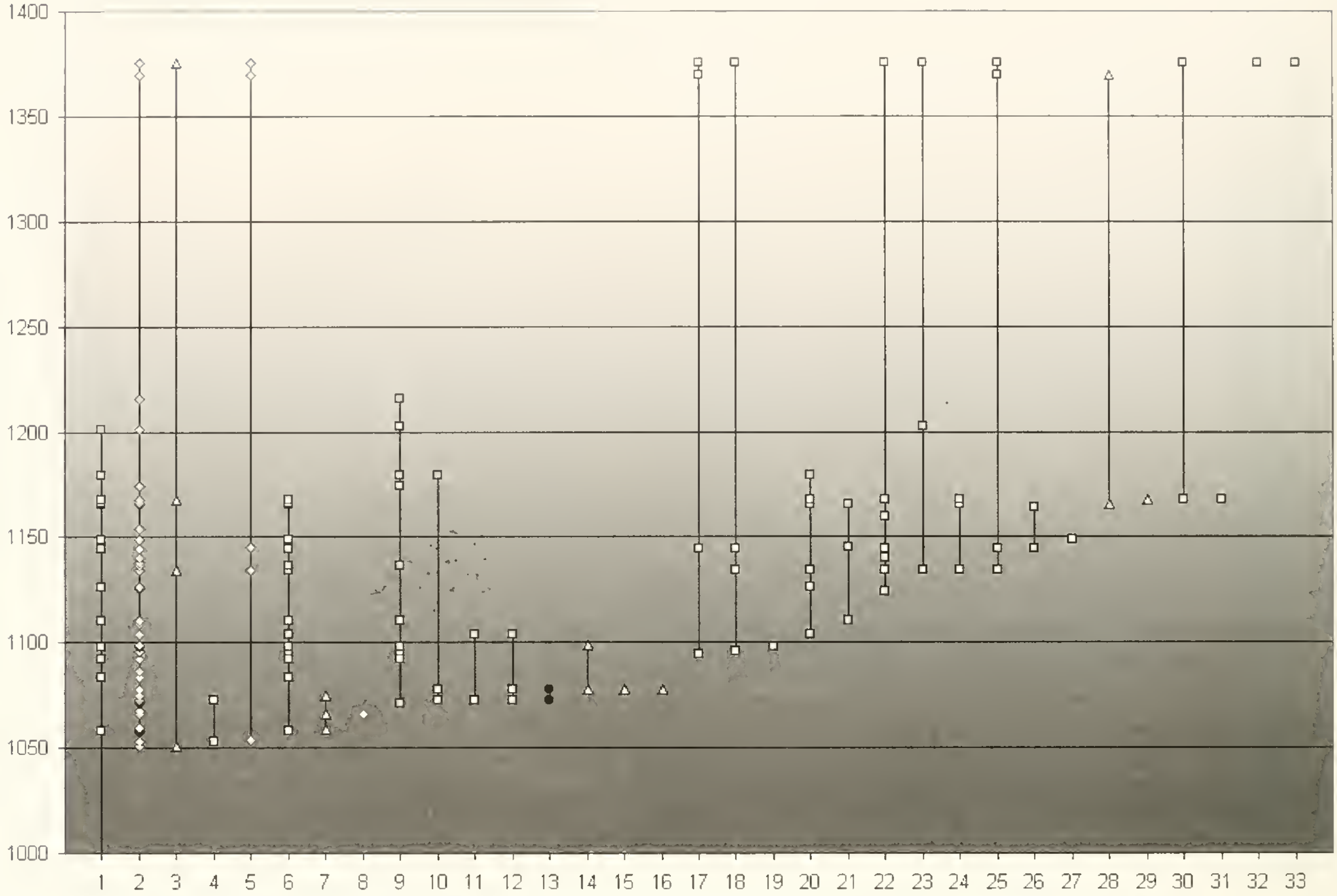


Text-figure 3.—Stratigraphic distribution and feeding strategies of Danian bivalves from the López de Bertodano and Sobral formations, with inferred life habits. Symbols: open square, suspension feeders; solid square, infaunal byssate; cross, epifaunal sessile; solid diamond, deposit feeder; open triangle, shallow infaunal. Acronyms: SF, suspension feeder; DI, deep infaunal; IB, infaunal byssate; SI, shallow infaunal; ES, epifaunal sessile; DF, deposit feeder. 1, *Panopea clausa* (SF-DI); 2, *Pinna freneixae* (SF-IB); 3, *Lahillia larseni* (SF-SI); 4, *Acesta webbi*, (SF-ES); 5, *Nucula (Leionucula) suboblonga* (DF-SI); 6, *Cucullaea ellioti* (SF-SI); 7, *Marwickia woodburnei* (SF-SI); 8, *Saxolucina antarctipleura* n. sp. (SF-SI); 9, *Ostrea* sp. (SF-ES); 10, *Jupiteria*? n. sp. (DF-SI); 11, *Ledina*? n. sp. (DF-SI); 12, *Nucula (Leionucula) hunickeni* (DF-IS); 13, *Periploma*? n. sp. (SF-DI); 14, *Thyasira austrosulca* n. sp. (SF-SI); 15, *Nucula* sp. (DF-SI); 16, *Australoneilo gracilis* (DF-SI); 17, *Lahillia huberi* (SF-SI); 18, *Australoneilo casei* (DF-SI); 19, *Nuculana antarctirostrata* n. sp. (DF-SI).

ments. See Text-figures 3 and 4 for the stratigraphic distribution of primary feeding strategies for the Danian bivalves and gastropods from the López de Bertodano unit 10 and the Sobral Formation.

The Paleocene gastropods from the upper units of the López de Bertodano Formation and the Sobral Formation were derived from predominantly sandy, shallow- to middle-shelf environments in temperate coastal waters of normal salinity. Mollusks generally occur in isolated local shell concentrations throughout the Danian part of the sequence, the only exception being the floods of opportunistic species, chiefly *Lahillia larseni* and *Struthiochenopus hurleyi* n. sp. immediately above the K-T Glauconite at the base of unit 10.

In descending order of species-level diversity and importance, suspension feeders dominate the bivalve fauna with 55% of the assemblage belonging to this category, followed by 45% of deposit feeders. Most of the suspension feeders are shallow infaunal forms attributed to the Cucullaeidae, Lucinidae, Thyasiridae, Cardiidae, Veneridae, and Periplomatidae (see Table 1). The diversity and abundance of epifaunal bivalves are surprisingly rare during the Danian. The occurrence of an undescribed species of *Ostrea* is restricted to the individuals associated with small biohermal concentrations of branching corals that are limited to immediately above the disconformity between unit 10 and the Sobral Formation. Epibyssate suspension feeders are rare and include the rare species, *Acesta webbi* Zinsmeister and Macellari, 1988 (Limidae). Equally uncommon are byssate representatives such as *Pinna freneixae* Zinsmeister and Macellari, 1988, and *Seymourtula antartica* (Wilckens, 1910). Deposit feeders are members of Nuculidae, Nuculanidae and Malletiidae, and are infaunal burrowers. This is consistent with the idea that epifaunal suspension feeders were particularly affected by the phytoplankton crash or the significant drop in primary production at the K-T boundary, leading to the demise of many suspension-feeding groups, compared with deposit feeders (see Rhodes and Thayer, 1991; Hansen *et al.*, 1993; Sheehan *et al.*, 1996). In the Southern Hemisphere, this pattern of selective extinction is corroborated in the K-



Text-figure 4.—Stratigraphic distribution and feeding strategies of Paleocene gastropods from the Lopez de Bertodano and Sobral formations. Symbols (and acronyms): open square, carnivore (C); open diamond, deposit feeder (DF); open triangle, epifaunal grazer (G); solid circle, ectoparasite (EP). 1, *Vanikoropsis arktowskiana* (Wilckens, 1910) (C); 2, *Struthiochenopus hurleyi* n. sp. (DF); 3, *Conotomaria* n. sp. C (EG); 4, *Amauropsis notoleptos* n. sp. (C); 5, *Mesalia virginiae* n. sp. (DF); 6, *Seymourosphaera bulloides* Oleinik & Zinsmeister, 1996 (C); 7, *Acmaea submesidia* n. sp. (EG); 8, *Turritella (Haustator?) parisi* n. sp. (DF); 9, *Seymourosphaera elevata* Oleinik & Zinsmeister, 1996, (C); 10, *Cosmasyrinx (Tholitoma) antarctigera* n. sp. (C); 11, *Cylichnania* cf. *C. impar* Finlay and Marwick, 1937, (C); 12, *Euspira antarctidia* n. sp. (C); 13, *Melanella seymourensis* n. sp. (EG); 14, *Bittium (Zebittium) brooksi* n. sp. (EG); 15, *Bittium (Bittium?) paleonotum* n. sp. (EG); 16, *Conotomaria* sp. A (EG); 17, *Taioma sobrali* n. sp. (C); 18, *Marshallaria variegata* n. sp. (C); 19, *Antarctiranella tessela* n. gen. n. sp. (C); 20, *Levifusus woolfei* n. sp. (C); 21, *Seymourosphaera subglobosa* Oleinik & Zinsmeister, 1996, (C); 22, *Zygomelon apheles* n. sp. (C); 23, *Paleopsephaea? nodoprosta* n. sp. (C); 24, *Probuccinum palaiocostatum* n. sp. (C); 25, *Serrifusus binodosum* n. sp. (C); 26, *Colus delrioae* n. sp. (C); 27, *Pseudofax? paucus* n. sp. (C); 28, *Antarctodarwinella austerocallosa* n. sp. (EG); 29, *Conotomaria* sp. B (EG); 30, *Seymourosphaera depressa* Oleinik & Zinsmeister, 1996 (C); 31, *Sycostoma pyrinota* n. sp. (C); 32, *Heteroterma?* n. sp. (C); 33, *Pyropsis? australis?* n. sp. (C).

T boundary and early Paleocene molluscan faunas of Antarctica and also New Zealand (see Stilwell, 1994).

No bivalves are particularly abundant at any locality apart from a flood of the presumed opportunistic bivalve *Lahillia larseni* (Sharman and Newton, 1897) in the early Danian. *Lahillia larseni* extends in the stratigraphic record from the late Maastrichtian across the K-T boundary into the Danian on Seymour Island, and although it is a relatively common member of the Maastrichtian benthic community, the bivalve is usually represented by fewer than five individuals at any given locality. In the Upper Glauconite on Seymour Island, *L. larseni* is locally abundant, occurring in floods of thousands of individuals. Although the number of individuals of *L. larseni* decreases dramatically above the Upper Glauconite, the species continues to be a prominent member of the Danian benthic community remaining. Only general comments about the Antarctic bivalve community can be made here, as it is a rather depauperate assemblage of only 18 species, and most of these species are generally represented by a few specimens of variable preservation. The number of articulated specimens of these bivalves is relatively high, suggesting that the environments in which they lived were below fair-weather wave base. Indeed, the absence of shallow-water sedimentary structures in

Table 1.—Systematic checklist of Paleocene bivalves from the López de Bertodano and Sobral formations, Seymour Island, Antarctic Peninsula, with inferred life habits. Identifications by J. D. Stilwell and W. J. Zinsmeister. Acronyms used: *DF*, deposit feeder: *IB*, infaunal byssate; *SF*, suspension feeder; *NSI*, nonsiphonate infaunal; *BY*, byssate; *EB*, epifaunal byssate; *SI*, siphonate infaunal.

Bivalvia	Inferred Life Habits
Nuculidae	
Nucula sp.	DF-IB
Nucula (*Leionucula*) *suboblonga* (Wilckens, 1905)	DF-IB
Nucula (*Leionucula*) *hunickeni* Zinsmeister and Macellari, 1988	DF-IB
Nuculanidae	
Nuculana antarctirostrata n. sp.	DF-IB
Ledina? sp.	DF-IB
Jupiteria? sp.	DF-IB
Malletiidae	
Australoneilo gracilis (Wilckens, 1905)	DF-IB
Australoneilo casei Zinsmeister and Macellari, 1988	DF-IB
Cucullaeidae	
Cucullaea ellioti Zinsmeister and Macellari, 1988	SF-NSI
Pinnidae	
Pinna freneixae Zinsmeister and Macellari, 1988	SF-NSI-BY
Limidae	
Acesta webbi Zinsmeister and Macellari, 1988	SF-EB
Seymourtula antarctica (Wilckens, 1910)	SF-EB
Ostreidae	
Ostrea sp.	SF-ES
Lucinidae	
Saxolucina antarctipleura n. sp.	SF-SI
Thyasiridae	
Thyasira austrosulca n. sp.	SF-SI
Cardiidae	
Lahillia larseni (Sharman and Newton, 1897)	SF-SI
Lahillia huberi Zinsmeister and Macellari, 1988	SF-SI
Veneridae	
Marwickia woodburnei Zinsmeister and Macellari, 1988	SF-SI
Panopea clausa Wilckens, 1910	SF-SI
Cyclorisma chaneyi Zinsmeister and Macellari, 1988	SF-SI
Periplomatidae	
Periploma? n. sp.	SF-SI

Unit 10 of the López de Bertodano Formation and the Sobral Formation corroborates this observation.

The Paleocene gastropods from the López de Bertodano and Sobral formations (Table 2) were derived from predominantly sandy, shallow- to middle-shelf environments in temperate coastal waters of normal salinity. In descending order of species-level diversity and importance, the gastropod fauna encompasses five general groupings: carnivores, epifaunal grazers, deposit feeders, epifaunal browsers, and a single ectoparasite. It is difficult to ascertain from the fossil record if some of these taxa were predominantly epifaunal or infaunal forms or at specific times during their life cycle could inhabit both realms (*e.g.*, Naticidae, Cerithiidae, Struthiolariidae). The carnivores dominated the Paleocene Antarctic shelf environments with just over 60% of recorded gastropod species belonging to this category. These families include the Naticidae, Tudiclidae, Buccinidae, Fasciolariidae, Volutidae, Mitridae, Turridae, and Cylichnidae. Most of these taxa are considered to be epifaunal mobile taxa, apart from the volutes and naticids, which could have been either infaunal or epifaunal comparable to Recent forms. Carnivores apparently dominated the immediate, post K-T boundary shelf environments, and were opportunistic, rapidly evolving species of so-called "bloom families" (*sensu* Hansen, 1988) that flourished in Paleocene marine environments. Epifaunal grazers such as the pleurotomariids and the single acmaeid make up 17% of the gastropod fauna, although it is possible that some pleurotomariids were either unspecialized omnivores or carnivores (see notes by Darragh and Kendrick, 1994, p. 5). Deposit feeders were a significant element in the Antarctic Paleocene community, but still represent only about 7% of the total species-level diversity; these include members of the Aporrhaidae and Struthiolariidae. Epifaunal browsers that fed largely on detritus make up a small proportion of the fauna at only 7% and these include cerithiids of the *Bittium* group. Turritellids are largely suspension feeders (Allmon, 1988), and make up about 6% of the species total. *Melanella* was in all likelihood an ectoparasite that lived on echinoderms, consistent with most living forms, and makes up the smallest category of Antarctic Paleocene gastropods at only 3% of the total. None of the recorded gastropods from the López de Bertodano and Sobral formations are particularly abundant at any locality, except for *Struthiochenopus hurleyi* n. sp. and *Bittium* (*Zebittium*) *brooksi* n. sp. *S. hurleyi* n. sp becomes locally abundant immediately above the upper glauconite horizon. Its abundance in association with the *Lahillia* floods suggests that it is one of the opportunistic species which appear in great number following the boundary event. Throughout the rest of the López de Bertodano and Sobral formations *S. hurleyi* n. sp. is locally abundant. *B.* (*Z.*) *brooksi* forms local nearly monotypic concentrations at several localities in the lower 50 m with its first appearance in the Fish Bone Horizon. This overall rarity and rather low species-level diversity of gastropods attests to the significant impact of the K-T boundary event and is a reflection of the decimation and general low diversity of

Table 2.—Systematic checklist of Paleocene gastropods from the Lopez de Bertodano and Sobral formations, Seymour Island, Antarctic Peninsula, with inferred life habits. Identifications by J.D. Stilwell and A.E. Oleinik. Acronyms used: DF, deposit feeder; SF, suspension feeder; C, carnivore; EB, epifaunal browser; EG, epifaunal grazer; EP, ectoparasite; E/I, epifaunal/infaunal; EM, epifaunal mobile.

Table 2.—Continued.

Gastropoda	Inferred Life Habits
Pleurotomariidae	
Conotomaria sp. A	EG-C?
Conotomaria sp. B	EG-C?
Conotomaria sp. C	EG-C?
Acmaeidae	
Acmaea submesidia n. sp.	EG
Cerithiidae	
Bittium (Bittium?) paleonotum n. sp.	E?B
Bittium (Zebittium) brooksi n. sp.	E?B
Turritellidae	
Turritella (Haustator?) parisi n. sp.	SF-E/I
Mesalia virginiae n. sp.	SF?-E/I?
Aporrhaidae	
Struthiochenopus hurleyi n. sp.	DF
Struthiolariidae	
Antarctodarwinella austerocallosa n. sp.	DF-E?/I?
Vanikoridae	
Vanikoropsis arktowskiana (Wilckens, 1910)	I?/E?-C
Naticidae	
Amauropsis notoleptos n. sp.	C-E?/I?
Euspira antarctidia n. sp.	C-E?/I?
Ranellidae	
Antarctiranella tessela n. gen. n. sp.	C-EM
Eulimidae	
Melanella seymourensis n. sp.	EP
Tudiclidae	
Heteroterma? n. sp.	C-EM
Pyropsis? australis n. sp.	C-EM
Buccinidae	
Colus delrioae n. sp.	C-EM
Pseudofax? paucus n. sp.	C-EM
Levifusus woolfei n. sp.	C-EM
Probuccinum palaiocostatum n. sp.	C-EM
Serrifusus binodosum n. sp.	C-EM
Sycostoma pyrinota n. sp.	C-EM
Seymourosphaera subglobosa Oleinik & Zinsmeister, 1996	C-EM
Seymourosphaera depressa Oleinik & Zinsmeister, 1996	C-EM
Seymourosphaera bulloides Oleinik & Zinsmeister, 1996	C-EM
Seymourosphaera elevata Oleinik & Zinsmeister, 1996	C-EM
Strepsidura? polaris n. sp.	C-EM
Fasciolariidae	
Paleopsephaea? nodoprosta n. sp.	C-EM
Taioma sobrali n. sp.	C-EM
Volutidae	
Zygomelon apheles n. sp.	C-EM
Mitridae	
Mitra (Eumitra?) antarctmella n. sp.	C-EM
Turridae	
Marshallaria variegata n. sp.	C-EM
Cosmasyrinx (Tholitoma) antarctigera n. sp.	C-EM
Cylichnidae	
Cylichnania cf. *C. impar* Finlay and Marwick, 1937	I?-C

invertebrate faunas during the earliest Danian resulting from the mass extinction.

COMPOSITION AND PALEOBIOGEOGRAPHY

Paleocene molluscan faunas are rare in the Southern Hemisphere, and earliest Paleocene faunas are particularly so, and are represented solely by the early Danian fauna of Seymour Island. This fauna is extremely important in that it not only fills a major gap in our knowledge of early Paleocene Austral molluscan faunas, but provides much new data on the steps of biotic recovery following the K-T boundary event. Other Austral Paleocene faunas have been thoroughly documented and/or await further attention, but are either late early to late Paleocene in age or not particularly well dated; these include the late early to late Paleocene faunas of New Zealand (Finlay and Marwick, 1937; Stilwell, 1993, 1994; JDS, unpublished data), late Paleocene of Chatham Islands (Campbell *et al.*, 1993; Stilwell and Grebneff, 1996; Stilwell, 1997, 2003a; JDS, unpublished data.), mid- to late Paleocene of Victoria and Western Australia, (Singleton, 1943; Darragh, 1994, 1997; Stilwell, 2003b; JDS, personal observation), and poorly dated Paleocene faunas of southern South America, predominantly southern Argentina (Olivero *et al.*, 1990; Camacho, 1992; Griffin and Hünicken, 1994; JDS, personal observation). The Paleocene fauna of Antarctica provides important information on the composition of immediate post K-T faunas during the early recovery phase following the mass extinction event.

The Antarctic gastropod fauna records taxa that are either the oldest member of respective genera (*e.g.*, *Bittium* (*Zebittium*), *Antarctodarwinella*, *Amauropsis?*, *Melanella*, *Heteroterma?*, *Pseudofax?*, *Colus*, *Levifusus*, *Probuccinum*, *Strepsidura?*, *Zygomelon*, *Vexillum* s.l., *Marshallaria*, *Cosmasyrinx* (*Tholitoma*), and *Cylichnania*) or some that survived the K-T event in the earliest Danian (*e.g.*, *Perotrochus*, *Conotomaria*, *Ac-*

maea, Struthiochenopus, Vanikoropsis, Euspira, "Pyropsis," Serrifusus, Sycostoma, Paleopsephaea, and *Taioma*). Others are either members of widespread genera that may have evolved in the high southern latitudes or of uncertain origin, representing Indo-Pacific/Tethyan or Temperate forms (*e.g., Perotrochus, Conotomaria, Amauropsis, Antarctiranella* n. gen., *Pyropsis?, Heteroterma?, Colus, Strepsidura?, Levifusus, Serrifusus,* and *Paleopsephaea*). Some 34% of genera and subgenera make up this category. Only four genera, *Antarctodarwinella, Antarctiranella* n. gen., *Probuccinum,* and *Seymourosphaera,* are endemic to Antarctica, and compose between 12.5% and 16% of the total fauna. *Antarctodarwinella austerocallosa* n. sp. is the progenitor of two Eocene species, *A. ellioti* Zinsmeister, 1976, recorded from Units II–III of the La Meseta Formation, and younger *A. nordenskjoldi* (Wilckens, 1911), distributed in Units III–V. *Antarctodarwinella* became extinct during the late Eocene. These taxa form a lineage with an observed gap in the late Paleocene to early Eocene record in Antarctica. This gap in the record may contribute to the observable difference in overall morphology in *A. austerocallosa* n. sp. and younger Eocene forms *A. ellioti* and *A. nordenskjoldi,* discussed in detail in the systematics section of this work (pp. 31–32). *Antarctiranella* n. gen. is distinct from other coeval and younger ranellid gastropods, so probably represents a short-lived group that evolved during an early stage of the radiation of this family and became extinct sometime during the Paleocene. *Seymourosphaera* is closely related to the pseudolivine gastropod, *Austrosphaera* from the Late Cretaceous to Paleocene of southern Argentina (Tierra del Fuego), and most likely is descended from *Austrosphaera* (Oleinik and Zinsmeister, 1996). *Probuccinum* has been recorded only in Antarctica where it spans the entire Cenozoic beginning in the earliest Paleocene and today has a circum-Antarctic distribution in depths of 140 m to more than 600 m (see Dell, 1990). However, there is a gap of nearly 65 m.y. in the fossil record of this group and it is surprising that there is no evidence of *Probuccinum* in the La Meseta Formation or younger Tertiary marine sediments. This may reflect the migration of mid-Tertiary forms to deeper waters, of which we have no record.

Paleoaustral gastropods dominate the fauna at 44% (including endemic taxa in accordance with Fleming's (1963) original ideas). Cosmopolitan groups make up 22% of the total fauna. At species level, however, all taxa are endemic. Thus, the composition of the fauna has generally a cosmopolitan or at least a widespread flavor at genus level with relatively few provincial forms. Further, few taxa recorded in the Antarctic Paleocene are present in the Cretaceous deposits in the James Ross Basin, apart from *Acmaea, Struthiochenopus, Euspira,* and *Taioma,* but some are known from other northern and southern regions in Cretaceous deposits (*e.g., Perotrochus, Conotomaria, Bittium, Turritella* s.l., *Mesalia, Amauropsis, "Pyropsis," Levifusus?, Serrifusus?, Paleopsephaea,* and *Cylichnania*). Thus, most of the Paleocene Antarctic gastropod fauna is composed of groups that originated in the Late Cretaceous or earliest Tertiary, either from southern circum-Pacific regions, or the north, or evolved in the Antarctic region and dispersed further afield during the Cenozoic. The patterns of composition of the fauna and biotic recovery in the Paleocene reflect several factors, among them the final breakup of the supercontinent Gondwana with ensuing changes to oceanic circulation and climate, and all of these factors play significant roles in the observed biodiversity patterns.

The marked endemism at species level for the Antarctic Peninsula region during the Paleocene points to a strong degree of provincialism and also isolation from other coeval recorded faunas around the southern circum-Pacific. However, on a higher grade of paleobiogeographic scale, there is a moderate degree of similarity of faunas around the southern circum-Pacific margin. This reinforces the proposition posed by Crame (1996) and Stilwell (1997) that the occurrence of disjunct species of congeners around the southern circum-Pacific reflects evolution in isolation, resulting from retracted distributions of cosmopolitan taxa during the latter part of the Cretaceous. Further, the breakup of Gondwana would have increased the sea-surface temperature gradient and maximized shelf area for dispersal of marine invertebrate taxa, but it would have also enhanced provinciality of faunas due to segmentation of presumed oceanic circulation patterns during the latest Cretaceous and early Tertiary (Stilwell, 1997). Progressive continental reshuffling and associated changes in oceanic circulation played a large role in disrupting biotic distributions late in the Mesozoic and early Cenozoic. This trend commenced during the latter part of the Mesozoic, especially during the mid- to Late Cretaceous period, when the final breakup of Gondwana was well underway. During this time the Antarctic fauna belonged to the Austral Province of Kauffman (1973).

Preliminary biodiversity and paleobiogeographic trends are relatively consistent with data on the tectonic and paleo-oceanographic history of the Austral region, but still require much refinement and rigorous testing. The Early Cretaceous period saw the breakup of East Gondwana, including Australasia, especially by 130 Ma when initial rifting had begun between Australia and greater India (see review of Gondwana breakup by Lawver *et al.,* 1992). Provinciality of shelf faunas increased throughout the Late Jurassic and Early Cretaceous when most of the Southern Hemisphere belonged to the Austral Province. Although this provinciality decreased from Aptian to Maastrichtian times in the Australian region (Kauffman, 1973; Veevers, 1984; Stilwell and Crampton *in* Henderson *et al.*, 2000; Stilwell and Henderson, 2002), so did the genus-level diversity, reflecting gradual contraction and withdrawal of shallow epicontinental seas with fluctuations throughout the Late Cretaceous (Frakes *et al.*, 1987). Seaways were most widespread during the Aptian-Albian in Australia, but were most extensive during the latest Cretaceous for Antarctica, New Zealand, Chatham Islands, and New Caledonia, reflecting the final fragmentation of these regions from the Gondwana margin and resultant thermal subsidence and transgression. As such, there was increased shelf area resulting from the transgression, but oceanic circulation patterns were becoming increasingly segmented.

Zinsmeister (1982) and Huber and Watkins (1992) proposed that the southern Pacific margin was dominated by counterclockwise circulation with a western boundary current flowing southward along Australia and New Zealand comparable to the present-day Kuroshio Current of the North Pacific. Hence, the southern circum-Pacific was, for the most part, isolated by the prevailing oceanic circulation from other major oceans in the Southern Hemisphere. However, during the late Campanian and early Maastrichtian (c. 79 Ma), microfossil evidence, including the presence of latest Cretaceous microfossils in reworked glacial diamictites in the Transantarctic Mountains (Huber and Watkins, 1992), points to circum-Antarctic flow of shallow surface waters and the presence of a Trans-Antarctic seaway.

Stilwell (1997) presented two scenarios for dispersal of molluscan larvae along shallow, southern circum-Pacific shelves during the latest Cretaceous. First, it is possible that larvae were dispersed from currents flowing from the New Zealand–Chatham Rise region to the margins of Marie Byrd Land–Antarctic Peninsula and through the shallow gateway between the Antarctic Peninsula and southern South America. Second, currents originated from the New Zealand–Chatham Rise region and eventually progressed northward through the Trans-Antarctic seaway to reach the Antarctic Peninsula. Because part of Western Antarctica was thought to be a series of islands (Zinsmeister, 1987), larvae may have been distributed through these areas, notwithstanding the probability of a Trans-Antarctic seaway. But did this occur? The distances between the New Zealand–Chatham Rise and Antarctic Peninsula/southern South America regions were still immense during the Late Cretaceous, despite their high-latitude position (approximately 90° of longitude or an estimated 4000 km), such that of macroinvertebrates, only those with planktotrophic teleplanic larvae capabilities would have been the most successful of marine organisms to make the long journey along the increasingly dissected Gondwana margin. No species-level gastropods have a wide distribution in the Southern Hemisphere during the latest Cretaceous and only four recorded gastropods traversed the nearly 1000-km distance along the Chatham Rise–New Zealand subcontinent (Stilwell, 1997, 1998).

With the final breakup of Gondwana at the close of the Mesozoic, the Austral Province lost its identity. One of the smaller faunal provinces, the Weddellian Province (Zinsmeister, 1979), resulting from the dissolution of the Austral Province, occupied the region south of the northeastern coast of Australia and New Zealand, extending westward and including the continental shelf areas along Antarctica and southern South America. The concept of the Province can be expanded to include New Caledonia and Chatham Islands, based on quantitative analyses of molluscan similarities (Stilwell, 1991, 1994, 1997). Another recent study on Maastrichtian gastropods of Antarctica supports the existence of the Weddellian Province during the latest Cretaceous (Fricker, 1999).

Faunal comparisons around the southern circum-Pacific indicate that Western Australia can be excluded from the Weddellian Province. Evidence supports the idea that there was virtually no faunal interchange between Western Australia and the southern circum-Pacific during the latest Cretaceous (Darragh and Kendrick, 1991), and also Paleocene faunas of southeastern Australia and other Austral localities (Darragh, 1994, 1997). Molluscan evidence (Stilwell, 1994, and JDS, unpublished data) supports the contention that the Weddellian Province was probably short-lived, existing only through the Campanian-Maastrichtian time, after which the province was either reduced quite considerably or had broken up into smaller biogeographic entities by the earliest Tertiary, much earlier than the Eocene proposed by Zinsmeister (1979, 1982). Distributions of Paleogene Austral mollusks indicate that the Weddellian Province was reduced during the earliest Tertiary to the area of southeastern Australia, New Zealand, and possibly the Chatham Islands, and that the Antarctic Peninsula and southern South America probably also belonged to separate provinces or subprovinces (Stilwell, 1991, 1994). This pattern most likely reflects the environmental perturbations at the end of the Cretaceous resulting from the continental redistribution (Stilwell, 1997).

The Paleocene bivalve fauna of Antarctica is the oldest recorded Austral Cenozoic assemblage and as such, provides an important data set for early Paleocene faunal composition and paleobiogeographic distributions. As stated by Stilwell (2000), the Paleocene molluscan faunas of Antarctica yield significant information on the composition of immediate post-K-T faunas in the Southern Hemisphere, not found elsewhere, and also patterns of the early recovery phases following the mass extinction event. The composition of the bivalve fauna corroborates the findings of Stilwell (2000) on the paleobiogeographic history of Paleocene Antarctic gastropods, the details of which will not be repeated herein.

In summary, at species level all Antarctic Paleocene bivalves are endemic, indicating that this marked endemism points to a strong degree of provinciality and also isolation of the Antarctic Peninsula faunas with other Paleocene faunas around the southern circum-Pacific. The Paleocene Antarctic faunas, in all likelihood, belonged to a distinct biotic province by Paleocene time. The distribution of Paleogene Austral mollusks suggests that the Weddellian Province of Zinsmeister (1979) was greatly reduced by the early Tertiary and had dissipated into separate biotic entities by this time (see Stilwell, 1997).

At genus level the composition of the bivalve fauna has a strong cosmopolitan flavor with a weaker Paleoaustral component. Widespread and long-ranging bivalves dominate the assemblage at approximately 75% of the recorded genera of bivalves, including *Nucula, Leionucula, Nuculana, Ledina*?, *Jupiteria*?, *Cucullaea, Pinna, Acesta, Saxolucina, Thyasira,* and *Periploma*?. Most of these genera provide new and additional records of these groups in the fossil record of Antarctica by extending stratigraphic ranges. As an example, *Saxolucina* and *Periploma*? were previously recognized in the Eocene of Seymour Island (Stilwell and Zinsmeister, 1992), but the Paleocene records expand the range to include first occurrences in the Danian. The possible record of *Ledina* may indicate an Austral origin for this nuculanid group, previously reported from the late early Paleocene of New Zealand (see review by Stilwell, 1994), and subsequent younger Paleogene deposits elsewhere.

Only 25% of the bivalves are Paleoaustral forms with a long history in the Southern Hemisphere; these include *Australoneilo, Lahillia, Marwickia* and *Cyclorisma*. Of note, three groups, apart from *Marwickia*, have latest Cretaceous representatives in the Austral realm, indicating that they crossed the K-T boundary into the Tertiary. *Australoneilo* and *Cyclorisma* disappeared from the fossil record sometime during the Eocene in Antarctica, whereas *Lahillia* became extinct during the Miocene in South America. The earliest Paleocene Antarctic record of *Marwickia* predates the New Zealand record (Beu and Maxwell, 1990; Stilwell, 1994) by a few million years. Thus, many of the bivalve and gastropod groups present in the Antarctic Paleocene originated in the Late Cretaceous, either from southern circum-Pacific regions, or the north. Some taxa such as *Pinna* have had a very long history in Antarctica, being first recorded in Upper Jurassic sediments (Willey, 1975), but disappeared from the fossil record in the Eocene. The disappearance of *Australoneilo, Lahillia, Cyclorisma,* and other mollusk groups in the Eocene of Antarctica most likely corresponds to deteriorating climatic condition at the close of the Eocene.

One aspect of the Paleogene faunas of Antarctica that is not commonly recognized is that the shelf region along Antarctica was the source for a number of groups of benthic invertebrates that have a wide and varied distribution in mid- and low latitudes during the latter part of the Cenozoic. Zinsmeister and Feldmann (1984) discussed the phenomenon of heterochroneity of the marine faunas of the Southern Hemisphere. The recognition of the earliest occurrence of a number of mollusks, arthropods and echinoderms on Seymour Island clearly indicates that the high southern latitudes around Antarctica during the Paleogene were the site of diversification of the marine faunas associated with climatic change and the development of marked seasonality. These newly evolved groups were restricted to the shelf region around Antarctica until conditions in the mid-latitudes cooled enough to allow them to migrate northward. In addition to the northward migration of shallow-water taxa, a number of taxa (*Metacrinus* (crinoid), *Zoroaster* and *Ctenophoraster* (sea stars), and *Lyreidus* (decopod)) migrated into deep marine environments as cooling of the deep-sea environment developed during the Eocene.

SUMMARY

The early Danian molluscan fauna from the López de Bertodano and Sobral formations provides a unique insight into the origin of the Cenozoic marine fauna following the terminal Cretaceous extinction event. It is clear that climatic cooling during the Maastrichtian and the final breakup of Gondwana had initiated major changes in the composition of marine faunas in the southern high latitudes and set the stage of the mass extinction at the end of the Cretaceous. Although diversity dropped dramatically at the K-T boundary, ~39% of the molluscan fauna survived the boundary event. Initial recovery of the shelf faunas was characterized by floods of opportunitistic groups such as *Lahillia* and *Struthiochenopus* followed by the reappearance of cosmopolitan and refugia Lazarus species. As the diversification within the faunas began to increase, the isolation of Antarctica became more pronounced as the other southern continents moved northward. Major changes in oceanic circulation associated with the final breakup of Gondwana enhanced the isolation of the marine faunas along Antarctica. Only with the onset of glacial conditions and marked cooling of both the shallow and deep-sea realms, did the Antarctic faunas begin to migrate northward into the mid-latitudes.

SYSTEMATIC PALEONTOLOGY

There are of number of nomenclatural problems with several of the taxa described and figured by Otto Wilckens (1910). To understand the source of these problems a brief review of field activities of the Swedish South Polar Expedition is necessary. Fossil material from Seymour Island was collected by Otto Nordenskjold, Gunnar Andersson and other members of the Swedish South Polar Expedition. Only Gunnar Andersson was a trained geologist and his work on the island was limited to the last days of the expedition's stay in Antarctica. Nordenskjold's field work on Seymour Island was hindered by circumstances which prevented them from recognizing the remarkable paleontologic record on the island.

During the two and a half years spent in the James Ross Basin only a limited amount of time was spent collecting fossils. Seven sledging trips to Seymour Island were made during this period; except for the last trip led by Gunnar Andersson during late October and early November of 1903, each visit was three days or less in length and none of the personnel on these visits was a trained geologist. Another factor that played a central role in the limited success of their work on Seymour Island was that all sledging trips along the coast were restricted to the east coast which is the least fossiliferous region of the island. The only exception was the Bodman party during November 21 through 25 of 1902, which went along the west coast of the island and crossed through Cross Valley to the east coast to collect penguin eggs at the penguin rookery. Although the Bodman party passed through some of the most fossil-rich regions of the Upper Cretaceous and Danian strata on the island, none of the personnel in Bodman's party had any scientific training and only a few fossils without any locality data were collected.

As a consequence, many of the fossils Wilckens described had only the most superficial locality data. Only during the last visit to Seymour Island in the spring of 1903 by Andersson were any fossils collected with adequate field data. Combined with the fact that nothing was known about stratigraphy of the Late Cretaceous/earliest Tertiary, several of Wilckens' taxa were based on material collected from different stratigraphic horizons and ages. Another factor that influences Wilckens' systematic study of the fauna was the common belief during the early part of the 20th century that the Danian was the uppermost part of the Cretaceous. It is interesting to note that Andersson (1904) felt that because of the absence of any ammonites, the fossils from the Swedish South Polar Expedition (SSPE) locality 9 were, indeed, Tertiary, but Wilckens included them with the Cretaceous taxa he described.

The mollusks described and figured in this paper are housed at the National Museum of Natural History, Washington, DC (USNM); Department of Earth and Atmospheric Sciences, Purdue University (PU); University of Buenos Aires, Argentina (UBA); Institute of Geological Sciences, London (IGS); and the Naturhisktoriska Riksmuseet, Stockholm, Sweden (Mo). Additional material from Seymour Island is housed in the British Museum of Natural History; British Antarctic Survey, Cambridge; and the Centro de Investigaciones en Recursos Geologicos, Buenos Aires, Argentina. The systematic paleontology section in this work incorporates a complete catalogue of all molluscan species recorded from the Paleocene of Antarctica. Where appropriate, in some species, the taxonomy is updated and modernized, in accordance with recent advances in molluscan systematics.

The Appendix (p. 51) contains stratigraphic data for Maastrichtian and Danian localities on Seymour Island, as well as individual occurrences and abundance data for Danian species.

Phylum **MOLLUSCA** Linnaeus, 1758

Class **BIVALVIA** Linnaeus, 1758

Subclass **PALAEOTAXODONTA** Korobkov, 1954

Order **NUCULOIDA** Dall, 1889

Superfamily **NUCULOIDEA** Gray, 1824

Family **NUCULIDAE** Gray, 1824

Subfamily **NUCULINAE** Gray, 1824

Genus **NUCULA** Lamarck, 1799

Type species (by monotypy).—*Arca nucleus* Linnaeus, 1758.

Subgenus **Leionucula** Quenstedt, 1930

Type species (by original designation).—*Nucula albensis* d'Orbigny, 1844

Nucula (Leionucula) suboblonga (Wilckens, 1907)

Plate 1, Figures 1–4, 8

Nucula suboblonga Wilckens, 1907, pp. 53; 1910, pp. 22–24, pl. 2, figs. 1a,b, 2; Zinsmeister and Macellari, 1988 p. 256, figs. 3.1–5.

Nuculoma (*Palaeonucula*) *poyaensis* Freneix, 1958 (1956), pp. 157–158, pl. figs. 1a, b.
Leionucula poyaensis (Freneix). Freneix, 1980, pp. 75–77, pl. 1, figs. 1–4.

Dimensions.—Hypotype USNM 404809, length 44 mm; height 30 mm.

Type.—Lectotype MO 1424a.

Localities.—9, 459, 477, 497, 514, 725, 754, 757, 762, 776, 777, 1119, 1130, 1131, 1134, 1135, 1136, 1148, 1430, 1431, 1432, 1467, 1473, 1502, 1505, 1506, 1510, 1519, 1697, 1529, 1531, 1533, 1534, 1535, 1536, 1537, 1548, 1586.

Material.—150 specimens.

Stratigraphic distribution.—1040 to 1216 m.

Discussion.—This species was originally described from the Upper Cretaceous sequence at Cerro Cazado in southern Patagonia (Wilckens, 1907). In the same paper, Wilckens described a second species of *Nucula* (*L.*) *oblonga* and separated the two by the more centrally located umbones of *N.* (*L.*) *suboblonga*. Unfortunately he did not figure *N.* (*L.*) *suboblonga* because he did not have a "perfect" specimen. Wilckens (1910) subsequently reported the occurrence of this species on Seymour Island and included the first figure of the species. Freneix (1958) described a similar species (*N.* (*L.*) *poyaensis*) from New Caledonia. Because the dimensions of *N.* (*L.*) *poyaensis* and *N.* (*L.*) *suboblonga* are nearly identical, we believe that the two are conspecific.

Nucula (*L.*) *suboblonga* has an extensive range on Seymour Island, first appearing in the middle part of the Maastrichtian of the López de Bertodano and extending through the Sobral Formation. Although it is not very abundant in the Maastrichtian, it becomes a very common element throughout the Danian on Seymour Island.

Nucula (Leionucula) hunickeni Zinsmeister and Macellari, 1988
Plate 1, figures 6, 7

Nucula (*Leionucula*) *hunickeni* Zinsmeister and Macellari, 1988, 256–257, figs. 3.10, 3.11.

Dimensions.—Holotype USNM 404814; length 23 mm, height 17 mm, width of paired valves 12 mm.

Type.—Holotype USNM 404814.

Stratigraphic occurrence.—Middle part of unit 1 of the Sobral Formation.

Localities.—9 (type), 497, 746, 1104, 1505, 1519, 1534.

Material.—31 specimens.

Stratigraphic range.—1072 to 1375 m.

Discussion.—This species of *Leionucula* may be distinguished from *Nucula* (*L.*) *suboblonga* by its smaller size and straighter anterior, which slopes at a steeper angle. *Nucula* (*L.*) *hunickeni* has only been encountered in a dark-brown silty sandstone facies of the Sobral Formation.

Nucula species
Plate 1, figures 13, 16

Locality.—1535.

Material examined.—One poorly preserved specimen.

Stratigraphic range.—1078 m.

Discussion.—The affinity of this poorly preserved, minute nuculid bivalve is uncertain, as the delicate, disarticulated shell is partly immersed in fine matrix. The specimen is 2.5 mm in length and 2.0 mm high, circular to slightly ovate, gently inflated, with ornamentation of closely spaced commarginal riblets that become coarser and broader near the ventral margin. There is also evidence of a poorly developed radial element. The specimen is reminiscent of *Linucula*? *mcmurdoensis* Stilwell, 2000 (p. 265, pl. 1, figs. D, J) from the Eocene of East Antarctica in size and outline, but *Nucula* sp. has more developed commarginal ornamentation. The sculpture of *Nucula* sp. is comparable to *Nucula* (*Leionucula*) *palmeri* (Zinsmeister, 1984) (pp. 1501–1502, fig. 3A, B; Stilwell and Zinsmeister, 1992, pp. 47–48, pl. 1, figs. a, b), from Unit III of the La Meseta Formation, also Eocene, of Seymour Island, but *Nucula* sp. is more ovate, whereas *N.* (*L.*) *palmeri* has a subtrigonal outline and more evenly spaced commarginal riblets of mostly equal strength. More material is needed to assess the relationships of this species in detail. *Nucula* sp. is distinct from *N.* (*L.*) *suboblonga* (Wilckens, 1907) and *N.* (*L.*) *hunickeni* Zinsmeister and Macellari, 1988, both recorded from the Danian of Seymour Island.

Superfamily **NUCULANOIDEA** H. and A. Adams, 1858

Family **NUCULANIDAE** H. and A. Adams, 1858

Subfamily **NUCULANINAE** H. and A. Adams, 1858

Genus **NUCULANA** Link, 1807

Type species (by original designation).—*Arca rostrata* Chemnitz, 1774 (= *Arca pernula* Müller, 1771).

Nuculana antarctirostrata, new species
Plate 1, figures 11, 12, 15

Diagnosis.—Small- to medium-sized *Nuculana* with a narrowly elongate, moderately rostrate, moderately inflated shell; posterior end moderately pointed; umbones strongly opisthogyrous, small; escutcheon bordered by moderately developed, weakly concave umbonal ridge; ornamentation of closely spaced commarginal riblets, overprinted by discordant riblets that become more concordant anteriorly and posteriorly; posterior part of hinge 70% of length of shell.

Description.—Shell small- to medium-sized for genus (length 10.3 mm), thin, narrowly elongate, moderately rostrate; shell moderately inflated, more so centrally on disk becoming less so at anterior and posterior margins; umbones small, strongly opisthogyrous, located more anteriorly; lunule poorly developed; escutcheon long, narrow, with weak threads, bordered by gently convex to nearly straight umbonal ridge; anterodorsal margin short, steeply sloping, scarcely convex, more straight, merging with well-rounded anterior margin; posterodorsal margin long, gently concave, merging with narrowly rounded to subangular, pointed posterior margin; ventral margin moderately broadly convex; more rounded near anterior margin; sculpture of closely spaced commarginal riblets (>10 per 1 mm) with some marked growth pauses, and moderately pronounced discordant riblets, more distinctive on central part of disc and ventrally; discordant riblets become more concordant near anterior and posterior margins; posterior hinge 70% of length of shell; many chevron-shaped hinge teeth becoming weaker near posterior and anterior margins; pallial line poorly developed; inner margins smooth.

Dimensions.—Holotype USNM 517001, length 10.3 mm, height 6.5 mm, width of paired valves 6.0 mm; paratype USNM 517002, length 7.5 mm, height 5.0 mm (internal).

Types.—Holotype USNM 517001; paratype USNM 517002.

Locality.—1589.

Material examined.—Two specimens.

Stratigraphic range.—1149 m.

Discussion.—*Nuculana antarctirostrata* n. sp., one of three nuculanid species newly recorded from the Antarctic Paleocene, belongs to a characteristic latest Cretaceous–early Paleogene group ornamented with discordant commarginal riblets. *Nuculana* n. sp. of Stilwell (1994, pp. 268–270, pl. 3, figs. 1–2, 5) from the Maastrichtian of Northland, New Zealand, is morphologically very similar to *N. antarctirostrata*, differing in the Antarctic species being slightly smaller with a more narrowly rounded and convex ventral margin and more unevenly spaced, commarginal riblets that are more discordant along the central part of the disc. No other Paleocene nuculanid has a comparable sculptural configuration.

Etymology.—Species named for its endemic Antarctic occurrence and its moderately developed rostrum.

Genus **LEDINA** Dall, 1898

Type species (by original designation).—*Leda eborea* Conrad, 1860 (*non* Conrad, 1846) (= *Leda* (*Ledina*) *smirna* Dall, 1898).

Ledina? species

Plate 1, figures 5, 9, 10

Description.—Shell relatively small (length 7.5 mm nearly complete), thin, polished, subtrigonally elongate-ovate, moderately inflated, scarcely rostrate; umbones subcentral, just more anterior, suborthogyrous, just slightly curved toward posterior; lunule and escutcheon poorly differentiated; anterodorsal margin short, steep, gently convex; anterior margin incomplete on available specimen; posterodorsal margin moderately long and steep, very gently convex to nearly straight, merging with blunt, narrowly rounded, posterior margin; ventral margin broadly rounded; sculpture of many, closely spaced commarginal threads and riblets, becoming more spaced and raised ventrally; hinge details unknown; inner margin smooth.

Dimensions.—USNM 517003, length 7.5 mm, height 5.5 mm, width of paired valves 4.5 mm.

Locality.—1519.

Material.—One specimen.

Stratigraphic range.—1072 m.

Discussion.—This new species is probably assignable to the Paleocene to Eocene genus *Ledina* Dall, 1898, but as there are no internal details available and part of the anterior end of the shell is missing, only a tentative assignment is made here. The subovate outline and slightly rostrate shell, sculpture of slightly variable commarginal riblets, and poorly defined lunule and escutcheon in the Antarctic species are all characteristics of *Ledina*, type species *L. smirna* (Dall, 1898) (see Puri *in* Moore, 1969, p. N237, fig. A7-3; Toulmin, 1977, pp. 149–150, pl. 2, figs. 8–9) from the Paleocene of North America. *Ledina smirna* is larger with finer ornamentation, a slightly broader ventral margin, and a scarcely more developed rostrum, compared with *Ledina*? sp. The rostrum in *Ledina*? sp. is more pronounced, compared with *L. taioma* (Finlay and Marwick, 1937) (pp. 16–17, pl. 1, figs. 1, 3, 6; Fleming, 1966, p. 106, pl. 4, fig. 59–61; Stilwell, 1994, pp. 727–730, pl. 47, figs. 16, 19–20) from the late early Paleocene of New Zealand, which is also twice the size of the Antarctic species with more pronounced growth pauses and a more inflated shell. *Ledina paucigradata* (Singleton, 1943) (p. 268, pl. 12, fig. 1a-b; Darragh, 1994, pp. 77, 79, fig. 1H–I, O–P, R–S, U–V) from the mid-Paleocene of southeastern Victoria, Australia, is not a closely related form, as it has a much larger, more elongated shell and more indistinct commarginal ornamentation, compared with *Ledina*? n. sp.

Genus **JUPITERIA** Bellardi, 1875

Type species (by subsequent designation, Dall, 1898).—*Nucula concava* Bronn, 1831.

Jupiteria? species

Plate 1, figures 14, 17

Description.—Shell average-sized for family (8 mm in length), thin, moderately inflated, subtrigonally elongate–broadly ovate; length to height ratio 1.15:1; very weakly rostrate; umbones slightly inflated, subcentral, weakly opisthogyrous; umbonal ridge poorly developed; anterodorsal margin moderately sloping, very weakly convex, merging with rounded anterior margin; posterodorsal margin moderately long and descending, nearly straight; ventral margin broadly convex; shell polished, weakly ornamented with many, closely spaced commarginal striae; inner details unknown.

Dimensions.—USNM 517004, length 8.0 mm, height 7.0 mm, width of single left valve, ~2.3 mm.

Type.—Hypotype USNM 517004.

Localities.—1519, 1538.

Material examined.—One specimen.

Stratigraphic range.—1072 m.

Discussion.—This probable new nuculanid species is of uncertain affinity. Only one nearly complete external valve is available. Without hinge details, it is often difficult to distinguish nuculanid genera, but the scarcely rostrate, broad, subtrigonally ovate, smooth and polished shell of closely spaced commarginal striae in this species is reminiscent of Tertiary species of *Jupiteria* Bellardi, 1875, type species *J. concava* Bronn, 1831, from the Pliocene of Italy. We can find no closely related species in the Paleogene record in the Southern Hemisphere. Some species of *Jupiteria*, such as *Jupiteria* sp. of Maxwell (1992, p. 57, pl. 2, fig. k) from the late Eocene of New Zealand, have similar sculpture or near lack thereof, but *Jupiteria*? sp. has a more elongate shell and more developed rostrum, compared with the Antarctic species. Further, few North American species are similar apart from a superficial resemblance to *Tindaria* sp. 2 of Peterson and Vedelsby (2000, pp. 34–35, fig. 19A–B) from the Paleocene of Nuussuaq, Greenland, but *Jupiteria*? n. sp. from Seymour Island has less well-defined commarginal sculpture, less inflated umbones and a less steeply sloping posterodorsal margin, compared with the Greenland species.

Family **MALLETIIDAE** H. and A. Adams, 1858

Genus **AUSTRALONEILO** Zinsmeister, 1984

Type species (by original designation).—*Australoneilo rossi* Zinsmeister, 1984.

Discussion.—*Australoneilo* is much more widespread than previously recognized, being recorded from the latest Cretaceous? to Paleocene of southern Argentina and Paleocene to Eocene of Antarctica (Zinsmeister and Macellari, 1988), latest Cretaceous of New Zealand (Stilwell, 1994), and mid-Paleocene of southeastern Australia (Darragh, 1994). Reduction in valve inflation and lengthening of shell seem to be the most prominent changes in *Australoneilo* species from late Campanian? or Maastrichtian to Eocene time, after which the group disappears from the fossil record. *Australoneilo gracilis* (Wilckens, 1905) and *A. casei* Zinsmeister and Macellari, 1988, also from the Paleocene of Antarctica, appear to be morphologically intermediate forms between an undescribed species from New Zealand and *A. rossi* Zinsmeister, 1984, which both share a moderate degree of valve inflation and shell elongation. *Australoneilo gracilis*, *A. casei*, and *A. cultrata* Darragh, 1994, are of close lineal descent and *Australoneilo* n. sp. may be ancestral as indicated by their close morphological affinity.

Australoneilo gracilis (Wilckens, 1905)

Plate 1, figures 19, 20, 23

Malletia gracilis Wilckens, 1905, p. 35, pl. 5, fig. 10; Wilckens, 1910, p. 25, pl. 2, fig. 4.

Australoneilo gracilis (Wilckens). Zinsmeister and Macellari, 1988, p. 258, fig. 3.6, 3.7; Stilwell. 1994, p. 302.

Neilo (*Australoneilo*) *gracilis* (Wilckens). Darragh, 1994, p. 79.

Dimensions.—USNM 517005, length 34.0 mm, height 17.0 mm (right valve and part of hinge).

Localities.—9, 497, 1104 1137, 1138, 1414, 1434.

Material.—27 specimens.

Stratigraphic distribution.—1107 to 1375 m.

Discussion.—Zinsmeister and Macellari (1988, p. 258) re-evaluated *Australoneilo gracilis* (Wilckens, 1905), which is recognized both in uppermost Cretaceous?–Paleocene deposits of southern Patagonia and in the Danian of Seymour Island. New well-preserved material from Seymour Island and the discovery of a similar species in New Zealand improves our knowledge of the relationships of this species. *Austaloneilo gracilis* is most closely related to *Austaloneilo* n. sp. of Stilwell (1994, pp. 300–303, pl. 4, figs. 14, 15, pl. 5, figs. 1–6) from the Maastrichtian of Northland, New Zealand. *Australoneilo gracilis* is slightly more elongate and more compressed with a slightly concave posterodorsal margin and slightly more pointed posterior margin, compared with the new New Zealand species. See Plate 1, figure 23 for the complete external form of *A. gracilis* and partial hinge details, previously not figured for this species.

Australoneilo casei Zinsmeister and Macellari, 1988

Plate 1, figures 18, 21, 22, 24

Australoneilo casei Zinsmeister and Macellari. 1988, p. 258, figs. 3.8, 3.9; Stilwell, 1994, pp. 302–303.

Neilo (*Australoneilo*) *casei* (Zinsmeister and Macellari). Darragh, 1994, p. 79.

Dimensions.—USNM 517006, length 36.0 mm, height 18.0 mm, width of paired valves 15.5 mm (partial hinge exposed); USNM 517007, length 28.5 mm, height 17.0 mm, width of paired valves 13.0 mm.

Types.—Hypotype USNM 517006; hypotype USNM 517007.

Material examined.—Eight specimens.

Locality.—746.

Stratigraphic range.—1168 m.

Discussion.—*Australoneilo casei* Zinsmeister and Macellari, 1988, is most closely allied with *A. cultrata* Darragh, 1994 (p. 79, fig. 1A–G) from the mid-Paleocene of southestern Australia, but is differentiated from the Australian species in having a slightly larger shell and a smooth shell nearly void of ornamentation apart from very fine commarginal striae. The outlines and convex ventral margins of *A. casei* and *A. cultrata* are strikingly similar. The dorsal margin and partial hinge of *A. casei* are depicted herein in Plate 1, figs. 21, 22 to illustrate the hinge teeth, external ligament and articulated left and right valves, not clearly visible in Zinsmeister and Macellari (1988).

Subclass **PTERIOMORPHIA** Beurlen, 1944

Order **ARCOIDA** Stoliczka 1871

Superfamily **ARCOIDEA** Larmarck, 1809

Family **CUCULLAEIDAE** Stewart, 1930

Genus **CUCULLAEA** Lamarck, 1801

Type species (by subsequent designation, Children, 1823).—*Cucullaea auriculifera* Lamarck, 1801.

Cucullaea ellioti Zinsmeister and Macellari, 1988
Plate 2, figures 1–6

Cucullaea ellioti Zinsmeister and Macellari, 1988, p. 261, figs. 5.1–10.

Cucullaea n. sp. Zinsmeister and Macellari, 1983, p. 68, Fig. 2a1.

Dimensions.—USNM 404838, length 51 mm, height 35 mm, width of single valve 16 mm.

Type.—Holotype USNM 404838.

Localities.—9 (type), 477, 485, 496, 497, 631, 746, 1119, 1130, 1131, 1135, 1136, 1161, 1189, 1192, 1430, 1431, 1434, 1435, 1508, 1510, 1529, 1531, 1534, 1536, 1537, 1601.

Material.—158 specimens.

Stratigraphic distribution.—1051 to 1369 m.

Discussion.—*Cucullaea ellioti* is easily separated from the Maastrichtian *C. antarctica* by its smaller size, less inflation of valves, greater elongation, and narrow ligamental region. The absence of a myophoric flange also serves to distinguish *C. ellioti* from *C. antarctica*.

Cucullaea ellioti makes its first appearance within the "K-T Glauconite" and forms an important element of the Danian bivalve fauna in Unit 10 and the Sobral Formation. Although it was originally believed to have made its first appearance below the K-T boundary (Zinsmeister and Macellari, 1983), *C. ellioti* is now considered to make its first appearance in the Danian. All occurrences in the "K-T Glauconite" are above the Lower Glauconite which marks the K-T boundary.

Order **MYTILOIDA** Férussac, 1822

Superfamily **PINNOIDEA** Leach, 1819

Family **PINNIDAE** Leach, 1819

Genus **PINNA** Linnaeus, 1758

Type species (by subsequent designation, Children, 1823).—*Pinna rudis* Linnaeus, 1758.

Discussion.—*Pinna* had a long presence in Antarctica, with the oldest records extending into the Late Jurassic (Tithonian) (Willey, 1975), and disappeared in the fossil record during the late Eocene (see Stilwell and Zinsmeister, 1992).

Pinna freneixae Zinsmeister and Macellari, 1988
Plate 2, figures 7–10

Pinna freneixae Zinsmeister and Macellari, 1988, p. 265, fig. 3.16; Stilwell, 1994, p. 354; Stilwell, 1998, p. 37.

Dimensions.—USNM 517008, length 83.5 mm incomplete; USNM 517009, length 83.0 mm.

Type.—Hypotype USNM 517008; hypotype USNM 517009.

Localities.—497, 746, 769, 772, 776, 763, 764, 1132, 1134, 1136, 1139, 1150, 1179, 1181, 1698.

Material examined.—18 specimens.

Stratigraphic range.—431 to 1369 m.

Discussion.—*Pinna freneixae* Zinsmeister and Macellari, 1988, previously thought to have become extinct at the close of the Maastrichtian, is now known to have crossed the K-T boundary in the earliest Danian. Adding to discussion of this species by Zinsmeister and Macellari (1988, p. 265), *P. freneixae* has also an apical angle ranging from 23° to 26°, very close to *Pinna* sp. of Stilwell (1994, pp. 353–354, pl. 9, fig. 1, 3; Stilwell, 1998, pp. 36–37, fig. 3F, G), from the Campanian? to Maastrichtian of New Zealand and Chatham Islands, which has an apical angle of 20°. *Pinna sobrali* Zinsmeister, 1984 (p. 1510, fig. 5G, H; Stilwell and Zinsmeister, 1992, pp. 59–60, pl. 3, figs. j, k) from the uppermost Unit VII of the La Meseta Formation (upper Eocene) of Seymour Island, is a closely related species and probably the descendant of *P. freneixae*.

Order **PTERIOIDA** Newell, 1965

Suborder **PTERIINA** Newell, 1965

Superfamily **LIMOIDEA** Rafinesque, 1815

Family **LIMIDAE** Rafinesque, 1815

Genus **ACESTA** Adams and Adams, 1858

Type species (by monotypy).—*Ostrea excavata* Fabricius, 1780.

Acesta webbi Zinsmeister and Macellari, 1988

Acesta webbi Zinsmeister and Macellari, 1988, pp. 267–268, figs. 9.1–3.

Dimensions—USNM 405769, length 56 mm, height 71 mm, width of paired valves 30 mm.

Type.—Holotype USNM 405769.

Localities.—1119, 1134, 1135, 1139, 1548.

Material.—Seven specimens.

Stratigraphic range.—900–1145 m.

Discussion.—*Acesta webbi* is easily separated from *A. shackeltoni* by its smaller size, more elongated shell outline, and near absence of radial sculpture. The almost total absence of radial ornamentation is uncommon among members of the family Limidae. "*Lima*" cf. *L. latgens* Feruglio 1936 (pl. 14, figs. 10, 11) from the Maastrichtian of Lago Argentino in Patagonia is very similar to *A. webbi*, but the posterior auricle is not as broad and the shell is not as inflated.

Genus **SEYMOURTULA** Zinsmeister *in* Zinsmeister and Macellari, 1988

Type species (by original designation).—*Lima antarctica* Wilckens, 1910.

Seymourtula antarctica (Wilckens, 1910)

Lima (Limatula) antarctica Wilckens, 1910, pp. 16–17, pl. 1, fig. 8; Fleming, 1978, p. 52, fig. 26 (not *S. antarctica* Wilckens).
Seymourtula antartica (Wilckens, 1910), Zinsmeister and Macellari, 1988, figs. 8.12, 8.13.

Dimensions.—USNM 405787, length 32 mm, height 18 mm.

Types.—Holotype Mo 1636; hypotypes USNM 405787, 405788, 405789, 405790.

Localities.—754, 757, 763, 776, 1109, 1110, 1116, 1143, 1172, 1178, 1190, 1468, 1591, 1620, 1632.

Material.—33 specimens.

Stratigraphic range.—692 to 1053 m.

Discussion.—Although *Seymourtula antarctica* is not a common bivalve and is not represented by a large number of individuals, it does have has an extensive range through all the Maastrichtian on Seymour Island and finally disappears in the earliest Danian in the Fish bed horizon of the "K-T Glauconite." When encountered, *S. antarctica* normally is represented by several individuals. The co-occurrence of several individuals probably represents the gregarious habit of some species of limids of attaching in clusters to some solid surface.

Suborder **OSTREINA** Ferussac, 1822

Superfamily **OSTREOIDEA** Rafinesque, 1815

Family **OSTREIDAE** Rafinesque, 1815

Subfamily **OSTREINAE** Rafinesque, 1815

Genus **OSTREA** Linnaeus, 1758

Type species (by subsequent designation, ICZN Opinion 94).—*Ostrea edulis* Linnaeus, 1758.

Ostrea species

Localities.—1131, 1483.

Material.—Two specimens.

Stratigraphic occurrence.—1065 to 1125 m.

Discussion.—Oysters are very rare in the Danian of either the López de Bertodano or Sobral formations. Likewise they are also very rare in the Maastrichtian of the López de Bertodano and the Eocene La Meseta formations. The near absence in the Maastrichtian and the Danian probably reflects unfavorable facies for the group, but the limited occurrence of oysters in the shallow-water tidal-dominated facies of the La Meseta Formation is puzzling. The rareness of the ostreids on Seymour Island may reflect the high-latitude location of the island during the Late Cretaceous and early Cenozoic.

Subclass **HETERODONTA** Neumayr, 1884

Order **VENEROIDA** H. and A. Adams, 1856

Suborder **LUCININA** Dall, 1889

Superfamily **LUCINOIDEA** Fleming, 1828

Family **LUCINIDAE** Fleming, 1828

Subfamily **LUCININAE** Fleming, 1828

Genus **SAXOLUCINA** Stewart, 1930

Type species (by original designation).—*Lucina saxorum* Lamarck, 1806.

Saxolucina antarctipleura, new species

Plate 3, figures 7–13

Diagnosis.—Medium-sized lucinid with subcircular shape and near 1:1 length to height ratio; lunule pronounced, narrow, subclavate; escutcheon long, narrow; sculpture of closely spaced, mostly even commarginal riblets (about 3 per 1 mm), and many secondary threads; ligament external, narrow, elongated, pencil-shaped.

Description.—Shell medium-sized for family (up to 30 mm in length), moderately thick, subcircular, discoidal, moderately compressed; equivalved; length to height ratio nearly 1:1; lunule well-developed, but narrow, elongated, subclavate, slightly depressed, moderately deep, escutcheon long, narrow, moderately deep; anterodorsal margin short, slightly concave, moderately steep, merging with well-rounded anterior margin; posterodorsal margin moderately long, nearly straight, margin with somewhat bluntly angular posterior margin; ventral margin strongly convex; ornamentation of evenly spaced, moderately developed, primary riblets (~3 per 1 mm) and many weak, interstitial striae, primaries gradually strengthening from umbones to ventral margin; left valve with two cardinal teeth, anterior one triangular and posterior one elongated, details of teeth uncertain as hinges poorly preserved; external ligament strongly developed, elongated, narrow, pencil-shaped; inner margin smooth.

Dimensions.—Holotype USNM 517010, length 21.0 mm, height 18.5 mm, width of paired valves ~8.0 mm; paratype USNM 517011, length 30.0 mm, height 28.0 mm; paratype USNM 517012, length 22.0 mm, height 22.0 mm, width of paired valves 8.0 mm.

Types.—Holotype USNM 517010; paratypes USNM 517011, 517012.

Localities.—746, 1105, 1131 (type), 1137, 1161, 1430, 1467, 1535.

Material examined.—33 specimens.

Stratigraphic range.—1065 to 1369 m.

Discussion.—The ancestor-descendant relationship of *Saxolucina antarctipleura* n. sp. and *S. sharmani* (Wilckens, 1911) (p. 12, pl. 1, fig. 11; Zinsmeister, 1984, p. 1513, fig. 7M–N; Stilwell and Zinsmeister, 1992, p. 64, pl. 4, figs. j, n; Stilwell, 2000, pp. 278–279, pl. 3, fig. C–D, F, H), from the middle to late Eocene of Seymour Island and McMurdo Sound, East Antarctica, is secure. There is little to distinguish between *S. antarctipleura* n. sp. and *S. sharmani*, except that the Paleocene species is generally larger with a slightly more inflated shell and the commarginal riblets tend to flatten out slightly posteroventrally, compared to the circum-Antarctic Eocene species. *Lucina scotti* (Wilckens, 1910) (p. 57, pl. 3, fig. 2a, b; Zinsmeister and Macellari, 1988, p. 273, figs. 9.5, 9.6) from the late Maastrichtian of Seymour Island is not a closely related form, as the umbones are nearly central and the ornamentation is of much more pronounced commarginal ribs. The Tertiary South American species, *Lucina promaucana* Philippi, 1887 (p. 175, pl. 24, fig. 6; see Ortmann, 1902, pp. 130–131, pl. 27, fig. 4a, b), is also a closely related form and may be congeneric, differing from the Paleocene Antarctic species in having a longer anterodorsal margin and more projecting umbones.

Etymology.—Species named for its endemic presence in Antarctica and from the Greek *pleuron* (equivalent to "rib, side") for its closely spaced, commarginal riblets.

Family THYASIRIDAE Dall, 1901

Genus THYASIRA Leach *in* Lamarck, 1818

Type species (by original designation).—*Amphidesma flexuosa* Lamarck, 1818.

Thyasira austrosulca, new species

Plate 3, figures 14–17

Diagnosis.—Minute, moderately inflated, subcircular thyasirid (maximum height 5.5 mm), umbones strongly prosogyrous; posterior sulcus strongly developed, situated nearly flush with posterior margin; shell polished with poorly developed ornamentation of commarginal threads that increase in strength slightly from umbones to ventral margin.

Description.—Shell small for genus and family (up to 5.5 mm high), thin, moderately inflated, subcircular; length to height ratio nearly 1:1; umbones small, slightly pointed, situated centrally along dorsal margin; strongly prosogyrous, anterodorsal margin steeply sloping, short, very gently concave, merging with strongly convex anterior margin; posterodorsal margin with strong sulcation, positioned nearly flush with posterior margin about 10% of distance of length of shell from posterior margin; posterior margin moderately long, only marginally convex, merging with bluntly truncated sulcation; outer margins of posterior sulcus gently concave; ventral margin well-rounded, convex; shell polished, mostly smooth, apart from very weak ornamentation of many, commarginal threads, increasing in strength slightly from umbones to ventral margin, where they become a bit more spaced and unequal; hinge and inner details unknown.

Dimensions.—Holotype USNM 517013, length 5.3 mm, height 5.5 mm; paratype USNM 517015, length 5.3 mm, height 4.5 mm.

Types.—Holotype USNM 517013, paratype USNM 517015.

Locality.—1519 (type).

Material examined.—Two specimens.

Stratigraphic range.—1073 m.

Discussion.—This new small thyasirid bivalve is represented by one articulated specimen and also by a slightly decorticated left valve. *Thyasira austrosulca* n. sp. has no recorded close relative in the Cenozoic record of Antarctica, and seems to be most closely allied to a Recent circum-Antarctic species, *T. dearborni* Nicol, 1965 (p. 79, pl. 8, figs. 1, 2; Nicol, 1966, p. 62, figs. 7, 8; Dell, 1964, p. 207, fig. 4, nos. 10, 11; Dell, 1990, p. 56, figs. 91, 92), found today in depths between 351 and 836 m. *Thyasira austrosulca* is a bit smaller and has a slightly broader posterior sulcus compared with *T. dearborni*, but there is little else to distinguish these closely related forms. In all likelihood, *T. austrosulca* is the ancestor of *T. dearborni*. Dell (1990) noted intraspecific variation in the morphology of the posterior sulcus in *T. dearborni*, but we can find no differences in the two specimens of *T. austrosulca*. Another closely related Austral species is *Thyasira* sp. of Darragh (1994, p. 89, fig. 4P, Q) from the mid-Paleocene of Australia, which reaches a length and height of 7.2 mm. *Thyasira* sp. of Darragh (1994) has a more circular, slightly larger shell and a marginally weaker sulcus compared with the Paleocene Antarctic species, but again there is little to differentiate these taxa, which are seemingly from the same stock. *Thyasira austrosulca* may be separated from the Maastrichtian *T. townsendi* White from the López de Bertodano Formation by its small size and the absence of a broad, very deep sulcus that characterizes the posterioventral margin of *T. townsendi*.

Etymology.—Species named for its Austral occurrence and from the Latin *sulcus* (equivalent to "furrow, groove") for its prominent posterior sulcus.

Superfamily **CARDIOIDEA** Lamarck, 1809

Family **LAHILLIIDAE** Finlay and Marwick, 1937

Genus **LAHILLIA** Cossmann, 1899

Type species (by subsequent designation, Finlay and Marwick, 1937).—*Amathusia angulata* Philippi, 1887.

Lahillia larseni (Sharman and Newton, 1897)

Plate 2, figures 11–14

Cyprina larseni Sharman and Newton, 1897, pp. 59–60, pl. 1.

Lahillia lusia Wilckens, 1910, pp. 58–63, pl. 3, figs. 4, 5, 6, 7a–c, 11; Zinsmeister and Macellari, 1983, p. 68, fig. 2, B3.

Lahillia larseni (Sharman and Newton). Zinsmeister and Macellari, 1988, pp. 276–277, figs. 15.1–5.

Dimensions.—USNM 405803, length 105 mm, height 94 mm, width of paired valves 72 mm.

Type.—Holotype IGS 4053.

Type locality.—No locality given by Sharman and Newton (1897) other than Seymour Island.

Localities.—9, 477, 485, 496, 631, 757, 776, 777, 778, 1130, 1131, 1134, 1135, 1136, 1137, 1148, 1161, 1192, 1430, 1431, 1432, 1435, 1473, 1499, 1501, 1504, 1510, 1529, 1531, 1532.

Material.—110 specimens.

Stratigraphic range.—867 to 1200 m.

Discussion.—*Lahillia larseni* was originally described by Sharman and Newton (1897) from a medium-sized paired-bivalved specimen collected by Captain A. Larsen during his first visit to Seymour Island during the austral summer of 1892–93. Since the material Sharman and Newton had previously described from Seymour Island was Tertiary and they were not aware of Cretaceous strata on the island, they assumed that the undescribed species of *Lahillia* was also of Tertiary age. The existence of Cretaceous age sediments was not recognized until the Swedish South Polar Expedition at the beginning of the 20th century. As a consequence, Sharman and Newton referred *L. larseni* to the Tertiary, which Wilckens (1911) followed. Wilckens (1911) referred the Cretaceous species collected by the Swedish South Polar expedition to the South American species *L. lusia*. Examination of Larsen's specimen and the collection of a large number of additional specimens from the Eocene La Meseta Formation has revealed that Larsen's specimen is distinct from the Eocene species. Comparison of the Sharman and Newton specimen with the Maastrichtian/Danian *Lahillia* clearly shows the two to be conspecific. It is also clear that the Seymour Island species is distinct from the *L. lusia* from Patagonia (Zinsmeister and Mascellari, 1988). As a consequence, the specific name *L. larseni* is now applied to the Maastrichtian/Danian species of *Lahillia* in the López de Bertodano and Sobral formations. The eroded nature of the shell together with extensive fieldwork on Seymour Island suggest that the specimen of *L. larseni* that Larsen found most likely was found on the beach north of Penguin Point. Eroded Cretaceous fossils are occasionally encountered along the beach in this area. This is the area where Larsen and his men landed on their first visit to the island.

Lahillia larseni makes its first appearance in unit 8 of the López de Bertodano Formation and though present at most localities, it forms a relatively minor component of the molluscan fauna. In the lowermost Danian, immediately above the "K-T Glauconite," the abundance of *L. larseni* increases dramatically and is characterized by floods of thousands of individuals. This sudden increase in abundance is believed to reflect the opportunistic nature of the species. The absence of competition following the mass extinction at the end of the Cretaceous enabled *L. larseni* to become the dominant element in the shelf faunas in the Seymour Island region during the earliest Danian. With the diversification and appearance of new benthic taxa, the floods of lahillia disappeared. Although *L. larseni* remains an important element of the Danian shelf faunas in the Seymour Island region, the floods of thousands of individuals are restricted to the interval during the period immediately following the extinction event.

Lahillia huberi Zinsmeister and Macellari, 1988

Plate 3, figures 1, 2

Dimensions.—USNM 405817, length 71 mm, height 64 mm, width of paired valves 44 mm.

Types.—Holotype USNM 405817; paratypes USNM 405818, 405819.

Localities.—9, 496, 631, 746 (type), 1136, 1148, 1192, 1698.

Material.—41 specimens.

Stratigraphic range.—1134 to 1179 m.

Discussion.—*Lahillia huberi* may be distinguished from *L. larseni* by its smaller size, subtrigonal shell outline, orthogyrate beaks, and an only moderately concave anterior margin. The nymph of *L. larseni* is considerably more massive, longer, and extends above the margin of the valves.

Suborder **ARCTICINA** Newell, 1965

Superfamily **VENEROIDEA** Refinesque, 1815

Family **VENERIDAE** Rafinesque, 1815

Subfamily **PITARINAE** Stewart, 1930

Genus **MARWICKIA** Finlay, 1927

Type species (by original designation).—*Finlaya parthiana* Marwick, 1927.

Marwickia woodburnei Zinsmeister and Macellari, 1988

Plate 3, figures 3–6

Astarte cf. *A. venatorum* Wilckens, 1910, pp. 49–50, pl. 2, figs. 28a, b, *not* figs. 29 a, b.

Dimensions.—USNM 405804, length 30 mm, height 29 mm, width of paired valves 16 mm.

Types.—Holotype USNM 405804; paratypes USNM 405805, 405834.

Localities.—9 (type), 746, 1130, 1131, 1134, 1135, 1136, 1137, 1138, 1139, 1148, 1149, 1189, 1414, 1432, 1434, 1435, 1448, 1467, 1502, 1504, 1507, 1508, 1510, 1529, 1530, 1531, 1532, 1533, 1534, 1536, 1537, 1538, 1586, 1589, 1695, 1697.

Material.—137 specimens.

Stratigraphic range.—1052 to 1216 m.

Discussion.—Venerid bivalves are rare in the López de Bertodano and Sobral formations and are characterized by a similar inflated ovate shell. Species are separated by variation of the hinge elements. Wilckens (1910) tentatively referred specimens from SSPE locality 8 on Snow Hill Island and SSPE 9 on Seymour Island to the genus *Astarte*. Zinsmeister and Macellari (1988) believed that the assignment of the specimens from Seymour Island to *Astarte* was based on the astarte-like hinge of the fragmented specimens from Snow Hill Island. The presence of an anterior lateral tooth on specimens from Seymour Island clearly shows that they belong to the venerid subfamily Pitarinae and not in the family Astartidae. *Marwickia woodburnei* is easily separated from the Maastrichtian venerid species *Cyclorisma chaneyi* Zinsmeister and Macellari, 1988, by the presence of an elongated anterior lateral and by a more centrally located umbone.

Order **MYOIDA** Stoliczka, 1870

Suborder **MYINA** Stoliczka, 1870

Superfamily **HIATELLOIDEA** Gray, 1824

Family **HIATELLIDAE** Gray, 1824

Genus **PANOPEA** Ménard de la Groye, 1807

Type species.—*Mya glycimeris* Born, 1778.

Panopea clausa Wilckens, 1910

Plate 3, figures 20–22

Panopea (*Pleuromya*?) *clausa* Wilckens, 1910, 68–69, pl. 3, figs. 10a, b.

Panopea clausa Wilckens, Woods, 1917, p. 33, pl. 18, figs. 6a, b, 7; Freneix, 1958, p. 343, pl. 3, fig. 6; Warren and Speden, 1978, p. 40, fig. 26–13; Zinsmeister and Macellari 1988, pp. 280–282, figs. 16.1–3.

Localities.—458, 459, 757, 769, 776, 1116, 1146, 1176, 1178, 1180, 1190, 1426, 1471, 1476, 1489, 1492, 1540, 1584, 1595, 1614, 1615, 1620, 1622.

Material.—15 specimens.

Stratigraphic range.—344 to 1056 m.

Discussion.—Although *Panopea clausa* is not a common bivalve and is not represented by a large number of individuals, it does have an extensive range through all the Maastrichtian on Seymour Island and finally disappears in the earliest Danian in the "K-T Glauconite" fish bed horizon. Surprisingly, *P. clausa* or related species of *Panopea* are not present in either Danian of Unit 10 or the Sobral Formation. The genus reappears in the Eocene La Meseta formation at the north end of the island.

Subclass **ANOMALODESMATA** Dall, 1889

Order **PHOLADOMYOIDA** Newell, 1965

Superfamily **PANDOROIDEA** Rafinesque, 1815

Family **PERIPLOMATIDAE** Dall, 1895

Genus **PERIPLOMA** Schumacher, 1817

Type species (by monotypy).—*Corbula margaritacea* Lamarck, 1801.

Periploma, new species

Plate 3, figures 18, 19

Description.—Shell moderate-sized for family and genus (25.0 mm long), thin, slightly inflated, obliquely subovate, attenuate and compressed anteriorly; nearly equivalved; inequilateral; umbones small, scarcely inflated, prosogyrous; anterodorsal margin short, moderately sloping, straight, merging with obliquely truncated anterior margin; posterodorsal margin moderately long, gently sloping, broadly convex, merging with well-rounded posterior margin; ventral margin strongly convex; ornamentation of low, rounded, closely spaced, commarginal riblets, growing in strength only slightly towards ventral margin; posterior gape only slightly developed; internal details unknown.

Dimensions.—USNM 517014, length 25.0 mm, height 21.8 mm, width of paired valves 9.5 mm.

Locality.—1138, 1484, 1519, 1538.

Material examined.—Four specimens.

Stratigraphic range.—1051 to 1104 m.

Discussion.—This new species represents a member of the Periplomatidae, and is tentatively assigned to *Periploma* Schumacher, 1817, as it has the characteristic thin, obliquely subovate shell with an attenuate, compressed and slightly truncated anterior end; slightly gaping posterior end; small umbones; and closely spaced commarginal riblets, comparable to Cenozoic members of the family and genus. In outline, no other Antarctic fossil or Recent form approaches *Periploma*? n. sp. *Periploma topei* Zinsmeister, 1984 (pp. 1525–1526, fig. 10F, G; Stilwell and Zinsmeister, 1992, p. 89, pl. 10, fig. e, l) and *Periploma* n. sp.? cf. *P. topei* Zinsmeister of Stilwell (2000, p. 290, pl. 5, fig. G) from the middle Eocene of Seymour Island and McMurdo Sound have much larger, more compressed and obliquely ovate shells, compared with *Periploma*? n. sp. *Periploma topei* is doubtfully the descendant of *Periploma*? sp. *Thracia subgracilis* (Whitfield, 1880) (p. 419, pl. 11, figs. 29–30; Stanton, 1920, pp. 26–27, pl. 3, figs. 4a, b, 5a, b, *Anatina*; Cvancara, 1966, pp. 357–358, pl. 9, figs. 19, 20, *Laternula*?) from the Paleocene of North America has a similar outline and sculpture, more so than any other coeval forms from the Northern or Southern Hemisphere, except that *T. subgracilis* has a slightly less circular shell with a corresponding more convex posterodorsal margin and marginally more attentuate anterior margin, compared with *Periploma*? n. sp. The genus-level assignment of *T. subgracilis* is in a state of flux. The compressed nature of both *T. subgracilis* and *Periploma*? n. sp. is identical. Of note, *Thracia subgracilis* doubtfully belongs in *Thracia*, and is most likely a member of Periplomatidae.

Class **GASTROPODA** Cuvier, 1797

Subclass **STREPTONEURA** Spengel, 1881

Order **ARCHAEOGASTROPODA** Thiele, 1925

Suborder **PLEUROTOMARIINA** Cox and Knight, 1960

Superfamily **PLEUROTOMARIOIDEA** Swainson, 1840

Family **PLEUROTOMARIIDAE** Swainson, 1840

Genus **CONOTOMARIA** Cox, 1959

Type species (by original designation).—*Pleurotomaria mailleana* d'Orbigny, 1843.

Conotomaria species A

Plate 4, figures 1, 2

Description.—Shell large with maximum diameter to 106.7 mm, thin (0.9 mm at base of last whorl), trochiform, broadly conical, as broad as high; spire angle ~69.8°; 7½ whorls preserved; region between suture and selenizone convex; region between selenizone and periphery straight; suture abutting below peripheral keel; selenizone moderately broad (5.6 mm; 0.15 ramp width), entirely below peripheral keel, flush to slightly convex; sculpture of fine spiral cords strongest at shoulder, 10–12 between selenizone and suture, along keel; base very weakly convex with only axial growth lines; periphery with pronounced keel; columellar callus thin, nacreous, spanning 0.25 mm base radius; aperture ovate (height/width = 0.69 mm); umbilicus deep and narrow.

Dimensions.—USNM 511842, height 62.5 mm, diameter of last whorl 106.7 mm.

Localities.—9, 1105, 1535.

Material.—Three specimens.

Stratigraphic range.—1077 to 1169 m.

Discussion.—This species, assignable to *Conotomaria*, differs from *Pleurotomaria tardensis* Stanton, 1901 (pp. 29–30, pl. 7, figs. 1, 2), from the Upper Cretaceous Belgrano Beds of Argentina (Patagonia), in having a higher spire, thinner and much larger shell, narrower selenizone, lack of spiral sculpture on the base of the shell, presence of a sharp peripheral keel, and in having a narrower and thinner columellar callus. It is also distinguished from *Perotrochus*? *larseniana* (Wilckens, 1910), from the late Maastrichtian and early Paleocene of Seymour Island, in having a more angular outline, convex whorls, broader umbilicus, and position of selenizone on the mid-whorl, as well as the presence of thin, but prominent spiral threads. *Conotomaria* sp. A is closely allied with the Cretaceous type species, *C. mailleana* (d'Orbigny, 1842) (pp. 253–254, pl. 195), from France, but has slightly more convex whorls, a less distinct selenizone, and a slightly less developed peripheral keel.

Conotomaria species B

Plate 4, figures 3, 4

Description.—Shell small (maximum diameter of last whorl 44.8 mm), relatively thick (1.2 mm on ramp of last whorl), trochiform, broadly conical, extrapolated to be broader than high; spire angle ~86.4°; three whorls preserved; region between suture and selenizone and periphery straight to concave; suture abutting below peripheral keel; selenizone moderately broad (1.8 mm; 0.16 mm ramp width), spanning mid-whorl; sculpture of numerous, thin, spiral cords (8 between suture and selenizone, 3 on selenizone, 6 between selenizone and periphery) and fine, oblique growth lines; periphery with prominent rounded keel; base poorly preserved, weakly convex, with fine spiral cords; shell anomphalous, with remains of strong columellar callus; aperture narrowly ovate, height to width ratio of 0.40:1.

Dimensions.—USNM 511843, height 32.5 mm, diameter of last whorl 44.8 mm.

Locality.—9.

Material.—Four specimens.

Stratigraphic occurrence.—1168 m.

Discussion.—This small species is very distinct among all other Pleurotomariidae on Seymour Island, in having a comparatively small size, distinctly angulated appearance, and prominent spiral sculpture. It also has a significantly thicker shell, in proportion to the size. In outline and size, *Conotomaria* sp. B is comparable with *Pleurotomaria gurgitis* Brongniart *in* Cuvier and Brongniart, 1822 (p. 96, pl. 9, fig. 7A, B; d'Orbigny, 1842, pp. 249–250, pl. 192, figs. 4–6) from the Gault region, France, but the whorls in *Conotomaria* sp. B are slightly more flush and less convex, and the ornamentation is a bit weaker, compared with *P. gurgitis*. The specimen figured in Cuvier and Brongniart (1822) (see especially pl. 9, fig. 7A) is higher spired with no details of a selenizone.

Conotomaria species C

Plate 4, figures 5, 6

Description.—Shell medium- to large-sized (maximum diameter of last whorl 89.2 mm), thick (~1.3 mm on ramp of last whorl), broadly conical, slightly broader than high; spire angle ~81.9°; 8.5 whorls preserved; region between suture and selenizone convex, between selenizone and periphery straight to slightly convex; suture shallow, canaliculate; selenizone moderately broad (2.7 mm, 0.18 mm ramp width), slightly concave spanning mid-whorl; sculpture of thin, raised cords (from 7 on juvenile specimen to 16–18 on adults) between suture and selenizone, from 6–7 on juvenile to 11–12 on adults between selenizone and periphery, and fine, oblique growth lines; periphery marked with prominent angulated shoulder; base weakly convex, with fine spiral cords and axial growth lines; remains of the columellar callus nacreous and thin; umbilicus closed; aperture broad, roundly rectangular.

Dimensions.—USNM 511844, height 69.0 mm, diameter of last whorl 86.9 mm.

Material.—Eight specimens.

Localities.—9, 746, 1104, 1149.

Stratigraphic range.—1052 to 1375 m.

Discussion.—This species closely resembles *Conotomaria* sp. A. It differs, however, in having a broader, distinctly concave selenizone, canaliculated suture, thicker shell, presence of spiral threads on the base, generally lower and more compressed spire, closed umbilicus, and broader subrectangular aperture. As with *Conotomaria* sp. A and B, this species is left in open nomenclature until better preserved specimens are collected.

Order **PATELLOGASTROPODA** Lindberg, 1986

Suborder **DOCOGLOSSA** Troschel, 1866

Superfamily **PATELLOIDEA** Rafinesque, 1815

Family **ACMAEIDAE** Carpenter, 1857

Genus **ACMAEA** Eschscholtz, 1830

Type species (by subsequent designation).—*Acmaea mitra* Eschscholtz, 1833.

Discussion.—*Acmaea* species are characterized by variably smooth or radially ribbed limpet-like shells with generally an ovate outline and subcentral apex (Abbott, 1974, p. 28; see Lindberg, 1988). The geologic range of *Acmaea* is Cenomanian to Recent (Dockery, 1993, p. 43), although some workers suggest that fossil *Acmaea*-like gastropods belong elsewhere (Lindberg, 1988; W. Ponder, personal communication, 2001). The range of the group in Antarctica is restricted to the latest Cretaceous to the earliest Paleocene on Seymour Island.

Acmaea submesidia, new species

Plate 5, figures 1–4

Acmaea n. sp. 2 Zinsmeister *et al.*, 1989, p. 733, fig. 2.

Diagnosis.—Somewhat small *Acmaea* species with a maximum shell diameter of just over 10 mm and a thin, ovate shell of 0.5 mm thick; apex, although subcentral, is more anterior, located about a quarter of the length of shell from anterior margin; differs from type, *A. mitra*, in having a less elevated shell, a more ovate outline and more anteriorly situated apex.

Description.—Shell relatively thin, porcelaneous, ovate with maximum diameter of just over 10 mm; conic in shape with rounded base; apex strongly elevated and pointed, but not sharply so, subcentral, situated approximately a quarter of length of shell from anterior margin; surface of shell smooth, as is interior;

muscle scars broadly crescent-shaped, connected by thin anterior line which is elevated above the base.

Dimensions.—Holotype USNM 511846, length 14.5 mm, maximum diameter 15.5 mm, height 7.5 mm; paratype USNM 511847, length 7.25 mm, maximum diameter 6.0 mm, height ~3.5 mm.

Types.—Holotype USNM 511846; paratype USNM 511847.

Localities.—477, 1131, 1534, 1548, 1560 (type).

Stratigraphic range.—1058 to 1074 m.

Material.—23 mostly decorticated specimens.

Discussion.—*Acmaea submesidia* n. sp. is curiously quite distinct from *Acmaea* n. sp. of Zinsmeister (1990, fig. 1) from the uppermost López de Bertodano Formation, and lacks the crenulate margin present in the older latest Maastrichtian species. *Acmaea submesidia* n. sp. is smaller, less rounded in outline and has a more anterior apex.

Etymology.—Species named from the Greek *mesidios* (equivalent to "middle") for its subcentrally located apex.

Order **CAENOGASTROPODA** Cox, 1959

Suborder **NEOTAENIOGLOSSA** Haller, 1892

Superfamily **CERITHIOIDEA** Fleming, 1822

Family **CERITHIIDAE** Fleming, 1822

Genus **BITTIUM** Gray, 1847

Type species (by subsequent designation, Gray, 1847).—*Murex reticulatus* Montagu (= *Strombiformis reticulatus* Da Costa, 1778).

Subgenus **BITTIUM** *sensu stricto*

Bittium (Bittium?) paleonotum, new species

Plate 5, figure 5

Cerithium n. sp. Zinsmeister, 1998a, p. 565, fig. 9.

Diagnosis.—Moderately sized *Bittium* species with high spire of at least 8 well-rounded convex whorls, and spire angle of some 22°; sculptural configuration of approximately 25 somewhat clathrose, pustule-bearing axial ribs and 7 closely spaced spirals with interstitial threads; differs from closely related *B. antarctonodosum* Stilwell and Zinsmeister, 1992, in having a slightly smaller shell, more pronounced clathrose sculpture, more spirals, and more impressed sutures.

Description.—Shell medium-sized for genus (~18 mm high), rather thin- to medium-shelled, high-spired turritelliform; spire high, consisting of at least 8 moderately rounded, inflated, convex, and slightly compressed whorls; sutures impressed; spire whorl inflation mostly constant; spire angle ~22°; protoconch details unknown; last whorl incomplete, but moderately inflated and convex; growth lines weakly developed, opisthocyrt; ornamentation of ~25 moderately strong nodulose axial ribs extending from suture to suture and 7 closely and evenly spaced, moderately strong spirals and fine interstitial spiral threads, most abapical rib subsuturally the weakest; sculpture attains a somewhat clathrose pattern with the even crossing of axials and spirals, creating weakly nodulose ribs; aperture details wanting on holotype.

Dimensions.—Holotype USNM 511848, height 18.0 mm nearly complete, diameter of last whorl 6 mm.

Type.—Holotype USNM 511848.

Type locality.—1581.

Material.—One specimen.

Stratigraphic range.—1165 m.

Discussion.—*Bittium* (*Bittium*?) *paleonotum* n. sp. was collected in association with a dense coral colony and is represented solely by the partially decorticated holotype. Despite the imperfect nature of the holotype, the preserved features of this cerithioid gastropod compare well with *Bittium* Gray, 1847, which is characterized by high-spired shells with dominant axial ribs that are overridden by spiral riblets or threads that are swollen into beads, creating a moderately strong clathrose pattern. *Bittium* (*Bittium*?) *paleonotum* n. sp. is apparently closely related to *B. antarctonodosum* Stilwell and Zinsmeister, 1992 (p. 98, pl. 12, figs. c, d), from Unit V of the La Meseta Formation on Seymour Island, differing in having a slightly smaller shell, fewer spirals, and slightly less impressed sutures. The clathrose sculpture is stronger in *B. paleonotum* n. sp. Although the subgenus is in question, *B.* (*B.*?) *paleonotum* n. sp. is strikingly similar to many extant North American species of the genus (see Abbott, 1974, pp. 106–107, figs. 1012–1031). We know of no other Paleocene species of the genus in the Southern Hemisphere apart from *B.* (*B.*?) *paleonotum* n. sp.

Etymology.—Species named from its early occurrence in the fossil record of Antarctica and from the Greek *notos* (equivalent to "south").

Subgenus **ZEBITTIUM** Finlay, 1927

Type species (by original designation).—*Cerithium exilis* Hutton, 1873.

Discussion.—The presence of *Bittium* (*Zebittium*) in the Sobral Formation of Seymour extends the range from the middle Eocene of Antarctica and New Zealand (Stilwell and Zinsmeister, 1992) to the earliest Paleocene. *Bittium* (*Zebittium*) is rather common today in shallow to deep (up to 260 m) New Zealand waters (Powell, 1979, p. 132).

Bittium (Zebittium) brooksi, new species

Plate 5, figures 11–15

Diagnosis.—Moderately sized, high-spired *Bittium* (*Zebittium*) with a spire of 6 convex whorls, ornamented with 12–13 sinuous axial ribs and 6–7 spiral threads, that create weak clathrose pattern, but axials still stronger than spirals; aperture ovate to subrhomboid with poorly developed canal; differs from Recent type species, *B.* (*Z.*) *exile* (Hutton, 1873), in having less impressed sutures, more spirals, and rounded, opisthocyrt-trending axials.

Description.—Shell average-sized for genus, but small for family (~6.5 mm high), moderately robust, high-spired turritelliform; spire relatively high with at least 6 moderately convex, moderately compressed, well-rounded whorls; spire angle approximately 27°; whorl inflation gradual from early teleoconch whorls to last whorl; sutures impressed; protoconch details eroded in available material; last whorl slightly inflated, ornamented with 12–13 poorly developed, sinuous axial ribs with an apex situated midway on the last whorl at maximum diameter or outer periphery, and ~13 narrowly and semi-equally spaced spiral threads; adapical slope on last whorl steep, short; axials on last whorl weaker than on teleoconch whorls; growth lines weak and strongly opisthocyrt; teleoconch whorls with 6–7 spiral threads, including sutural and subsutural ones, and opisthocyrt-trending axials; the crossing of axials and spiral create a weakly clathrose pattern of poorly developed nodulose ribs; basal constriction generally gradual; aperture small, ovate to subrhomboid-shaped, with a poorly developed and very weak notch; columella smooth, short, concave; outer lip thin.

Dimensions.—Holotype USNM 511849, height 4.5 mm incomplete, diameter of last whorl 2.25 mm; paratype USNM 511850, height 4.5 mm incomplete, diameter of last whorl ~2.3 mm; paratype USNM 511851, diameter of last whorl (apertural view) ~2.25 mm; paratype USNM 511852, height of shell 4.0 mm incomplete (showing aperture and sectioned whorls); paratype USNM 511853, height of spire fragment 3.5 mm; paratype USNM 511910, length of block with many specimens, ~68 mm.

Types.—Holotype USNM 511849; paratypes USNM 511910, 511850–511853.

Type locality.—1535 (type locality), 1537.

Material.—Several hundred mostly incomplete specimens.

Stratigraphic distribution.—1078 to 1099 m.

Discussion.—*Bittium* (*Zebittium*) *brooksi* n. sp. from the Sobral Formation is not only the earliest member of this Austral cerithiid group, but is also the most abundant of Antarctic Paleocene mollusks with dense nearly monotypic concentrations of these gastropods present at Loc. 1535. As the minute shell of *B.* (*Z.*) *brooksi* is rather fragile, no complete specimen with protoconch preserved is available for study. However, enough characters are preserved in the type material to enable us to easily differentiate this early species with other members of the group. *Bittium* (*Zebittium*) *brooksi* is a distinct member of this subgenus, as the axial ribs are generally just slightly more developed than the spirals, which is generally not the case in most species of *Bittium* (*Zebittium*), in which the spirals tend to dominate the axials resulting in a relatively weaker or obsolete nodulation (Powell, 1979, p. 132).

The Recent type species, *B.* (*Z.*) *exile* (Hutton, 1873) (p. 27; Powell, 1979, p. 132, fig. 32-1) is strikingly similar to *B.* (*Z.*) *brooksi* n. sp., and differs predominantly in whorl shape and minor sculptural differences. *Bittium* (*Zebittium*) *brooksi* is slightly larger with less impressed sutures and has more spirals that are also less nodulose, compared to *B.* (*Z.*) *exile.* The whorl outline of *B.* (*Z.*) *brooksi* is more reminiscent of the Recent New Zealand (Three Kings Islands) species, *B.* (*Z.*) *editum* (Powell, 1930) (see Powell, 1979, p. 132, pl. 29, fig. 15), with a steep subsutural adapical slope, but the axials in the Antarctic species are more pronounced and opisthocyrt.

The only other Antarctic species of *Bittium* (*Zebittium*), *B.* (*Z.*) *granchii* Stilwell and Zinsmeister, 1992 (p. 98–99, pl. 12, figs. l, m), from Unit V of the La Meseta Formation, is quite distinct from, and probably not closely related to, *Z.* (*B.*) *brooksi,* as the Sobral Formation species is much smaller with more but weaker spirals, and has more impressed sutures. A lineage from *B.* (*Z.*) *brooksi* to *B.* (*Z.*) *granchii* is unlikely.

Etymology.—Species named for Velma May Brooks Paris for her continued support of WJZ over the years.

Family **TURRITELLIDAE** Woodward, 1851

Subfamily **TURRITELLINAE** Woodward, 1851

Genus **TURRITELLA** Lamarck, 1799, p. 74

Type species (by monotypy).—*Turbo terebra* Linnaeus, 1758.

Subgenus **HAUSTATOR** Montfort, 1810

Type species (by original designation).—*Haustator gallicus* Montfort, 1810 (= *Turritella imbricataria* Lamarck, 1804).

Discussion.—Genus-level systematics and nomenclature in turritellines are as yet unresolved and in a state of flux (Allmon, 1996). We have therefore chosen to use the generic name *Turritella* s.l. Only one specimen of a turritelline was collected from the Sobral Formation and it is incomplete. This specimen, USNM 511854, has characteristic features of generally flattened to very gently convex and solid whorls, weakly impressed sutures, and strong spiral sculpture, similar to *Turritella* (*Haustator*), type species *Turritella* (*Haustator*) *gallicus* (Montfort, 1810), but it is assigned to *Turritella* (*Haustator*?) until better material is obtained.

Turritella (Haustator?) parisi, new species
Plate 5, figure 17

Turritella n. sp. Zinsmeister, 1998a, p. 565, fig. 9.

Diagnosis.—Moderately sized turritellid with acute spire of more than 5 gently convex to nearly subquadrate whorls, ornamented with dominantly spiral sculpture of 5 primary cords with excavated and gently wavy interspaces and a weak axial, nodulose component in early whorls; growth lines shallowly opisthocyrt with apex of sinus in lower third of whorls; differs from Eocene type species, *T.* (*H.*) *imbricataria* Lamarck, in having a shorter spire, slightly stronger spiral cords, and broader opisthocyrt growth lines.

Description.—Shell medium-sized for family, moderately thick, moderately high-spired turritelliform; spire moderately high to high of more than 5 subquadrate, gently convex to nearly flush whorls; spire angle acute at approximately 23°; protoconch unknown; sutures very slight impressed to almost flush; last whorl incomplete; spire whorls sculptured with 5 pronounced primary spiral cords that have slightly wavy, excavated interspaces, generally weakening only slightly adapically; in early whorls a weakly nodulose axial component of poorly developed opisthocyrt-trending growth elements that become weaker on younger whorls where there are very fine growth lines; apex of growth lines on lower third of each whorl; base with rapid constriction that is nearly flat to gently convex; aperture incomplete, but remnants indicate a subquadrate outline.

Dimensions.—Holotype USNM 511854, height 16.0 mm incomplete, diameter of last whorl 7.5 mm.

Type.—Holotype USNM 511854.

Type locality.—1716.

Material.—Holotype.

Stratigraphic range.—1066 m.

Discussion.—The whorl profile, outline and sculpture of this new Antarctic turritellid, named here *Turritella* (*Haustator*?) *parisi*, matches coeval and slightly younger Eocene species of *Turritella* (*Haustator*), type species *T.* (*H.*) *imbricataria* Lamarck, 1804 (p. 216; Montfort, 1810, pp. 182–184, full-page woodcut (p. 182); Cossmann, 1888, p. 300; see Wenz, 1939, pp. 653–654, fig. 1860), from the middle Eocene of France, in having a relatively high-spired shell with subquadrate to gently convex, nearly flush, whorls. The sutures are, indeed, only weakly impressed to almost flush in *T.* (*H.*) *imbricataria*. The Antarctic species has these features and also the prominent spiral cords found in the type, but with respect to the growth lines the apex of the sinus is shallower than the type.

Few other Paleocene taxa compare well with *T.* (*H.*?) *parisi* n. sp. apart from the highly variable species *T.* (*H.*) *nigeriensis* Adegoke, 1977 (pp. 95–96, pl. 16, especially fig. 7) from the Paleocene of Nigeria, but the Antarctic species has fewer and comparatively weaker spiral cords and less impressed sutures. There are no other related Antarctic turritellids.

Etymology.—Species named in honor of Dr. David Paris MD for his untiring support of WJZ during the early years of his career.

Subfamily **PAREORINAE** Finlay and Marwick, 1937

Genus **MESALIA** Gray, 1847

Type species. (by original designation).—*Cerithium mesal* Adanson (= *Turritella brevialis* Lamarck, 1822).

Mesalia virginiae, new species
Plate 5, figures 6–10

Mesalia n. sp. B, Zinsmeister et al., 1989, p. 734, fig. 3.

Diagnosis.—Moderately sized, high-spired, rather delicate thin-shelled *Mesalia* with at least 7 strongly unicarinate whorls, ornamented with 3–4 spiral cords and weaker, beaded, spiral threads on upper adapical half, strongest cord at peripheral angulation, becoming weaker abapically; growth lines broadly opisthocyrt; canal distinct, narrow and small, spout-like, twisted obliquely and abaxially.

Description.—Shell medium-sized for genus (less than 30 mm high), relatively thin-walled, broadly high-spired of at least 7 strongly carinate, subquadrate, compressed whorls; spire angle 33°; protoconch incomplete, but apparently polygyrate of smooth, rounded whorls; whorl inflation moderately rapid; sutures impressed; last whorl slightly to moderately inflated, strongly unicarinate with only spiral sculpture of 6 marked spiral cords on lower abapical half of shell, the strongest cord at peripheral angulation, and weak, beaded, spiral threads on short steep, weakly concave, adapical ramp; teleoconch whorls ornamented with weak spiral threads on upper halves of whorls and 3 to 4 moderately strong primary cords, cord at angulation the strongest, and quite weak secondary spiral threads; adapical slopes on teleoconch whorls steep, short; growth lines poorly developed, weak, closely spaced, broadly opisthocyrt; basal constriction rapid, culminating in a short, narrow, twisted, abaxially-trending, spout-like canal; aperture broadly D-shaped;

columella short, mostly straight with narrow callus; outer lip thin.

Dimensions.—Holotype USNM 511855, height 28.0 mm, diameter of last whorl 13.5 mm; paratype USNM 511911, height 21.5 mm, diameter of last whorl 16.5 mm incomplete; paratype USNM 511912, height 29.5 mm, diameter of last whorl 12.5 mm; USNM 511913, length of block of specimens 80.5 mm.

Types.—Holotype USNM 511855; paratypes USNM 511911, USNM 511912, USNM 511913.

Localities.—497, 746, 1104, 1139, 1548, 1591, 1715 (type).

Material.—20 specimens.

Stratigraphic range.—1053 to 1375 m.

Discussion.—*Mesalia* is recognized in the fossil record of Antarctica for the first time, represented by the relatively rare occurrence of *M. virginiae* n. sp., except at locality 1139 where it occurs in large numbers. In the Southern Hemisphere, species of *Mesalia* are an uncommon element of Paleocene faunas. *Mesalia virginiae* n. sp. is easily distinguished from other coeval species in having strongly unicarinate whorls and a short, but distinct, spout-like siphonal canal that is twisted obliquely and abaxially. *Mesalia* sp. 1 and 2 of Kollmann and Peel (1983, pp. 42–43, figs. 70, 71) from the Paleocene of Greenland have nearly the same outline with a similar spire angle, but the whorls are nearly flush with sculpture of even spiral cords. The canal is not nearly as distinct in the Greenland species. No unicarinate species are present in the Paleocene of Nigeria (Adegoke, 1977), and all have relatively regular spiral sculpture. The Recent African type species, *M. brevialis* (Lamarck, 1822) (p. 58, not figured; Wenz, 1939, p. 651, fig. 1851; Abbott and Dance, 1983, p. 59, figure upper left corner), has a much higher spire, more rounded whorl profiles, a more rudimentary siphonal canal, and flatter spiral ribs, compared to *M. virginiae*. The phylogeny of *M. virginiae* is uncertain, as it disappeared from the Antarctic fossil record after the Paleocene.

Etymology.—This species is named in honor of Dr. Virginia Ann Paris Zinsmeister for keeping the home fires going during my numerous trips to Seymour Island and for also providing support to JS and AO while they were graduate students at Purdue University.

Superfamily **STROMBOIDEA** Rafinesque, 1815

Family **APORRHAIDAE** Gray, 1850

Genus **STRUTHIOCHENOPUS** Zinsmeister and Griffin, 1995

Type species (by original designation).—*Perissoptera nordenskjoldi* Steinmann and Wilckens, 1908.

Discussion.—*Struthiochenopus* Zinsmeister and Griffin, 1995, is one of few aporrhaid gastropods that survived the K-T boundary well into the Tertiary with species spanning Campanian to early Miocene time from Antarctica to South America (Chile, Argentina). In Antarctica, the group spans the Campanian to Paleocene interval, represented by *S. nordenskjoldi* (Wilckens) (Campanian), from Snow Hill Island (possibly also Vega and James Ross islands), and *S. hurleyi* n. sp. (Wilckens, 1910) (latest Maastrichtian to Paleocene) of Seymour Island.

Struthiochenopus hurleyi, new species

Plate 5, figures 18–20; Plate 6, figures 1–6

Perissoptera nordenskjoldi Wilckens, 1910, pp. 83–86, pl. 4, fig. 5 only; Macellari, 1984, pl. 34, figs. 5–8; Zinsmeister and Macellari, 1983, fig. B4; Zinsmeister *et al.*, 1989, p. 733, fig. 2, p. 734, fig. 3, p. 736, fig. 6.

Aporrhaidae spp. Palamarczuk *et al.*, 1984, p. 401.

Struthiochenopus nordenskjoldi (Wilckens). Zinsmeister and Griffin, 1995, pp. 699–700, fig. 3.11–3.19.

Description.—Shell medium-sized with moderately low spire consisting of 7 to 8 convex whorls, spire angle 45° to 47°; protoconch of 2.5 smooth whorls with faint keel; keel strengthens rapidly becoming sharp on later whorls eventually merging with posterior digitation, second less pronounced more abapically keel developed on body whorl, merges with anterior digitation; 20 to 24 weak rounded nodes present on primary keel becoming obsolete on body whorl; shoulder posterior to primary keel flat merging with slightly impressed suture; medial portion of whorl between keels flat to concave; body whorl anterior to secondary keel drawn out into narrow siphon; surface covered with faint narrow spiral threads; aperture elongated, pyriform with moderately long and straight canal; outer lip expanded into broad moderately thick wing, inclined at about 50° or more to shell axis; moderately broad shallow sinus along posterior margin of wing; primary keel merges with long curved posterior digitation; posterior digitation frequently dorsally curved; anterior digitation blunt, anteriorly oriented; posterior margin of wing between posterior digitation and suture thickened; medial apertural surface of wing digitation thickened; inner lip of aperture covered with moderate callus.

Dimensions.—USNM 405836, height 57.0 mm, width of last whorl without wing 16.0 mm (figured specimen).

Types.—Holotype 405857; paratypes USNM 405858, PU783/2.

Localities.—9, 447, 497, 783, 1104, 1119, 1131, 1134, 1135, 1136, 1137, 1148, 1161, 1189, 1205, 1430, 1431, 1433, 1434, 1435, 1442, 1456, 1467, 1479, 1502, 1503, 1505, 1506, 1507, 1508, 1510, 1519, 1529, 1531, 1532, 1534, 1535, 1536, 1537, 1538, 1548, 1574, 1577, 1587, 1589, 1601, 1697, 1698, 1699, 1700.

Material.—327 specimens.

Stratigraphic range.—1037 to 1375 m.

Discussion.—Although Zinsmeister and Griffin (1995) referred all of the aporrhaid gastropods figured by Wilckens (1910) to *S. nordenskjoldi*, it is clear from the examination of Nordenskjold's material that there are two distinct species. Wilckens' figures 2, 3, and 4 on plate 4 come from latest Campanian to early Maastrichtian from Snow Hill Island while figure 5 without the wing is distinct and comes from the Danian of Seymour Island. This confusion stems from the fact that Andersson and Nordenskjold had only crude understanding of the stratigraphic relationships between Snow Hill and Seymour islands and locality information was limited. Locality data concerning many of the fossils collected by Nordenskjold's party prior to the arrival of Andersson in 1903 are absent and the stratigraphic horizon from which these fossils were collected can only be estimated from the nature of preservation and the supposed track of the field parties to Seymour Island in 1902. It is now known that there are two horizons on Snow Hill and Seymour islands where *Struthiochenopus* occurs.

The specimens referred to as *S. nordenskjoldi* in Wilckens (1910), figures 2–4, and Zinsmeister and Griffin (1995), figures 3.9 and 3.10, are from Snow Hill Island, where they typically occur as casts and molds in dark reddish brown concretions. Wilckens's figure 3 actually shows a steinkern of *S. nordenskjoldi* in one of these concretions. His figures 2 and 4 are casts made from these steinkerns. It is interesting to note that the locality where this material was collected is only a short distance from Nordenskjold's hut on Snow Hill Island and is probably the first fossil locality that Nordenskjold discovered on his arrival on the island. The two specimens figured by Zinsmeister and Griffin are latex molds from concretions collected by Zinsmeister from near Nordenskjold's hut in a visit to Snow Hill Island in 1981. *Struthiochenopus hurleyi* n. sp., Wilckens's figure 5 and Zinsmeister and Griffin's figures 3.11–3.19, is restricted to the uppermost Maastrichtian level of unit 9 of the López de Bertodano Formation and the Danian unit 10 of the López de Bertodano Formation and the Sobral Formation.

Although *Struthiochenopus hurleyi* and *S. nordenskjoldi* are closely related, *S. hurleyi* is about two-thirds the size of *S. nordenskjoldi*. The shoulder of *S. nordenskjoldi* is typically concave between the primary keel and the suture. In addition, the siphonal canal of *S. nordenskjoldi* is long and straight compared to the relatively shorter and curved siphon of *S. hurleyi*.

It is possible that *Rostellaria patagonensis* von Ihering, 1903 (p. 209, 221, not figured; 1904, pp. 13–14, fig. 11; 1907, p. 29), and *R. chubutensis* von Ihering, 1903 (p. 220, pl. 2, fig. 17; 1907, p. 29), from the Paleocene Roca and Salamanca formations of Patagonia belong to *Struthiochenopus*, but the poor preservation of these taxa prevents an accurate assessment. The mostly smooth unicarinate teleoconch whorls that are ornamented with poorly developed axial ribs are, however, consistent with *Struthiochenopus*.

The disjunct stratigraphic distribution of *Struthiochenopus* on Snow Hill and Seymour islands is a bit surprising. Although the genus is absent throughout the Maastrichtian on Seymour Island except for its reappearance in the uppermost part of unit 9 just below the K-T boundary, *Austroaporrhais*, another genus of aporrhaid gastropod, is extremely abundant throughout the late Maastrichtian, but disappears prior to the reappearance of *Struthiochenopus*. Immediately following the K-T extinction, *S. hurleyi* becomes very abundant and remains a prominent element in the Danian molluscan assemblage on Seymour Island.

Etymology.—This species is named in honor of phenomenal photographer, Frank Hurley, on Ernst Shackleton's ill-fated attempt to cross the continent of Antarctica. The photographs that Hurley took during the expedition are considered to be some of the finest ever taken in Antarctica.

Family **STRUTHIOLARIIDAE** Fischer, 1887

Genus **ANTARCTODARWINELLA** Zinsmeister, 1976

Type species (by original designation).—*Antarctodarwinella ellioti* Zinsmeister, 1976.

Discussion.—Presence of *Antarctodarwinella* in the Sobral Formation extends the stratigraphic range of this endemic characteristic struthiolariid into the early Paleocene. The heavily callused and globose nature of *Antarctodarwinella* is reminiscent of only one other struthiolariid gastropod, *Conchothyra*, recorded from the Campanian (or possibly Santonian) to Danian, of New Zealand. Although beyond the scope of this paper, the relationships between species of *Conchothyra*, *Antarctodarwinella*, and Australian *Tylospira* (especially early forms such as *T. glomerata* Darragh, 1991, from the early Miocene) require further assessment and clarification. The absence of Cretaceous struthiolariids in the fossil record of Antarctica suggests that its dispersal from New Zealand was associated with the population of the shelf faunas along the southern Pacific margin during the recovery stage following the K-T boundary event.

Antarctodarwinella austerocallosa, new species
Plate 6, figures 7–15

Conchothyra or *Antarctodarwinella* sp. Palamarczuk *et al.*, 1984, p. 401.
Antarctodarminella n. sp. Stilwell, 2002, p. 404.

Diagnosis.—Medium-sized, robust, subglobose *Antarctodarwinella* with at least 4 weakly angled to gently rounded whorls; last whorl bicarinate with strongly projecting wing, ornamented with poorly developed tubercle development, slightly stronger on adapical keel; last whorl with sinuous growth rugae, stronger near wing and more spaced on older whorls; adapical or posterior sinus angle approximately 52.5°; callus development pronounced, partially enveloping spire, but only to penultimate whorl; distinguished from type species, *A. ellioti* Zinsmeister, 1976, in having a narrower less globose shell, stronger tubercle development, higher spire, and broader aperture.

Description.—Shell moderately sized for genus and family (up to 35 mm high), semi-globose, thick and robust, low to moderately elevated spire of at least 4 compressed, weakly angled to gently convex, strongly ornamented whorls; protoconch paucispiral, smooth, only partially preserved in available material; spire angle variable from approximately 62° to just over 80°; whorl inflation rapid, especially from penultimate to last whorl; sutures encroaching on succeeding whorls, moderately declivous; last whorl capacious, well-inflated with diameter of last whorl just under height of shell; last whorl bicarinate with projected wing, strongly ornamented with rugose, sinuous, varix-like growth increments, posterior or adapical sinus angle ~52.5 °; moderately spaced, rather blunt, axially extending tubercles, present only on poorly developed carinae that are 5 mm apart, and with interspaces smooth; growth increments closer spaced on last whorl, especially more bunched on wing, compared to more spaced ones on older whorls; last whorl with distinct digitation, that is partially truncated to weakly convex and rounded on the distal portion of wing abaxially; spire whorls with sparse sculpture apart from 10–12 weakly developed, only slightly axially extending, tubercles that commence on antepenultimate whorl; last whorl with extensive callus that encroaches on earlier whorls, extending completely over penultimate whorl, but does not completely envelop the spire, still creating a subglobose outline; fasciole forms a moderately developed low ridge on the abapical part of the last whorl; aperture moderately small, sublenticular to narrowly subovate with distinct raised callus pad extending to the parietal region, becoming slightly narrower at poorly developed canal; columella very gently curved, especially in the parietal area; outer lip thickened.

Dimensions.—Holotype USNM 511856, height 35.5 mm, diameter of last whorl including wing 30.5 mm; paratype USNM 511857, height 32.5 mm, diameter of last whorl 22.5 mm (without wing preserved); paratype USNM 511858, height 33.25 mm, diameter of last whorl 22.5 mm; paratype USNM 511859, height 30.5 mm, most of last whorl incomplete; paratype USNM 511914, external mold height of specimen 34.5 mm, height of concretion 61.0 mm.

Types.—Holotype USNM 511856; paratypes USNM 511858, USNM 511859, USNM 511914.

Localities.—497, 1434 (type).

Material.—Four moderately well-preserved specimens and one external mold.

Stratigraphic distribution.—1166 to 1369 m.

Discussion.—The presence of a species of *Antarctodarwinella,* herein named *A. austerocallosa* n. sp., in the Paleocene of Antarctica not only extends the stratigraphic range from the Eocene to the Paleocene, but also presents new data on the phylogeny of this biostratigraphically significant group. Although only three species of *Antarctodarwinella* have been recorded, *A. austerocallosa* n. sp., *A. ellioti* Zinsmeister, 1976 (Units II, III only, La Meseta Formation), and *A. nordenskjoldi* (Wilckens, 1911) (Units III–V, La Meseta Formation), the phylogeny of the genus is curiously not at all clear-cut, as the oldest Paleocene species, *A. austerocallosa* n. sp., is enigmatically much more similar to the youngest species, *A. nordenskjoldi.* The growth line symmetry is nearly identical in all three species. However, the adapical or posterior sinus angle (PSA) is similar in *A. austerocallosa* and *A. nordenskjoldi* at just over 50°, whereas in the oldest Eocene species the angle is approximately 30°. Zinsmeister and Camacho (1980, pp. 3–4) presented evidence of a large increase in the PSA through time in *Antarctodarwinella,* but measurements on the new Paleocene species falsifies this perceived trend. *Antarctodarwinella ellioti* is larger and much more globose with a lower spire, compared to both *A. austerocallosa* and *A. nordenskjoldi.* The extensive callus development in *A. ellioti* is more reminiscent of *Conchothyra parasitica* Hutton, 1877, from the Santonian?–Campanian, and *C. australis* (Marshall, 1916) of New Zealand, in which the callus nearly envelops the spire. It seems likely that *A. nordenskjoldi* was derived from *A. austerocallosa,* as growth lines and sculpture are comparable, except for the more developed wing in *A. austerocallosa.* Also, the last whorl in *A. austerocallosa* is more strongly bicarinate with a marginally sharper abapical keel and the labial callus less developed than in *A. nordenskjoldi.* The disparity in morphology between the three species of *Antarctodarwinella* indicates that the fossil record of this group is far from complete, and other intermediate forms probably existed, of which we have no fossil record. Indeed, no *Antarctodarwinella*-like struthiolariids are recorded from upper Paleocene to lower Eocene deposits, as there is a paucity of deposits of this age in the Southern Hemisphere.

Etymology.—Species named from the Latin *callosus* (equivalent to "hard skin, callus") and Latin *auster* (equivalent to "south") for its heavily callused shell and endemic presence in Antarctica.

Superfamily **VANIKOROIDEA** Gray, 1840

Family **VANIKORIDAE** Gray, 1840

Genus **VANIKOROPSIS** Meek, 1876

Type species (by original designation).—*Natica tuomeyana* Meek and Hayden, 1856.

Discussion.—*Vanikoropsis* is one of the oldest Cretaceous gastropods with records extending back to the Barremian–Aptian of Japan (Tracey *et al.*, 1993, p. 148). *Vanikoropsis* had a wide distribution during the Cretaceous with reports of the genus from Europe, West India, North America, Australia, New Zealand and Antarctica (see Wenz, 1938; Fricker, 1999). The genus survived the K-T boundary extinction event and apparently inhabited northern and southern polar regions only (Kollmann and Peel, 1983; Zinsmeister *et al.*, 1989).

Vanikoropsis arktowskiana (Wilckens, 1910)

Plate 6, figures 16–19

Eunaticina? *arktowskiana* Wilckens, 1910, pp. 78–80, pl. 3, figs. 29a, b, pl. 4, figs. 17, 18.

Eunaticina arctowskiana Wilckens. Macellari, 1984, pl. 34, figs. 11–12, pl. 35, fig. 11, error *pro V. arktowskiana*; Stilwell and Zinsmeister, 1987a, p. 9, error *pro V. arktowskiana*; Stilwell and Zinsmeister, 1987b, p. 8, error *pro V. arktowskiana*.

Eunaticina arctowskiana Wilckens. Zinsmeister *et al.*, 1989, p. 733, fig. 2, p. 734, fig. 3, p. 736, fig. 6, error *pro V. arktowskiana;* Stilwell, 1994, p. 661; Zinsmeister, 1998a, p. 565, fig. 9, error *pro V. arktowskiana*.

Vanikoropsis, n. sp. Fricker, 1999, pp. 146–152, pl. 3, figs. 5–10.

V. arctowskiana (Wilckens). Fricker, 1999, pp. 153–155, pl. 3, figs. 11, 12, pl. 4, figs. 1–3, error *pro V. arktowskiana* (Wilckens, 1910).

Dimensions.—USNM 511860, height 44.5 mm, diameter of last whorl 36.5 mm; USNM 511861, height 34.0 mm, diameter of last whorl 29.5 mm.

Types.—Mo 1330, Mo 1339, Mo. 1340.

Localities.—9, 496, 1134, 1135, 1205, 1414, 1430, 1431, 1432, 1434, 1505, 1506, 1507, 1508, 1510, 1548, 1589, 1596, 1601, 1698, 1700.

Material.—98 specimens.

Stratigraphic range.—900 to 1201 m.

Discussion.—The abundant, characteristic naticiform gastropod *Eunaticina*? *arktowskiana* Wilckens, 1910 (p. 78, pl. 3, fig. 29a, b, pl. 4, figs. 17, 18), from the latest Cretaceous to Danian of the James Ross Island Group (recorded from Snow Hill, Seymour and James Ross islands), was divided recently by Fricker (1999, pp. 145–155) into two species, one new. In our opinion, this division may not be warranted, especially given the variable nature of *Vanikoropsis* (see Sohl, 1967; Erickson, 1974). A scatter diagram of height versus diameter provided by Fricker (1999, p. 152) does not yield evidence for such a separation of *V. arktowskiana* and, for example, the figured specimen of *Vanikoropsis* n. sp. (see pl. 3, fig. 3a, b) can hardly be distinguished from *V. arktowskiana* depicted on the same plate (see fig. 9a, b). The sculptural configuration of *V. arktowskiana* is diverse with differences from individual to individual of strength, width, spacing, and number of spirals. The convexity of the whorl outline is also variable in the species, as is the expanded nature of the outer lip.

Vanikoropsis arktowskiana is one of the longest ranging species in Antarctica with records extending from probably Campanian time to at least the early Danian, crossing the K-T boundary unscathed. We can cite no differences in Paleocene forms, compared with their Cretaceous counterparts. The affinity of probable older Antarctic forms such as *Vanikoropsis*? sp. of Thomson (1971) from Alexander Island is uncertain, as the material is poorly preserved.

Superfamily **NATICOIDEA** Gray, 1840

Family **NATICIDAE** Gray, 1840

Subfamily **POLINICINAE** Gray, 1847

Genus **AMAUROPSIS** Mörch, 1857, p. 81

Type species (by subsequent designation, Dall, 1909).—*Natica helicoides* Johnston, 1835 (= *Nerita islandica* Gmelin, 1791).

Discussion.—*Amauropsis* is one of few gastropods with a stratigraphic range of Paleocene to Recent in Antarctica (see extant species described by Dell, 1990). Of note, *Amauropsis* is not present in the Eocene La Meseta Formation. Dell (1990, pp. 139–140) could see no evidence to separate the Arctic and Antarctic forms of *Amauropsis*, despite the absence of a channeled suture in Antarctic species, and advised that the concept of *Amauropsis* be expanded rather than to divide the northern and southern forms when the state of present knowledge of the significance of sutural differences has not been adequately evaluated.

Amauropsis notoleptos, new species
Plate 6, figures 20–22

Diagnosis.—Early, small *Amauropsis* with a moderately high spire of at least three convex whorls, and spire angle of ~92°; no sculpture as shell polished and smooth apart from weak prosocline growth lines and equally weak, numerous microscopic growth lines; umbilicus poorly developed; labial callus well raised, but rather narrow extending to parietal area; differs from closely related *A. rossiana* Smith, 1907, in having a much smaller shell, slightly less developed spiral sculpture of microscopic threads, a more raised callus, and slightly shallower umbilicus.

Description.—Shell relatively small for genus (less than 10 mm high), thin, polished, strong, moderately high-spired naticiform, umbilicate; ratio of height to diameter of last whorl 1.25:1; spire moderately high, consisting of at least three convex whorls with narrowly channeled sutures or subsutural furrows; spire angle ~92°; apical whorls low, paucispiral, worn in available material; inflation rapid, especially from penultimate to last whorl; last whorl moderately inflated, convex, smooth apart from weak prosocline growth lines and weak microscopic spiral threads; sculpture on penultimate whorls similar of very weak growth lines and spirals; aperture holostomatous, moderately ovate, open; columella gently concave; labium with raised, well-defined, moderately narrow callus; outer lip thin.

Dimensions.—Holotype USNM 511862, height 8.0 mm, diameter of last whorl 7.0 mm; paratype USNM 511863, height 6.5 mm, diameter of last whorl 5.0 mm.

Types.—Holotype USNM 511862; paratype USNM 511863.

Localities.—1519, 1531 (type).

Material.—Two specimens and other fragments.

Stratigraphic distribution.—1053 to 1073 m.

Discussion.—*Amauropsis notoleptos* n. sp. is the oldest record of the genus in Antarctica and the only species known from the Paleogene. *A. notoleptos* is apparently allied to and is probably the ancestor to living Antarctic species such as *A. rossiana* Smith, 1907 (p. 5, pl. 1, figs. 6, 6a; Dell, 1990, p. 140, figs. 247, 276), and *A. powelli* Dell, 1990 (p. 144, figs. 246, 268), but differs in its much smaller size and narrower, slightly taller spire. The aperture and callus of *A. rossiana* is strikingly similar to *A. notoleptos*, but the Paleocene species has a marginally more developed umbilicus. The Recent (also known as fossil, but ages unknown) type species, *A. islandica* (Gmelin, 1791) (p. 3675; Wenz, 1938–1944, p. 1035, fig. 2965; Marincovich, 1977, pp. 217–218, pl. 17, figs. 1–4, pl. 22, fig. 1, text-fig. 12), is largely a magnified version of and is very similar to *A. notoleptos* n. sp., and differs in having a much larger shell with a higher spire and more distinct prosocline growth lines. Other Paleocene species of *Amauropsis*, such as *A. meierensis* Zinsmeister, 1983 (pp. 1292–1293, fig. 2L, M) and *A. martinezensis* Dickerson, 1914 (p. 142, pl. 13, fig. 4a, b; Marincovich, 1977, pp. 221–222; pl. 17, figs. 5–10), from the Paleocene of Western North America have higher spires and much larger shells, compared to *A. notoleptos*, and are not closely related. The origin of *A. notoleptos* is uncertain, given the patchy stratigraphic distribution of the group in the earliest Tertiary.

Etymology.—Species named from the Greek word *notos* (equivalent to "south") and Greek word *leptos* (equivalent to "fine, small") for its endemic Antarctic occurrence and small size for the genus.

Genus **EUSPIRA** Agassiz *in* J. Sowerby, 1837

Type species (by subsequent designation, Bucquoy, Dautzenberg, and Dollfus, 1883)—*Natica glaucinoides* J. Sowerby, 1812 (*non* Deshayes, 1832) (= *Natica labellata* Lamarck, 1804) (Kabat, 1991, p. 429).

Euspira antarctidia, new species
Plate 7, figures 7–10

Diagnosis.—Relatively small but robust *Euspira* with nearly 1:1 ratio of height to diameter of last whorl; weakly channeled sutures, and dome-like protoconch of no more than 2 whorls; no sculpture, just weak prosocline growth lines and microscopic spirals; umbilicus moderately developed; funicle present; aperture D-shaped to broadly oval-shaped; differs from closely related Antarctic species, *Euspira* n. sp. of Fricker (1999), in being minute in comparison, with weaker growth lines, a funicle, and a more D-shaped aperture.

Description.—Small-to medium-sized for genus (up to 13.0 mm high), moderately high-spired, robust, globose naticiform, umbilicate; spire of at least 2 small, weakly inflated, convex whorls with weakly channeled sutures; ratio of height to diameter of last whorl just over 1.1:1; protoconch paucispiral, dome-like, smooth, slightly covered in matrix on holotype; spire angle obtuse of approximately 112.5°; whorl inflation quite rapid, especially from penultimate to last whorl; last whorl greatly inflated, with faint, weak microscopic threads and prosocline growth lines only; teleoconch whorls similarly smooth with only prosocline growth lines; aperture large, holostomatous; broadly ovate to D-shaped; umbilicus moderately deep; columella distinctly curved with distinct but rather thin funicle; parietal region with thin glaze; outer lip thin.

Dimensions.—Holotype USNM 511864, height 13.0

mm, diameter of last whorl 11.5 mm; paratype USNM 511865, height 7.0 mm, diameter of last whorl 6.5 mm; paratype USNM 511866, height 6.0 mm, diameter of last whorl 5.5 mm.

Types.—Holotype USNM 511864; paratypes USNM 511865, USNM 511866.

Localities.—1519 (type), 1535, 1538.

Material.—Seven specimens.

Stratigraphic range.—1072 to 1130 m.

Discussion.—*Euspira* is recognized in Antarctic Paleocene deposits for the first time, previously recorded from the latest Cretaceous (Fricker, 1999) and mid-Eocene (Stilwell, 2000). *Euspira antarctidia* n. sp., described herein from the Sobral Formation, is closely related to *Euspira* n. sp. of Fricker (1999, pp. 158–161, pl. 4, figs. 4a, b, 5a, b) from the Maastrichtian (perhaps even older record of Campanian, also) of the López de Bertodano Formation, but is comparatively small to moderate in size with more defined prosocline growth lines, a slightly more compressed last whorl, a more D-shaped aperture, and a less open umbilicus. *Euspira bohatyi* Stilwell, 2000 (p. 303, pl. 8, figs. a–c) from the middle Eocene of McMurdo Sound, East Antarctica, has a much larger shell, a more compressed last whorl, stronger prosocline growth lines, and a much wider umbilicus. The European Eocene type species, *E. labellata* (Lamarck, 1804) (see Brown, 1849, p. 89 (error p. 99 in index), pl. 43, figs. 30–31, *Natica glaucinoides*; Wenz, 1941, p. 1042, fig. 2986), is also quite comparable to *E. antarctidia*, but differs again in its much larger size, a more inflated spire, and stronger growth lines.

Other Austral Paleocene species are apparently only distantly related to *E. antarctidia* n. sp.; these include *E. fyfei* (Marwick, 1924) from South Island, New Zealand, *Euspira* sp. cf. *E. pueyrredonensis* (Stanton, 1901) of Griffin and Hünicken (1994) from southwestern Patagonia, and *E. saxosulensis* Darragh, 1997, from Victoria, Australia. These records indicate that the genus was well distributed and established in Southern Hemisphere Paleocene shallow waters.

Etymology.—Species named from the Latin diminutive prefix *-idium* and for its occurrence in Antarctica.

Superfamily **TONNOIDEA** Suter, 1913

Family **RANELLIDAE** Gray, 1854

Subfamily **CYMATIINAE**? Iredale, 1913

Genus **ANTARCTIRANELLA,** new genus

Type species (by original designation).—*Antarctiranella tesella* n. gen. n. sp.

Diagnosis.—Moderately high-spired ranelliform or fusiform shell with highly ornamented shell of cancellate sculpture that approaches a tesselate or "checker-board" pattern on the central part of last whorl and penultimate whorl with rounded nodes at the intersection of spiral and axial elements; spiral ornamentation of two strong carinae and spiral cords; outer lip broken on available material, but preserved sections indicate a definite flare or varix; inner lip with moderately broad callus, concave; aperture broadly ovate; inner labrum with furrows corresponding to spiral elements; siphonal canal moderately long, slightly twisted, narrowly notched.

Discussion.—*Antarctiranella* n. gen. is erected herein for an enigmatic Paleocene Antarctic gastropod with a moderately twisted siphonal canal, flared outer lip and shell form reminiscent of groups within the Ranellidae. Only one specimen of this gastropod was available for study, but a new species described by Fricker (1999) from the López de Bertodano Formation of Seymour Island is probably congeneric if not perhaps conspecific as well, but the penultimate whorl is more convex and the sutures more impressed. Fricker (1999) (pp. 175–177) considered the Maastrichtian Antarctic species to be an aberrant member of the Ranellidae as it does not appear to have either a definite varix, columellar plications, or a rugose inner lip callus compared with many ranellid gastropods. Fricker suggested that a possible relationship to Buccinidae cannot be discounted, but we suggest that the overall form and flared outer lip is more indicative of Ranellidae. Further, Fricker was apparently unaware of a specimen collected from the Paleocene Sobral Formation of Seymour Island. This individual has an outer lip that can be described as a definite varix. There is no other member of the Ranellidae that approaches this new group apart from *Cymatium* s.l. (A. Beu, personal communication, 2000), so it is highly likely that *Antarctiranella* n. gen. was short-lived and became extinct sometime during the Paleocene.

Etymology.—Named based on its sole early presence in Antarctica and for its relationship to Ranellidae.

Antarctiranella tessela, new species

Plate 7, figures 5, 6

Diagnosis.—As for genus.

Description.—Shell moderately large for family (slightly more than 38 mm high), robust, moderately thick-shelled, ranelliform to fusiform; spire moderately high of more than 2 unicarinate, nearly quadrate, slightly convex whorls, about a third of total height of shell; whorl inflation rapid from penultimate to last whorl; spire angle approximately 66.5°; protoconch unknown; suture barely impressed, slightly clasping, last whorl wrapping around noded axials of penultimate whorl; sculpture elaborate of tesselate or "checker-board" pattern of cancellate spiral ribs and equally strong axials, especially centrally on last whorl, bearing 10–11 axially aligned nodes on the two central carina, which are concave between; last whorl with more than 17 strong, but unequally developed spiral cords and many microscopic interstitial threads; last whorl broadly convex with 10–11 axials and nodes, slightly concave between carinas; sutural ramp moderately steep, gently concave, merging with carina; axials on penultimate whorl extend from adapical carina abapically to suture; some 12 nodes on penultimate whorl; axials on penultimate whorl not aligned with those on last whorl; growth lines poorly defined; base of last whorl strongly contracted to moderately short, slightly twisted, narrowly notched canal; aperture broadly ovate with narrow channels corresponding to carina on last whorl; labium with moderately narrow callus; columella seemingly smooth, concave; outer lip flared abaxially into thickened varix, smooth internally.

Dimensions.—Holotype USNM 511867, height slightly more than 38.0 mm if complete, diameter of last whorl 29.0 mm.

Type.—Holotype USNM 511867.

Type locality.—1431.

Material.—Holotype

Stratigraphic range.—1144 m.

Discussion.—*Antarctiranella tessela* n. gen. n. sp. represents an early member of the Ranellidae that has no other coeval or older Late Cretaceous relatives. It is probably a short-lived taxon that evolved during the K-T boundary marine revolution that became extinct sometime during the Paleocene. As reviewed by Beu (1988), the oldest recorded ranellid is Turonian in age, *Sassia kanabensis* (Stanton, 1893) from the Western Interior of North America, and most of the six recorded species are Maastrichtian. None of these approach the new Antarctic Paleocene species. Paleocene members of the group are rare and consist of *Gyrineum*? *judithae* Zinsmeister, 1983, from the Danian, *Sassia* sp. of Darragh (1997, p. 74, fig. 3G, H) from the mid-Paleocene of southeastern Australia, and *Ranella louellae* Beu, 1988, from the late Paleocene of California. Ranellids described by Kollmann and Peel (1983) from the Paleocene of Greenland do not belong in this family (A. Beu, personal communication, 2000).

Etymology.—Species named from the Latin *tesella* (equivalent to "inlaid with small, square stones, checkered") for its checkered sculptural configuration of axials and spirals on the last and penultimate whorls.

Superfamily **EULIMOIDEA** Philippi, 1853

Family **EULIMIDAE** Philippi, 1853

Genus **MELANELLA** Bowdich, 1822, p. 120

Type species (by monotypy).—*Melanella dufresnei* Bowdich, 1822 (*non dufresnii*, error, Abbott, 1974, p. 125).

Discussion.—The Paleocene distribution of this eulimid is extended to Antarctica, previously recorded from the Paleocene of New Zealand (Finlay and Marwick, 1937), and Eocene to Recent of Europe, North Africa, South India, Japan, West Indies, and North and South America (Wenz, 1940, p. 835). *Balcis* Leach, 1847, is a synonym (Warén, 1984; Maxwell, 1992). Unless the available fossil material is well-preserved, in practice it is often difficult to distinguish *Melanella* from pyramidellid groups such as *Odostomia* Fleming, 1817, which has a variably strong plait on the adapical part of the columella. The Antarctic material, which is nicely preserved, belongs in *Melanella*.

Melanella seymourensis, new species

Plate 7, figures 1–4

Diagnosis.—High-spired *Melanella* with more than five gently inflated, subtrapeziform whorls with only slightly impressed sutures; whorls polished, smooth, with only closely spaced microscopic spiral threads, opisthocyrt growth lines and a few groove-like varices; aperture tear-shaped; easily distinguished from *M. pontilis* Maxwell, 1992, in having opisthocyrt growth lines and more swollen whorls that have more impressed sutures.

Description.—Species small- to medium-sized for genus, thin-shelled, high-spired, subulate, polished, imperforate; spire high, subgradate, of at least five subtrapeziform, gently swollen whorls; spire angle acute; sutures only slightly impressed; whorl inflation gradual; protoconch unknown, broken on available material; last whorl weakly inflated and convex, mostly smooth apart from many, closely spaced microscopic spiral threads and closely spaced, sinuous opisthocyrt growth lines; teleoconch whorls similarly sculptured; aperture moderately small, tear-shaped, holostomatous; pillar smooth, straight to only slightly concave, with very narrow, slightly raised callus; outer lip thin, smooth.

Dimensions.—Holotype USNM 511868, height 5.5 mm, diameter of last whorl 2.0 mm; paratype USNM 511869, height 6.25 mm, diameter of last whorl 2.5 mm; paratype USNM 511870, height 4.0 mm incomplete.

Types.—Holotype USNM 511868; paratypes, USNM 511869, USNM 511870.

Localities.—1519, 1535 (type).

Material.—Two mostly complete specimens and several fragments.

Stratigraphic range.—1072 to 1078 m.

Discussion.—The oldest records of *Melanella* are in the Southern Hemisphere and are represented by *M. seymourensis* n. sp. from the Sobral Formation, *M. lautoides* Finlay and Marwick, 1937, from the late early Paleocene of the Wangaloa Formation of New Zealand, and *Melanella*? n. sp. of Stilwell (1994) from the mid-Paleocene Kauru Formation, also of New Zealand. The Kauru Formation species (Stilwell, 1994, pp. 937–938, pl. 68, fig. 6) is most like *M. seymourensis* in having a subulate, high-spired, polished shell, but the growth lines of *M. seymourensis* are opisthocyrt, whereas those of *Melanella*? n. sp. are more opisthocline. The Kauru Formation species was tentatively placed in *Melanella* as the aperture in the only known specimen is incomplete. All preserved features of this shell point to an allocation to *Melanella*. *M. lautoides* Finlay and Marwick, 1937 (p. 66, pl. 5, fig. 11; Fleming, 1966, p. 388, pl. 145, fig. 1748; Stilwell, 1994, pp. 935–937, pl. 68, figs. 1–5) has a much lower spired shell with a more gradate spire and deeper, more orthocline growth lines, and more channeled sutures. *Melanella pontilis* Maxwell, 1992 (p. 120, pl. 16, figs. e, f) from the late Eocene of New Zealand is strikingly like *M. seymourensis*, but *M. pontilis* has a taller spire, more flush whorls and less distinctive opisthocline growth lines, compared to the Antarctic species.

Of note, *Melanella* sp. of Finlay and Marwick (1937, p. 66, pl. 5, figs. 18, 19; Fleming, 1966, p. 388, figs. 1749, 1750) from the mid-Paleocene of Boulder Hill, South Island, New Zealand, doubtfully belongs to *Melanella* and may represent a species of *Odostomia* because of the preserved plait situated high on the pillar adapically.

Etymology.—Species named for its endemic occurrence on Seymour Island.

Superfamily **MURICOIDEA** Rafinesque, 1815

Family **TUDICLIDAE** Cossmann, 1901, emend. Finlay and Marwick, 1937

Genus **HETEROTERMA** Gabb, 1869

Type species (by monotypy).—*Heteroterma trochoidea* Gabb, 1869.

Heteroterma?, new species
Plate 7, figures 13, 14

Description.—Shell small- to medium-sized (up to 18.5 mm), moderately thick-shelled, low-spired biconic; spire moderately low, of at least 3 weakly convex, noded whorls; protoconch paucispiral, smooth, only partially preserved on available specimen; spire angle approximately 77°; whorl inflation rapid from penultimate to last whorl; suture slightly impressed, last whorl nearly clasping around noded penultimate whorl; sutural ramp steep; last whorl uniangulate, inflated, with noded central keel; ornamentation of 12 well-developed tubercles centrally on keel and more than 25 spiral cords that are more bunched on base; growth lines weak, opisthocyrt; tubercled keel on penultimate whorl located just adapical of suture; base contracting to short neck; aperture broad, ovate; columella obscured by matrix; outer lip slightly thickened at keel.

Dimensions.—USNM 511871, height 18.5 mm, diameter of last whorl 14.5 mm.

Locality.—1104.

Material.—One specimen.

Stratigraphic occurrence.—1375 m.

Discussion.—The biconic outline and sculpture of strong tubercles and spiral cords of this probable tudiclid approaches *Heteroterma trochoidea* Gabb, 1869 (p. 152, pl. 26, figs. 30, 30a; see review by Saul, 1988a, pp. 13–14, figs. 12, 72–76) and *H.*? *acrita* Saul, 1988a (pp. 14–16, figs. 13, 77–84) from the late Paleocene of California, but the shell of *Heteroterma*? n. sp. is somewhat abraded with loss of part of the siphonal canal and sculpture details. It is not known whether or not a fasciole is present in this new Antarctic species. The suture of *Heteroterma*? n. sp. is somewhat clasping with the nodose keel of the penultimate whorl just visible, as in *H. trochoidea*, whereas in *H.*? *acrita* the last whorl envelops the nodose keel of the penultimate whorl and takes the form of a steep collar or subsutural welt. More specimens are needed to confirm a genus-level assignment.

Genus **PYROPSIS** Conrad, 1860

Type species (by monotypy).—*Tudicla* (*Pyropsis*) *perlata* Conrad, 1860.

Discussion.—Although beyond the scope of this paper, further research on the problematic "Wangaloan" Paleocene New Zealand species *Heteroterma zelandica* Marshall, 1917, and related Cretaceous and Paleocene taxa such as *Cominella*? *praecursor* Wilckens, 1905 (= *Struthilariopsis*? *tumida* Wilckens, 1905), *Heteroterma elegans* Griffin and Hünicken, 1994, *Pyropsis*? *gabbi* (Stanton, 1896) [*Heteroterma*] and *Heteroterma*? *acrita* Saul, 1988a, is necessary to clarify relationships of these closely related groups (Stilwell, 1993, 1994). *Heteroterma zelandica* is not a *Heteroterma* as it is very much distinct from the type species, *H. trochoidea* Gabb, 1869, which has a developed fasciole, narrower and less expanded lip, moderately short siphonal canal, and a suture that does not cover the adapical series of nodes, very much distinct from *H.*

zelandica. The new Antarctic species, *Pyropsis? australis* n. sp. described below, is very closely related to *H. zelandica* and both are congeneric and probably derived from the same stock. A full review of these taxa is being prepared by one of us (JDS), and until this work is completed in conjunction with the well-preserved New Zealand material, the Austral forms will be retained in closely allied *Pyropsis*.

Pyropsis? australis, new species

Plate 7, figures 9, 10

Diagnosis.—Moderately sized, robust, low-spired *Pyropsis*? with apical angle of 82°; 12–13 axially extending tubercles and some 25 wavy spirals; steep subsutural ramp that wraps around tubercles of penultimate whorl yielding a band that has a wavy appearance, penultimate whorl with slightly swollen subsutural band giving a gently concave profile; distinguished from closely allied New Zealand species, "*P*." *zelandica* (Marshall, 1917), in having a higher spire, steeper adapical slope, less developed sutural band and fewer axials and spirals.

Description.—Shell medium-sized for family (up to 47.5 mm high), relatively robust, thick, pyriform; spire low, conical, consisting of at least 4 compressed, gently convex whorls; protoconch small, paucispiral, conical, a bit eroded on holotype; spire angle 82°; whorl inflation very rapid from penultimate to last whorl; suture complex with ill-defined, relatively blunt, axially extending tubercles, bounded adapically by narrow, wavy zone on extreme abapical part of last whorl that essentially wraps around adapical nodulation of penultimate whorl like a wavy band, on swollen, mostly spirally sculptured, obliquely truncated, abapical angulation; last whorl capacious with short, rather steep adapical ramp that is gently concave, merging with distinctly angled periphery of ~12–13 moderately strong, broad, axially extending tubercles and spiral ornamentation of more than 25 wavy spiral cords that are more spaced on angulation; penultimate whorl with 6 narrow spiral cords; growth lines on last whorl opisthocyrt on ramp becoming orthocline and just slightly sinuous on angulation and canal; basal constriction rapid; growth lines on teleoconch whorls opisthocyrt; aperture well open, broadly lenticular, with mostly straight columella; callus moderately thick, spreading into parietal glaze; siphonal canal moderately long, narrow, tapered; outer lip thickened.

Dimensions.—Holotype USNM 511872, height 47.5 mm, diameter of last whorl 30.0 mm.

Type.—Holotype USNM 511872.

Locality.—1104.

Material.—One specimen.

Stratigraphic occurrence.—1375 m.

Discussion.—*Pyropsis? australis* n. sp. is congeneric with, and most closely allied to, *Heteroterma zelandica* Marshall, 1917 (pp. 453–454, pl. 35, figs. 20, 21; Finlay and Marwick, 1937, pp. 84–85, pl. 10, figs. 8–10; Fleming, 1966, p. 322, pl. 112, figs. 1367–1369; Beu and Maxwell, 1990, pp. 84–86, pl. 2, fig. p; Stilwell, 1994, pp. 986–997, pl. 70, figs. 5, 9, 13–18) (= n. gen. aff. *Pyropsis*), one of the most characteristic and commonly figured Paleocene gastropods of New Zealand. These two taxa are strikingly similar, and differ mainly in height of spire and minor sculptural attributes. *Pyropsis? australis* is distinguished from *P.? zelandica* in having a slightly higher spire, a slightly steeper adapical ramp on the last whorl, a less developed sutural band, fewer axially extending tubercles, and fewer spiral cords. The Antarctic species is probably slightly older than the New Zealand species, which is considered to be late early Paleocene in age (Stilwell, 1994). *Heteroterma elegans* Griffin and Hünicken, 1994 (pp. 267–269, figs. 7.1, 7.2) from the Paleocene of Patagonia is also a congeneric form that has a longer siphonal canal, poorly developed tubercles, a less swollen subsutural band, compared to *P.? australis* and *P.? zelandica*. Of note, the only species comparable to *P.? australis* in the Northern Hemisphere are *H.? acrita* Saul, 1988a (pp. 14–16, figs. 13, 77–84) (= *Pyropsis*?) and *H. striata* Stanton, 1896 (p. 1046, pl. 67, fig. 5; Dickerson, p. 151, pl. 17, fig. 1; Zinsmeister, 1983, p. 1299, figs. 3O, P; Saul, 1988b, pp. 885–886, figs. 2.3, 3.26–3.30) (= *Pyropsis*?), from the Paleocene of California, but these taxa have smaller shells, slightly more developed tubercles, and a more swollen subsutural band, compared to *P.? australis*. The distribution of these species of *Pyropsis*? suggests that the group was well established in Danian shallow waters extending from western North America to the southern rim of the southern circum-Pacific.

Etymology.—Species named for its Austral occurrence.

Superfamily **BUCCINOIDEA** Rafinesque, 1815

Family **BUCCINIDAE** Rafinesque, 1815

Subfamily **BUCCININAE** Rafinesque, 1815

Genus **COLUS** Röding, 1798

Type species (by original designation).—*Colus islandicus* (Gmelin, 1791).

Colus delrioae, new species

Plate 7, figures 15–20

Diagnosis.—Large smooth *Colus* with moderately high spire of at least 7 rather compressed and weakly convex to almost flush whorls; spire angle approximately 36° to 38°; shell nearly void of sculpture apart from widely spaced, very weak spirals, and equally weak growth lines; base well contracted; siphonal canal moderately long, gently twisted abaxially; columella smooth and concave; differs from Recent type species, *C. islandicus* (Gmelin, 1791) in having a higher spire with less convex and more flattened, flush whorls and weaker spiral ornamentation.

Description.—Shell large (up to 90 mm high), rather slender, moderately thick-shelled, high-spired fusiform; spire moderately high to high of at least 7 compressed, very weakly rounded to nearly flush whorls that approach a near gradate outline; protoconch partially present, paucispiral, smooth; spire angle acute of between 36° to 38°; whorl inflation moderately slow on spire increasing rapidly from penultimate to last whorl; sutures very weakly impressed; last whorl inflated, convex, smooth and polished apart from weak, but broad, spiral ribs that are widely spaced, and weak growth lines that are opisthocline medially becoming more prosocline near base; spire whorls void of sculpture apart from microscopic spiral threads and faint opisthocyrt growth lines; last whorl contracts abruptly at base, producing a moderately long, gently oblique and twisted canal that is narrowly channeled; columella moderately long, smooth, concave with narrow callus; outer lip thin, smooth.

Dimensions.—Holotype UBA 16816, height 90.0 mm, diameter of last whorl 44.0 mm; paratype USNM 511873, height 51.5 mm, diameter of last whorl 24.0 mm (immature individual); paratype USNM 511874, height 38.5 mm, diameter of last whorl 25.5 mm.

Types.—Holotype UBA 16816; paratypes, USNM 511873, USNM 511874.

Localities.—1431, 1535, 1556.

Material.—Three specimens.

Stratigraphic range.—1077 to 1144 m.

Discussion.—This enigmatic high-spired gastropod is rare in the Sobral Formation and is represented by three specimens, of which only one is moderately well preserved (an immature individual, USNM 511873). No other related species are recorded from the Antarctic fossil record or from the Recent. The outline and weak spiral sculpture is consistent with the Tertiary to Recent genus *Colus* Röding, 1798, type species *C. islandicus* (Gmelin, 1791) (see Abbott and Dance, 1983, p. 163, colored figure), from Labrador to Norway. The siphonal canal is longer in *C. islandicus* and the whorls are more convex, but the Seymour Island species fits comfortably in the group, acknowledging the variable nature of this buccinid. Few fossil members of *Colus* approach the Antarctic species, but *Fasciolaria rhomboidea* Rogers, 1839 (p. 376, pl. 30, fig. 3) (= *Colus*?) from the mid-Tertiary of Virginia is similar. *Colus*? *rhomboidea* has more rounded, convex whorls, compared with *C. delrioae* n. sp.

The evolutionary history of *Colus delrioae* is uncertain and the group apparently did not survive after the Paleocene in Antarctica. This species is in all likelihood a migrant species, but the imperfect preservation of the available material prevents an in-depth investigation of this unusual new group.

Etymology.—This species is named for Dr. Claudia del Rio, University of Buenos Aires, who found the magnificent holotype of this species.

Genus **PSEUDOFAX** Finlay and Marwick, 1937

Type species (by original designation).—*Phos ordinarius* Marshall, 1917.

Discussion.—*Pseudofax* was one of the most widespread buccinid gastropods in lower Tertiary shallow-marine deposits in the Southern Hemisphere. This group is represented in the early late Paleocene to middle Eocene of New Zealand, Paleocene of southern Patagonia, mid-Paleocene of southeastern Australia, and from this work from earliest Paleocene to middle Eocene of Antarctica (see Finlay and Marwick, 1937; Stilwell and Zinsmeister, 1992; Stilwell, 1994; Griffin and Hünicken, 1994; Darragh, 1997; Stilwell, 2000).

Pseudofax, a generalized buccinid, was recently reviewed in detail by Beu and Maxwell (1990, p. 83) and Stilwell and Zinsmeister (1992, pp. 124–125), so only a brief summary is appropriate here, with additional records of this representative of a post K-T boundary "bloom taxon." *Pseudofax*, as the name suggests, has an affinity with *Fax* Iredale, 1925, but protoconch differences separate the two groups: *Pseudofax* has a broadly conical protoconch, different from the cylindrical protoconch in *Fax*. *Pseudofax* is considered to be intermediate morphologically among *Nassicola*, *Zelandiella*, *Eucominia*, *Cominula*, and *Procominula*, all Finlay (1926) buccinid genera. Wenz (1941, p. 1176) believed *Pseudofax* to be a subgenus of *Phos* Montfort, 1810, type species *P. senticosus* (Linnaeus, 1758) (see Wenz, 1941, p. 1175, fig. 3338), but the distinctive highly ornamental shell and aperture of *P. senticosus* effectively separates these groups at genus level.

Pseudofax? paucus, new species

Plate 8, figures 25, 26

Diagnosis.—Average-sized *Pseudofax*, but small for Buccinidae, relatively thin-shelled, moderately high-spired fusiform to elongate-ovate in outline; more than 3 convex spire whorls; spire angle about 59°; ornamentation of some 15 equally spaced spiral cords and about 10 poorly developed, rounded axials; inner part of outer lip lirate; distinguished from type species, *P.*

ordinarius (Marshall, 1917), in having generally more inflated whorls, less wavy spiral cords, reflecting a more subdued axial component, and broader more ovate aperture.

Description.—Shell small for family (height 14 mm), broadly fusiform to elongate-ovate; spire moderately high of more than 3 rather squat, convex whorls; whorl inflation relatively rapid; spire angle approximately 59°; protoconch details unknown; sutures impressed; last whorl moderately inflated, convex, ornamented with 15 equally spaced spiral cords and incised interspaces, and about 10 rounded, poorly defined, axial ridges; growth lines weak, poorly defined, orthocline to barely opisthocyrt; spire whorls with 5–6 spiral cords and no perceptible axials; base contracted abruptly to short, notched, oblique, siphonal canal; columella short, concave with thin, narrow callus; fasciole poorly developed; aperture broad, ovate; inner part of outer lip lirate; outer lip relatively thin.

Dimensions.—Holotype USNM 511875, height 14.0 mm, diameter of last whorl 9.5 mm.

Type.—Holotype USNM 511875.

Type locality.—1589.

Material.—Holotype.

Stratigraphic range.—1149 m.

Discussion.—This rare species compares well with the Paleogene buccinid *Pseudofax*, type species *P. ordinarius* (Marshall, 1917) (p. 456, pl. 35, figs. 24, 25; Wenz, 1941, p. 1176, fig. 3341; Finlay and Marwick, 1937, p. 80, pl. 9, figs. 16, 18; Beu and Maxwell, 1990, p. 83, pl. 2, fig. t), but the shell outline of the new Antarctic species is relatively broader, the spiral cords are more uniform and less wavy, and the aperture is more open and ovate. *Phos conica* Marshall, 1917, was relegated to subspecies-level status by Finlay and Marwick, (1937, p. 80), who believed it to be a subspecies of *Pseudofax ordinarius*. Beu and Maxwell (1990) recognized the variability of *P. ordinarius* and considered *P. conicus* to be a morphotype, albeit extreme, of *P. ordinarius*. Stilwell (1994) supported Beu and Maxwell's conclusions by collecting a large number of these morphotypes. Other Paleocene Austral taxa, such as *P. costellatus* Griffin and Hünicken, 1994, from southwestern Patagonia, and *P.* cf. *P. ordinarius* from southeastern Australia, are not closely related. Although the preservation of the holotype is not overly well-preserved, there is evidence to suggest that *P. paucus*? n. sp. is the ancestor to *P. weddellensis* Stilwell and Zinsmeister, 1992, and *P. suroinflatus* Stilwell and Zinsmeister, 1992, from the La Meseta Formation. *Pseudofax*? *paucus* has narrower spiral cords and a much weaker axial component, compared with the Eocene Antarctic species. *Pseudofax weddellensis* (see Stilwell and Zinsmeister, 1992, pl. 16, figs. x–z) is morphologically very close to *P.*? *paucus* and probably represents a lineage.

Etymology.—Species named from the Latin *paucus* (equivalent to "few, little") for its rare occurrence on Seymour Island.

Subfamily **MELONGENIINAE** Gill, 1867

Genus **LEVIFUSUS** Conrad, 1865

Type species (by original designation).—*Fusus trabeatus* Conrad, 1833.

Discussion.—*Levifusus* is recorded from Antarctica for the first time, previously cited from Paleocene to Eocene rocks of southeastern United States (Toulmin, 1977), East and West Africa (Adegoke, 1977; Gliozzi and Malatesta, 1985), and probably Australia (Darragh, 1997). Southern Hemisphere records of the group are rare, compared to the much higher diversity in North America.

Levifusus woolfei, new species

Plate 9, figures 23–29

Diagnosis.—Relatively large *Levifusus*, with moderately high-spired, robust shell; whorls well shouldered with greatly inflated last whorl bearing 3 keels, the adapical one strongest with 11–12 spirally extending tubercles; spire angle 120°; rows of tubercles not all aligned; penultimate whorl with strong angulation, bearing 14 small nodes; siphonal canal short, twisted abaxially; outer lip relatively thin without tubercles; distinguished from type species, *L. trabeatus* (Conrad, 1833), in having a more inflated last whorl, lower spire, more projecting tubercles, and short canal.

Description.—Shell large (up to 57 mm high), robust, moderately high-spired for genus, pyriform, with modestly elevated spire of at least 3 nodulose, well-shouldered whorls; somewhat enveloped from succeeding whorls; spire angle obtuse, approximately 120°; whorl inflation very rapid from penultimate to last whorl; protoconch minute, paucispiral, domelike?; sutures clasping around succeeding whorls and wavy; last whorl capacious, very inflated, tricarinate, highly ornamented with rows of nodes that are not all aligned; adapical ramp of last whorl moderately steep, short, mostly straight to only marginally concave, merging with a strong adapical peripheral angulation of 11–12 variable, spirally extending, inflated tubercles, central angulation spaced ~5 mm from adapical angulation, ornamented with ~12 slightly weaker, spaced tubercles; lowermost abapical keel rather weak, close to medial one, spaced about 3–4 mm, ornamented with weak, only slightly raised tubercles; penultimate whorl with strong medial angulation, bearing ~14 projecting, closely spaced nodes with moderately steep adapical ramp and very steep, nearly vertical slope below angulation, meeting suture of last whorl; only weak angulation and poorly developed nodes on antepenultimate whorl; growth lines very weak, mostly prosocline; last whorl abruptly contracted by strong basal constriction to short, twisted canal; aperture large, broadly ovate to sublenticular; columella long, smooth, concave with broad callus pad, that spreads in parietal region over medial and abapical rows of tubercles; siphonal canal moderately broad, twisted slightly abaxially; outer lip relatively thin, void of tubercles in adult specimens.

Dimensions.—Holotype USNM 511876, height 57.0 mm, diameter of last whorl 43.5 mm; paratype USNM 511877, height 44.0 mm, diameter of last whorl 40.5 mm; paratype USNM 511878, height 51.5 mm, diameter of last whorl 43.0 mm.

Types.—Holotype USNM 511876; paratypes USNM 511877, USNM 511878.

Localities.—9 (type), 479, 496, 1434, 1435, 1505, 1538, 1587.

Material.—39 specimens.

Stratigraphic range.—1168 to 1179 m.

Discussion.—*Levifusus woolfei* n. sp. is most closely related to *L.*? *quadrifunifer* Darragh, 1997 (pp. 76–77, fig. 3S, U) from the Paleocene of Australia, the only other member of the group in the Southern Hemisphere. No post-Paleocene records of the genus are known in the Austral Realm. *Levifusus woolfei* has a tricarinate profile like *L.*? *quadrifunifer*, but it is not as well-developed as in the Australian species. The spire in *L. woolfei* is also higher, compared with *L.*? *quadrifunifer*, which further has less projecting tubercles. The type species, *L. trabeatus* (Conrad, 1833) (p. 53, pl. 18, fig. 1 (see Harris, 1893, for discussion of the pagination of this complicated and rare original work); Wenz, 1943, p. 1222, fig. 3473), has a more gracile, high-spired shell, a longer siphonal canal, and a less inflated last whorl, but the relationship of the Antarctic species to the type is secure. In our opinion, *L. mortonii* (I. Lea, 1833) (p. 145, pl. 5, fig. 145; see also Toulmin, 1977, pp. 289–290, pl. 48, fig. 8), and *L. mortoniopsis* (Gabb, 1860) (p. 377, pl. 67, fig. 15; see also Toulmin, 1977, p. 290, pl. 48, fig. 6) from the eastern Gulf Coast are probably not congeneric, as there is an axial component and strong spiral element along with a straight canal, not present in the type. *Levifusus maputi* Gliozzi and Malatesta, 1983 (pp. 105–106, pl. 7, figs. 3–5), from the Paleocene of Mozambique is also not a close relative of *L. woolfei*, as the Mozambique species has a very marked shoulder angulation and higher spire, unlike *L. woolfei*. The African species described in Adegoke (1977) (see pp. 180–182, pl. 28, figs. 16–19) may not belong in *Levifusus* either, as both the axial and spiral ornament is marked.

Etymology.—Species named in honor of our late young colleague, Ken Woolfe, James Cook University, who passed on tragically in December 1999, for his ceaseless enthusiasm and voluminous contributions to Antarctic geology.

Genus **PROBUCCINUM** Thiele, 1912

Type species (by original designation).—*Neobuccinum tenerum* Smith, 1907.

Probuccinum palaiocostatum, new species
Plate 10, figures 1–3

Diagnosis.—Teleoconch of 5 convex whorls, axial sculpture of broad folds, spiral ornamentation of thin threads, siphonal canal slightly curved, fasciole weak to inconspicuous.

Description.—Shell of small size (up to 50.2 mm high), thin to moderately thick in larger specimens, with up to 5 convex rounded whorls, separated by adpressed suture; protoconch not preserved; aperture semi-ovate, moderately wide; axial sculpture of straight to slightly curved folds, becoming wider and lower, to completely obsolete, in some specimens on the last whorl; spacing between folds is approximately equal to the width of the folds; examined specimens with 15–17 folds on last and penultimate whorls; spiral sculpture fine, slightly raised threads separated by interspaces of equal width; aperture subovate, tapering anteriorly and posteriorly; siphonal canal slightly curved, fasciole weak, inconspicuous on most specimens; outer lip thin, simple; inner lip smooth, gently concave; siphonal canal slightly curved sinistrally.

Dimensions.—Holotype USNM 511879, height 26.0 mm, diameter of last whorl 21.0 mm; paratype USNM 511880, height 54.0 mm, diameter of last whorl 31.0 mm; paratype USNM 511881, height 44.0 mm incomplete, diameter of last whorl 28.0 mm.

Types.—Holotype USNM 511879; paratypes 511880, USNM 511881.

Localities.—9, 746 1434, 1699, 1701.

Material.—Eight specimens.

Stratigraphic range.—1134 to 1167 m.

Discussion.—The holotype of *Probuccinum palaiocostatum* n. sp. is apparently an immature individual without distinct axial sculpture developed on the last whorl. It differs from the Recent circum-Antarctic species *P. costatum* Thiele, 1912 (p. 211, pl. 13, fig. 22; see Dell, 1990, p. 171, fig. 285), in having a lower spire, a more rounded and convex whorl profile, and wider axial folds, separated by interspaces of equal width. *Probuccinum palaiocostatum* is the oldest member of this endemic Antarctic group.

Etymology.—Species named from the Latin *palaios* (equivalent to "ancient, old") and Latin *costa* (equivalent to "rib").

Genus **SERRIFUSUS** Meek, 1876

Type species (by monotypy).—*Fusus dakotensis* Meek and Hayden, 1856.

Discussion.—*Serrifusus* is a rare gastropod, known previously from North America by two species, the type *S. dakotensis* (Meek and Hayden, 1856), from the latest Campanian-Maastrichtian of Wyoming (perhaps also known from Hormby Island, Vancouver Island area, Canada; see Whiteaves, 1879, and Sohl, 1967, p. B29), and *S. joaquinensis* Anderson, 1958, from the Campanian of California. The Antarctic record from the Sobral Formation is the only one outside North America and also the only record from the Tertiary.

Serrifusus binodosum, new species
Plate 9, figures 1–5, 8–10

Diagnosis.—Moderately sized *Serrifusus* with at least 4 shouldered whorls with steep adapical slopes; last whorl bicarinate with moderately developed closely spaced noded keels, small, sharp nodes nearly aligned with weakly opisthocyrt, sinuous growth lines; outer lip slightly thickened, sinuous, with moderately developed flare below lower keel; canal short, slightly twisted; distinguished from type, *S. dakotensis* (Meek and Hayden, 1856), in having a smaller shell, closer more sharply noded keels, and a shorter canal.

Description.—Shell medium-sized, short-spired fusiform, moderately thick; spire of at least 4 shouldered, compressed whorls with moderately steep slopes; protoconch medium-sized, dome-like, of at least one smooth whorl, slightly eroded in available material; whorl inflation very rapid from penultimate to last whorl; spire angle approximately 62°; sutures channeled, encroaching on penultimate whorl at outer lip; last whorl moderately inflated, bicarinate, keels closely spaced and slightly concave between, bearing 20–21 only slightly axially extending, small, sharp tubercles, that are nearly parallel and connected by slightly excavated raised rib, and follow the moderately weak opisthocyrt growth lines; adapical ramp of last whorl long, steep, contracting greatly to a short canal except for contour of outer lip which hardly contracts, and is slightly flared and convex; spiral sculpture weak of equally and closely spaced threads only apart from noded keels; additional weakly noded spirals variably present on last whorl, but subsidiary to noded keels; spire whorls of weak spiral lines and two weakly noded spiral ribs, located just adapical of suture; aperture large, ovate, some 70% of height of shell, contracting to short, slightly obliquely twisted, narrow canal; columella concave with moderately developed callus pad; outer lip sinuous, moderately thick and varix-like on adult holotype, and flared abapically just below lowermost row of tubercles producing a curved concavity.

Dimensions.—Holotype USNM 511882, height 41.0 mm, diameter of last whorl 26.5 mm; paratype USNM 511883, height 35.0 mm, diameter of last whorl 23.5 mm; paratype USNM 511884, height 38.0 mm, diameter of last whorl 24.0 mm (specimen showing severe repaired break); paratype USNM 511885, height 33.5 mm, diameter of last whorl 25.0 mm, most of canal missing; paratype USNM 511886, height 32.0 mm, diameter of last whorl 21.0 mm, immature individual.

Types.—Holotype USNM 511882; paratypes USNM 511883, USNM 511884, USNM 511885 USNM 511886.

Localities.—497, 746, 1104, 1138, 1431.

Material.—39 specimens.

Stratigraphic range.—1134 to 1375 m.

Discussion.—*Serrifusus binodosum* n. sp., a K-T boundary survivor, is the only Tertiary representative of this genus in the fossil record and can be separated from the latest Cretaceous North American type species, *S. dakotensis* (Meek and Hayden, 1856) (p. 65; Meek, 1876, p. 374, pl. 31, fig. 11, pl. 32, figs. a, c, also same paper *S. goniophorus* Meek, p. 375, pl. 32, fig. 7a, b?; Wenz, 1941, p. 1262, fig. 3594; Sohl, 1967, p. B29–B30, pl. 6, figs. 12, 13, 18–21), in having a smaller shell, more closely spaced noded keels, sharper nodes, and a more expanded sinuous outer lip. *Serrifusus joaquinensis* Anderson, 1958 (pp. 171–172, pl. 49, fig. 3) from the latest Cretaceous of the Pacific Coast is not closely allied with *S. binodosum*, as it has a much higher, more strongly unicarinate spire and last whorl. We believe that the Antarctic species falls into the limit of variability of this genus. Intraspecific variation is apparent in *S. binodosum* with various strengths of noded keels present in the type material. On the holotype, USNM 511882, a third adapical spiral row of nodes disappears gradually on the last whorl midway on the volution. Another specimen, paratype USNM 511884, has a severe repaired break, affecting the sculpture of the last whorl, making it quite irregular. This break was probably made by a "lip-peeler" such as a decapod crustacean.

Etymology.—Species named from the Latin *nodosus* (equivalent to "full of knots") for its distinctive two spiral rows of nodes or tubercles.

Genus **SYCOSTOMA** L. R. Cox 1931

Type species (by original designation).—*Fusus bulbiforme* Lamarck, 1803.

Discussion.—*Sycostoma* has been recorded in Upper Cretaceous to Paleogene rocks of Europe, Madagascar and North America (Wenz, 1943, p. 1222), uppermost Cretaceous rocks of New Zealand (Fleming *in* Wellman, 1959; Stilwell, 1994), and Paleocene of Greenland (Kollmann and Peel, 1983). *Austroficopsis* Stilwell and Zinsmeister, 1992, may be a closely related form. Melongenine gastropods are rare in Austral Cretaceous and Paleogene deposits. *Sycostoma* is reported herein from Antarctica for the first time.

Sycostoma pyrinota, new species
Plate 8, figures 23, 24

Diagnosis.—Small to moderately sized *Sycostoma* with low spire with at least two weakly convex whorls; spire angle about 74°; length of last whorl about 80% total height of shell; sculpture of rather weak, closely spaced, spiral threads, ~3 per mm; siphonal canal moderately long and broadly notched; most closely related to latest Cretaceous New Zealand species, *S.* n. sp. of Stilwell (1994), differing by the new Antarctic species being half the size with weaker spirals and longer canal.

Description.—Shell small- to medium-sized for genus (27 mm high), low-spired, moderately robust, pyriform; spire obtuse, low, paucispiral, of at least two weakly convex, steeply sided whorls; whorl inflation rapid, especially from penultimate to last whorl; protoconch unknown; spire angle approximately 74°; sutures weakly impressed; last whorl length about 80% of total height of shell; last whorl moderately inflated, ovately elongated, moderately convex, sutural ramp steep, ornamented with equally and closely spaced, weak spiral cords, ~3 per mm, equally strong from canal to suture; penultimate whorl similarly sculptured; growth lines very weak, nearly opisthocline; base contracted to a moderately long neck; siphonal canal moderately broad, notched; columella smooth, convex, long; outer lip thin.

Dimensions.—Holotype USNM 511887, height, 27.5 mm, diameter of last whorl 17.0 mm.

Type.—Holotype USNM 511887.

Locality.—9.

Material.—One specimen.

Stratigraphic occurrence.—1168 m.

Discussion.—*Sycostoma pyrinota* n. sp. is the only member of this genus in Antarctica and is closely related to a slightly older Maastrichtian form, *Sycostoma* n. sp., from Northland, New Zealand (see Stilwell, 1994, pp. 673–676, pl. 43, figs. 1–4). *Sycostoma pyrinota* may be the descendant of *Sycostoma* n. sp. from New Zealand, as the outline and sculpture is nearly identical, except that the Antarctic species is half the size with a slightly shorter, broader canal. No other member of this group has been recorded from the Southern Hemisphere, so the genus may have evolved in the north, where there is a much better and diverse record. The European Eocene type species, *S. bulbiforme* (Lamarck, 1803) (p. 287; see Swainson, 1840, p. 308, fig. 75; Cossmann, 1889, p. 168; Wenz, 1943, p. 1222, fig. 3475; Oleinik and Zinsmeister, 1996, p. 927, fig. 4), is also larger than *S. pyrinota* with a higher spire, slightly more inflated whorls, and a more developed labial callus. *Sycostoma jonesi* Adegoke, 1977 (pp. 146–147, pl. 23, figs. 1–6) from the Paleocene of Nigeria is not a closely related species and has much more compressed spire whorls and is more globose, compared with *S. pyrinota*. *Sycostoma* disappeared from the fossil record in Antarctica after the early Paleocene.

Etymology.—Species named for its pyriform outline and from the Greek *notos* (equivalent to "south") for its sole presence in Antarctica.

Subfamily **PSEUDOLIVINAE?** Cossmann, 1901

Genus **SEYMOUROSPHAERA** Oleinik and Zinsmeister, 1996

Type species (by original designation).—*Seymourosphaera bulloides* Oleinik and Zinsmeister, 1996.

Discussion.—*Seymourosphaera* is seemingly allied with *Austrosphaera* Camacho, 1949, and is distinguished from the Argentine group in having "[a] more concave columella, generally broader and thicker callus, narrower and shallower parietal and siphonal canals, lacking a fasciole, and prominent spiral sculpture" (Oleinik and Zinsmeister, 1996, p. 926). This characteristic endemic group is associated with the repopulation phase in Antarctica immediately following the K-T boundary (WJZ and JDS). *Seymourosphaera* shares features in common with both Buccinidae and Nassariidae, so it is tentatively placed in Buccinidae Pseudolivinae. Four species have been recognized in the Paleocene sequence of Seymour Island. Details are provided below. See Oleinik and Zinsmeister (1996) for detailed discussion of distinguishing features of these species, and their relationships to other closely related forms, not repeated herein.

Seymourosphaera bulloides Oleinik and Zinsmeister, 1996
Plate 8, figures 1–7

Seymourosphaera bulloides Oleinik and Zinsmeister, 1996, pp. 926, 929–930, figs. 2.1, 2.3, 5.1–5.6, 5.10–5.11, 5.20, 5.21.

Dimensions.—Holotype USNM 487298, height 41.3 mm, diameter of last whorl 27.3 mm (see Table 1, Oleinik and Zinsmeister, 1996, p. 930) for dimensions of paratypes.

Types.—Holotype USNM 487298; paratypes

USNM 487294, USNM 487296, USNM 487289, USNM 487300, PU 496, PU 746, PU 995, PU 1135, PU 1430, PU 1432.

Localities.—9, 119, 496, 746, 1134, 1135, 1136, 1430, 1431, 1432 (type), 1434, 1506, 1538, 1589, 1601, 1694, 1700.

Material.—98 specimens.

Stratigraphic distribution.—1058 to 1168 m.

Discussion.—*Seymourosphaera bulloides* is easily separated from *Austrosphaera glabra* Comacho, 1949, by having a more elevated and wider callus, generally elongated shape, lack of fasciole and presence of well-developed spiral sculpture on the upper part of the body whorl. *Austrosphaera patagonica* (Feruglio, 1936) has a narrower callus, and a much wider aperture, well-developed fasciole and siphonal notch. *Seymourosphaera subglobosa* Oleinik and Zinsmeister, 1996, has a less elongated shell, lower spire, and wider apical angle. *Seymourosphaera elevata* Oleinik and Zinsmeister, 1996, has a more elongated shell, elevated spire, smaller apical angle and four rather than five whorls. *Seymourosphaera depressa* Oleinik and Zinsmeister, 1996, has a lower spire, broader aperture and lacks radial sculpture on the spire whorls.

Seymourosphaera subglobosa Oleinik and Zinsmeister, 1996

Plate 8, figures 10–13, 20

Seymourosphaera subglobosa Oleinik and Zinsmeister, 1996, p. 930, figs. 2.2, 5.9, 5.12–5.17.

Dimensions.—Holotype USNM 487292, height 33.3 mm, diameter of last whorl 26.3 mm.

Types.—Holotype USNM 487292; paratypes USNM 487293, USNM 487295, USNM 487297, PU 9, PU 496, PU 1135, PU 1430

Localities.—1133, 1136 (type), 1430.

Material.—15 specimens.

Stratigraphic range.—1145 to 1165 m.

Discussion.—*Austrosphaera glabra* Camacho, 1949, differs from *Seymourosphaera subglobosa* in lacking distinct spiral sculpture, narrower callus, broader aperture, straight columella, and by the presence of a fasciole. *Seymourosphaera depressa* has a less elevated spire, broader apical angle. *Austrosphaera patagonia* (Feruglio, 1936) has a fasciole, siphonal notch, and a narrower callus and a generally more elongated shell.

Seymourosphaera depressa Oleinik and Zinsmeister, 1996

Plate 8, figures 8, 9

Seymourosphaera depressa Oleinik and Zinsmeister, 1996, p. 930, figs. 5.7–5.8.

Dimensions.—Holotype USNM 487290, height 38.3 mm, diameter of last whorl 28.7 mm.

Type.—Holotype USNM 487290; paratypes PU 9, PU 1135.

Localities.—9, 1104, 1434 (type).

Material.—Five specimens.

Stratigraphic distribution.—1168 to 1375 m.

Discussion.—*Austrosphaera glabra* Camacho, 1949, differs in having a generally narrow and thicker callus, absence of spiral sculpture on the spire whorls and by the presence of a fasciole. The shell of *Seymourosphaera subglobosa* is more inflated and the aperture is narrower with a more concave columella. *Seymourosphaera bulloides* may be separated by is narrower aperture, higher spire, and more prominent spiral sculpture.

Seymourosphaera elevata Oleinik and Zinsmeister, 1996

Plate 8, figures 14–19, 21, 22

Seymourosphaera elevata Oleinik and Zinsmeister, 1996, p. 931, figs. 5.18, 5.19, 5.22–5.27.

Dimensions.—Holotype USNM 487288, height 37.4 mm, diameter of last whorl 26.0 mm.

Type.—Holotype USNM 487288, paratypes, USNM 487287, USNM 487291, USNM 487299, PU 9, PU 496, PU 1430.

Localities.—496, 1119, 1135 (type), 1136, 1148, 1189, 1430, 1432, 1433, 1506, 1577, 1586.

Material.—42 specimens.

Stratigraphic range.—1071 to 1215 m.

Discussion.—This is the most distinctive and easily recognizable species of *Seymourosphaera* on Seymour Island. It differs from the other species by the absence of regular spiral sculpture, smaller apical angle, and higher spire consisting of five whorls. *Seymourosphaera elevata* differs from *Austrosphaera glabra* Camacho, 1949, in having a more elongated shape, higher spire, and broader callus with a concave columella. Compared to *A. patagonica* (Feruglio, 1936), *S. elevata* has a more elongated shell, higher spire, concave columella and the absence of regular spiral sculpture, a well-developed fasciole and a siphonal notch.

Genus **STREPSIDURA** Swainson, 1840

Type species (by original designation).—*Murex turgidus* (Solander, 1766).

Strepsidura? polaris, new species

Plate 8, figures 27, 28

Diagnosis.—Relatively small to moderately sized buccinid with moderately high, slightly concave to near papillate, spire and subfusiform outline; spire angle about 54°; last whorl inflated with broadly cancellate sculpture of rounded, broad axial costae and many incised spirals; base contracted to notched, oblique, spout-like canal; differs from type species, *Strepsidura turgida* (Solander, 1766), in having a higher, more concave spire, more robust ornamentation, and a shorter siphonal canal.

Description.—Shell small- to medium-sized (23.5 mm high), moderately high-spired, moderately robust, subfusiform to somewhat inflated biconical outline; spire with slightly concave to near papillate outline, of at least 4, nearly stacked whorls; spire angle approximately 54°; whorl inflation slow then rapid from penultimate to last whorl; protoconch apparently large, incomplete on holotype; suture weakly impressed; last whorl moderately inflated, convex, ornamented with near opisthocline-trending, cancellate, broad, axial ribs and many incised, equally spaced, spiral ribs; spire whorl sculpture obscured by diagenetic alteration of shell; base contracted gradually to curved, abaxially twisted, spout-like, moderately broadly notched canal; columella moderately short, concave; smooth; outer lip smooth, thin.

Dimensions.—Holotype USNM 511888, height 23.5 mm, diameter of last whorl 16.0 mm.

Type.—Holotype USNM 511888.

Locality.—9.

Material.—One specimen.

Stratigraphic occurrence.—1167 m.

Discussion.—The only collected specimen of this species of buccinid gastropod has been slightly diagenetically altered such that the ornamentation is not clearly preserved, especially on the spire. The subfusiform outline and cancellate sculpture is consistent with members of the Pseudolivinae, and the Tertiary genus *Strepsidura* may be a likely candidate for genus-level assignment, as apart from the apparent lack of a plication on the columella, there is general agreement in shell outline, sculpture and the oblique-trending, notched siphonal canal. The Eocene European type species, *S. turgida* (Solander, 1766) (p. 26, pl. 4, fig. 51; see also Sowerby, 1821, pl. 291, fig. 7; Cossmann, 1889, pp. 162–163; Wenz, 1943, p. 1270, fig. 3611) has a lower spire, two columellar plaits, and a slightly longer siphonal canal. This species may represent a new group, but more material is needed to make a more concrete assessment. Other Paleocene species such as *S. kerstingi* Oppenheim, 1914 (p. 58, pl. 5, figs. 4a, b; Adegoke, 1977, pp. 158–159, pl. 24, figs. 22–26), from Nigeria and *Strepsidura* sp. of Kollmann and Peel (1983) (pp. 86–87, fig. 192) from Greenland are not closely related forms.

Etymology.—Species named for its polar occurrence.

Family **FASCIOLARIIDAE** Gray, 1853

Subfamily **FASCIOLARIINAE** Gray, 1853

Genus **PALEOPSEPHAEA** Wade, 1926

Type species (by original designation).—*Paleopsephaea mutabilis* Wade, 1926.

Paleosephaea? nodoprosta, new species
Plate 9, figures 6, 7, 11–16

Paleopsephaea n. sp. Zinsmeister *et al.*, 1989, p. 733, fig. 2, p. 734, fig. 3.

Diagnosis.—Moderately sized *Paleopsephaea* with moderately low spire of more than 5 strongly noded whorls; spire whorls and last whorl bearing 12–14 projecting tubercles, some more axially extending; siphonal canal short, only gently twisted, with moderately broad notch; columella with at least two oblique plaits; distinguished from type species, *P. mutabilis*, in having peripheral projecting nodes most of which do not axially extend and a much shorter, notched canal.

Description.—Shell medium-sized (up to ~45 mm high), solid, moderately high-spired biconic-fusiform; spire of more than 5 strongly noded whorls, about 40% of total shell height; protoconch incomplete, but seemingly polygyrate of more than 2 smooth whorls; whorl inflation generally constant, increasing from penultimate to last whorl; spire angle varies from 43° to 52°; sutures gently declivous, encroaching on previous whorls; last whorl with steep, moderately concave adapical slope, merging with strongly noded medial periphery; basal constriction moderately rapid below medial angulation; sculpture on last whorl of 12–14 variably sharp to axially extending nodes and weak spiral threads; growth lines with broad sinus, apex situated at center of periphery on nodes; spire whorls with medial or just adapical of suture angulation bearing 13–14 strong tubercles, some slightly extending axially; aperture moderately narrow, sublenticular, with moderately short broadly notched, only slightly twisted, canal; columella long, mostly straight, bearing at least two oblique folds; outer lip moderately thick, smooth.

Dimensions.—Holotype USNM 511889, height 39.5 mm, diameter of last whorl 20.5 mm; paratype USNM 511890, height 44.5 mm, diameter of last whorl 24.5 mm; paratype USNM 511891, height 38.5 mm, diameter of last whorl 23.5 mm.

Type species.—Holotype USNM 511889; paratypes USNM 511890, USNM 511891, USNM 511892.

Localities.—746, 1104, 1586, 1701.

Material.—12 specimens.

Stratigraphic distribution.—1134 to 1375 m.

Discussion.—The siphonal canal of *Paleopsephaea*?

nodoprosta n. sp. is relatively short and the peripheries of spire whorls and last whorl bear strong tubercles, compared to the latest Cretaceous type species, *P. mutabilis* Wade, 1926 (p. 123, pl. 40, figs. 4, 5, 8; Wenz, 1943, p. 1328, fig. 3772; Sohl, 1964, pp. 209–210, pl. 28, figs. 1–6) from the Gulf Coast of North America, but the slender outline, contracted whorls, and position of columellar folds are consistent with *Paleopsephaea*. Further, *P. mutabilis* has three columellar folds, but only two are visible on *P.? nodoprosta*. A possible fourth specimen of *P.? nodoprosta*, USNM 511892 (see Plate 6, figures 15, 16), is recorded from Loc. 746-4 and is incomplete, but is more slender with axially extending peripheral nodes.

Etymology.—Species named from the Latin *prosto* (equivalent to "stand out, project") and the Latin *nodus* (equivalent to "knot, swelling") for its protruding tubercles or nodes.

Subfamily **FUSININAE** Swainson, 1840?

Genus **TAIOMA** Finlay and Marwick, 1937

Type species (by original designation).—*Taioma tricarinata* Finlay and Marwick, 1937.

Discussion.—The family-level placement of *Taioma* is contentious in the literature as this characteristic Austral Late Cretaceous to Paleogene group has been placed in its own family Taiomidae (Finlay and Marwick, 1937; Stilwell and Zinsmeister, 1992; Griffin and Hünicken, 1994), Fasciolariidae: Taiominae (Wenz, 1943), Turridae: Thatcheriinae (Stilwell, 1994), and Fasciolariidae: Fusininae (Fricker, 1999). This confusion of relationship between *Taioma* and especially the Turridae and Fasciolariidae hinges on common features shared between these groups. Until a detailed study of this genus is completed, we concur with Wenz (1943) and Fricker (1999) that *Taioma* can be included in the Fasciolariidae as it shares a similar size and shell form, a long siphonal canal, a smooth columella and a similar growth line sinus that many fasciolariids have and can be confused with Turridae. However, the turrid genus *Clinura* Bellardi, 1875, combines features of *Taioma* and Turridae, and cannot be easily dismissed as unrelated. *Taioma* is recorded from the Late Cretaceous to Eocene of Antarctica, Paleocene of New Zealand, Paleocene of Patagonia, and perhaps the Paleocene of Greenland (see Stilwell, 1994, for review).

Taioma sobrali, new species

Plate 9, figures 17–22

Diagnosis.—Moderately sized, rather tumid, pagodaform to broadly fusiform *Taioma* with at least 5 noded, low-keeled, pagodaform whorls; whorls partially enveloped by succeeding whorls, so that abapical part of whorl just below tubercled keels are hidden, marked by suture line; last whorl bicarinate, spiral sculpture weaker than growth lines, spiral ribs more spaced abapically below keel; growth lines separate and in some instances dissect tubercles; separated from likely descendent, *T. bicarinata* Stilwell and Zinsmeister, 1992, in having a smaller shell, weaker spiral sculpture and tubercle development.

Description.—Shell medium-sized for genus (more than 39.0 mm high), solid, tumid, broadly fusiform to pagodaform; spire moderately high, of at least 5 noded, keeled, slightly compressed, pagodaform whorls; whorl inflation very rapid from penultimate to last whorl; protoconch conical, small, paucispiral of seemingly two smooth whorls; spire angle approximately 75°; sutures partially clasping, abutting against keel of previous whorls; last whorl capacious, moderately inflated, bicarinate, subsutural ramp very steep, short, shoulder steep and mostly straight, merging with a strong, projecting, noded keel with some 18–20 poorly to moderately defined tubercles, excavated below abapically, merging with secondary abapical angulation or rather week keel; basal constriction moderately rapid; spiral ornamentation weak of closely spaced, weakly beaded threads and rather broadly spaced cords on lower abapical half of last whorl below primary keel; growth lines strong, especially between each tubercle, broadly opisthocyrt, with moderately deep sinus with apex situated midway on shoulder; spire whorls with strong subsutural keel bearing sharp nodes sitting directly on suture; whorls partially envelop succeeding whorl, so that area of whorl abapical of keel hidden; aperture moderately open, broadly lenticular to subovate; siphonal canal incomplete; columella broadly concave, smooth, with moderately broad callus; outer lip moderately thick with distinct sinus on shoulder.

Dimensions.—Holotype USNM 511893, height 40.0 mm, diameter of last whorl 30.5 mm; paratype USNM 511894, height 23.5 mm, diameter of last whorl 16.5 mm; paratype USNM 511895, height 27.0 mm nearly complete, diameter of last whorl 21.5 mm.

Types.—Holotype USNM 511893; paratypes USNM 511894, USNM 511895.

Localities.—497, 1104 (type), 1105, 1130, 1431.

Material.—19 specimens.

Stratigraphic range.—1095 to 1375 m.

Discussion.—*Taioma sobrali* n. sp. fills a gap in the Antarctic lineage of this Late Cretaceous to Eocene group. Until this record from the Sobral Formation, *Taioma* was recognized from the Campanian–Maastrichtian deposits of Seymour, Humps and James Ross islands (Macellari, 1984; Stilwell and Zinsmeister, 1987c; Aguirre-Urreta and Olivero, 1992) and Eocene shallow-marine deposits of Seymour Island (Zinsmeister, 1982; Stilwell and Zinsmeister, 1992). A lineal relationship between *T. sobrali* and *T. bicarinata* Stilwell and Zinsmeister, 1992 (pp. 137–138, pl. 19, figs. a–d) is highly probable, as these taxa are extremely close morphologically. Minor differences in size of shell, tubercle development and spiral ornamentation serve to distinguish these Antarctic taxa. *Taioma sobrali* has a smaller shell, less developed tubercles creating a slightly weaker keel, and weaker spiral sculpture, compared with *T. bicarinata.* Although the holotype and two other recorded specimens of *T. sobrali* are slightly crushed from compaction, a bit abraded and slightly incomplete, it would be rather difficult to differentiate these specimens from others of *T. bicarinata* if they were recovered from the same unit. *Taioma charcotianus* (Wilckens, 1910) (pp. 91–93, pl. 4, figs. 6a, b, 8, 11; Macellari, 1984, pl. 35, figs. 6–8; Fricker, 1999, pp. 202–205, pl. 6, figs. 6, 7) from the Campanian–Maastrichtian of Antarctica is much closer in age to *T. sobrali* than this species is to *T. bicarinata,* but a close relationship is not probable, as *T. charcotianus* has a very high-spired fusiform shell with more centrally located keels, unlike the tumid nature of *T. sobrali* and *T. bicarinata.* The New Zealand Paleocene type species, *T. tricarinata* Finlay and Marwick, 1937 (p. 72, pl. 10, figs. 5–7; Wenz, 1943, p. 1256, fig. 3579; Fleming, 1966, p. 320, pl. 111, figs. 1361–1363; Stilwell, 1994, pp. 1087–1090, pl. 76, figs. 10–17), also has a high spire and is tricarinate, unlike *T. sobrali.* Of note, *Clinura* sp. 1 of Kollmann and Peel (1983) (p. 97, fig. 220, especially C, D) from the Paleocene of Greenland may be a congeneric form, but the position of the keel on the spire whorl is more adapically positioned above the suture and has stronger spiral sculpture, but weaker growth lines, compared with *T. sobrali.*

The greatly disjunct, bi-polar distribution of *Taioma* during the Paleocene is difficult to reconcile if *Clinura* sp. 1 proves to be more appropriately allocated to *Taioma.* Perhaps *Taioma* had a more widespread distribution during the Late Cretaceous than previously thought, or the groups are indeed homeomorphs.

Etymology.—Species named for its presence in the Sobral Formation.

Superfamily **VOLUTOIDEA** Rafinesque, 1815

Family **VOLUTIDAE** Rafinesque, 1815

Subfamily **ZIDONINAE** Pilsbry and Olsson, 1954

Genus **ZYGOMELON** Harasewych and Marshall, 1995

Type species (by original designation).—*Zygomelon zodion* Harasewych and Marshall, 1995.

Discussion.—The stratigraphic range of *Zygomelon* is extended into the early Paleocene with the description herein of *Z. apheles* n. sp. from the Sobral Formation. The genus is represented only by *Z. suropsilos* (Stilwell and Zinsmeister, 1992), from the Eocene La Meseta Formation (Units V–VI), and the New Zealand type species, *Z. zodion* Harasewych and Marshall, 1995.

Zygomelon apheles, new species

Plate 10, figures 4–10

Diagnosis.—Teleoconch of 6–7 smooth, rounded or weakly angulated whorls, callus thin, columella with a single oblique fold, and siphonal fasciole inconspicuous.

Description.—Shell of medium size (up to 77.2 mm), moderately thin for size, biconic, with fusiform spire, rounded anteriorly; protoconch not preserved; teleoconch of up to 7 convex, rounded or weakly angulated whorls. Suture adpressed; shell surface smooth except for thin axial growth lines; aperture ovate, tapering anteriorly and posteriorly; siphonal fasciole weak and inconspicuous on some specimens; outer lip smooth and simple; columella smooth with one oblique fold, located in the middle or slightly below the middle.

Dimensions.—Holotype USNM 511896, height 53.0 mm, diameter of last whorl 25.0 mm; paratype USNM 511897, height 58.0 mm, diameter of last whorl 26.0 mm; paratype USNM 511898, height 70.5 mm, diameter of last whorl incomplete; paratype USNM 511899, height, 40.0 mm, diameter of last whorl 20.0 mm; paratype USNM 511900, height 47.0 mm nearly complete, diameter of last whorl 23.0 mm.

Types.—Holotype USNM 511896; paratypes USNM 511897, USNM 511898, USNM 511899, USNM 511900.

Localities.—9, 746, 1104, 1192, 1431, 1442, 1601.

Stratigraphic range.—1124 to 1375 m.

Material.—13 specimens.

Discussion.—*Zygomelon apheles* n. sp. is distinguished from the Recent New Zealand type species, *Zygomelon zodion* Harasewych and Marshall, 1995 (pp. 145–150, figs. 1–13), in having a larger size, thicker shell, lack of spiral and axial sculpture, other than growth lines, single oblique columellar plait, and narrower aperture tapering anteriorly and posteriorly.

Etymology.—Named from the Greek *apheles* (equivalent to "even, smooth, simple" for its smooth, unornamented shell.

Family **MITRIDAE** Swainson, 1831

Subfamily **MITRINAE** Swainson, 1831

Genus **MITRA** Swainson, 1831

Type species (by tautonomy).—*Voluta mitra* Linnaeus, 1758.

Subgenus **EUMITRA** Tate, 1889

Type species (by subsequent designation, Cotton, 1957).—*Mitra alokiza* Tenison-Woods, 1880.

Mitra (Eumitra?) antarctmella, new species
Plate 10, figures 11–14

Diagnosis.—Moderately sized mitrid with a ovately fusiform outline and characteristic telescoped whorl profiles; spire subgradate; sculpture poorly defined of weak spiral threads and mostly orthocline growth lines; short canal with distinct notch; columella with two folds (a possible adapical third poorly preserved); distinguished from *Mitra* (*Eumitra*) *sadleri* Stilwell and Zinsmeister, 1992, in having a higher spire, more elongate last whorl, weaker spiral sculpture and distinct telescoped whorls.

Description.—Shell medium-sized for genus and subgenus (at least 33.0 mm high), moderately robust, moderately high-spired elongate-fusiform; spire of at least 3, gradate, telescoped, subsuturally swollen, subquadrate whorls; spire 38% of total shell height; whorl inflation relatively rapid from penultimate to last whorl; spire angle acute, approximately 35°; sutures weakly impressed to nearly channeled; protoconch unknown; last whorl capacious, but only moderately inflated axially, with subsutural swollen "collar" just abapical of suture, becoming concave with a constriction between swollen "collar" and lower abapical swollen region followed by moderate tapering of siphonal canal; sculpture poorly defined on holotype, but of weak spiral threads and mostly orthocline growth lines; only growth lines on spire whorls; aperture nearly half of length of shell, narrowly lenticular; canal short, with moderately broad spout; columella gently concave, with at least two, closely spaced, moderately developed, columellar folds, a possible third adapical plait present, but poorly preserved on holotype, and a narrow callus; outer lip thin.

Dimensions.—Holotype USNM 511901, height 33.0 mm, diameter of last whorl 16.0 mm; paratype USNM 511902, height 19.5 mm, diameter of last whorl 9.5 mm.

Types.—Holotype USNM 511901; paratype USNM 511902.

Localities.—1108, 1635. Material for both localities was collected as surface float. Precise stratigraphic horizon can only be approximated: locality 1108~1210 m, locality 1635~1175 m.

Material.—Two specimens.

Discussion.—The holotype and paratype of *Mitra* (*Eumitra*?) *antarctmella* n. sp. are coarsely preserved and worn, so that detail of ornamentation and columella are ill defined. Thus, although clearly a member of the *Mitra* Lamarck, 1798, group, a subgenus-level assignment is tentative at the time of this writing. The specimens have a moderately high-spired fusiform outline, at least two folds (a possible adapical third poorly preserved on the holotype), a subgradate spire, irregular growth lines, a distinct notch, a slightly produced canal, all characters consistent with *Mitra* (*Eumitra*) (see review by Cernohorsky, 1970, pp. 36–37). If positively identified, this specimen is the oldest member of this Tertiary group that became extinct in Australia and New Zealand during the early Pliocene. Previously, the oldest record was from the Eocene of Antarctica, where two species were described, *M.* (*E.*) *monoplicata* and *M.* (*E.*) *sadleri*, by Stilwell and Zinsmeister (1992) from the La Meseta Formation.

Mitra (*Eumitra*?) *antarctmella* n. sp. is most closely allied with *M.* (*E.*) *sadleri* Stilwell and Zinsmeister, 1992 (p. 148, pl. 21, fig. e) from Units II–V of the La Meseta Formation, but the Sobral species has a higher spire, more elongate last whorl with a swollen subsutural collar, and also spire whorls that are more subquadrate and telescoped. The sculpture and whorl shape of *M.* (*E.*?) *antarctmella* is also reminiscent of *M.* (*E.*) *waitematiaensis* (Powell and Bartrum, 1929) (see Cernohorsky, 1970, p. 37, pl. 3, fig. 5) from the Miocene of New Zealand, but the Antarctic species is slightly smaller with more telescoped whorls and more developed subsutural "collars."

Etymology.—Species named from the Latin *mellum* (equivalent to "collar"), for its swollen, collar-like subsutural inflation and for its Antarctic occurrence.

Order **STYLOMATOPHORA** A. Schmidt, 1865

Suborder **TOXOGLOSSA** Troschel *in* Troschel and Ruthe, 1848

Superfamily **CONOIDEA** Rafinesque, 1815

Family **TURRIDAE** Swainson, 1840

Subfamily **PSEUDOTOMINAE** Bellardi, 1875

Genus **MARSHALLARIA** Finlay and Marwick, 1937

Type species (by original designation).—*Verconella spiralis* Allan, 1926.

Discussion.—A solely Austral group, the geographic range of *Marshallaria* Finlay and Marwick, 1937, is expanded herein to include the Paleocene of Antarctica, previously recorded from the late early Paleocene to late early Miocene of New Zealand (Beu and Maxwell, 1990) and mid-Paleocene to early Oligocene of Victoria, Australia (Long, 1981; Darragh, 1997). Beu and Maxwell (1990, p. 124) stated that the few records of this turrid indicate that species during the Tertiary favored mid-shelf to upper bathyal zones;

however, *M. multicincta* (Marshall, 1917) from the New Zealand Paleocene and *M. variegata* n. sp. from the Antarctic Paleocene lived in nearshore, subtidal environments along the inner shelf suggesting a possible gradual shift from shallower to deeper waters throughout the Tertiary.

Further research on early Tertiary turrids is required to clarify the relationships of seemingly closely related groups such as *Marshallaria* and the Tertiary European *Pseudotoma* Bellardi, 1875. Species of *Marshallaria* have a slightly more produced siphonal canal and a narrower callus on the inner lip compared to species of *Pseudotoma* which have shorter less produced siphonal canals and broader labial calluses. Additional study on these taxa may result in the abandonment of *Marshallaria* or at least reduction to subgenus level especially in light of the marked similarities between these two groups. Of note, another closely related group, *Austrotoma* Finlay, 1924, has a ridge-margined fasciole and a pronounced siphonal notch compared with *Marshallaria* (Beu and Maxwell, 1990, p. 124). *Marshallena* Allan, 1927, is another closely related taxon, but *Marshallena* has a more poorly defined sinus and a regularly conic polygyrate protoconch in contrast to *Marshallaria* which has a more defined shallowly concave sinus on the adapical shoulder slope and polygyrate dome-shaped protoconch (see Powell, 1966, p. 27).

Marshallaria variegata, new species
Plate 10, figures 17–22

Diagnosis.—Relatively big *Marshallaria* with moderately high spire of at least 4.5 angulate, subtrapeziform whorls; whorls partially envelop succeeding whorls variably, so that angulation on penultimate whorl either nearly abutting suture or well above adapically; spire angle varies from 56° to 67°; last whorl with strong medial angulation, bearing poorly developed tubercles and weaker secondary one just below at onset of basal constriction; spiral sculpture stronger than growth lines; callus narrow, but rather thick; notch barely developed; outer lip moderately thick with sinus on shoulder; distinguished from closely allied type species, *M. spiralis* (Allan, 1926) in having a stronger peripheral angulation and an additional secondary angulation below abapically, lower spire, and a longer, steeper, more concave adapical ramp on shoulder.

Description.—Shell large for genus (up to 46.5 mm high), moderately thick-shelled, robust, relatively tumid, biconic-fusiform; spire moderately high of at least 4.5, angulate, moderately compressed, subtrapeziform whorls that partially envelop succeeding whorl; protoconch relatively large, dome-shaped, probably polygyrate, smooth, incomplete on available material; spire angle varies from 56° to 67°; whorl inflation relatively rapid, especially from penultimate to last whorl; sutures slightly impressed, gently declivous; last whorl capacious, biangulate, adapical ramp steep, moderately long, concave, merging with strong peripheral angulation, bearing weak axially extending tubercles, and lower abapical secondary angulation, marked by onset of basal constriction, gently concave between angulations; sculpture of ~37–40 evenly and closely spaced spiral cords, more bunched on adapical sutural ramp on last whorl, and sinuous growth lines; sinus moderately concave on shoulder slope; spiral sculpture stronger than growth lines; ornamentation on spire whorls of ~15 spiral ribs and ~20 rather poorly defined tubercles on abapically positioned angulation; angulation on penultimate whorl variably positioned either just above suture or occupying a more medial whorl position; aperture over half the length of shell at 57% of shell height, moderately open, sublenticular with parietal canal and short, straight, virtually unnotched canal; columella long, concave above, straight below on pillar, callus narrow, thick, even along columella; fasciole poorly developed; outer lip moderately thick with sinus on shoulder.

Dimensions.—Holotype USNM 511904, 46.5 mm, diameter of last whorl 28.0 mm; paratype USNM 511905, height 45.0 mm, diameter of last whorl 28.5 mm; paratype USNM 511906, height 41.5 mm, diameter of last whorl 27.0 mm.

Types.—Holotype USNM 511904; paratypes USNM 511905, USNM 511906.

Locality.—746 (type), 1104, 1119, 1431, 1548.

Material.—16 specimens.

Stratigraphic range.—1096 to 1375 m.

Discussion.—*Marshallaria variegata* n. sp., the oldest member of this group, fits comfortably in this Paleocene to Miocene genus, and greatly expands its geographic range. The late Eocene type species, *M. spiralis* (Allan, 1926) (p. 340, pl. 76, fig. 9; Wenz, 1943, p. 1389, fig. 3925; Powell, 1966, p. 27, pl. 1, fig. 13; Beu and Maxwell, 1990, p. 124, pl. 8, fig. x; Maxwell, 1992, p. 155, pl. 22, figs. b, c, l) has a higher spire, steeper and longer shoulder, and single angulation on the last whorl, compared with *M. variegata*. These two taxa are closely allied forms. *Marshallaria multicincta* (Marshall, 1917) (p. 457, pl. 35, fig. 30; Finlay and Marwick, 1937, p. 84, pl. 11, figs. 10–12; Fleming, 1966, p. 368, pl. 135, figs. 1588–1590) (= *Daphnella ovata* Marshall, 1917, p. 457, pl. 35, figs. 28, 29) from the New Zealand Paleocene and *M. tumefacta* Darragh, 1997 (p. 82, 84, fig. 5Q, X, Y) from the Australian Paleocene are not closely related forms, but *Marshallaria* sp. a of Darragh (1997) (p. 84, fig.

5M, N) from the early Eocene is reminiscent of *M. variegata*, differing in the Australian species having a more tumid shell and a steeper, more concave, longer adapical ramp. Although the Turridae is speciose in the Antarctic Eocene, no *Marshallaria* species have been recorded, although *Austrotoma oliveroi* Stilwell and Zinsmeister, 1992 (pp. 155–156, pl. 23, figs. a–d) comes closest to *M. variegata*, but has a much weaker peripheral angulation, narrower callus, and longer steeper adapical slope. Further, the available material of *M. variegata* reveals some interesting intraspecific variation, mainly in shell outline (either tumid or less so), strength of tubercles on angulation, and position of angulation on penultimate whorl (*e.g.*, extent to which last whorl envelops penultimate whorl).

Etymology.—Species named from the Latin *variegatus* (equivalent to "of different sorts") for its variable nature in terms of shell outline and especially ornamentation.

Subfamily **TURRINAE** Swainson, 1840

Genus **COSMASYRINX** Marwick, 1931

Type species (by original designation).—*Cosmasyrinx monilifera* Marwick, 1931.

Subgenus **THOLITOMA** Finlay and Marwick, 1937

Type species (by original designation).—*Tholitoma dolorosa* Finlay and Marwick, 1937.

Discussion.—Recent work on *Cosmasyrinx* (*Tholitoma*) indicates that this subgenus is more widespread than previously thought. The presence of the group in the Paleocene of Antarctica extends its range from middle to late Eocene, recorded by *C. brychiosinus* Stilwell and Zinsmeister, 1992. Darragh (1997) described *C.* (*T.*) *levicristata* from the Paleocene Pebble Point Formation of Victoria, Australia, and *Cosmasyrinx* (*Tholitoma*) sp. of Long (1981) is the only known late Eocene species from Victoria, Australia. In New Zealand, *Cosmasyrinx* (*Tholitoma*) ranges from late early Paleocene to late Eocene (see Finlay and Marwick, 1937; Maxwell, 1992; Stilwell, 1994).

Cosmasyrinx (Tholitoma) antarctigera,
new species

Plate 10, figures 15, 16

Diagnosis.—Small- to medium-sized for group, somewhat fusiform to pagodaform; spire angle about 63°; last whorl inflated with strong angulation or keel, bearing about 18 strong tubercles or nodes, some axially extending, and spiral ornamentation of about 25 gemmuliform threads; apex of moderately deep anal sinus on middle part of shoulder slope, positioned just above appearance of tubercles; distinguished from type species, *Cosmasyrinx* (*Tholitoma*) *dolorosa* Finlay and Marwick, 1937, in having a more tumid pagodaform outline, stronger keel, weaker spiral ornamentation, and less developed subsutural submoniliform spiral cord.

Description.—Shell small- to medium-sized for genus and subgenus, moderately thin, polished in well-preserved specimens, moderately fusiform to pagodaform; spire moderately high of at least four keel whorls, bearing strong tubercles; whorl inflation rapid; spire angle approximately 63°; suture moderately impressed, gently descending; protoconch moderately large, incomplete on types, but apparently polygyrate, dome-shaped; last whorl capacious, strongly unicarinate with prominent keel bearing ~18 moderately developed, slightly axially extending, collabral tubercles, and rather weak sculpture of 25 somewhat irregular, gemmuliform, closely spaced riblets; adapical shoulder slope of last whorl steep, slightly concave, merging with strong peripheral angulation and contracting rapidly abapically below to moderately long neck; presence of subsutural riblets poorly developed, closely spaced gemmules on margining submoniliform inflated cord; gemmules on subsutural cord trend opposite to tubercles on periphery and generally follow growth lines; growth lines moderately strong with deep sinus midway on shoulder slope; spire whorls strongly carinate with 16 nodules on slightly inflated keel sitting directly on suture and some 20 weak spiral threads; aperture long, narrow, sublenticular; outer lip thin; anal sinus moderately deep, U-shaped, apex situated just abapical of midpoint on adapical ramp, just above the appearance of collabral tubercles.

Dimensions.—Holotype USNM 511907, height 7.0 mm, diameter of last whorl 5.5 mm; paratype USNM 511908, height 6.5 mm, diameter of last whorl 4.5 mm.

Types.—Holotype USNM 511907; paratype USNM 511908.

Localities.—496, 1519 (type), 1535.

Material.—Three specimens.

Stratigraphic distribution.—1073 to 1179 m.

Discussion.—*Cosmasyrinx* (*Tholitoma*) *antarctigera* n. sp. is the oldest recorded member of the group, as it is present in the early Danian of Antarctica. The next oldest species is the type, *C.* (*T.*) *dolorosa* Finlay and Marwick, 1937 (pp. 85–86, pl. 12, figs. 6, 7; Fleming, 1966, p. 364, pl. 133, figs. 1570–1572; Powell, 1966, p. 37, pl. 3, fig. 22; Stilwell, 1994, pp. 1059–1063, pl. 75, figs. 1–8), from the late early Paleocene of New Zealand, which differs from *C.* (*T.*) *antarctigera* in having a slightly larger, more slender, more high-spired shell, a stronger subsutural moniliform spiral cord, and a more prominent keel. Another closely related species is the mid-Paleocene species, *C.* (*T.*) *levicristata* Darragh, 1997 (p. 82, fig. 5R, V, W, Z) from Victoria, Australia, but differs from the Sobral Formation species in having a more slender, higher spired shell, and fewer, more spaced collabral tubercles on the peripheral angulation. *Cosmasyrinx* (*Tholitoma*) *antarctigera* is a most likely candidate as the ancestor of *C. brychiosinus* Stilwell and Zinsmeister, 1992 (p. 159, pl. 22, figs. i–l), from Units III–VII of the La Meseta Formation of Seymour Island, and is separated from the younger Eocene *C. brychiosinus* in having a larger more inflated last whorl, a shorter spire, finer spiral ornamentation, and stronger tubercles on the keel.

Etymology.—Species named from the Greek *geras* (equivalent to "old") for its earliest recorded occurrence in Antarctica.

Subclass **OPISTHOBRANCHIA** Milne-Edwards, 1848

Order **CEPHALOSPIDEA** Fischer, 1883

Suborder **ACTEONOIDA** d'Orbigny, 1842

Superfamily **PHILINOIDEA** Gray, 1850

Family **CYLICHNIDAE** A. Adams, 1850

Genus **CYLICHNANIA** Marwick, 1931

Type species (by original designation).—*Cylichnania bartrumi* Marwick, 1931.

Discussion.—*Cylichnania* Marwick, 1931, is recorded from Antarctica for the first time, previously known only from the Late Cretaceous to late Pliocene? of New Zealand (Stilwell, 1994) and mid-Paleocene to late Eocene of Australia (Darragh, 1997). *Cylichnania* is distinct in having a subcylindrical outline, ornamentation of even, low, flat-topped spiral cords, and its deep apical depression, with labrum extending well adapically to the labium (Beu and Maxwell, 1990, p. 238). Species of closely related *Cylichna* Lovén, 1846, are characterized by small and cylindrical shells with a truncated abapical end, an involute spire reflecting a tightly coiled and multi-whorled shell, a small apical concavity and a columella with a single oblique fold (Abbott, 1974, p. 314; *cf.* Stilwell and Zinsmeister, 1992, p. 173). Species of *Cylichnania* are eurybathyal, ranging from at least inner shelf to upper bathyal environments (*cf.* Beu and Maxwell, 1990, p. 238). Paleocene representatives *C. impar* Finlay and Marwick, 1937, and *Cylichnania* n. sp. of Stilwell (1994), from the Wangaloa and Kauru formations of New Zealand are present in sandstones interpreted to have been deposited along the inner shelf in a protected environment (Stilwell, 1994, p. 1159). *Cylichnania* cf. *C. impar* described below is also from an inner shelf environment.

Cylichnania cf. C. impar Finlay and Marwick, 1937

Plate 10, figure 23

Description.—Shell average-sized for genus (10 mm high), thin, moderately slender, subcylindrical to narrowly ovate, involute, apex sunken (eroded on available specimen), subhorizontally truncated; ornamentation of many, closely spaced, slightly wavy, revolving spiral riblets (~15 per mm), generally weaker centrally on last whorl; growth lines weak becoming slightly stronger on edge of labrum, mostly orthocline apart from tendency to become weakly prosocline abapically near base; aperture very narrow, constricting with parallel sides adapically, widening greatly at base; aperture at abapical end ovate; columella mostly straight, short, slightly truncated below, bearing a moderately developed plait, situated flush against columellar wall at base (covered by matrix more adapically); umbilicus poorly developed; outer lip thin, probably finely crenulated, partially fragmented on available specimen; large break in shell during growth (damage by lip peeler?), which affected growth only slightly pathologically, in which spiral riblets along break are "warped."

Dimensions.—USNM 511915, height, 10.0 mm, diameter of last whorl 5.5 mm.

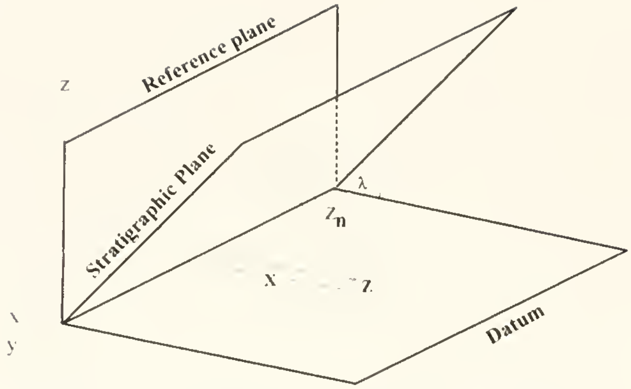
Type.—Hypotype USNM 511915.

Localities.—1519, 1538.

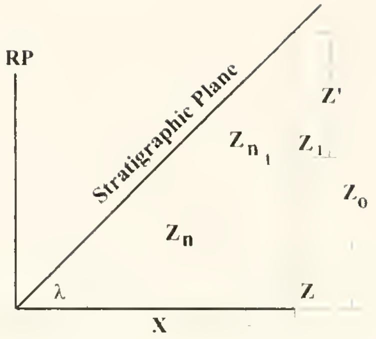
Material.—Three specimens.

Stratigraphic range.—1073 to 1104 m.

Discussion.—Only one opisthobranch gastropod has been reported from the Paleocene of Antarctica. It is surprising that acteonid and ringiculid gastropods are absent in Antarctic Paleocene deposits, being present in uppermost Cretaceous units in Antarctica and also in coeval shallow-marine deposits of New Zealand, Australia, and South America, where opisthobranchs are moderately to highly diverse. The sole specimen belongs to the Cylichnidae and has a close affinity with *Cylichnania impar* Finlay and Marwick, 1937 (p. 93, pl. 13, fig. 1; Fleming, 1966, p. 382, pl. 142, fig. 1690; Stilwell, 1994, pp. 1159–1161, pl. 81, figs. 1–3) and *Cylichnania* n. sp. of Stilwell (1994, pp. 1161–1163, pl. 81, figs. 4, 5, 9, 13, 18) from the late early Paleocene of New Zealand, differing slightly in ornamentation and shell outline. The Antarctic species has a slightly smaller, less ovate and more cylindrical shell with finer and more abundant, wavy spiral riblets, compared to *C. impar* and *Cylichnania* n. sp. of Stilwell (1994), but overall is more comparable to *C. impar.* Although probably a new species, the Antarctic species is left in open nomenclature until more material is discovered.



Text-figure 5.—Stratigraphic plane analysis is a graphical technique that produces two-dimensional geometric projections to visualize simultaneously spatial and stratigraphic distribution of fossil occurrences using two intersecting planes (Reference and Stratigraphic) with a datum, which is defined by a specified elevation. The Reference Plane is a vertically oriented plane parallel to the strike of the sequence and is used to locate the spatial occurrence of *x*, *y*, and *z* coordinates of locality Z, where the *y*-axis is the strike of the sequence, the *x*-axis is normal to *y*, and the vertical *z*-axis defines the elevation. The Stratigraphic Plane is an arbitrarily designated plane oriented parallel to the regional strike and dip of the bedding, where λ is the angle of dip. X is the distance from the Reference Plane to Z and Z_n represents the stratigraphic interval between locality Z and the Stratigraphic Plane.



$$Z_0 = \tan\lambda X$$
$$Z_n = \cos\lambda(Z_0)$$

Text-figure 6.—Determination of Z_n values (relative stratigraphic occurrence): Z, location of the locality, is equal to the elevation at that point; X, distance from Z to the Reference Plane RP; λ, angle of dip of the Stratigraphic Plane (equal to dip of bedding); Z_0, vertical distance from Z located on the datum to the stratigraphic plane; Z_n, the stratigraphic distance from Z to the stratigraphic plane. If Z is located above the datum (Z_1), the value of Z′ is equal to the difference between the elevation Z_1 and Z_0 (when Z is located on the datum, Z_1 equals Z_0). The conversion of spatial to stratigraphic data is expressed by the formulae to the right of the figure.

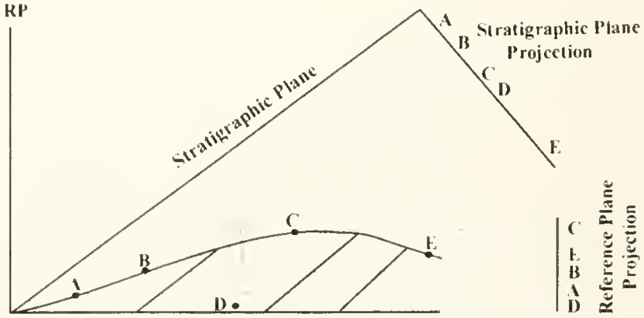
APPENDIX

Maastrichtian/Danian Seymour Island Data Base

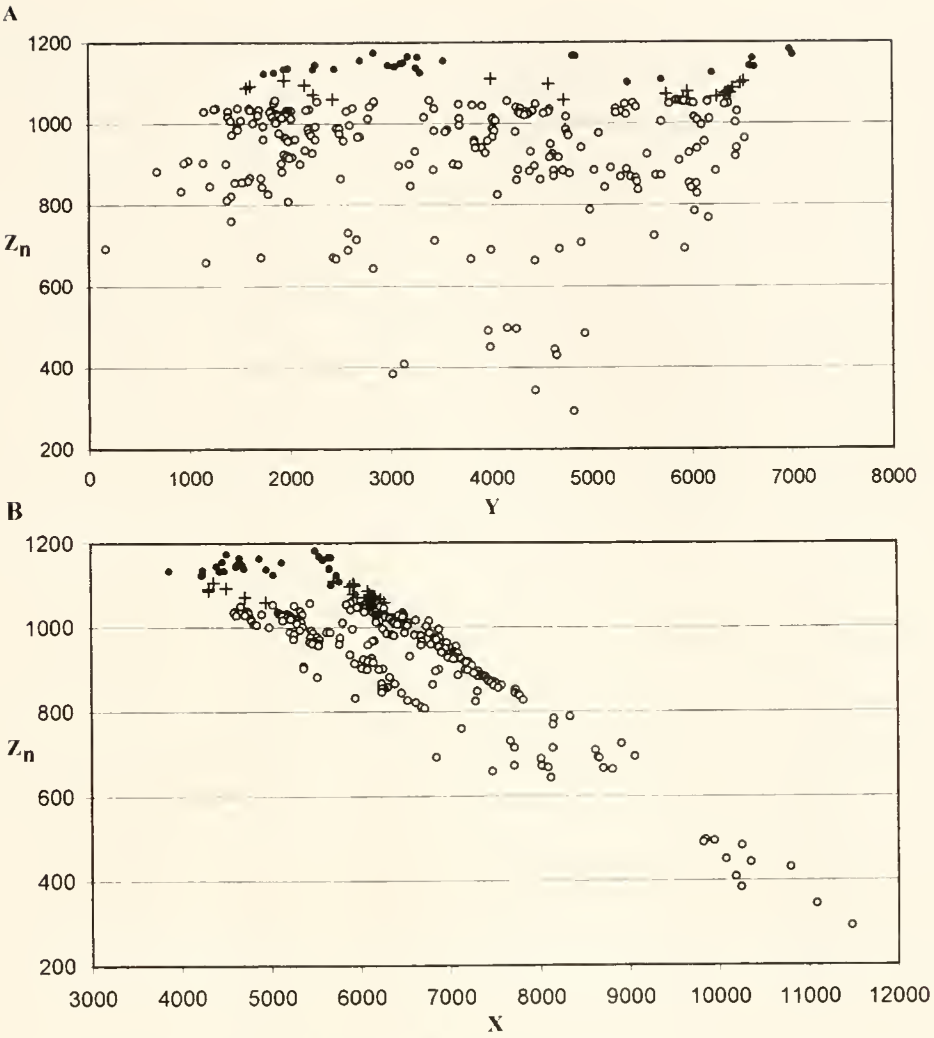
William J. Zinsmeister

The controversy about the nature, sequence, and timing of the extinction event at the K-T boundary has revealed several inherent limitations in the traditional biostratigraphic methods. The foundation of biostratigraphy has been the measured section. Range data from measured sections, by convention, are combined into composite range charts that are intended to represent the temporal ranges of the taxa portrayed in the chart. An inherent problem with the use of measured sections is the integration of data that do not occur along any of the sections. The traditional approach when constructing composite range figures is to determine the stratigraphic interval between an isolated fossil locality and a horizon that can be correlated into the measured section. In those cases where it is not practical or possible to assign a locality to a known horizon, the stratigraphic location of the fossil occurrence is, as a consequence, estimated. In both approaches, the accuracy of the stratigraphic location of an isolated fossil locality is less than that obtained along a measured section.

Another serious limitation in presenting occurrence data in composite range charts is the loss of the geographic component with the data set. Although the data represented in a composite range chart may have been based on a number of measured sections from a broad geographic area, the spatial components within the data are suppressed when the data are merged in a single-dimensional (temporal) range chart. Zinsmeister (1996) discussed the need to evaluate biostratigraphic data from a spatial perspective and presented the first two-dimensional figures (spatial and stratigraphic) of the distribution of ammonites from Seymour Island. Zinsmeister (1998b) proposed a graphical technique, Projection Plane Analysis, which uses orthographic projections to locate simultaneously spatial and stratigraphic fossil occurrences. This technique allows for the determination of the relative stratigraphic occurrence of any locality not located along a measured section. For a detailed description of the tech-



Text-figure 7.—Geometric relationship of stratigraphic plane with spatial occurrence of location data. Regardless of the location of the data point, when the data are projected against the Stratigraphic Plane, the relative stratigraphic position of the data point in relation to other data points may be determined. Stratigraphic projections also highlight any stratigraphic or structural anomalies which may compromise the data set.



Text-figure 8.—Two-dimensional projections of Maastrichtian/Danian fossil localities on Seymour Island. A, Z_nY projection of occurrence data along strike. B, projection of the data in A in a Z_nX projection perpendicular to strike. Z_n, stratigraphic occurrence (m) of localities; Y, distance (km) along strike; and X, distance (km) perpendicular to strike and from the intersection of the Stratigraphic and Reference planes with the datum horizon. The Stratigraphic Plane corresponds to the upper margin of the figures. Solid circles, Maastrichtian, and crosses, Danian localities in the López de Bertodano Formation; open circles, Danian localities in the Sobral Formation.

nique refer to Zinsmeister (2001). A brief summary of the Stratigraphic Plane Analysis is provided here as an introduction to stratigraphic data presented in this appendix.

The objectives of Projection Plane Analysis are to increase precision in the location of stratigraphic data not located along a measured section and to provide a technique to retain the spatial component in the evaluation of a biostratigraphic data set over large geographic areas. The technique is based on patterns produced by orthographic projections of biostratigraphic data using two intersecting planes (Reference and Projection planes) with a datum, which is defined by a specified elevation, typically sea level (Text-fig. 5). The Reference Plane is used to locate fossil localities spatially while the Projection Plane is a stratigraphic plane employed to locate the stratigraphic occurrence (Zn value) of a locality (Text-fig. 6). In traditional biostratigraphy, the data are plotted relative to a stratigraphic horizon, such as an ash bed or lithologic contact, which is considered to be a time horizon. The possibility exists that subtle surface relief along the stratigraphic horizon caused either by subtle changes of attitude or the bedding planes or pre-depositional erosion may compromise the stratigraphic integrity of data projected this way. Biostratigraphic errors caused by subtle surface relief along the horizon are magnified as the geographic area increases. As an example, a half of one degree of slope on a surface used to plot biostratigraphic data will produce an error of 8.7 m over

Table 3.—Maastrichian-Danian locality registry. Geographic and relative stratigraphic locations (Z_n) of Maastrichtian and Danian localities from the López de Bertodano and Sobral formations. All Maastrichtian localities from the López de Bertodano Formation have been included because a number of the Danian taxa have ranges that extend into the Maastrichtian. The X, Y, and Z values in Table 3 provide the geographic location of each locality. The coordinates are based on the location of the Reference Plane, which was oriented N38°30′E. The intersection of the Stratigraphic and Reference planes is located 525 m east of conical hill (56°42′54.2″ and 64°15′75.5″) located at the head of Cross Valley. The point at the head of Cross Valley is an arbitrary geographic point to locate the intersection of the Reference and Stratigraphic planes and to insure that all the localities would be located below the Stratigraphic Plane. The conical hill is located at a point 7000 m from the 0 m point on the Reference Plane. See Zinsmeister (2001) for in-depth discussion of the location and orientation of the Reference and Stratigraphic planes when using Stratigraphic Plane Analysis technique.

Locality	Y	X	Z	Z_n
9	7010	5550	47	1167.94
37	4690	8320	77	770.78
38	4720	7890	82	832.30
458	6440	7210	25	919.08
459	6170	8150	3	769.01
468	6530	6970	36	963.16
477	5920	6055	30	1058.45
485	5880	6110	36	1056.12
496	7000	5490	51	1179.42
497	7110	3810	22	1369.31
631	6630	5660	40	1138.29
648	6980	5500	55	1181.68
724	6030	8160	24	784.60
725	5930	9060	51	692.54
746	1950	3870	5	1134.22
754	5030	7310	48	885.08
755	4490	7580	82	862.98
756	5450	7530	43	866.53
757	5560	7040	35	925.34
758	5650	7460	34	873.15
759	4620	7130	82	926.22
760	4600	6950	83	949.59
761	4600	7170	81	919.27
762	4590	7190	82	917.29
763	6450	7080	29	940.04
764	4680	7190	79	917.91
765	6130	7070	52	955.59
767	4630	10360	15	444.17
768	4930	10260	30	483.56
769	4650	10800	58	430.94
770	4750	6780	92	986.36
771	6100	6880	69	996.08
772	4900	8620	45	708.53
773	5400	7460	38	868.91
774	6030	6770	76	1015.19
775	6580	6970	27	955.47
776	4070	7280	23	825.14
777	6060	7090	40	939.14
778	5980	7090	31	927.90
779	5990	6120	29	1051.14
780	6050	7740	37	852.16
781	5980	7730	39	853.40
783	5750	5970	38	1072.17
785	6000	7770	32	841.89
786	6060	7820	23	828.26
860	3990	10080	13	451.01
884	3200	6020	100	1022.06
1104	7140	3790	25	1375.46
1105	7080	3790	20	1369.29
1109	1460	6240	63	855.43
1110	1730	6460	64	845.44
1116	2060	5540	42	962.53
1119	1970	5440	37	964.97
1120	1970	5175	70	1031.83
1125	2020	5350	70	1012.34
1128	1590	6310	67	858.81
1130	2150	4510	36	1094.66
1131	2090	4690	34	1065.89
1133	1570	4310	39	1087.34
1134	1360	4290	46	1083.14
1135	1610	4310	41	1091.90
1136	1990	4250	54	1136.32
1137	1850	4250	52	1125.70
1138	1950	4365	42	1107.16
1139	2260	4400	66	1145.11
1140	2240	4440	61	1133.82
1143	1610	6240	65	867.12
1146	2510	6810	82	865.07
1148	2670	4210	89	1215.89
1150	1380	6680	82	812.34
1151	1640	4990	36	1001.28
1157	1740	5330	66	993.59
1159	1950	6040	76	925.14
1161	5420	6100	44	1050.70
1164	1990	6100	77	920.86
1166	1970	5320	76	1019.10
1167	1980	6090	76	920.54
1170	1990	5540	41	957.28
1171	2260	5460	50	992.72
1172	1960	5490	46	966.84
1173	1900	5450	55	977.22
1174	1870	5360	70	1001.83
1175	1930	5340	76	1014.07
1176	2200	5520	46	977.47
1177	1930	5320	80	1020.61
1178	2190	5480	51	986.99
1180	1890	5230	70	1019.81
1182	2000	5940	50	915.30
1183	1860	5300	70	1008.94
1184	1990	5200	72	1031.81
1185	1990	6720	44	808.28
1186	1420	6620	81	821.71
1187	2230	6130	73	927.46
1188	1740	5470	52	961.68
1189	1980	4615	36	1070.85
1190	2220	5550	43	961.68
1192	1750	4230	54	1124.00
1194	2500	5670	59	988.52
1195	2200	5090	49	1035.83
1196	1970	5190	71	1030.89
1197	1610	4760	40	1032.95
1198	2170	5100	50	1033.75
1199	2280	5030	55	1054.24
1201	1960	5220	71	1026.41
1204	1850	4670	31	1050.78

Table 3.—Continued.

Locality	Y	X	Z	Z_n
1205	1600	4750	44	1037.56
1206	2470	5630	56	988.98
1207	1415	4850	38	1006.71
1211	5450	6130	36	1039.91
1404	1750	5650	42	929.21
1412	1980	5180	70	1031.79
1420	4030	6370	97	1013.94
1424	1530	6270	63	856.12
1425	1370	6250	37	822.44
1426	3130	10190	27	408.97
1427	3970	6680	84	958.42
1428	5250	6190	37	1026.32
1429	4300	6180	84	1037.33
1430	4580	5890	96	1098.20
1431	2980	4620	53	1144.26
1432	2970	4940	61	1110.44
1433	2840	4515	77	1174.05
1434	4850	5680	126	1165.61
1435	3180	4660	69	1165.45
1436	1720	6390	77	866.71
1437	3960	6780	102	962.94
1438	4020	6390	97	1010.92
1439	3850	6910	102	941.16
1439	3840	6790	106	960.12
1440	1870	5190	71	1024.72
1441	4400	7050	86	931.48
1442	3050	4710	57	1140.34
1443	4260	6160	86	1040.17
1448	4020	6500	88	987.83
1451	6450	6490	43	1029.92
1452	3680	5970	95	1047.31
1453	2540	6090	81	958.51
1454	2840	5270	52	1052.02
1455	2780	5810	85	1011.92
1456	3530	5130	101	1154.22
1457	2430	4950	42	1060.38
1458	2800	5900	126	1042.09
1460	4280	6255	85	1027.80
1461	4420	6280	85	1030.50
1462	4370	6330	86	1022.95
1463	4380	6360	90	1023.48
1464	4340	6340	86	1020.40
1465	4300	6285	85	1024.79
1466	2630	5340	59	1038.37
1467	2730	5220	57	1030.43
1468	2160	5890	54	935.37
1469	2600	5920	94	996.69
1470	2680	6140	89	967.87
1471	2700	6160	91	968.39
1472	1790	6530	51	827.31
1473	4000	5710	110	1110.49
1474	1830	5140	59	1016.77
1475	1810	5135	71	1028.06
1476	3840	6880	111	953.48
1477	4250	6680	94	980.70
1478	1490	5270	66	985.29
1479	1480	5220	64	989.09
1480	1430	5260	56	972.74
1481	950	5370	33	903.36
1482	990	5370	36	909.10
1483	6210	5740	48	1125.14

Table 3.—Continued.

Locality	Y	X	Z	Z_n
1484	2700	4470	61	1156.30
1485	2580	7670	54	730.50
1486	2430	8020	48	670.93
1487	2460	8090	52	667.60
1488	2830	8120	11	643.75
1489	3020	10250	15	383.58
1490	3970	9830	22	491.23
1491	4250	9950	29	495.08
1492	3800	8710	61	666.35
1493	5080	6890	84	976.70
1494	4350	6275	86	1029.19
1496	5350	6210	32	1022.25
1497	5340	6110	45	1047.68
1498	5300	6180	37	1029.35
1499	3860	5740	126	1116.11
1501	3730	5780	130	1108.86
1502	3640	5820	129	1098.44
1504	6060	5720	57	1132.44
1505	5870	5710	55	1126.18
1506	5630	5770	54	1110.01
1509	3130	4160	60	1218.33
1510	2990	4200	55	1200.87
1512	4000	8660	69	689.89
1513	5700	6530	44	1004.43
1514	4630	7400	75	884.90
1515	6180	6540	38	1011.36
1516	6060	6450	27	1008.67
1517	4530	6480	101	1025.14
1518	4170	6070	94	1055.80
1519	4150	6010	104	1072.57
1520	3690	6180	87	1012.80
1521	3570	6300	81	985.64
1522	3440	6360	93	983.44
1523	3340	6220	113	1016.32
1524	4580	6430	96	1028.65
1525	4590	6480	109	1035.51
1527	4750	6620	102	1016.88
1528	4770	6830	86	974.75
1529	4730	6270	100	1059.19
1530	5370	5680	41	1100.12
1531	6330	6270	34	1046.22
1532	6330	6230	50	1067.23
1533	6340	6170	48	1073.24
1534	6390	6140	44	1074.45
1535	6370	6110	44	1077.79
1536	6410	6090	49	1086.36
1537	6490	5940	40	1098.79
1538	6520	5930	43	1103.80
1539	5970	6085	34	1060.02
1540	5910	6100	32	1054.34
1541	2110	6210	64	901.07
1542	1920	6260	84	902.89
1543	1930	6330	72	882.59
1544	2030	6150	78	917.85
1545	1210	6240	71	846.77
1546	3090	6840	86	896.86
1547	3190	6880	90	900.86
1548	3630	7170	105	900.28
1549	3680	7200	105	898.81
1552	4790	7420	64	877.72
1553	4630	7500	74	871.03

Table 3.—Continued.

Locality	Y	X	Z	Z_n
1555	5460	7540	34	856.65
1556	5470	7780	46	837.98
1557	4720	7370	68	885.39
1558	5140	7730	57	843.91
1559	4990	8340	86	788.62
1560	5960	5930	33	1078.70
1561	5250	6150	42	1036.43
1562	6020	6145	30	1049.78
1563	6370	6230	30	1048.45
1564	4440	7320	84	896.39
1565	4390	7400	83	883.01
1566	4270	7320	82	887.23
1567	1420	7120	84	837.98
1570	3820	6060	98	885.39
1572	1820	4910	45	843.91
1573	1490	4740	50	1037.68
1574	3260	4960	76	1137.86
1575	1250	4595	45	1035.54
1576	4450	6225	95	1048.74
1579	1390	4720	46	1029.74
1581	3280	4880	91	1164.05
1582	3430	7090	91	886.94
1583	3200	7310	92	847.98
1584	4440	11090	17	344.39
1585	1390	4795	42	1016.12
1586	2990	4480	93	1202.49
1587	2450	4490	56	1134.66
1589	3110	4630	52	1148.82
1590	6160	6130	29	1054.69
1591	6160	6140	29	1053.40
1592	5950	6110	32	1054.23
1593	3690	6260	81	996.55
1594	3550	6380	87	980.31
1595	3250	6560	77	932.26
1596	1370	6080	94	900.86
1598	3440	6050	107	1037.25
1599	3390	5900	111	1058.05
1600	6580	5660	44	1141.05
1601	6610	5590	53	1159.72
1603	3950	6980	94	928.79
1604	5300	7470	43	869.16
1605	5700	7430	28	872.65
1607	5880	7250	36	909.29
1608	4910	7050	76	941.86
1609	5360	7310	39	887.86
1610	6440	6740	48	1002.42
1612	5700	5770	50	1108.26
1613	1520	4820	28	1007.51
1614	1170	7470	44	658.88
1615	4160	9850	22	497.11
1616	4040	6610	96	982.49
1617	4260	7490	79	861.93
1620	4680	8650	41	692.18
1621	1720	7720	53	671.61
1622	3910	6910	100	941.94
1623	920	5940	39	833.81
1624	170	6840	68	692.14
1625	2580	8010	56	688.70
1626	4440	8810	42	662.83
1628	2660	7720	40	714.67
1629	4820	5650	124	1166.34
1630	5630	8910	73	724.43
1631	2500	5780	61	976.33
1679	3440	8150	53	713.23
1690	680	5520	51	882.85
1694	3300	5040	72	1125.62
1695	2260	5770	58	960.73
1697	3440	8150	53	713.23
1700	4830	5660	125	1166.43
1703	4780	6850	85	971.57
1705	2020	5120	60	1032.05
1706	4050	6420	96	1007.41
1707	4020	6690	92	967.32
1708	3920	6120	100	1044.14
1709	1270	4600	46	1037.23
1710	1150	4620	48	1028.56
1711	2840	5850	130	1054.67
1712	5780	6130	34	1048.52
1713	1890	5230	73	1022.79
1714	1980	5230	73	1028.33
1716	6250	6140	39	1065.78
1717	6230	6130	38	1065.53
1718	5930	6110	32	1053.64
1719	1700	4760	35	1033.73
1720	2240	4720	35	1071.97
1721	6240	7380	17	883.99
1722	1860	5440	137	1057.35
1723	5850	6090	35	1056.80
1725	5600	4970	161	1318.19
1726	4920	4970	162	1295.41
1727	4870	4970	163	1294.51
1728	4800	5340	159	1240.21
1729	5210	7260	41	891.07
1758	1690	4785	26	1020.95

a distance of 1 km. Plotting the stratigraphic data in respect to the Projection Plane, which is by definition a plane, eliminates any possibility of compromising faunal range as a consequence of surface relief along a physical datum (Text-fig. 7).

By using Projection Plane techniques it is possible to merge both spatial and stratigraphic components of paleontologic data into two-dimensional figures (ZnY and ZnX projections). The ability to retain the spatial component within a data set has the potential to provide insights into paleontologic or stratigraphic relationships that are obscured by conventional single-dimensional graphical presentations of biostratigraphic data. Text-figure 8 presents the relative stratigraphic location of 327 Maastrichtian and Danian fossil occurrences located over approximately 70 km^2 of the southern two-thirds of Seymour Island. Geographic and stratigraphic locations of Maastrichtian and Danian localities are listed in Table 3, and individual occurrences and abundances in Tables 4 and 5.

Table 4.—Danian locality/species occurrence registry.

Locality	Meters	Species	No. speci-mens	
9	1167.94	*Australoneilo gracilis*	7	
		Conotomaria sp. A	1	
		Conotomaria sp. C	3	
		Coral	1	
		Crinoids (numerous)		
		Cucullaea ellioti	25	
		Echinoid spines	11	
		Lahillia huberi	10	
		Lahillia larseni	1	
		Levifusus woolfei n. sp.	21	
		Marwickia woodburnei	45	
		Nucula (Leionucula) hunickeni	1	
		Nucula (Leionucula) suboblonga	1	
		Probuccinum palaiocostatum n. sp.	1	
		Seymourosphaera bulloides	27	
		Seymourosphaera depressa	2	
		Strepsidura polaris	1	
		Struthiochenopus hurleyi n. sp.	104	
		Sycostoma pyrinota n. sp.	1	
		Vanikoropsis arktowskiana	37	
		Zygomelon apheles n. sp.	3	
		Total		303
447	1058.45	Brachiopod	17	
		Lahillia larseni	20	
		Nucula (Leionucula) suboblonga	1	
		Struthiochenopus hurleyi n. sp.	10	
		Acmea submesidia n. sp.	1	
		Cucullaea ellioti	6	
		Total		55
477		*Cucullaea ellioti*	3	
		Lahilla larsensi	15	
		Total		18
496	1179.42	*Cosmasyrinix antarctigera* n. sp.	1	
		Cucullaea ellioti	1	
		Lahillia huberi	4	
		Levifusus woolfei n. sp.	1	
		Seymourosphaera elevata	1	
		Vanikoropsis arktowskiana	6	
		Total		14
497	1369.31	*Antarctodarwinella austerocallosa* n. sp.	1	
		Australoneilo gracilis	9	
		Cucullaea ellioti	3	
		Levifusus woolfei n. sp.	1	
		Mesalia virginiae n. sp.	1	
		Nucula (Leionucula) hunickeni	18	
		Pinna freneixae	1	
		Scaphopod	4	
		Serrifusus binodosum n. sp.	3	
		Struthiochenopus hurleyi n. sp.	8	
		Taioma sobrali n. sp.	15	
		Total		64
631	1138.29	*Cladocera antarctica*	1	
		Cucullaea ellioti	1	
		Lahillia huberi	2	
		Total		4
746	1134.22	*Australoneilo casei*	1	
		Conotomaria sp. C	1	
		Cucullaea ellioti	38	
		Lahillia huberi	19	
		Lahillia larseni	4	
		Marshallaria variegata n. sp.	5	
		Marwickia woodburnei	2	
		Mesalia virginiae n. sp.	1	
		Nucula (Leionucula) hunickeni	5	
		"*Paleopsephaea*" *nodoprosta* n. sp.	8	
		Pinna freneixae	2	
		Probuccinum palaiocostatum n. sp.	1	
		Saxolucina antarctipleura n. sp.	1	
		Serrifusus binodosum n. sp.	33	
		Seymourosphaera bulloides	9	
		Struthiochenopus hurleyi n. sp.	9	
		Zygomelon apheles n. sp.	5	
		Total		144
783	1072.17	*Struthiochenopus hurleyi* n. sp.	9	
		Total		9
1104	1375.46	*Australoneilo gracilis*	1	
		Conotomaria sp. C	1	
		"*Heterotrema*" sp.	1	
		Marshallaria variegata n. sp.	2	
		Mesalia virginiae n. sp.	1	
		Nucula (Leionucula) hunickeni	1	
		"*Paleopsephaea*" *nodoprosta* n. sp.	1	
		Pyropsis australis n. sp.	1	
		Scaphopod	3	
		Serrifusus binodosum n. sp.	1	
		Seymourosphaera depressa	2	
		Struthiochenopus hurleyi n. sp.	3	
		Taioma sobrali n. sp.	1	
		Zygomelon apheles n. sp.	1	
		Total		20
1105	1369.29	*Conotomaria* sp. A	1	
		Saxolucina antarctipleura n. sp.	1	
		Taioma sobrali n. sp.	1	
		Total		3
1161	1050.70	*Conotomaria* sp. C	1	
		Cucullaea ellioti	19	
		Lahillia larseni	9	
		Marwickia woodburnei	1	
		Nucula (Leionucula) suboblonga	2	
		Panopea clausa	1	
		Saxolucina antarctipleura n. sp.	2	
		Struthiochenopus hurleyi n. sp.	1	
		Total		36
1119	1095.70	*Cucullaea ellioti*	3	
		Lahillia larseni	2	
		Marshallaria variegata n. sp.	1	
		Nucula (Leionucula) suboblonga	1	
		Seymourosphaera bulloides	2	
		Seymourosphaera elevata	11	
		Struthiochenopus hurleyi n. sp.	3	
		Acesta webbi	1	
		Total		24
1130	1094.66	*Cucullaea ellioti*	1	
		Lahillia larseni	1	
		Marwickia woodburnei	5	

Table 4.—Continued.

Locality	Meters	Species	No. specimens	
		Nucula (Leionucula) suboblonga	1	
		Taioma sobrali n. sp.	1	
		Total		9
1131	1065.89	*Acmea submesidia* n. sp.	1	
		Cucullaea ellioti	3	
		Lahillia larseni	1	
		Marwickia woodburnei	4	
		Nucula (Leionucula) suboblonga	13	
		Ostrea sp.	1	
		Saxolucina antarctipleura n. sp.	1	
		Struthiochenopus hurleyi n. sp.	2	
		Total		26
1133	1087.34	*Lahillia larseni*	2	
		Total		2
1134	1083.14	*Acesta webbi*	3	
		Coral	1	
		Lahillia larseni	10	
		Marwickia woodburnei	1	
		Nucula (Leionucula) suboblonga	1	
		Pinna freneixae	2	
		Seymourosphaera bulloides	2	
		Struthiochenopus hurleyi n. sp.	2	
		Vanikoropsis arktowskiana	1	
		Total		23
1135	1091.90	*Acesta webbi*	1	
		Cucullaea ellioti	1	
		Lahillia larseni	18	
		Marwickia woodburnei	2	
		Nucula (Leionucula) suboblonga	2	
		Seymourosphaera bulloides	4	
		Seymourosphaera elevata	1	
		Struthiochenopus hurleyi n. sp.	13	
		Total		42
1136	1136.32	Crinoids		
		Cucullaea ellioti	5	
		Lahillia huberi	2	
		Marwickia woodburnei	3	
		Nucula (Leionucula) suboblonga	2	
		Pinna freneixae	1	
		Seymourosphaera bulloides	3	
		Seymourosphaera elevata	1	
		Struthiochenopus hurleyi n. sp.	9	
		Wood	1	
		Total		27
1137	1125.70	*Australoneilo gracilis*	6	
		Marwickia woodburnei	8	
		Saxolucina antarctipleura n. sp.	2	
		Struthiochenopus hurleyi n. sp.	13	
		Total		29
1138	1107.16	*Australoneilo gracilis*	1	
		Marwickia woodburnei	13	
		Nucula (Leionucula) suboblonga	13	
		Periploma? n. sp.	1	
		Serrifusus binodosum n. sp.	1	
		Total		29
1139	1145.11	*Acesta webbi*	1	
		Marwickia woodburnei	1	

Table 4.—Continued.

Locality	Meters	Species	No. specimens	
		Mesalia virginiae n. sp.	10	
		Pinna freneixae	2	
		Seymourosphera subglobosa	2	
		Total		16
1148	1215.89	*Lahillia huberi*	3	
		Marwickia woodburnei	3	
		Nucula (Leionucula) suboblonga	9	
		Seymourosphaera elevata	1	
		Struthiochenopus hurleyi n. sp.	6	
		Total		22
1189	1070.85	*Cucullaea ellioti*	2	
		Marwickia woodburnei	9	
		Nucula (Leionucula) suboblonga	16	
		Seymourosphaera elevata	2	
		Struthiochenopus hurleyi n. sp.	2	
		Total		31
1192	1124.00	*Cucullaea ellioti*	1	
		Lahillia huberi	1	
		Zygomelon apheles n. sp.	1	
		Total		3
1430	1098.20	*Cucullaea ellioti*	8	
		Lahillia larseni	8	
		Nucula (Leionucula) suboblonga	16	
		Saxolucina antarctipleura n. sp.	10	
		Seymourosphaera bulloides	22	
		Seymourosphaera elevata	11	
		Struthiochenopus hurleyi n. sp.	4	
		Vanikoropsis arktowskiana	1	
		Total		80
1431	1144.26	*Antarctiranella tessela* n. gen. n. sp.	1	
		Colus delrioae n. sp.	1	
		Crinoids		
		Cucullaea ellioti	3	
		Lahillia larseni	1	
		Marshallaria variegata n. sp.	1	
		Nucula (Leionucula) suboblonga	1	
		Serrifusus binodosum n. sp.	2	
		Seymourosphaera bulloides	2	
		Struthiochenopus hurleyi n. sp.	2	
		Taioma sobrali n. sp.	1	
		Vanikoropsis arktowskiana	1	
		Zygomelon apheles n. sp.	1	
		Total		17
1432	1110.44	*Marwickia woodburnei*	7	
		Nucula (Leionucula) suboblonga	5	
		Seymourosphaera elevata	3	
		Vanikoropsis arktowskiana	1	
		Total		16
1433	1174.05	*Seymourosphaera elevata*	4	
		Struthiochenopus hurleyi n. sp.	1	
		Total		5
1434	1165.61	*Antarctodarwinella austerocallosa* n. sp.	3	
		Australoneilo gracilis	2	
		Cucullaea ellioti	1	
		Echinoid spines	2	
		Lahillia larseni	1	
		Levifusus woolfei n. sp.	7	

Table 4.—Continued.

Locality	Meters	Species	No. speci-mens	
		Marwickia woodburnei	7	
		Probuccinum palaiocostatum n. sp.	1	
		Seymourosphaera bulloides	11	
		Seymourosphaera depressa	1	
		Struthiochenopus hurleyi n. sp.	10	
		Vanikoropsis arktowskiana	19	
		Total		65
1435	1165.45	*Cucullaea ellioti*	2	
		Lahillia larseni	1	
		Levifusus woolfei n. sp.	3	
		Marwickia woodburnei	2	
		Seymourosphera subglobosa	3	
		Struthiochenopus hurleyi n. sp.	3	
		Total		14
1442	1140.34	*Struthiochenopus hurleyi* n. sp.	1	
		Zygomelon apheles n. sp.	1	
		Total		2
1456	1154.22	*Struthiochenopus hurleyi* n. sp.	1	
		Total		1
1467	1057.40	*Marwickia woodburnei*	9	
		Nucula (Leionucula) suboblonga	1	
		Saxolucina antarctipleura n. sp.	14	
		Struthiochenopus hurleyi n. sp.	2	
		Total		26
1473	1110.49	*Lahillia larseni*	1	
		Nucula (Leionucula) suboblonga	1	
		Seymourosphera subglobosa	1	
		Total		3
1483	1125.13	*Cladocera antarctica*	100	
		Ostrea sp.	1	
		Total		101
1484		*Periploma*? n. sp.	1	
		Total		1
1499	1116.11	*Lahillia larseni*	3	
		Total		3
1501	1108.86	*Struthiochenopus hurleyi* n. sp.	1	
		Total		1
1502	1098.44	*Marwickia woodburnei*	2	
		Nucula (Leionucula) suboblonga	2	
		Struthiochenopus hurleyi n. sp.	3	
		Total		7
1504	1132.44	*Marwickia woodburnei*	1	
		Total		1
1505	1126.18	*Levifusus woolfei* n. sp.	1	
		Nucula (Leionucula) hunickeni	1	
		Nucula (Leionucula) suboblonga	2	
		Struthiochenopus hurleyi n. sp.	3	
		Vanikoropsis arktowskiana	3	
		Total		10
1506	1110.01	Crinoids		
		Nucula (Leionucula) suboblonga	1	
		Seymourosphaera bulloides	1	
		Seymourosphaera elevata	1	
		Struthiochenopus hurleyi n. sp.	1	
		Vanikoropsis arktowskiana	1	
		Total		5
1510	1200.87	*Cucullaea ellioti*	1	

Table 4.—Continued.

Locality	Meters	Species	No. speci-mens	
		Lahillia larseni	1	
		Marwickia woodburnei	1	
		Nucula (Leionucula) suboblonga	13	
		Struthiochenopus hurleyi n. sp.	5	
		Vanikoropsis arktowskiana	1	
		Total		22
1519	1072.57	*Amauropsis notoleptos* n. sp.	1	
		Cosmasyrinix antarctigera n. sp.	1	
		Cylichnania cf. *C. impar*	1	
		Euspira antarctidia n. sp.	1	
		Jupiteria? sp.	1	
		Lahillia larseni	2	
		Ledina? n. sp.	1	
		Melanella seymourensis n. sp.	1	
		Nucula (Leionucula) hunickeni	4	
		Nucula (Leionucula) suboblonga	4	
		Periploma? n. sp.	1	
		Struthiochenopus hurleyi n. sp.	2	
		Thyasira austrosulca n. sp.	1	
		Total		21
1529	1059.19	*Cucullaea ellioti*	10	
		Lahillia larseni	9	
		Marwickia woodburnei	4	
		Nucula (Leionucula) suboblonga	3	
		Struthiochenopus hurleyi n. sp.	9	
		Total		35
1530	1100.12	*Lahillia larseni*	1	
		Marwickia woodburnei	2	
		Total		3
1531	1052.66	*Amauropsis notoleptos* n. sp.	1	
		Cucullaea ellioti	4	
		Lahillia larseni	2	
		Marwickia woodburnei	3	
		Nucula (Leionucula) suboblonga	4	
		Struthiochenopus hurleyi n. sp.	2	
		Total		16
1532	1067.23	*Lahillia larseni*	2	
		Marwickia woodburnei	2	
		Struthiochenopus hurleyi n. sp.	2	
		Total		6
1533	1046.22	*Marwickia woodburnei*	1	
		Nucula (Leionucula) suboblonga	4	
		Wood	1	
		Total		6
1534	1074.45	*Acmea submesidia* n. sp.	1	
		Cucullaea ellioti	1	
		Marwickia woodburnei	4	
		Nucula (Leionucula) hunickeni	1	
		Nucula (Leionucula) suboblonga	2	
		Struthiochenopus hurleyi n. sp.	6	
		Total		15
1535	1077.79	*Bittium (Zebittium) brooksi n. sp.*	50	
		Colus delrioae n. sp.	1	
		Conotomaria sp. A	1	
		Cosmasyrinix antarctigera n. sp.	1	
		Euspira antarctidia n. sp.	2	
		Melanella seymourensis n. sp.	3	

Table 4.—Continued.

Locality	Meters	Species	No. specimens	
		Nucula (Leionucula) suboblonga	1	
		Nucula sp.	1	
		Saxolucina antarctipleura n. sp.	1	
		Struthiochenopus hurleyi n. sp.	1	
		Total		62
1536	1086.36	*Cucullaea ellioti*	1	
		Marwickia woodburnei	7	
		Nucula (Leionucula) suboblonga	9	
		Struthiochenopus hurleyi n. sp.	2	
		Total		19
1537	1098.79	*Bittium (Zebittium) brooksi n. sp.*	*10*	
		Cucullaea ellioti	2	
		Lahillia larseni	1	
		Marwickia woodburnei	5	
		Nucula (Leionucula) suboblonga	6	
		Struthiochenopus hurleyi n. sp.	1	
		Total		25
1538	1103.80	*Cylichnania* cf. *C. impar*	1	
		Euspira antarctidia n. sp.	1	
		Jupiteria? sp.	1	
		Lahillia larseni	1	
		Levifusus woolfei n. sp.	1	
		Marwickia woodburnei	6	
		Periploma? n. sp.	1	
		Seymourosphaera bulloides	3	
		Struthiochenopus hurleyi n. sp.	18	
		Total		33
1574	1137.86	Bryozoa	10	
		Struthiochenopus hurleyi n. sp.	1	
		Wood	1	
		Total		12
1581	1164.05	*Bittium paleonotum* n. sp.	1	
		Total		1
1586	1202.49	*Marwickia woodburnei*	3	
		Nucula (Leionucula) suboblonga	4	
		Paleopsephaea? *nodoprosta* n. sp.	2	
		Seymourosphaera elevata	1	
		Total		10
1587	1134.66	*Levifusus woolfei* n. sp.	2	
		Struthiochenopus hurleyi n. sp.	3	
		Total		5
1589	1148.82	*Marwickia woodburnei*	3	
		Nuculana antarctirostrata n. sp.	2	
		Pseudofax? *paucus* n. sp.	1	
		Seymourosphaera bulloides	1	
		Struthiochenopus hurleyi n. sp.	2	
		Vanikoropsis arktowskiana	1	
		Total		10
1591	1053.39	*Mesalia virginiae* n. sp.	1	
		Seymourtula antarctica	1	
		Total		2
1599	1058.05	Wood	1	
		Total		1
1601	1159.72	*Cucullaea ellioti*	1	
		Seymourosphaera bulloides	7	
		Struthiochenopus hurleyi n. sp.	12	
		Vanikoropsis arktowskiana	4	
		Zygomelon apheles n. sp.	1	
		Total		25
1700	1166.43	Crinoids		
		Seymourosphaera bulloides	1	
		Struthiochenopus hurleyi n. sp.	4	
		Total		5
1715		*Mesalia virginiae* n. sp.	1	
		Total		1
1716	1065.78	*Turritella (Haustator?) parisi* n. sp.	1	
		Total		1

Table 5.—Danian species occurrence registry.

Taxon	Locality	No. specimens
Acesta webbi	1119	1
	1134	3
	1135	1
	1139	1
Total		6
Acmea submesidia n. sp.	477	1
	1131	1
	1534	1
	1560	1
Total		4
Amauropsis notoleptos n. sp.	1519	1
	1531	1
Total		2
Antarctodarwinella austerocallosa n. sp.	497	3
	1434	1
Total		4
Antarctiranella tessela n. gen. n. sp.	1431	2
Total		2
Australoneilo casei	746	8
Total		8
Australoneilo gracilis	9	6
	497	9
	1104	1
	1137	6
	1138	1
	1414	1
	1434	2
Total		26
Bittium (Bittium?) paleonotum n. sp.	1581	1
Total		1
Bittium (Zebittium) brooksi n. sp.	1535	50
	1537	10
Total		60
Colus delrioae n. sp.	1431	1
	1535	1
	1556	1
Total		3
Conotomaria sp. A	9	1
	1105	1
	1535	1
Total		3
Conotomaria sp. B	9	4
Total		4
Conotomaria sp. C	9	3
	746	1
	1104	4
Total		8
Tholitoma (Cosmasyrinix) antarctigera n. sp.	496	1
	1519	1
	1535	1
Total		3
Cucullaea ellioti	9	25
	477	6
	485	1
	496	1
	497	3
	631	1
	746	38
	1119	3
	1130	1
	1131	3
	1135	1
	1136	5
	1161	13
	1189	2
	1192	1
	1430	8
	1431	3
	1434	1
	1435	2
	1510	1
	1529	10
	1531	4
	1534	1
	1536	1
	1537	2
	1601	1
Total		138
Cylichnania cf. *C. impar*	1519	1
	1538	3
Total		4
Euspira antarctidia n. sp.	1519	1
	1535	2
	1538	1
Total		4
Heteroterma? n. sp.	1104	1
Total		1
Jupiteria? n. sp.	1519	1
	1538	1
Total		2
Lahillia huberi	9	10
	496	4
	631	2
	746	19
	1136	2
	1148	3
	1192	1
Total		41
Lahillia larseni	9	4
	447	20
	746	4
	777	3
	1119	2
	1130	1
	1131	1
	1133	2
	1134	10
	1135	18
	1161	9
	1414	1
	1430	8
	1431	1
	1434	1
	1435	1
	1473	1
	1499	3
	1510	2

Table 5.—Continued.

Table 5.—Continued.

Taxon	Locality	No. specimens
	1508	1
	1519	1
	1529	9
	1530	1
	1531	2
	1532	2
	1538	1
	1537	1
Total		110
Ledina? sp.	1519	1
Total		1
Levifusus woolfei n. sp.	9	21
	479	1
	496	1
	1434	7
	1435	3
	1505	1
	1538	1
	1587	2
Total		38
Marshallaria variegata n. sp.	746	5
	1104	2
	1119	1
	1431	1
	1548	2
Total		11
Marwickia woodburnei	9	16
	746	2
	1130	5
	1131	4
	1134	1
	1135	2
	1136	3
	1137	8
	1138	13
	1139	1
	1149	1
	1161	1
	1189	9
	1432	7
	1434	7
	1435	2
	1448	2
	1467	9
	1502	2
	1504	1
	1510	1
	1529	4
	1530	2
	1531	3
	1532	2
	1533	1
	1534	4
	1536	7
	1537	5
	1538	6
	1586	3
	1589	3
Total		137
Melanella seymourensis n. sp.	1519	3

Table 5.—Continued.

Taxon	Locality	No. specimens
	1535	1
Total		4
Mesalia virginiae n. sp.	497	1
	746	1
	1104	1
	1139	10
	1548	1
	1591	1
	1715	1
Total		16
Mitra (Eumitra?) antarctinella n. sp.	1108	2
	1635	1
Total		3
Nucula (Leionucula) hunickeni	9	1
	497	18
	746	5
	1104	1
	1505	1
	1519	4
	1534	1
Total		31
Nucula (Leionucula) suboblonga	9	1
	447	1
	777	1
	1119	1
	1130	1
	1131	13
	1134	1
	1135	2
	1136	2
	1138	13
	1148	9
	1149	2
	1189	16
	1430	16
	1431	1
	1432	5
	1473	1
	1505	2
	1506	1
	1467	1
	1502	2
	1510	13
	1519	4
	1529	3
	1536	9
	1531	4
	1533	4
	1534	2
	1535	1
	1537	6
	1548	1
	1586	4
	1695	5
	1697	2
Total		150
Nucula sp.	1535	1
Total		1
Nuculana antarctirostrata n. sp.	1589	2
Total		2

Table 5.—Continued.

Taxon	Locality	No. specimens
Ostrea sp.	1131	1
	1483	1
Total		2
Paleopsephaea? nodoprosta n. sp.	746	8
	1104	1
	1586	2
	1701	1
Total		12
Panopea clausa	1161	1
Total		1
Periploma sp.	1138	1
	1519	1
	1484	1
	1538	1
Total		4
Pinna freneixae	497	1
	746	2
	1132	1
	1134	2
	1136	1
	1139	2
	1150	1
	1179	1
	1181	1
Total		12
Probuccinum palaiocostatum n. sp.	9	1
	746	1
	1434	1
	1699	1
	1701	1
Total		5
Pseudofax? paucus n. sp.	1589	1
Total		1
Pyropsis? australis n. sp.	1104	1
Total		1
Saxolucina antarctipleura n. sp.	262	1
	746	1
	1105	1
	1131	1
	1137	2
	1161	2
	1430	10
	1467	14
	1535	1
Total		33
Serrifusus binodosum n. sp.	497	3
	746	33
	1138	1
	1104	1
	1431	2
Total		40
Seymourosphaera bulloides	9	25
	746	9
	1119	2
	1134	2
	1135	4
	1136	3
	1430	22
	1431	2
	1432	1
	1434	11
	1506	1
	1538	3
	1589	1
	1601	7
	1694	1
	1700	1
Total		95
Seymourosphaera depressa	9	1
	1104	1
	1434	2
Total		4
Seymourosphaera elevata	496	1
	1119	11
	1135	1
	1136	1
	1148	1
	1189	2
	1430	11
	1432	3
	1433	4
	1506	1
	1577	3
	1586	1
Total		40
Seymourosphera subglobosa	1133	2
	1136	3
	1430	1
Total		6
Seymourtula antarctica	1591	3
Total		3
Strepsidura? polaris n. sp.	9	1
Total		1
Struthiochenopus hurleyi n. sp.	9	104
	447	10
	497	8
	746	9
	777	4
	783	9
	1104	3
	1119	3
	1131	2
	1134	2
	1135	13
	1136	9
	1137	13
	1148	6
	1161	1
	1189	2
	1205	4
	1430	4
	1431	2
	1433	1
	1434	10
	1435	3
	1442	1
	1456	1
	1467	2
	1479	1

Table 5.—Continued.

Taxon	Locality	No. specimens
	1502	3
	1503	2
	1505	3
	1506	1
	1507	1
	1508	10
	1510	5
	1519	2
	1529	9
	1531	2
	1532	2
	1534	6
	1535	1
	1536	2
	1537	1
	1538	18
	1548	4
	1574	1
	1577	2
	1587	3
	1589	2
	1601	12
	1697	1
	1698	1
	1699	1
	1700	4
Total		327
Sycostoma pyrinota n. sp.	9	1
Total		1
Taioma sobrali n. sp.	497	15
	1104	1
	1105	1
	1130	1
	1431	1
Total		19
Thyasira austrosulca n. sp.	1519	1
Total		1
Turritella (Haustator?) parisi	1716	1
Total		1
Vanikoropsis arktowskiana	9	36
	261	1
	496	6
	1134	1
	1205	1
	1335	3
	1414	1
	1430	1
	1431	1
	1432	1
	1434	19
	1505	3
	1506	1
	1507	2
	1508	2
	1510	1
	1548	5
	1589	1
	1596	1
	1601	4
	1698	3
	1700	4
Total		62
Zygomelon apheles n. sp.	9	3
	746	5
	1104	1
	1192	1
	1431	1
	1442	1
	1601	1
Total		13

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REFERENCES CITED

Abbott, R.T.

1974. American Seashells. Second Edition. Van Nostrand Reinhold Company, New York, 663 pp.

Abbott, R.T., and Dance, S.P.

1983. Compendium of Seashells. New York, 248 pp.

Adams, A.

1850. Monograph of the family Bullidae. *In* G. B. Sowerby, ed., Thesaurus Conchyliorum, vol. 2, pp. 553–608, pls. 119–125.

Adams, H., and Adams, A.

1853–1858. The Genera of Recent Mollusca. London, vol. 1 (1853–1854), 484 pp., vol. 2 (1854–1858), 661 pp., vol. 3 (1858), 136 pls.

Adegoke, O.S.

1977. Stratigraphy and paleontology of the Ewekoro Formation (Paleocene) of southwestern Nigeria. Bulletins of American Paleontology, vol. 71, no. 295, 379 pp., 50 pls.

Aguirre-Urreta, M.B., and Olivero, E.B.

1992. A Cretaceous hermit crab from Antarctica: predatory activities and bryozoan symbiosis. Antarctic Science, vol. 4, pp. 207–214.

Allan, R.S.

1926. Fossil Mollusca of the Waihao Greensands. Transactions of the New Zealand Institute, vol. 56, pp. 338–346.

1927. The geology and paleontology of the lower Waihao Basin, South Canterbury, New Zealand.Transactions of the New Zealand Institute vol. 57, pp. 265–309.

Allmon, W.D.

1988. Ecology of living turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications. Palaios, vol. 3, pp. 259–284.

1996. Evolution and systematics of Cenozoic American Turritellidae (Gastropoda). I. Paleocene and Eocene species related to "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad" from the U.S. Gulf and Atlantic Coastal Plains. Palaeontographica Americana, no. 59, 134 pp.

Anderson, F.M.

1958. Upper Cretaceous of the Pacific Coast. The Geological Society of America Memoir 71, 378 pp., 75 pls.

Andersson, J.G.

1904. Swedish Antarctic Expedition. III. The scientific operations on board the 'Antarctic' in the summer of 1902–1903. IV. The sledge-expedition from the 'Antarctic.' Geographic Journal of London, vol. 23, pp. 215–220.

Bellardi, L.

1875. Monografia delle nuculidi trovate finore nei terrini terziari del Piemonte e della Liguria. II R. Liceo Gioberti nell' Anno scolastico 1874–1875, Torino, 32 pp., 1 pl.

Beu, A.G.

1988. Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and Bursidae. Part 5. Early history of the families, with four new genera and recognition of the family Personidae. Saito Ho-on Kai Special Publication (Professor Tamio Kotaka Commemorative volume), pp. 69–96, pls. 1–4.

Beu, A.G., and Maxwell, P.A.

1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey Paleontological Bulletin 58, 518 pp., 57 pls.

Beurlen, K.

1944. Beitäge zur Stammgeschichte der Muscheln. Bayerische Akademie der Wissenschäftliche Sitzungsberichte, vol. 1, pp. 133–145.

Born, I. Von

1778. Index Rerum Naturalium Musei Caesarei Vindibonsis Pars 1. Testacea. Vindobonae, 458 pp.

Bowdich, T.E.

1822. Elements of Conchology, including the fossil genera and the animals. Paris and London, vol. 1, 79 pp., 19 pls.; vol. 2, 40 pp., 8 pls.

Bronn, H.G.

1831. Ergebnisse meiner naturhistorischo-okonomischen reisen. K. Groos, Heidelberg, 176 pp., 1 pl.

Brown, T.

1849. Illustrations of the Fossil Conchology of Great Britain and Ireland. London, 273 pp., 98 pls.

Bucquoy, E., Dautzenberg, P., and Dollfus, G.

1882–1883. Les mollusques marins du Roussillon. 1. Gastropodes. Paris, 570 pp.

Camacho, H.H.

1949. La fáunula Cretácica del Hito XIX (Tierra del Fuego). Revista de la asociación Geológica Argentina, vol. 4, pp. 249—254.

1992. Algunas consideraciones acerca de la transgression marina Paleocena en la Argentina. Academia Nacional de Ciencias (Córdoba, Argentina), Miscelanea no. 85, 41 pp.

Campbell, H.J., Andrews, P.B., Beu, A.G., Maxwell, P.A., Edwards, A.R., Laird, M.G., Hornibrook, N. de B., Mildenhall, D.C., Watters, W.A., Buckeridge, J.S., Lee, D.E., Strong, C.P., Wilson, G.J., and Hayward, B.W.

1993. Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. Institute of Geological and Nuclear Sciences Monograph 2, 269 pp.

Carpenter, P.P.

1857. Catalogue of the Collection of Mazatland Shells in the British Museum collected by Frederick Reigen. London, Printed by the Order of the Trustees, 552 pp.

Cernohorsky, W.O.

1970. Systematics of the families Mitridae and Volutomitridae. Bulletin of the Auckland Institute and Museum, no. 8, 190 pp., 18 pls.

Chemnitz, W.A., and Chemnitz, J.H.

1769–1795. *In* F.H. Martini, W.A. Chemnitz and J.H. Chemnitz, Neues systematisches Conchylien-Cabinet. Nuremberg, 11 vols.

Children, J.G.

1823–1824. Lamarck's genera of shells translated from the French with plates from original drawings by Miss Anna Children. Quarterly Journal of Science, vol. 14, pp. 64–86(1822), 14, pp. 298–322(1823), 15, pp. 23–52(1823), 15, pp. 216–258(1823), 16, pp. 49–79(1823), 16, pp. 241–264(1824).

Conrad, T.A.

1832–1835. Fossil shells of the Tertiary formations of North America, illustrated by figures drawn from stone from nature. Philadelphia (see Wenz, 1938–1944, p. 1523 for parts).

1846. Descriptions of new species of fossil and Recent shells and corals. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 3, no. 1, pp. 19–27, pl. 1 [published 1848].

1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Journal of the Academy of Natural Sciences, Philadelphia, 2nd series, vol. 4, pp. 275–298, pls. 46–47.

1865. Descriptions of some new Eocene shells of the United States. American Journal of Conchology, vol. 1, pp. 142–149.

Cossmann, M.

1886–1913. Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. Annales de la Société royale Malacologique, Belgique (see Wenz, 1938–1944, p. 1525 for parts and dates).

1901. Essais de paléoconchologie comparée. Paris, vol. 4, 293 pp.

Costa, E.M. Da

1778. Historia Naturalis Testaceorum Britanniae, or the British Conchology; containing the descriptions and other particulars of the natural history of Shells of Great Britain and Ireland; illustrated with figures. In English and French. Millan, B. White; London, Elmsley and Robson, 254 pp., and index.

Cotton, B.C.

1957. No. 12. Family Mitridae. Royal Society of South Australia Malacological Section, 7 pp., 1 pl.

Cox, L.R.

1931. Sycostoma, a renamed genus of Lower Tertiary Gastropoda. Proceedings of the Malacological Society of London, vol. 19, p. 291.

1959. Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London, vol. 33, pp. 239–261.

Cox, L.R., and Knight, J.B.

1960. Suborders of the Archaeogastropoda. Proceedings of the Malacological Society of London, vol. 33, pp. 262–264.

Crame, J.A.

1996. Evolution of high-latitude molluscan faunas. *In* J.D. Taylor, ed., Origin and Evolutionary Radiation of the Mollusca, Oxford University Press, Oxford, pp. 119–131.

Cuvier, G.

1797. Tableau Élémentaire de l'Histoire Naturelle des Animaux. Paris, 710 pp.

Cuvier, G., and Brongniart, A.

1822. Description Géologique des Environs de Paris. Nouvelle Edition. G. Dufour et E. D'Ocagne, Paris, 428 pp., 11 pls.

Cvancara, A.M.

1966. Revision of the fauna of the Cannonball Formation (Paleocene) of North and South Dakota. Contributions from the Museum of Paleontology, The University of Michigan, vol. 22, no. 1, pp. 1–97, 9 pls.

Dall, W.H.

1889. On the hinge of pelecypods and its development, with an attempt toward a better division of the group. American Journal of Science, vol. 38, pp. 445–462.

1890–1903. Contributions to the Tertiary fauna of Florida, with special reference to the Miocene Silex beds of Tampa and the Pliocene beds of Caloosahatchie River. Transactions of the Wagner Free Institute of Science, Philadelphia (see Keen, 1958, p. 564 for details of parts).

1909. Contributions to the Tertiary Paleontology of the Pacific Coast. I. The Miocene of Astoria and Coos Bay, Oregon. United States Geological Survey Professional Paper 59, 278 pp., 23 pls.

Darragh, T.A.

1991. A revision of the Australian genus Tylospira Harris, 1897 (Gastropoda: Struthiolariidae). Alcheringa, vol. 15, pp. 151–175.

1994. Paleocene bivalves from the Pebble Point Formation, Victoria, Australia. Proceedings of the Royal Society of Victoria, vol. 106, pp. 71–103.

1997. Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Paleocene Pebble Point Formation, Victoria, Australia. Proceedings of the Royal Society of Victoria, vol. 109, no. 1, pp. 57–108.

Darragh, T.A., and Kendrick, G.W.

1991. Maastrichtian Bivalvia (excluding Inoceramidae) from the Miria Formation, Carnarvon Basin, north Western Australia. Records of the Australian Museum Supplement 36, 108 pp.

1994. Maastrichtian Scaphopoda and Gastropoda from the Miria Formation, Carnarvon Basin, northwestern Australia. Records of the Western Australian Museum Supplement 48, 76 pp.

Dell, R.K.

1964. Antarctic and sub-Antarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Discovery Reports, vol. 33, pp. 99–250.

1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. Bulletin of the Royal Society of New Zealand, vol. 27, pp. 1–311.

Deshayes, G.P.

1830–1832. Encyclopédie méthodique ou par ordre de matières. Histoire Naturelle de Vers et Mollusques. Paris, 850 pp.

Dickerson, R.E.

1914. Fauna of the Martinez Eocene of California. University of California, Bulletin of the Department of Geological Sciences, vol. 8, no. 6, pp. 61–180.

Dockery, D.T. III

1993. The streptoneuran gastropods, exclusive of the Stenoglossa, of the Coffee Sand (Campanian) of Northeastern Mississippi. Mississippi Department of Environmental Quality Office of Geology Bulletin 129, 191 pp., 42 pls.

Elliot, D.H., Askin, R.A., Kyte, F.T., and Zinsmeister, W.J.

1994. Iridium and dinocysts at the Cretaceous-Tertiary boundary on Seymour Island, Antarctica: implications for the K-T event. Geology, vol. 22, pp. 675–678.

Erickson, J.M.

1974. Revision of the Gastropoda of the Fox Hills Formation, Upper Cretaceous (Maestrichtian) of North Dakota. Bulletins of American Paleontology, vol. 66, no. 284, pp. 129–253, pls. 14–20.

Eschscholtz, J.F.

1830. Appendix. Review of the Zoological Collection. *In* O. von Kotzebue, A New Voyage Around the World, in the years 1823, 24, 25, and 26. Vol. 1, 341 pp.; Vol. 2, 362 pp., with Appendix, pp. 325–362. London, H. Colburn and R. Bentley (also in German, same year).

1833. Genus Acmaea. *In* H. Rathke, Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuen Thierarten, wahrend des Flottecapitains von Kotzebue Zweiter Reise um die Welt . . . in . . . 1823–26 beobachten von . . . F. Eschscholtz. Weimar?, Part 5, pp. 1–28.

Fabricius, O.

1780. Fauna Groenlandica . . . I. G. Rothe, Hafniae et Lipsiae, 452 pp., 1 pl.

Feruglio, E.

1936. Paleontolografia patagonica. Memorie dell'Istituto Geologicao Della R. Università Di Padova, pp. 195–381.

Férussac, A.D. De.

1822. Tableau systématiques des animaux mollusques. Paris and London, 111 pp.

Finlay, H.J.

1924. New shells from New Zealand Tertiary beds. Transactions of the New Zealand Institute, vol. 55, pp. 450–479.

1926. New shells from New Zealand Tertiary beds. Part II. Transactions of the New Zealand Institute, vol. 56, pp. 227–258.

1927. New specific names for Austral Mollusca. Transactions of the New Zealand Institute, vol. 57, pp. 488–533.

Finlay, H.J., and Marwick, J.

1937. The Wangaloan and associated fauna of the Kaitangata–Green Island Subdivision. New Zealand Geological Survey Paleontological Bulletin 15, 140 pp., 17 pls.

Fischer, P.

1880–1887. Manuel de conchyliologie et de paléontologie conchyliologique. F. Savy, Paris, 1369 pp.

Fleming, C.A.

1963. The nomenclature of biogeographic elements in the New Zealand biota. Transactions of the Royal Society of New Zealand, General Series, vol. 1, pp. 13–22.

1966. Marwick's Illustrations of New Zealand shells with a checklist of New Zealand Cenozoic Mollusca. New Zealand Department of Scientific and Industrial Research Bulletin 173, 456 pp., 145 pls.

1978. The bivalve mollusk genus *Limulata*: a list of described species and a review of living and fossil species in the southwest Pacific. Journal of the Royal Society of New Zealand, vol. 8, pp. 17–91.

Fleming, J.

1817. Conchology. *In* Edinburgh Encyclopedia by J. D. Brewster. Edition 7, vol. 12, pp. 55–107, pls. 203–206.

1822. The Philosophy of Zoology, or a General View of the Structure, Functions, and Classifications of Animals, vol. 1, 432 pp., vol. 2, 618 pp., London.

1828. A History of British Animals, exhibiting the descriptive characters and systematic arrangement etc. Bell and Bradfute, Edinburgh, 565 pp.

Frakes, L.A., Burger, D., Apthorpe, M., Wiseman, J., Dettmann, M., Alley, N., Flint, R., Gravestock, D., Ludbrook, N., Backhouse, J., Swarko, S., Schreibnerová, V., McKinn, A., Moore, P.S., Bolton, B.R., Douglas, J. G., Christ, R., Wade, M., R.E. Molnar, R.E., McGowran, B., Balme, J.G., and Day, R.A.

1987. Australian Cretaceous shorelines stage by stage. Paleogeography, Paleoclimatology, Paleoecology, vol. 59, pp. 31–48.

Freneix, S.

1958. Contribution à l'étude des Lamellibranches du Crétacé de Nouvelle-Calédonie. Science de la Terre, vol. 4 (1956), pp. 153–207.

1980. Bivalves Néocrétacés de Nouvelle Calédonie. Signification biogéographique, biostratigraphique, paléoécologique. Annales de Paléontology Invertébrés, vol. 66, pp. 67–134.

Fricker, C.A.

1999. Composition and paleobiology of a Late Cretaceous (Maastrichtian) gastropod faunule from the Lopez de Bertodano Formation of Seymour Island, Antarctic Peninsula. Unpublished Master of Science thesis, Purdue University, West Lafayette, Indiana, USA, 280 pp., 7 pls.

Gabb, W.M.

1860. Descriptions of some new species of Cretaceous fossils from South America in the collection of the Academy. Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 4, pp. 197–198, pl. 3.

1869. Cretaceous and Tertiary Fossils. Geological Survey of California. Paleontology, vol. 2, 299 pp.

Gill, T.N.

1867. On the genus *Fulgur* and its allies. American Journal of Conchology, vol. 3, pp. 141–152.

Gliozzi, E., and Malatesta, A.

1985. I molluschi del Paleocene di Baixa Chinhauanine nel Bacino del Rio Massintonto (Maputo-Mozambico). Geologica Romana, vol. 22, pp. 85–145, 13 pls.

Gmelin, J.F.

1791. Caroli a Linné . . . Systema naturae per regna tria naturae . . . 13th Edition, Leipzig, vol. 1, no. 6, pp. 3021–3910.

Gray, J.E.

1824. Supplement to the Appendix. Parry's First Voyage, 1819–1820. London, 37 pp.

1840. Synopsis of the contents of the British Museum, 42nd edition. British Museum, London, 370 pp.

1847. A list of the genera of Recent Mollusca, their synonyms and types. Proceedings of the Zoological Society of London, vol. 15, pp. 129–219.

Gray, M.E.

1842–1857. Systematic arrangement of the figures. *In* Figures of Molluscous Animals, M. E. Gray, *ed.*, London, 5 vols.

Griffin, M., and Hünicken, M.A.

1994. Late Cretaceous–early Tertiary gastropods from southwestern Patagonia, Argentina. Journal of Paleontology, vol. 68, pp. 257–274.

Haller, B.

1892. Die Morphologie der Prosobranchier, gesammelt auf einer Erdumsegelung durch die Königl. Italienische Korvette "Vettor Pisani." Morphologie Jahrbuch, vol. 18, no. 3, pp. 451–543, pls. 13–19.

Hansen, T.A.

1988. Early Tertiary radiation of marine molluscs and the long-term effects of the Cretaceous-Tertiary extinction. Paleobiology, vol. 14, pp. 37–51.

Hansen, T.A., Upshaw, B., Kauffman, E.G., and Gose, W.

1993. Patterns of molluscan extinction and recovery across the Cretaceous-Tertiary boundary in east Texas; report on new outcrops. Cretaceous Research, vol. 14, pp. 685–706.

Harasewych, M.G., and Marshall, B.A.

1995. *Zygomelon zodion*, a new genus and species of bathyal volute from New Zealand. The Veliger, vol. 38, no. 2, pp. 145–151.

Harris, G.D.

1893. Republication of Conrad's Fossil Shells of the Tertiary Formations of North America. Washington, R. H. Darby, 121 pp., 20 pls.

Henderson, R.A., Crampton, J.S., Dettmann, M.E., Douglas, J.G., Haig, D., Shafik, S., Stilwell, J.D., and Thulborn, R.A.

2000. Biogeographic observations on the Cretaceous biota of Australasia. *In* A.J. Wright, J. A. Talent, G.C. Young, and J.R. Laurie, *eds.*, Palaeobiogeography of Australasian Faunas and Floras. Memoir of the Association of Australasian Palaeontologists, vol. 23, pp. 355–404.

Huber, B.

1988. Upper Campanian–Paleocene foraminifera from the James Ross Island region, Antarctic Peninsula. *In* R.M. Feldmann and M.O. Woodburne, *eds.*, Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America Memoir 169, pp. 163–252.

Huber, B., and Watkins, D.K.

1992. Biogeography of Campanian-Maastrichtian calcareous plankton in the region of the Southern Ocean: paleogeographic and paleoclimatic implications. *In* J.P. Kennett and D.A. Warnke, *eds.*, A Perspective on Global Change. American Geophysical Union Antarctic Research Series, vol. 56, pp. 31–60.

Hutton, F.W.

1873. Catalogue of the marine Mollusca of New Zealand, with diagnoses of the species. Wellington, Government Printer, of the Colonial Museum and Geological Survey Department, 116 pp., 1 pl.

1877. Report on the geology of the north-east portion of the South Island, from Cook Straits to the Rakaia. Reports of the Geological Explorations during 1873–4, Wellington, New Zealand, pp. 27–58.

Ihering, H. von

1903. Les mollusques des terrains crétaciques superieur de l'Argentine Orientale. Anales del Museo Nacional, Buenos Aires, ser. 3, vol. 2, pp. 193–229.

1904. Nuevos observaciones sobre moluscos cretáceos y terciarios de la Patagonia. Rev. Museo de la Plata, vol. 11, pp. 227–244.

1905–1907. Les mollusques fossiles du Tertiaire et du Crétacés superieur de l'Argentine. Anales del Museo Nacional, Buenos Aires, ser. 3, vol. 7, pp. 1–611, 18 pls. [Published in 39 parts, November 21, 1905–September 13, 1907: date of each part appears on bottom of first page of each part].

Iredale, T.

1913. A collation of the molluscan parts of the Synopsis of the Contents of the British Museum, 1838–1845. Proceedings of the Malacological Society of London, vol. 10, pp. 294–309.

1924. Mollusca from the continental shelf of Eastern Australia. Records of the Australian Museum, vol. 14, pp. 179–278, pls. 31–36.

Johnston, R.M.

1835. Description of *Natica helicoides*, a new British shell. History of the Berwickshire Naturalists' Club, vol. 1, p. 69 (only), pl. 1.

Jonkers, H.A.

1998a. The Cockburn Island Formation; Late Pliocene interglacial sedimentation in the James Ross Basin, northern Antarctic Peninsula. Newsletters on Stratigraphy, vol. 36, pp. 63–76.

1998b. Stratigraphy of Antarctic late Cenozoic pectinid-bearing deposits. Antarctic Science, vol. 10, no. 2, pp. 161–170.

1999. Aligned growth positions in Pliocene *Laternula elliptica* (King and Broderip) (Bivalvia: Anomalodesmata: Laternulidae). Antarctic Science, vol. 11, no. 4, pp. 463–464.

Kabat, A.R.

1991. The classification of the Naticidae (Mollusca: Gastropoda): review and analysis of the supraspecific taxa. Bulletin of the Museum of Comparative Zoology, vol. 152, pp. 417–449.

Kauffman, E.G.

1973. Cretaceous Bivalvia. *In* A. Hallam, *ed.*, Atlas of Paleobiogeography, Elsevier, pp. 353–383.

Kauffman, E.G., and P.J. Harries

1996. Importance of crisis progenitors in recovery from mass extinction. *In* M.B. Hart, *ed.*, Biotic Recovery from Mass Extinction events, Geological Society Special Publication, no. 102, pp. 15–39.

Keen, A.M.

1958. Sea Shells of Tropical West America. Marine Mollusks from Lower California to Columbia. Stanford University Press, California, 619 pp.

Kollmann, H.A., and Peel, J.S.

1983. Paleocene gastropods from Nûgssuaq, West Greenland. Grønland Geologiske Undersøgelse Bulletin, vol. 146, pp. 1–115.

Korobkov, I.A.

1954. Handbook and Methodological Guide to Tertiary Mollusca. Lamellibranchiata. Leningrad, 444 pp. [in Russian]

Lamarck, J.B. de.

1798. Tableau encyclopédique et méthodiquedes trois régnes de la nature. Vers, Coquilles, Mollusques, et Polypiers. Liste des objets. Paris, 16 pp., pls. 287–390 (to pls. 488, 1816).

1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction apropriée des caractères génériques, et l'establissement d'un grand nombre des genres nouveaux. Mémoire de la Société d'Histoire Naturelle de Paris, 1799, pp. 63–90.

1801. Système des Animaux sans Vertèbres, ou Tableau Général des Classes, des Orders et des Genres de ces Animaux. Paris, 432 pp.

1802–1806. Mémoires sur les fossiles des environmens de Paris. Annales du Muséum National d'Histoire Naturelle. Paris [see Wenz, 1944, p. 1555 for parts].

1809. Philosophie Zoologique. Paris, vol. 1, 422 pp., vol. 2, 473 pp.

1815–1822. Histoire Naturelle de Animaux sans Vertèbres. Paris, 7 vols. [see Wenz, 1944, pp. 1555–1556 for collation of parts].

Lawver, L.A., Gahagan, L.M. and Coffin, M.F.

1992. The development of paleoseaways around Antarctica. *In* J.P. Kennett and D.A. Warnke, *eds.*, The Antarctic Paleoenvironment: A Perspective on Global Change. American Geophysical Union Antarctic Research Series, vol. 56, pp. 7–30.

Lea, I.

1833. Contributions to Geology. Philadelphia, Carey, Lea and Blanchard, 227 pp., 6 pls.

Leach, W. E.

1819. Appendix II. Zoology Memoir. *In* C.J. Ross, *ed.*, A Voyage of Discovery in H.M.S. Isabella and Alexander [in 1818] for purposes of exploring Baffin's Bay and inquiring into the probability of a north-west Passage, 252 pp.

1847. *In* J.E. Gray, The classification of the British Mollusca by W. E. Leach, 1818. Annual Magazine of Natural History, vol. 20, pp. 267–273.

Lindberg, D.R.

1986. Name changes in the 'Acmaeidae.' The Veliger, vol. 29, pp. 142–148.

1988. The Patellogastropoda. Malacological Review, Supplement 4, pp. 35–63.

Lindberg, D.R., and Hickman, C.S.

1985. A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). Journal of Paleontology, vol. 60, pp. 661–668.

Link, H.F.

1806–1808. Beschreibung der Naturalien-Sammlung der Universität zu Rostock. Rostock, 160 pp. (1806), 38 pp. (1807), 38 pp. (1808).

Linnaeus, C. von (Linné, C.)

1758. Systema Naturae. Edition 10. Laurentii Salvii, Holmiae, 823 pp.

Long, D.C.

1981. Late Eocene and Early Oligocene Turridae (Gastropoda: Prosobranchiata) of the Brown's Creek and Glen Aire Clays, Victoria, Australia. Memoirs of the National Museum of Victoria, vol. 42, pp. 15–55.

Lovén, S.L.

1846. Index Molluscorum litora Scandinaviae occidentalia habitantium. Ofversigt af Finska vetenskaps-societatens förhandlingar. Helsingfors, Holmiae, 50 pp.

McArthur, J.M., Thirwall, M.F., Engkilde, M., Zinsmeister, W.J., and Howarth, R.J.

1998. Strontium isotope profiles across the K/T boundary sequences in Denmark and Antarctica. Earth and Planetary Science Letters, vol. 160, pp.179–192.

Macellari, C.E.

1984. Late Cretaceous stratigraphy, sedimentology, and macropaleontology of Seymour Island, Antarctic Peninsula. Unpublished Ph. D. dissertation, The Ohio State University, 599 pp.

1988. Stratigraphy, sedimentology, and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Island. *In* R.M. Feldmann and M.O. Woodburne, *eds.*, Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America, Memoir 169, pp. 25–53.

Macellari, C.E., and Zinsmeister, W.J.

1983. Sedimentology and macropaleontology of the Upper Cretaceous to Paleocene sequence of Seymour Island. Antarctic Journal of the United States of America, vol. 18, pp. 69–71.

Marincovich, L.

1977. Cenozoic Naticidae (Mollusca: Gastropoda) of the northwestern Pacific. Bulletins of American Paleontology, vol. 83, no. 294, pp. 165–494, pls. 17–42.

Marshall, P.

1916. Some new fossil gastropods. Transactions of the New Zealand Institute, vol. 48, pp. 100–119.

1917. The Wangaloa beds. Transactions of the New Zealand Institute, vol. 49, pp. 450–460.

Marwick, J.

1924. The Struthiolariidae. Transactions of the New Zealand Institute, vol. 55, pp. 161–190.

1927. The Veneridae of New Zealand. Transactions of the New Zealand Institute, vol. 57, pp. 567–635, 21 pls.

1931. The Tertiary Mollusca of the Gisborne District. New Zealand Geological Survey Paleontological Bulletin 13, 177 pp.

Maxwell, P.A.

1992. Eocene Mollusca from the vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: paleoecology and systematics. New Zealand Geological Survey Paleontological Bulletin 65, 280 pp., 30 pls.

Medina, F.A., and del Valle, R.A.

1985. Scaphopoda (Mollusca) from the Upper Cretaceous found at the James Ross Group of islands–Antarctica. Instituto Antartico Argentino Contribucion No. 314, 9 pp.

Meek, F.B.

1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri Country. U. S. Geological Survey of the Territories, Reports, vol. 9, pp. 1–629.

Meek, F.B., and Hayden, F.V.

1856. Descriptions of new fossil species of Mollusca collected by Dr. F. V. Hayden, in Nebraska Territory together with a complete catalogue of all the remains of invertebrate hitherto described and identified from the Cretaceous and Tertiary formations of that region. Proceedings of the National Academy of Sciences, Philadelphia, vol. 8, pp. 265–286.

Ménard de la Groye

1807. Annales du Muséum National d'Histoire Naturelle. Paris, p.135.

Milne-Edwards, H.

1848. Note sur la classification naturelle des mollusques gastéropodes. Annales des Sciences Naturelles Zoologiques, Series 3, pp. 102–112.

Montfort, D. de

1808–1810. Conchyliogie systématique, et classification méthodique des coquilles; affrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. I. Coquilles univalves, cloisonnées [1808, 409 pp.]. II. Coquilles univalves, non cloisonnées [1810, 676 pp.]. Paris, Chez F. Schoell, Libraire.

Mörch, O.A.L.

1857. Fortegnelse veor Gronlands Blöddyr. *In* H.J. Rink, *ed.*, Gronland geographisk og Statistik beskrevet,. 2 (Appendix), no. 4, pp. 75–100, Copenhagen. [As separate, "Prodromus Faunae Molluscorum Grönlandiae", pp. 3–28.

Moore, R.C., Ed.

1969. Treatise on Invertebrate Paleontology. Part 6. Volumes 1–2. Bivalvia. Geological Society of America and University of Kansas Press, Lawrence, 952 pp.

Neumayr, R.M.

1884. Zur morphologie des Bivalvenschlosses. Mathematischen und Naturforschungen Klasse der Kaiserlichen Akademie der Wissenschaften in Wien, Sitzungs Berichte, vol. 88, pp. 385–419.

Newell, N.D.

1965. Classification of the Bivalvia. American Museum Novitates, vol. 2206, pp. 1–25.

Nicol, D.

1965. A new Thyasira (Pelecypoda) from the Ross Sea, Antarctica. Nautilus, vol. 78, pp. 79–81.

1966. Descriptive ecology and geographic distribution of some Antarctic pelecypods. Bulletins of American Paleontology, vol. 51, no. 231, pp. 1–102.

Oleinik, A.E., and Zinsmeister, W.J.

1996. Paleocene diversification of bucciniform gastropods on Seymour Island, Antarctica. Journal of Paleontology, vol. 70, pp. 923–934.

Olivero, E.B., Medina, F.A., and Camacho, H.H.

1990. Nuevos hallazgos de moluscos con afinidades australes en la Formación Lefipán (Cretácico Superior, Chubut): significado paleogeográfico. Actas del 5° Congreso Argentino de Paleontogía y Bioestratigrafía, vol. 1, pp. 129–135.

Oppenheim, P.

1914. Die eocäne Invertebraten-Fauna des Kalksteins in Togo. Beiträge zur geologischen Erforschung der Deutschen Schutzgebiete, vol. 12, pp. 1–126, 5 pls.

Orbigny, A.D. d'

1842–1843. Paléontologie Française. Description zoologique et géologique de tous les Animaux Mollusques et Rayonnés fossiles de France. Terrains Crétacés. Pteropoda, Gasteropoda. II. Paris, Chez Victor Masson, 456 pp. (text volume, dated 1842), pls. 149–236 (Atlas volume, dated 1842–1843).

1843–1847. Paléontologie Française. Terrains crétacés. Mollusques et rayonnés fossiles. Lamellibranches, Tome Troisième. Victor Masson, Paris, 807 pp.

Ortmann, A.E.

1902. Tertiary macroinvertebrates, pp. 45–332, pls. 11–39. *In* W. B. Scott, *ed.*, Reports of the Princeton Expedition to Patagonia 1896–1899. Volume 4. Paleontology 1. Part 2. Princeton, New Jersey and E. Schweizerbart'sche Verlagshandlung, Stuttgart.

Palamarczuk, S., Ambosini, G., Villar, H., Medina, F., Martínez Macchiavello, and Rinaldi, C.

1984. Las formaciones Lopez de Bertodano y Sobral en la Isla Vicecomodoro Marambio, Antartida. Noveno Congreso Geologico Argentino, S. C. Bariloche, Actas, vol. 1, pp. 399–419.

Petersen, G.H., and Vedelsby, A.

2000. An illustrated catalogue of the Paleocene Bivalvia from Nuussuaq, Northwest Greenland: their paleoenvironments and the paleoclimate. Steenstrupia, vol. 25, no. 1, pp. 25–120.

Philippi, R.A.

1853. Handbuch der Conchyliologie und Malakozoologiae. Halle, 547 pp.

1887. Fósiles Terciarios y Cuartarios de Chile. F. A. Brockhaus, Leipzig, 256 pp., 58 pls.

Pilsbry, H.A., and Olsson, A.A.

1954. Systems of the Volutidae. Bulletins of American Paleontology, vol. 35, no. 152, pp. 275–307, pls. 25–28.

Powell, A.W.B.

1930. New species of New Zealand Mollusca from shallow-water dredgings. Transactions and Proceedings of the New Zealand Institute, vol. 60, pp. 532–543.

1966. The molluscan families Speightiidae and Turridae. An evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. Bulletin of the Auckland Institute and Museum, vol. 5, pp. 1–184.

1979. New Zealand Mollusca: Marine, Land and Freshwater Shells. Collins, Auckland-Sydney-London, 500 pp., 82 pls.

Powell, A.W.B., and Bartum, J.A.

1929. The Tertiary (Waitematan) molluscan fauna of Onero, Waiheke Island. Transactions of the Royal Society of New Zealand, vol. 60, pp. 395–447.

Quenstedt, W.

1930. Die Anpassung an die grabende Lebenweise in der Geschichte der Solenmyiden und Nuculaceen. Geologische und Paleontologische Abhandlungen (N. F.), vol. 18, pt. 1, pp. 1–119.

Rafinesque, C.S.

1815. Analyses de la nature ou tableau de l'universe et des corps organises. Palermo, 224 pp.

Rhodes, M.C., and Thayer, C.W.

1991. Mass extinctions: ecological selectivity and primary production. Geology, vol. 19, pp. 877–880.

Röding, P.F.

1798. Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Frid. Bolten, M. D., p. d., Pars Secunda. Johan Christi Trapii, Hamburg, 119 pp.

Rogers, W.B.

1839. Contributions to the Geology of the Tertiary formations of Virginia. Second Series. Geology of the Peninsula between the Potomac and Rappa-Hannock Rivers. Transactions of the American Philosophical Society, held at Philadelphia, for promoting useful knowledge, vol. 4, New Series, pp. 347–380, pl. 26–30.

Saul, L.R.

1988a. New Late Cretaceous and early Tertiary Tudiclidae and Perissitytidae (Gastropoda) from the Pacific Slope of North America. Contributions in Science, Los Angeles County Museum, vol. 400, pp. 1–25.

1988b. Latest Cretaceous and early Tertiary Tudiclidae and Melongenidae (Gastropoda) from the Pacific Slope of North America. Journal of Paleontology, vol. 62, pp. 880–889.

Schmidt, A.

1865 (1855?). Der Geschlechtsapparat der Styllommatophoren in taxonomischer Hinsicht gewürdigt. Abhandlungen des Naturrwissenschaftlichen Vereines für Sachsen und Thüringen in Halle, vol. 1, pp. 1–52.

Schumacher, C.F.

1817. Essai d'un nouveau système des habitations des vers testacés. Copenhagen, 287 pp., 22 pls.

Sharman, G., and Newton, E.T.

1897. Notes on some additional fossils collected at Seymour Island, Graham's Land, by Dr. Donald and Captain Larsen. Proceedings of the Royal Society of Edinburgh, vol. 22, pp. 58–61.

Sheehan, P.M., Coorough, P.J., and Fastovsky, D.E.

1996. Biotic selectivity during the K-T and Late Ordovician extinction events. *In* G. Ryder *et al., eds.*, The Cretaceous-Tertiary boundary and other catastrophes in Earth History, Geological Society of America Special Paper 307, pp. 477–489.

Singleton, F.A.

1943. An Eocene molluscan fauna from Victoria. Proceedings of the Royal Society of Victoria, vol. 55, pp. 267–278, pls. 12–13.

Smith, E.A.

1907. Gastropoda. National Antarctic Expedition, 1901–1904, Natural History, vol. 2, pp. 1–12.

Sohl, N.F.

1964. Neogastropoda, Opisthobranchia, and Basammotophora from the Ripley, Owl Creek, and Prairie Bluff formations. United States Geological Survey Professional Paper 331-B, pp. 153–344, pls. 19–52.

1967. Upper Cretaceous gastropods from the Pierre Shale at Red Bird, Wyoming. United States Geological Survey Professional Paper 393-B, 46 pp., pls. 1–11.

Solander, D.C.

1766. *In* G. Brander, Fossilia Hantoniensia, collecta et in Musaeo Britannico deposita. London.

Sowerby, J. de C.

1812–1846. The Mineral Conchology of Great Britain: or coloured figures and descriptions of those remains of testaceous animals or shells which have been preserved at various times and depths in the earth. London, 7 vols.

1837. Mineral-Conchologie Grossbrittaniens, von James Sowerby; deutsche Bearbeitung, herausgegeben von Hercules Nicolet, durchgesehen von Dr. Agassiz. Neuchâtel, H. Nicolet, 52 pp., 21 pls. [reprinted 1839, along with remaining parts].

Spengel, J.W.

1881. Die Geruchsorgane und das Nervensystem der Mollusken. Zeitschrift für wissenschaftliche Zoologie, vol. 35, pp. 333–383.

Stanton, T.W.

1893. The Colorado Formation and its invertebrate fauna. Bulletin of the United States Geological Survey, no. 106, 288 pp., 45 pls.

1896. The faunal relations of the Eocene and Upper Cretaceous on the Pacific Coast. United States Geological Survey, 17th Annual Report Part 1, pp. 1011–1060.

1901. The marine Cretaceous invertebrates. *In* W.B. Scott, *ed.*, Reports of the Princeton University Expedition to Patagonia 1896–1899, vol. 4, Paleontology I, Part I, pp. 1–43, 10 pls.

1920. The fauna of the Cannonball Marine Member of the Lance Formation. United States Geological Survey Professional Paper 128-A, 66 pp., 10 pls.

Steinmann, G., and Wilckens, O.
1908. Kreide und Tertiärfossilien aus den Magellansländern, gesammelt von der schwedischen Expedition 1895–1897. Arkiv för Zoologi, vol. 4, pp. 1–119.

Stewart, R.B.
1930. Gabb's California Cretaceous and Tertiary type Lamellibranchs. Academy of the Natural Sciences of Philadelphia Special Publications, vol. 3, pp. 1–314, 17 pls.

Stilwell, J.D.
1991. Late Campanian to Eocene Mollusca of New Zealand: changes in composition as a consequence of the break-up of Gondwana. Eighth International Symposium on Gondwana, 24–28 June, 1991, Hobart, Tasmania. Abstract. Published on behalf of the Subcommission on Gondwana Stratigraphy (IUGS), C/-Gondwana 8, pp. 78–79.
1993. New Early Paleocene Mollusca from the Wangaloa Formation of South Island, New Zealand. Journal of Paleontology, vol. 67, pp. 360–369.
1994. Latest Cretaceous to earliest Paleogene molluscan faunas of New Zealand: changes in composition as a consequence of the break-up of Gondwana and extinction. Unpublished Ph. D. dissertation, The University of Otago, Dunedin, New Zealand, 1630 pp., 84 pls.
1997. Tectonic and palaeobiogeographic significance of the Chatham Islands, South Pacific, Late Cretaceous fauna. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 136, pp. 97–119.
1998. Late Cretaceous Mollusca from the Chatham Islands, New Zealand. Alcheringa, vol. 22, pp. 29–85.
2000. Eocene Mollusca (Bivalvia, Gastropoda and Scaphopoda) from McMurdo Sound: systematics and paleoecologic significance. *In* J.D. Stilwell and R.M. Feldmann, *eds.*, Paleobiology and Paleoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica, American Geophysical Union Antarctic Research Series volume 76, pp. 261–320.
2002. Early evolutionary history of *Monalaria* (Mollusca: Gastropoda: Struthiolariidae) from the Palaeogene of New Zealand. Alcheringa, vol. 25, pp. 395–405.
2003a. Patterns of biodiversity and faunal rebound following the K-T boundary extinction event in Austral Palaeocene molluscan faunas. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 195, pp. 319–356.
2003b. Macropaleontology of the *Trochocyathus-trematotrochus* band (Paleocene/Eocene boundary), Dillwyn Formation, Otway Basin, Victoria. Alcheringa, vol. 27, pp. 245–275.

Stilwell, J.D., and A. Gaździcki
1998. A new limid bivalve from the La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula. Acta Geologica Polonica, vol. 48, pp. 149–155.

Stilwell, J.D., and Grebneff, A.
1996. Records of Nautiloidea (Mollusca: Cephalopoda) across the Cretaceous-Tertiary boundary in Otago and Chatham Islands, New Zealand. New Zealand Journal of Geology and Geophysics, vol. 39, pp. 83–91.

Stilwell, J.D., and Henderson, R.A.
2002. Description and paleobiogeographic significance of a rare Cenomanian molluscan faunule from Bathurst Island, Northern Australia. Journal of Paleontology, vol. 76, pp. 447–471.

Stilwell, J.D., and Zinsmeister, W.J.
1987a. Late Cretaceous fossils from Cockburn Island collected during the 1986–1987 expedition to the Antarctic Peninsula. Antarctic Journal of the United States of America, vol. 22, no. 5, pp. 5–6.
1987b. Late Cretaceous fossils from Ula Point, James Ross Island, collected during the 1986–87 expedition to the Antarctic Peninsula. Antarctic Journal of the United States of America, vol. 22, no. 5, pp. 8–9.
1987c. Late Cretaceous faunal assemblage of Humps Island collected during the 1986–87 expedition to the Antarctic Peninsula. Antarctic Journal of the United States of America, vol. 22, no. 5, pp. 9–10.
1992. Molluscan systematics and biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. American Geophysical Union Antarctic Research Series vol. 55, 192 pp., 25 pls.
2000. Paleobiogeographic synthesis of Eocene fauna and flora, McMurdo Sound. *In* J.D. Stilwell and R.M Feldmann, *eds.*, Paleobiology and Paleoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica. American Geophysical Union Antarctic Research Series vol. 76, pp. 365–372.

Stoliczka, F.
1870–1871. Cretaceous fauna of Southern India. The Pelecypoda, with a review of all known genera of this class, fossil and Recent. Memoirs of the Geological Survey of India, Palaeontologia Indica, 6th series, 535 pp.

Suter, H.
1913–1915. Manual of the New Zealand Mollusca. With an Atlas of Quarto Plates. Wellington, Government Printer, 1120 pp., Atlas of 72 pls. (dated 1915).

Swainson, W.
1820–1833. Zoological Illustrations, or original figures and descriptions of new, rare, or otherwise interesting animals, selected chiefly principally from the Classes of Ornothology, Entomology, and Conchology. London [see Wenz, 1938–1944, p. 1586 for parts].
1840. A Treatise on Malacology; or the natural classification of shells and shell-fish. London, Lardiner's Cabinet Cyclopedia, 419 pp.

Tate, R.
1889. The gastropods of the older Tertiary of Australia. Transactions of the Royal Society of South Australia, vol. 11, pp. 116–174.

Tenison-Woods, J.E.
1880. On some Tertiary fossils. Proceedings of the Linnean Society of New South Wales, vol. 4, no. 1, pp. 1–26, pls. 1–4.

Thiele, J.
1912. Die antarktischen Schnecken und Muscheln. Deutsche Südpolar-Expedition 1901–1903, vol. 13, pp. 183–285.
1925–1956. Mollusca = Weichtiere. Handbuch der Zoologie, gegründet W. Kükenthal, vol. 5, pp. 15–258. Berlin, Leipzig.

Thomson, M.R.A.
1971. Gastropoda from the Lower Cretaceous sediments of southeastern Alexander Island. British Antarctic Survey Bulletin, no. 25, pp.45–58.

Toulmin, L.D.
1977. Stratigraphic distribution of Paleocene and Eocene fossils in the Eastern Gulf Region. Geological Survey of Alabama Monograph, vol. 13, 602 pp., 72 pls.

Tracey, S., Todd, J.A., and Erwin, D.H.
1993. Mollusca: Gastropoda. *In* M.J. Benton, *ed.*, The Fossil Record 2, Chapman and Hall, London, pp. 131–167.

Troschel, F.H.
1856–1893. Das Gebiß der Schnecken, zur Begründung einer natürlichen Classification untersucht von Dr. F. H. Troschel. Berlin, Nicolaische verlagsbuchhandlung, G. Parthey [4to. Viii, 252 pp., 20 pls. And 20 lines explanation

opposite. Published in 5 parts, lief. 1–4, each 2 th. 20 ngr., lief. 5, 3th; complete, 13 2/3th. Zweiten bandes erste [–] dritte lieferung, pp. 1–132, pls. 1–12, 1866–1869; lief. 1–3, each 3 th.] (see Gill, 1871, Smithsonian Miscellaneous Collections No. 227, p. 43).

Troschel, F., and Ruthe, J.F.

1848. A. F. A. Wiegmann's und J. F. Ruthe's Handbuch der Zoologie. Dritte Auflage. C. G. Lüderitz, Berlin, 652 pp.

Veevers, J.J., ed.

1984. Phanerozoic Earth History of Australia. Clarendon Press, Oxford, 418 pp.

Wade, B.

1926. The fauna of the Ripley Formation on Coon Creek, Tennessee. United States Geological Survey Professional Paper 137, 272 pp., 72 pls.

Warén, A.

1984. A generic revision of the family Eulimidae. Journal of Molluscan Studies, Supplement 13, 96 pp.

Warren, G., and Speden, I.G.

1978. The Piripauan and Haumurian stratotypes (Mata Series, Upper Cretaceous) and correlative sequences in the Haumuri Bluff district, South Marlborough. New Zealand Geological Survey Bulletin, vol. 92, 60 pp.

Wellman, H.W.

1959. Divisions of the New Zealand Cretaceous. Transactions of the Royal Society of New Zealand, vol. 87, nos. 1–2, pp. 99–163, pls. 10–12.

Wenz, W.

1938–1944. Gastropoda. *In* G. H. Schinderwolf, *ed.*, Handbuch der Paläozoologie, Bortraeger, Berlin, 1639 pp.

Whiteaves, J.F.

1879. On the fossils of the Cretaceous rocks of Vancouver and adjacent islands in the Strait of Georgia. Canada Geological Survey, Mesozoic Fossils, vol. 1, pp. 93–190, pls. 12–20.

Whitfield, R.P.

1880. Paleontology of the Black Hills of Dakota. *In* H. Newton and W.P. Jenney, Report on the Geology and Resources of the Black Hills of Dakota, pp. 325–468, pls. 1–16. Washington, United States Geological and Geographical Survey of the Rocky Mountain Region.

Wilckens, O.

1905–1907. Die Lamellibranchiaten, Gastropoden & c., der oberen Kreide Südpatagoniens. Berichte der Naturforschenden Gesellschaft zu Freiburg, vol. 15, pp. 97–166.

1910. Die anneliden, Bivalven und Gastropoden der Antarktischen Kreideformation. Wissentschaftliche Ergebnisse der Schwedische Südpolar Expedition 1901–1903, vol. 3, no. 12, pp. 1–42, pls. 1–4.

1911. Die Mollusken der antarktischen Tertiärformation. Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903, vol. 3, no. 13, pp. 1–62, 1 pl.

Willey, L.E.

1975. Upper Jurassic and Lower Cretaceous Pinnidae (Bivalvia) from southern Alexander Island. Bulletin of the British Antarctic Survey, nos. 41 and 42, pp. 121–131.

Woods, H.

1917. The Cretaceous fauna of north-eastern part of the South Island, New Zealand. New Zealand Geological Survey Paleontological Bulletin 4, 41 pp.

Woodward, S.P.

1851–1856. A Manual of the Mollusca: or rudimentary treatise of recent and fossils shells. London.

Zinsmeister, W.J.

1976. A new genus and species of the family Struthiolariidae, *Antarctodarwinella ellioti*, from Seymour Island, Antarctica. The Ohio Journal of Science, vol. 76, no. 3, pp. 111–114.

1979. Biogeographic significance of the Late Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. *In* J. Gray and A.J. Boucot, *eds.*, Historical Biogeography, Plate Tectonics, and the changing Environment. Oregon State University Press, pp. 349–355.

1982. Late Cretaceous-Early Tertiary molluscan biogeography of the southern circum-Pacific. Journal of Paleontology, vol. 56, pp. 84–102.

1983. New Late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology, vol. 57, pp. 1282–1303.

1984. Late Eocene bivalves (Mollusca) from the La Meseta Formation, collected during the 1974–75 joint Argentine-American expedition to Seymour Island, Antarctic Peninsula. Journal of Paleontology, vol. 58, pp. 1497–1527.

1987. Cretaceous paleogeography of Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 59, pp. 197–206.

1990. Note on the preservation of a limpet in living position from the Late Cretaceous, Seymour Island, Antarctica. Journal of Paleontology, vol. 64, pp. 477–478.

1996. Spatial biostratigraphy: empirical approach to approximating lineage terminations and evaluation of extinction patterns. Geological Society of America, Programs with Abstracts, vol. 27, no. 6, p. 249.

1998a. Discovery of fish mortality horizon at the K-T boundary on Seymour Island: re-evaluation of events at the end of the Cretaceous. Journal of Paleontology, vol. 72, pp. 556–571.

1998b. Event Plane Analysis: a technique for the spatial analysis of biostratigraphic data. Geological Society of America, Program with Abstracts, vol. 28, no. 6, p. 249.

2001. Projection Plane Analysis: a new biostratigraphic technique. Geology, vol. 109, pp. 213–229.

Zinsmeister, W.J., and Camacho, H.H.

1980. Late Eocene Struthiolariidae (Mollusca: Gastropoda) from Seymour Island, Antarctic Peninsula and their significance to the biogeography of early Tertiary shallow-water faunas of the Southern Hemisphere. Journal of Paleontology, vol. 54, pp. 1–14.

Zinsmeister, W.J., and Feldmann, R.M.

1984. Cenozoic high latitude heterochroneity of Southern Hemisphere marine faunas. Science, vol. 224, pp. 281–283.

Zinsmeister, W.J., and Griffin, M.

1995. Late Cretaceous and Tertiary aporrhaid gastropods from the southern rim of the Pacific Ocean. Journal of Paleontology, vol. 69, pp. 692–702.

Zinsmeister, W.J., and Macellari, C.E.

1983. Changes in the macrofossil faunas at the end of the Cretaceous on Seymour Island, Antarctic Peninsula. Antarctic Journal of the United States of America, vol. 18, no. 4, pp. 68–69.

1988. Bivalvia (Mollusca) from Seymour Island, Antarctic Peninsula. *In* R.M. Feldmann and M.O. Woodburne, *eds.*, Geology and Paleontology of Seymour Island, Antarctic Peninsula. Geological Society of America Memoir 169, pp. 253–284.

Zinsmeister, W.J., Woodburne, M.O., and Elliot, D.H.

1989. Latest Cretaceous/earliest Tertiary transition on Seymour Island, Antarctica. Journal of Paleontology, vol. 63, pp. 731–738.

PLATES

EXPLANATION OF PLATE 1

Figure Page

1–4, 8. *Nucula (Leionucula) suboblonga* (Wilckens, 1907) 16
1. Right valve, hypotype, USNM 404809, locality SSPE 9, Sobral Formation, ×1.
2. Left valve, hypotype, USNM 404810, locality SSPE 9, Sobral Formation, ×1.
3. Dorsal view of paired valves, hypotype, USNM 404813, locality SSPE 9, Sobral Formation, ×1.
4. Internal cast, hypotype, USNM 404811, locality SSPE 9, Sobral Formation, ×1.
8. Right hinge, hypotype, USNM 404812, locality SSPE 9, Sobral Formation, ×1.

6, 7. *Nucula (Leionucula) hunickeni* Zinsmeister and Macellari, 1988 17
6. Right valve, holotype, USNM 404814, locality 9, Sobral Formation, ×1.
7. dorsal view of paired valves, same specimen, ×1.

5, 9, 10. *Ledina*? species 18
5. SEM of microsculpture, hypotype, USNM 517003, locality 1519, ×8.
9. Left valve, hypotype, USNM 517003, locality 1519, ×2.4.
10. dorsal view of paired valves, same specimen, ×2.4

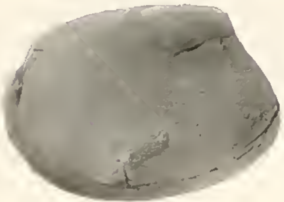
11, 12, 15. *Nuculana antarctirostrata* new species 17
11. Left valve, holotype, USNM 517001, locality 1589, Sobral Formation, ×1.8.
12. View of dorsal margin, same specimen, ×1.8.
15. Internal of right valve, paratype, USNM 517002, locality 1589, Sobral Formation, ×5.5.

13, 16. *Nucula* species 17
13. SEM of imperfect left valve, hypotype, USNM 517000, locality 1535, ×20.
16. SEM of commarginal riblets, same specimen, ×60.

19, 20, 23. *Australoneilo gracilis* (Wilckens, 1905) 19
19. Dorsal view, hypotype, USNM 404817, locality SSPE 9, Sobral Formation, ×1.
20. Right valve, same specimen, ×1.
23. Right valve and partial hinge, hypotype, USNM 517005, locality 1589, ×1.

18, 21, 22, 24. *Australoneilo casei* Zinsmeister and Macellari, 1988 19
18. Partial hinge, hypotype, USNM 517006, locality 746, Sobral Formation, ×2.
21. View of dorsal margin of paired with partial ligament preserved, hypotype, USNM 517007, locality 746, Sobral Formation, ×1.
22. Dorsal view, holotype, USNM 404818, locality 746, Sobral Formation, ×1.
24. Left hinge, same specimen, ×1.

14, 17. *Jupiteria*? species 18
14. SEM of left valve, hypotype, USNM 517004, locality 1519, ×7.
17. Same specimen, magnified anterodorsal margin showing fine, commarginal growth increments, ×∼15.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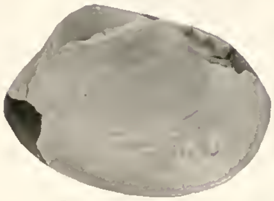
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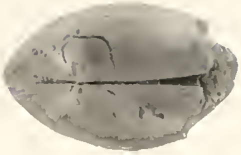
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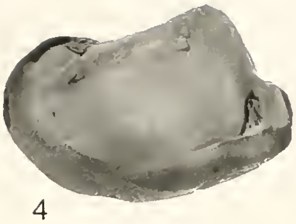
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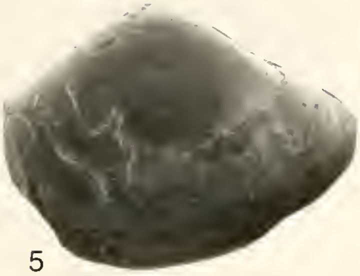
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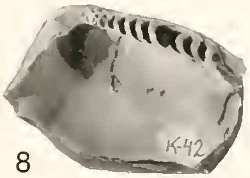

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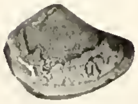
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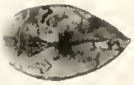
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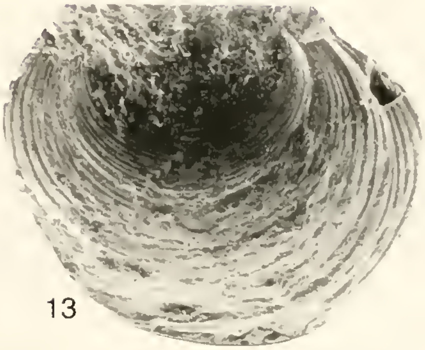
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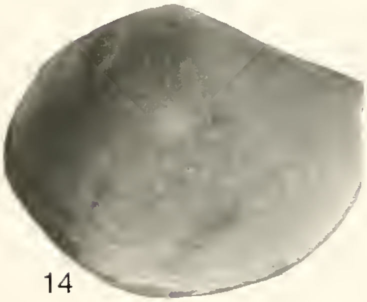
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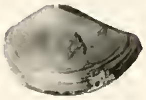
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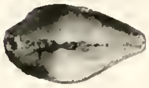
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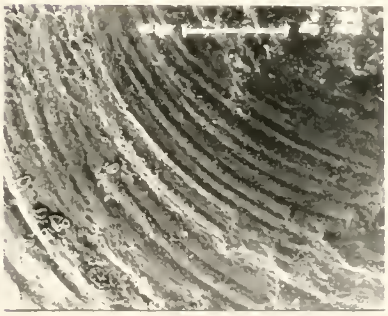
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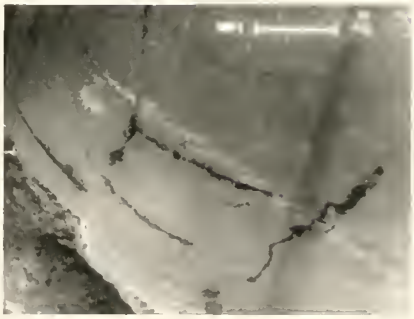
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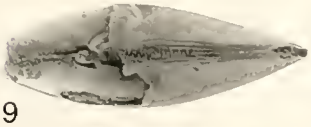
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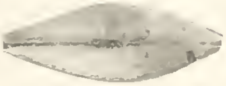
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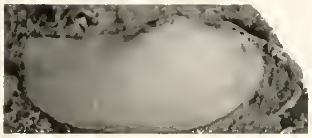
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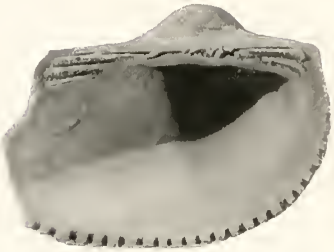

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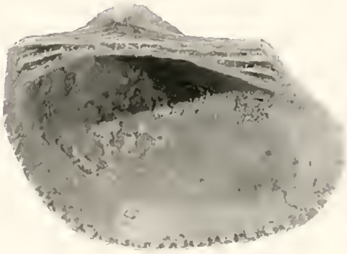

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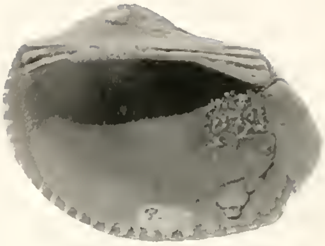

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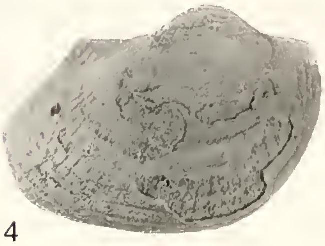

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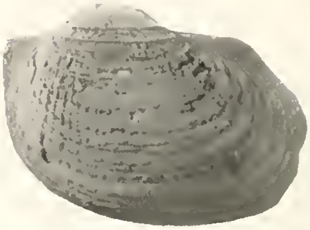

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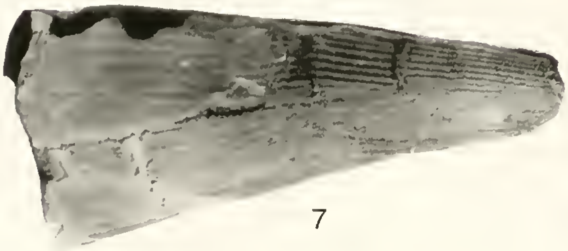

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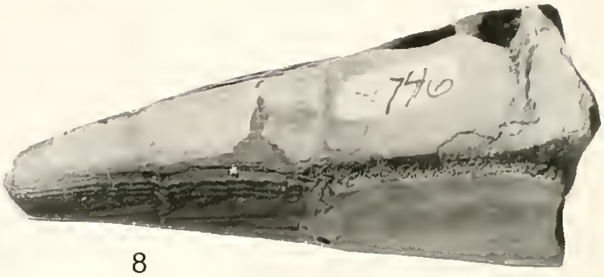

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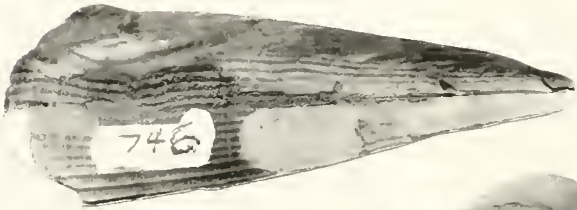

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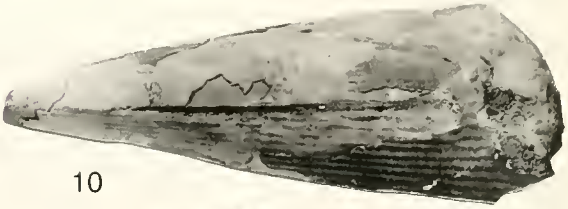

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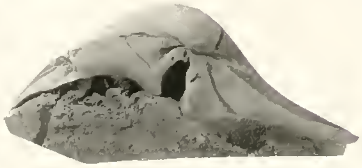

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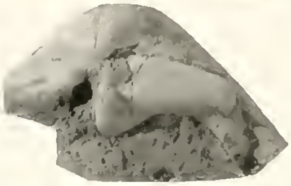

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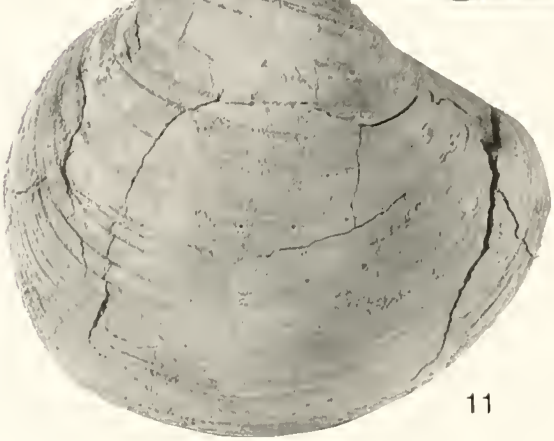

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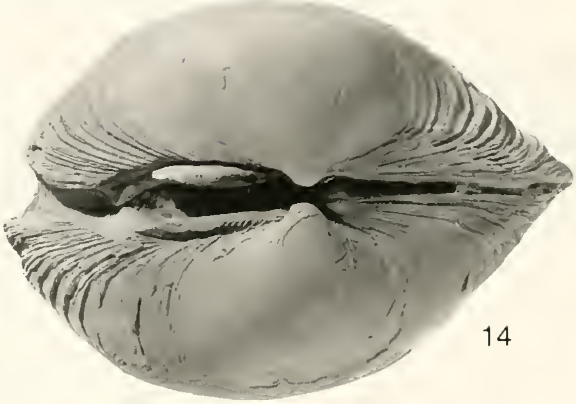

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EXPLANATION OF PLATE 2

Figure Page

1–6. *Cucullaea ellioti* Zinsmeister and Macellari, 1988 20
  1. Hinge view of left valve, paratype, USNM 404839, locality 9, Sobral Formation, ×1.
  2. Hinge view of right valve, holotype, USNM 404838, locality 9, Sobral Formation, ×1.
  3. Hinge view of right valve, paratype, USNM 404842, locality 9, Sobral Formation, ×1.
  4. Right valve, holotype, USNM 404838, locality 9, Sobral Formation, ×1.
  5. Left valve, paratype, USNM 404840, locality 9, Sobral Formation, ×1.
  6. Left valve, paratype, USNM 404841, locality 9, Sobral Formation, ×1.

7–10. *Pinna freneixae* Zinsmeister and Macellari, 1988 20
  7. External view of right valve, hypotype, USNM 517008, locality 746, Sobral Formation, ×1.
  8. Left valve, same specimen, ×1.
  9. External view of left valve, hypotype, USNM 517009, locality 746, Sobral Formation, ×1.
  10. External view of right valve, same specimen, ×1.

11–14. *Lahillia larseni* (Sharman and Newton, 1897) 23
  11. Right valve, hypotype, USNM 405803, locality 477, López de Bertodano Formation, ×1.
  12. Left hinge, hypotype, USNM 405801, locality 477, López de Bertodano Formation, ×1.
  13. Right hinge view, hypotype, USNM 405800, locality 477, López de Bertodano Formation, ×1.
  14. Dorsal view of paired valves, hypotype, USNM 405801, locality 477, López de Bertodano Formation, ×1.

EXPLANATION OF PLATE 3

Figure | Page

1, 2. *Lahillia huberi* Zinsmeister and Macellari, 1988 23
   1. Right hinge, Paratype, USNM 405819, locality 746, Sobral Formation, ×1.
   2. Right valve, holotype, USNM 405817, locality 746, Sobral Formation, ×1.

3–6. *Marwickia woodburnei* Zinsmeister and Macellari, 1988 24
   3. Left valve, holotype, USNM 405804, locality 9, Sobral Formation, ×1.
   4. Right valve, paratype, USNM 405805, locality 9, Sobral Formation, ×1.
   5. Right valve, paratype, USNM 405834, locality 9, Sobral Formation, ×1.
   6. Dorsal view of paired valves, same specimen, ×1.

7–13. *Saxolucina antarctipleura*, new species 21
   7. Left valve, paratype USNM 517012, locality 1131, ×2.

8, 9. Right valve and left valve, holotype, USNM 517010, locality 1131, ×2.
   10. Dorsal margin showing paired valves, holotype, USNM 517010, ×2.5.
   11. Left valve, paratype, USNM 517011, locality 1105, ×1.
   12. SEM of left valve, USNM 517022, locality 1131, ×9.
   13. Same specimen SEM of commarginal riblets, length = 5.0 mm, ×18.

14–17. *Thyasira austrosulca*, new species. 22
   14. Detail of posterior sulcus, paratype USNM 517015, locality 1519, ×~25.
   15. Left valve, paratype USNM 517015, locality 1519, ×6
   16. Right valve, holotype, USNM 517013, locality 1519, ×3.
   17. SEM of posterodorsal margin, holotype, USNM 517013, locality 1519, ×5.

18–19. *Periploma*? species 24
   18. Dorsal margin showing articulated valves, hypotype, USNM 517014, locality 1519, ×2.7.
   19. Left valve, same specimen, ×1.

20–22. *Panopea clausa* Wilckens, 1910 24
   20. Right valve, hypotype, USNM 405813, locality 459, ×1.
   21. Right valve, hypotype, USNM 405812, locality 459, ×1.
   22. Dorsal view of paired valves, hypotype USNM 405813, locality 459, ×1.


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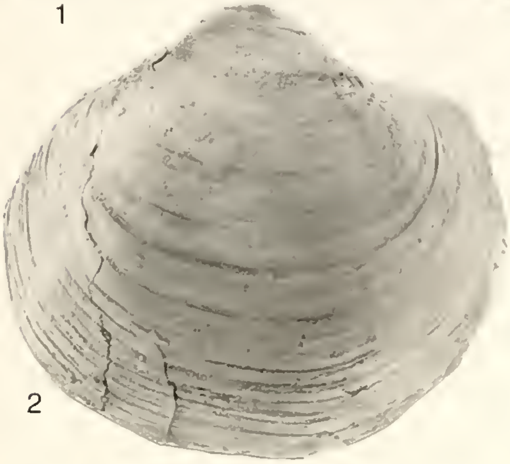
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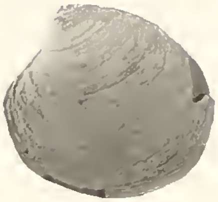
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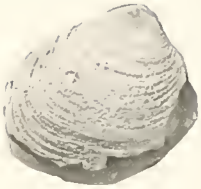
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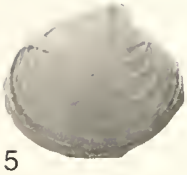
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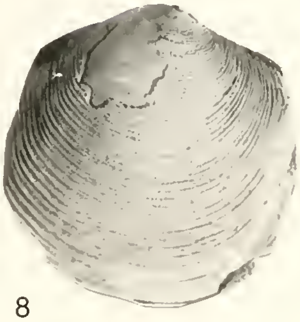
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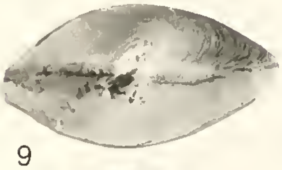
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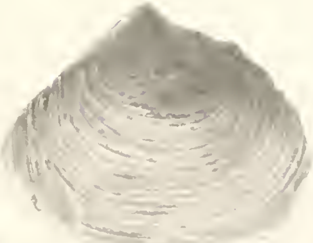
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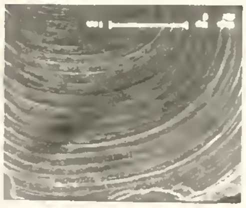
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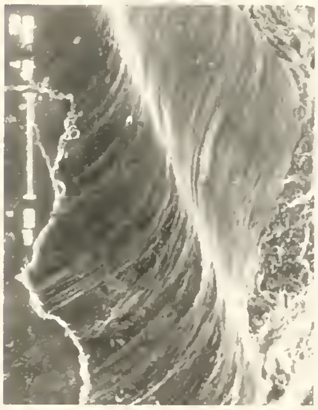
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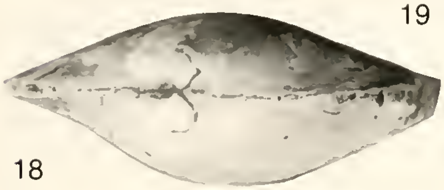
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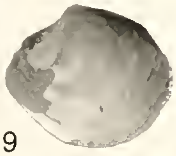
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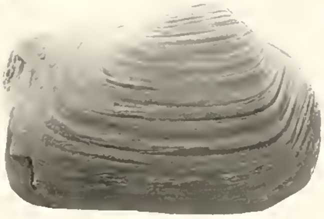
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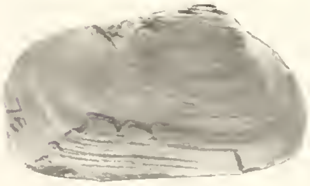
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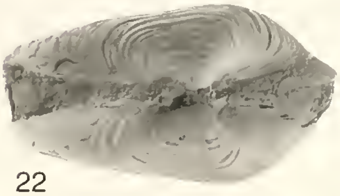
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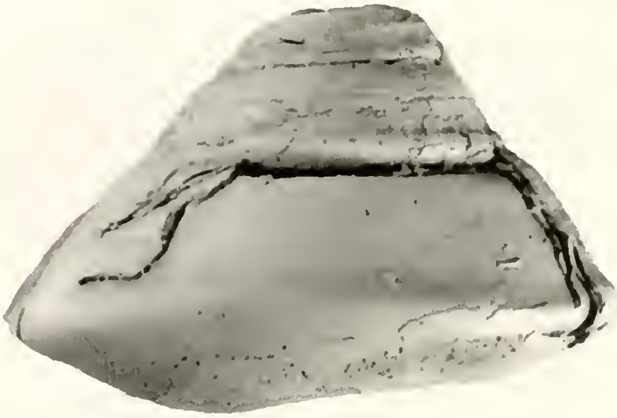

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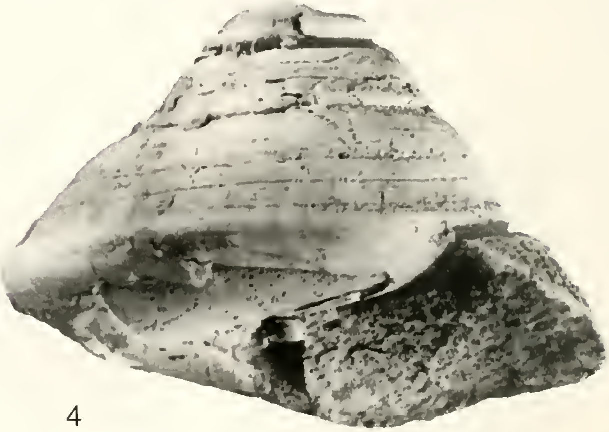

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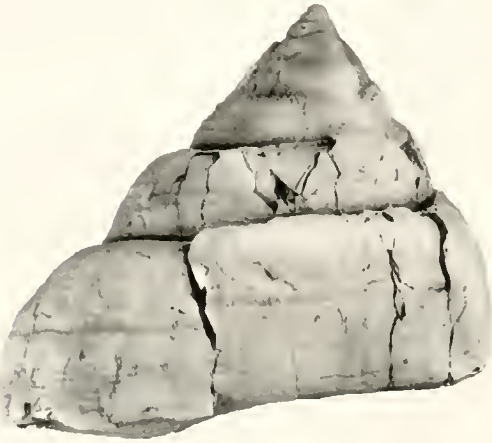

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EXPLANATION OF PLATE 4

Figure Page

1, 2. *Conotomaria* species A 25
  1. Abapertural view, USNM 511842, locality 1105, Sobral Formation, ×1.
  2. Apertural view, same specimen, ×1.

3, 4. *Conotomaria* species B 25
  3. Abapertural view, USNM 511843, locality 9, Sobral Formation, ×1.5
  4. Apertural view, same specimen, ×1.5.

5, 6. *Conotomaria* species C 26
  6. Abapertural view, USNM 511844, locality 746, Sobral Formation, ×1.
  7. Apertural view, same specimen, ×1.

EXPLANATION OF PLATE 5

Figure Page

1–4. *Acmaea submesidia*, new species 26
1. Internal apical view, holotype, USNM 511846, locality 1560, López de Bertodano Formation, ×2.
2. Internal apical view, paratype, USNM 511847, locality 1560, López de Bertodano Formation, ×4.5.
3. Lateral view, holotype, USNM 511846, locality 1560, López de Bertodano Formation, ×2.
4. View of holotype in matrix, ×1.

5. *Bittium (Bittium?) paleonotum*, new species 27
5. Abapertural view, holotype, USNM 511848, locality 1581, Sobral Formation, ×3.

6–10. *Mesalia virginiae*, new species 29
6. Apertural view, holotype, USNM 511855, locality 1715, López de Bertodano Formation, ×1,
7. Abapertural view, holotype, USNM 511855, locality 1715, López de Bertodano Formation, ×2.
8. Apertural view, paratype, USNM 511911, locality 1104, Sobral Formation, ×2.
9. Abapertual view, paratype, USNM 511912, locality 1591, López de Bertodano Formation, ×1.
10. Block of specimens, paratype, USNM 511913, locality 1548, Sobral Formation, ×1.

11–15. *Bittium (Zebittium) brooksi*, new species 27
11. Apertural view, paratype, USNM 511851, SEM, ×15.
12. Paratype, USNM 511910, length of block 68 mm, ×0.8.
13. SEM of microsculpture, holotype, USNM 511849, locality 1535, López de Bertodano Formation, ×15.
14. Apertural view, holotype, USNM 511849, locality 1535, López de Bertodano Formation, SEM, ×8,
15. Partial aperture and sectioned, paratype, USNM 511852, locality 1535, López de Bertodano Formation, SEM, ×10.

17. *Turritella (Haustator?) parisi*, new species 29
17. Apertural view, holotype, USNM 511854, locality 1716, López de Bertodano Formation, ×3.5.

18–20. *Struthiochenopus hurleyi* new species 30
18. Apertural view, holotype, USNM 405857, locality 783, ×1.
19. Apical view, same specimen, ×1.
20. Abapertural view, same specimen, ×1.


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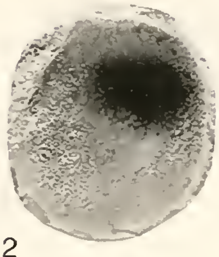
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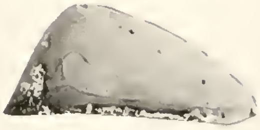
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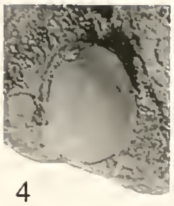
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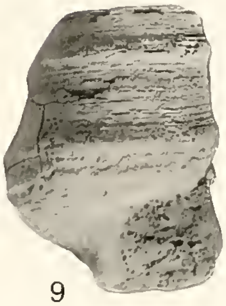
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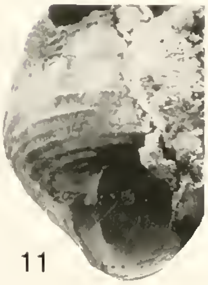
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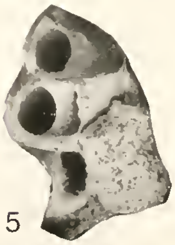
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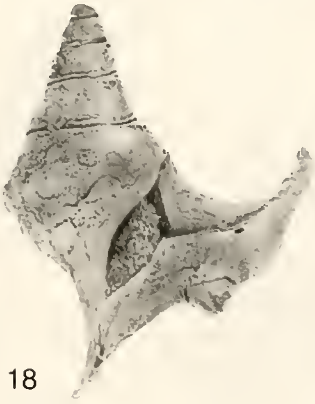
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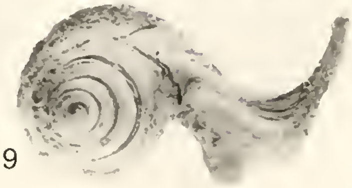
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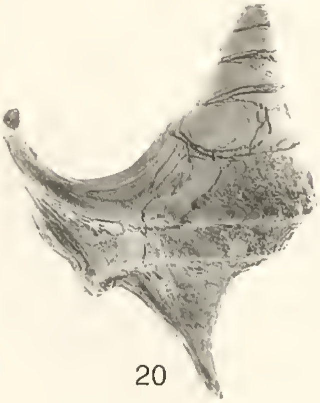
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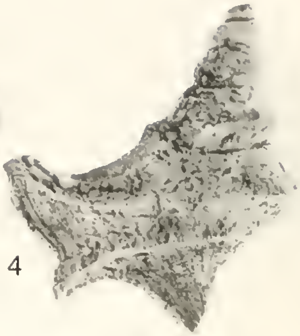
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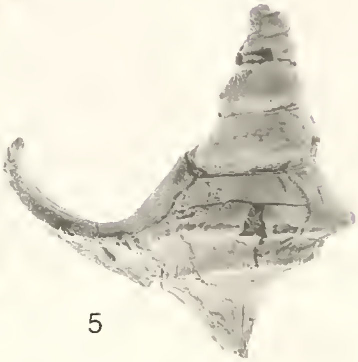
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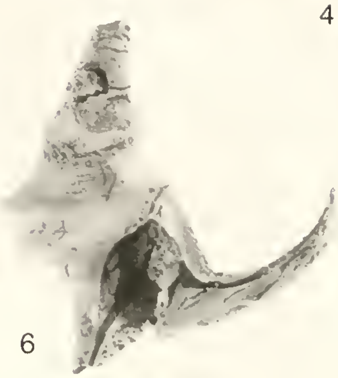
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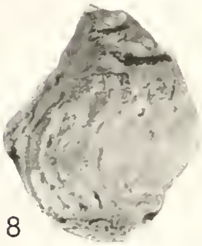
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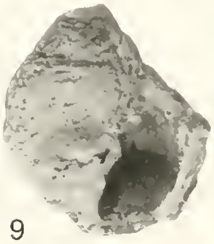
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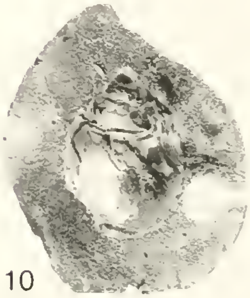
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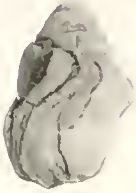
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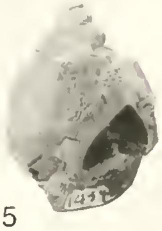
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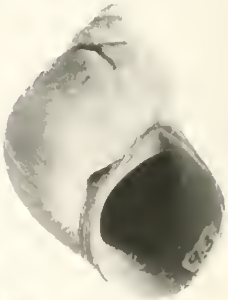
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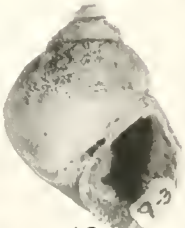
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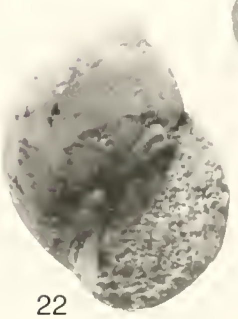
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EXPLANATION OF PLATE 6

Figure Page

1–6. *Struthiochenopus hurleyi*, new species 30

1, 3, 4. Apertural, apical, and abapertural views, respectively, paratype, PU783/2, locality 783, López de Bertodano Formation, ×1.

2, 5, 6. Apical, adapertural, and apertural views, respectively, paratype, USNM 405858, locality 783, López de Bertodano Formation, ×1.

7–15. *Antarctodarwinella austerocallosa*, new species 31

7, 8, 9. Lateral, abapertural, and apertural views, respectively, holotype, USNM 511856, locality 1434, Sobral Formation, ×1.

10. External mold in concretion, paratype, USNM 511914, locality 497, Sobral Formation, ×1.

11, 12. Abapertural and apertural views, respectively, paratype, USNM 511858, locality 1434, Sobral Formation, ×1.

13, 14, 15. Lateral view, apertural and abapertural views, respectively, paratype, USNM 511857, locality 1434, Sobral Formation, ×1.

16–19. *Vanikoropsis arktowskiana* (Wilckens, 1910) 33

16, 17. Abapertural and apertural views, respectively, hypotype, USNM 511860, locality 9, Sobral Formation, ×1.

18, 19. Abapertural and apertural views, respectively, hypotype, USNM 511861, locality 9, Sobral Formation, ×1.

20–22. *Amauropsis notoleptos*, new species 33

20, 21. SEM of abapertural and apertural views, respectively, paratype, USNM 511863, locality 1519, López de Bertodano Formation, ×7.5.

22. Apertural view, holotype, USNM 511862, locality 1531, López de Bertodano Formation, ×6.5.

EXPLANATION OF PLATE 7

Figure — Page

1–4. *Melanella seymourensis*, new species 36
1. SEM of apertural view, holotype, USNM 511868, locality 1535, López de Bertodano Formation, ×9.
2. SEM of apertural view, paratype, USNM 511869, locality 1519, López de Bertodano Formation, ×9.5.
3. SEM of apertural view, paratype, USNM 511870, locality 1519, López de Bertodano Formation, ×13.
4. SEM of spiral microsculpture and suture, paratype, USNM 511869, locality 1519, López de Bertodano Formation, ×~45.

5, 6. *Antarctiranella tessela*, new genus new species 35
5, 6. Abapertural and apertural views, respectively, holotype, USNM 511867, locality 1431, Sobral Formation, ×1.

7–10. *Euspira antarctidia*, new species 34
7. SEM of oblique apical view, paratype, USNM 511866, locality 1535, López de Bertodano Formation, ×10.
8, 10. SEM of abapertural and apertural views, respectively, paratype, USNM 511865, locality 1519, López de Bertodano Formation, × 4 and ×10, respectively.
9. Abapertural view, holotype, USNM 511864, locality 1519, López de Bertodano Formation, ×2.5.

9, 10. *Pyropsis? australis*, new species 37
9, 10. Apertural and abapertural views, respectively, holotype, USNM 511872, locality 1104, Sobral Formation, ×1.

13, 14. *Heteroterma*? new species 37
13. Adapertural view, USNM 511871, locality 1104, Sobral Formation, ×2.
14. Adapertural view, same specimen, slightly different view, ×2.

15–20. *Colus delrioae*, new species 38
15, 16. Abapertural and apertural views, paratype, USNM 511874, locality 1431, Sobral Formation, ×1.
17, 18. Apertural and abapertural views, respectively, paratype, USNM 511873, locality 1535, Sobral Formation, ×1.
19, 20. Abapertural and apertural views, respectively, holotype, UBA 16816, locality uncertain, Sobral Formation, ×1.


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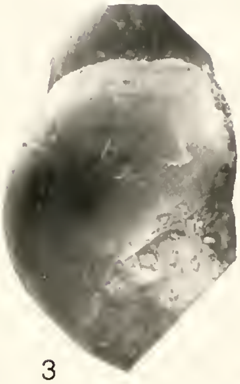
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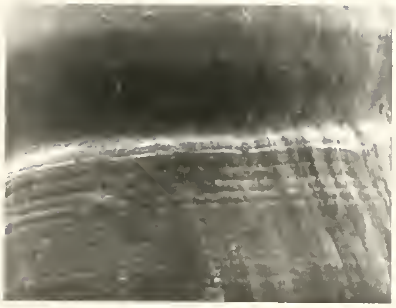
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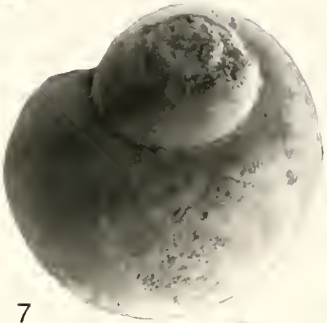
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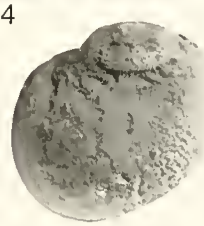
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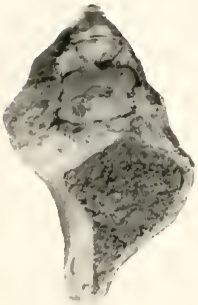
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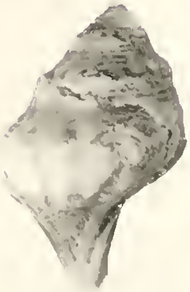
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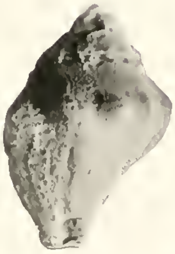
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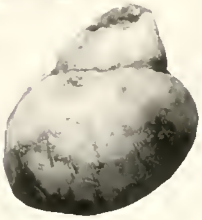
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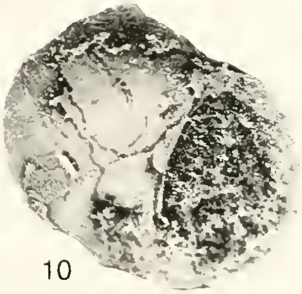
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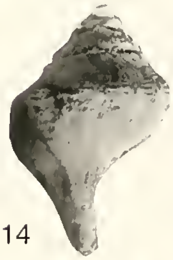
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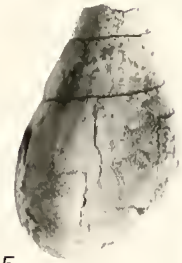
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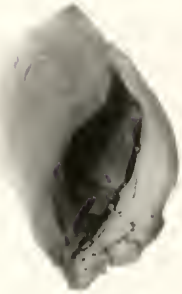
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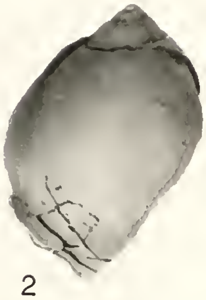
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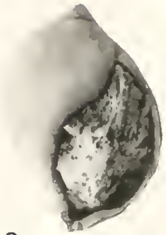
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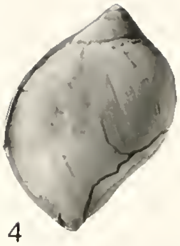
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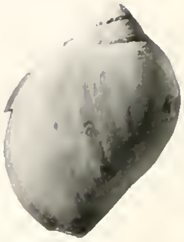
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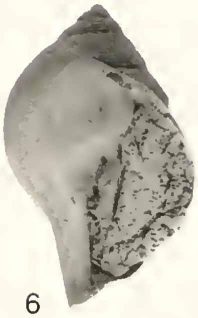
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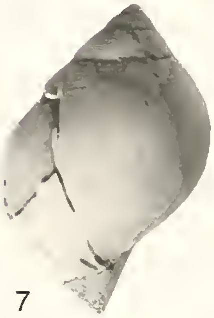
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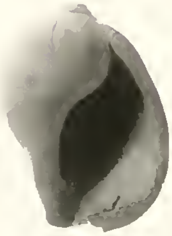
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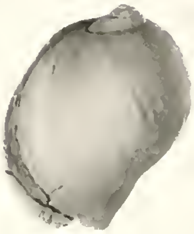
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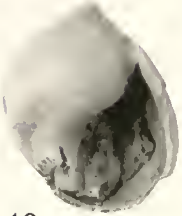
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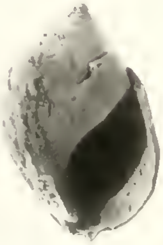
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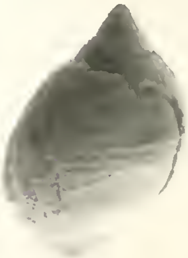
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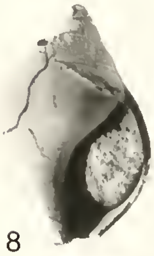
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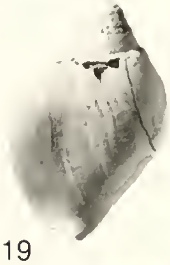
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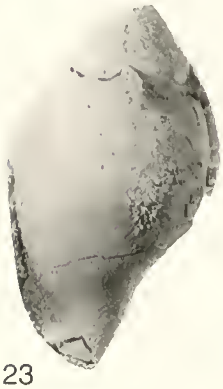
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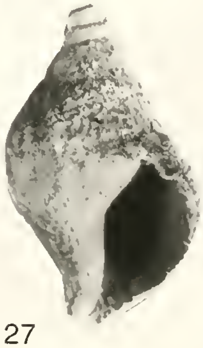
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EXPLANATION OF PLATE 8

Figure Page

1–7. *Seymourosphaera bulloides* Oleinik and Zinsmeister, 1996 43
  1, 2. Apertural and abapertural views, respectively, holotype, USNM 487298, locality 1432, Sobral Formation, ×1.
  3, 4. Apertural and abapertural views, respectively, paratype, USNM 487294, locality 1433, Sobral Formation, ×0.8.
  5. Abapertural view, paratype, USNM 487289, locality 9, Sobral Formation, ×1.
  6, 7. Apertural and abapertural views, respectively, paratype, USNM 487300, locality 9, Sobral Formation, ×1.5.

8, 9. *Seymourosphaera depressa* Oleinik and Zinsmeister, 1996 44
  8, 9. Apertural and abapertural views, respectively, holotype, USNM 487290, locality 1434, Sobral Formation, ×1.

10–13, 20. *Seymourosphaera subglobosa* Oleinik and Zinsmeister, 1996 44
  10, 11. Apertural and abapertural views, respectively, holotype, USNM 487292, locality 1136, Sobral Formation, ×0.8.
  12. Abapertural view, paratype, USNM 487293, locality 1133, Sobral Formation, ×0.6.
  13. Apertural view, paratype, USNM 487295, locality 1133, ×0.8.
  20. Abapertural view, paratype, USNM 487297, locality 1430, Sobral Formation, ×0.8.

14–19, 21, 22. *Seymourosphaera elevata* Oleinik and Zinsmeister, 1996 44
  14, 15. Apertural and abapertural views, respectively, holotype, USNM 487288, locality 1135, Sobral Formation, ×1.
  16, 17. Apertural and abapertural views, respectively, paratype, USNM 487291, locality 1188, López de Bertodano Formation, ×0.8.
  18, 19. Abapertural and apertural views, respectively, paratype, USNM 487291, locality 1430, Sobral Formation, ×0.6.
  21, 22. Abapertural and apertural views, respectively, paratype, USNM 487287, locality 1430, Sobral Formation, ×0.6.

23, 24. *Sycostoma pyrinota*, new species 42
  23, 24. Abapertural and apertural views, respectively, holotype, USNM 511887, locality 9, Sobral Formation, ×2.3.

25, 26. *Pseudofax*? *paucus*, new species 39
  25, 26. Abapertural and apertural views, respectively, holotype, USNM 511875, locality 1589, Sobral Formation, ×3.5 and ×3, respectively.

27, 28. *Strepsidura*? *polaris*, new species 44
  27, 28. Apertural and abapertural views, respectively, holotype, USNM 511888, locality 9, López de Bertodano Formation, ×2.5 and ×2.7, respectively.

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1–5, 8–10. *Serrifusus binodosum*, new species 42

1, 2. Abapertural and apertural views, respectively, holotype, USNM 511882, locality 746, Sobral Formation, ×1.

3. Apical view, paratype, USNM 511883, locality 746, Sobral Formation, ×1.

4, 5. Abapertural and apertural views, respectively, paratype, USNM 511885, locality 746, Sobral Formation, ×1.

8, 9. Abapertural view, illustrating repaired break made by probable lip peeler (decapod?), and apertural view, respectively, paratype, USNM 511884, locality 746, Sobral Formation, ×1.

10. Apertural view, paratype, USNM 511886, locality 746, Sobral Formation, ×1.

6, 7, 11–16. *Paleopsephaea? nodoprosta*, new species 45

6, 7. Abapertural and apertural views, respectively, paratype USNM 511891, locality 746, Sobral Formation, ×1.

11, 12. Abapertural and apertural views, respectively, holotype, USNM 511889, locality 746, Sobral Formation, ×1.

13, 14. Abapertural and apertural views, respectively, paratype, USNM 511890, locality 746, Sobral Formation, ×1.

15, 16. Abapertural and apertural views, respectively, paratype, USNM 511892, locality 746, Sobral Formation, ×1.

17–22. *Taioma sobrali*, new species 46

17, 18. Apertural and abapertural views, respectively, paratype, USNM 511894, locality 1104, Sobral Formation, ×1.

19, 20. Abapertural and apertural views, respectively, paratype, USNM 511895, locality 1105, Sobral Formation, ×1.

21, 22. Abapertural and apertural views, respectively, holotype, USNM 511893, locality 1431, Sobral Formation, ×2.

23–29. *Levifusus woolfei*, new species 40

23, 25. Apertural and adapertural respectively, paratype, USNM 511877, locality 9, Sobral Formation, ×0.9.

24, 26, 27. Apical, abapertural and apertural views, respectively, holotype, USNM 511876, locality 9, Sobral Formation, ×0.9.

28, 29. Abapertural and apertural views, respectively, paratype, USNM 511878, locality 9, Sobral Formation, ×0.8.

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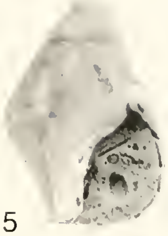
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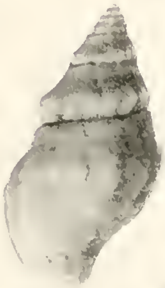
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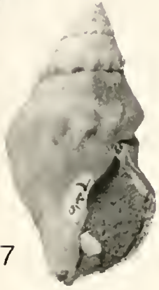
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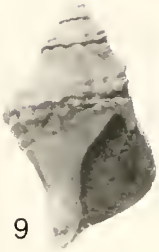
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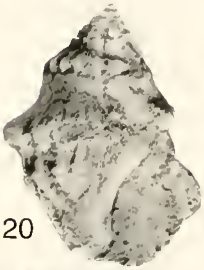
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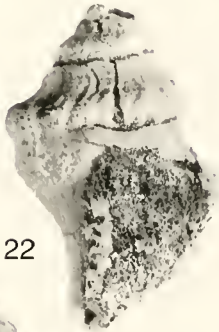
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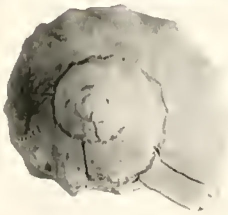
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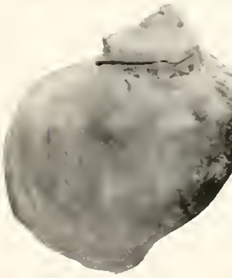
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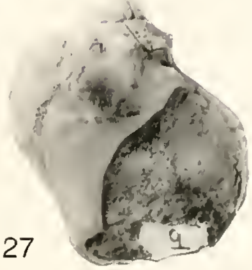
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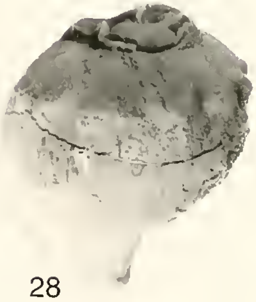
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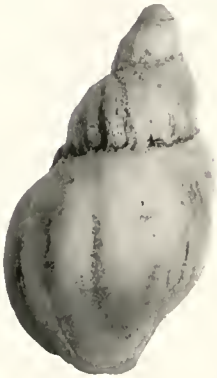
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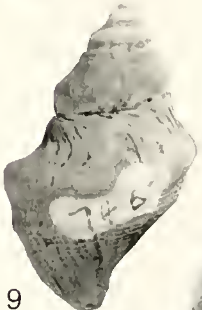
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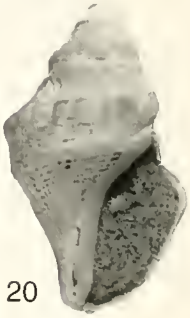
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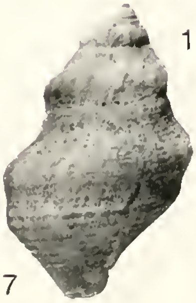
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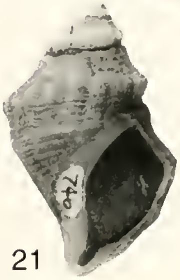
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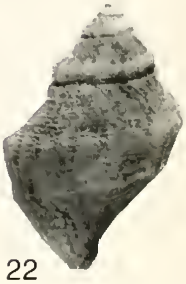
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PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

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ABSTRACT

Echinoderm faunas are described from 18 stratigraphic horizons of Viséan into Moscovian age from the Béchar Basin of northwestern Algeria. Two of these faunas are the first Bashkirian camerate-dominated faunas recognized when Pennsylvanian crinoid faunas worldwide are dominated by advanced cladids.

Additional results of this study include: 1. Emendation of the Actinocrinitidae, Sunwaptacrinidae, and Amphoracrinidae. 2. Upward extension of the ranges of *Ectocrinus*, *Aacocrinus*, *Sampsonocrinus*, and *Eucladocrinus* into the Bashkirian. 3. Downward extension of the ranges of *Hydriocrinus*, *Dicromyocrinus*, and *Mooreocrinus* into the Late Mississipppian (Serpukhovian). 4. First recognition of a partial cladid crown with three entoneural canals in the brachials. 5. First description and report of several genera from the northern border of Gondwana. 6. Discussion of biogeographic links between European/North American Early Carboniferous, as well as Japanese Morrowan and Atokan faunas, with the Tethyan Permian faunas.

New taxa proposed are the new family Ampullacrinidae; two new genera, *Hebohenocrinus* and *Ampullacrinus*; and 28 new species: *Ectocrinus mezereltensis*, *Ectocrinus redactus*, *Actinocrinites becharensis*, *Actinocrinites combinatus*, *Aacocrinus algeriaensis*, *Sampsonocrinus cheguigaensis*, *Blairocrinus grafensis*, *Pimlicocrinus octobrachiatus*, *Platycrinites reouienensis*, *Platycrinites aouidjaensis*, *Platycrinites djihaniensis*, *Platycrinites hamarensis*, *Pleurocrinus glomerosus*, *Pleurocrinus folliculus*, *Eucladocrinus? asymmetricus*, *Balearocrinus pareyni*, *Hebohenocrinus quasipatellus*, *Hydriocrinus? confusus*, *Ampullacrinus marieae*, *Ampullacrinus tritubulus*, *Dicromyocrinus vastus*, *Dicromyocrinus catillus*, *Dicromyocrinus? invaginatus*, *Mooreocrinus glomerosus*, *Ureocrinus commus*, *Paianocrinus? carinatus*, *Amphicrinus formosus*, and *Amphicrinus prinsi*.

INTRODUCTION

This study is based on 363 undescribed echinoderm specimens from three echinoderm collections from the Béchar Basin of northwestern Algeria made independently between 1952 and 1973. The largest and most diverse collection, approximately two-thirds of the specimens, was made by C. Pareyn (retired, formerly with the Université de Caen) during field studies between 1952 through 1954. This collection contains representatives from 16 of the 18 stratigraphic intervals from which echinoderms are herein reported (Appendix). The second collection is that made between 1964 and 1966 by M. Legrand-Blain, Université de Bordeaux III, and contains specimens that are mostly from the Bashkirian, especially from the upper and lower parts of the Hassi Kerma Formation. The third collection was made in 1973 by C. Winkler Prins, Nationaal Natuurhistorisch Museum, Leiden, and contains the only specimens from the Moscovian Oued Bel Groun Formation. Some specimens from all three collections were collected at the same localities, others were found in the same stratigraphic unit at different localities within a few kilometers proximity, and some specimens are exclusive. The collectors are identified for each of the taxa described under the *Material* sections in the systematics.

Pareyn (1961) provided lists, but no descriptions or illustrations, of Viséan to Bashkirian crinoids throughout the first volume of his descriptions of the Carboniferous massifs of northwestern Algeria and a stratigraphic list and brief analysis of some of the taxa identified by J. Wright and G. Ubaghs in the second volume. Breimer and Macurda (1972), as modified by Macurda (1983), described blastoids from the Viséan and Namurian of Algeria. Strimple and Pareyn (1982) described Namurian cibolocrinids from Algeria. Identified specimens in Pareyn (1961), Breimer and Macurda (1972), and Strimple and Pareyn (1982) are all from the Pareyn collections and except for the blastoids described by Breimer and Macurda (1972) are a part of the material studied herein. The Legrand-Blain and Winkler Prins collections have not been listed previously.

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Earlier descriptions and comparisons of Algerian echinoderms are few. Pomel (1885–1887) reported the first fossil echinoderms from Algeria, when he described some Cenozoic comatulids and ophiuroids from part of northern Africa which would later become Algeria. Carboniferous crinoid crowns, cups, and columnals were first reported from the Algerian part of Morocco by Termier and Termier (1950). Their descriptions or comparisons are minimal and illustrations are line sketches, which are mostly of insufficient quality for comparative studies. Many of the columnals are assigned generic identifications that are without comparative morphologic basis. Webster *et al.* (2001) noted a few mutual faunal occurrences between Iranian and North African Carboniferous faunas of Morocco and Algeria.

The Béchar Basin region (Text-fig. 1) was mapped by Deleau (1951) and later by Pareyn (1961). Mississippian and Pennsylvanian strata (Text-fig. 2) of the Béchar region are dominated by shallow-marine limestones, marls and claystones, with minor sandstones and siltstones (Pareyn, 1961; Legrand-Blain, 1967; Lemosquet and Pareyn *in* Weyant, 1985). Claystones and marls dominate the Tournaisian and Viséan parts of the section, including reefal limestones in the late Viséan and basal Serpukhovian. Marls and carbonates, interrupted and eroded by several fluvial channel systems which are filled by plant-bearing sandstone, increase upward and dominate the Serpukhovian into Moscovian part of the section. A few small reefs in a platform setting are also present (Lemosquet and Pareyn *in* Weyant, 1985). The stratigraphic terminology of Lemosquet and Pareyn *in* Weyant (1985) is followed herein for the Béchar Basin. Reference to earlier reports from North America and Europe cite the stratigraphic terms as used therein.

Pareyn (1961) reported several small reefs in the carbonates, especially in the lower part of the section, some with associated crinoids and other invertebrates. Among other invertebrates and floras, the stratigraphic section of the Béchar region has yielded numerous cephalopods, brachiopods, foraminifers, and conodonts, as summarized on individual range charts by several authors in Weyant (1985). The stratigraphic section is well dated on the basis of the diverse fauna, especially the ammonoids (Lemosquet and Manger *in* Weyant, 1985) and conodonts (Weyant *in* Weyant, 1985). Faunas reflect a moderate to shallow depth in a platform environment.

The purpose of this report is to provide a description of the Viséan to Moscovian crinoids, blastoids, and echinoids from the Béchar Basin area of western Algeria, relate them to correlative faunas worldwide, and establish a preliminary crinoidal biostratigraphic framework in the Béchar Basin to complement those completed for other phyla by various authors in Weyant (1985). Interested readers are referred to the numerous excellent air photos, cross-sections of local stratigraphic sections, photographs of exposures, and geologic maps of the Béchar Basin and adjacent area given in Pareyn (1961) and updated information, especially on the associated faunas in Weyant (1985).

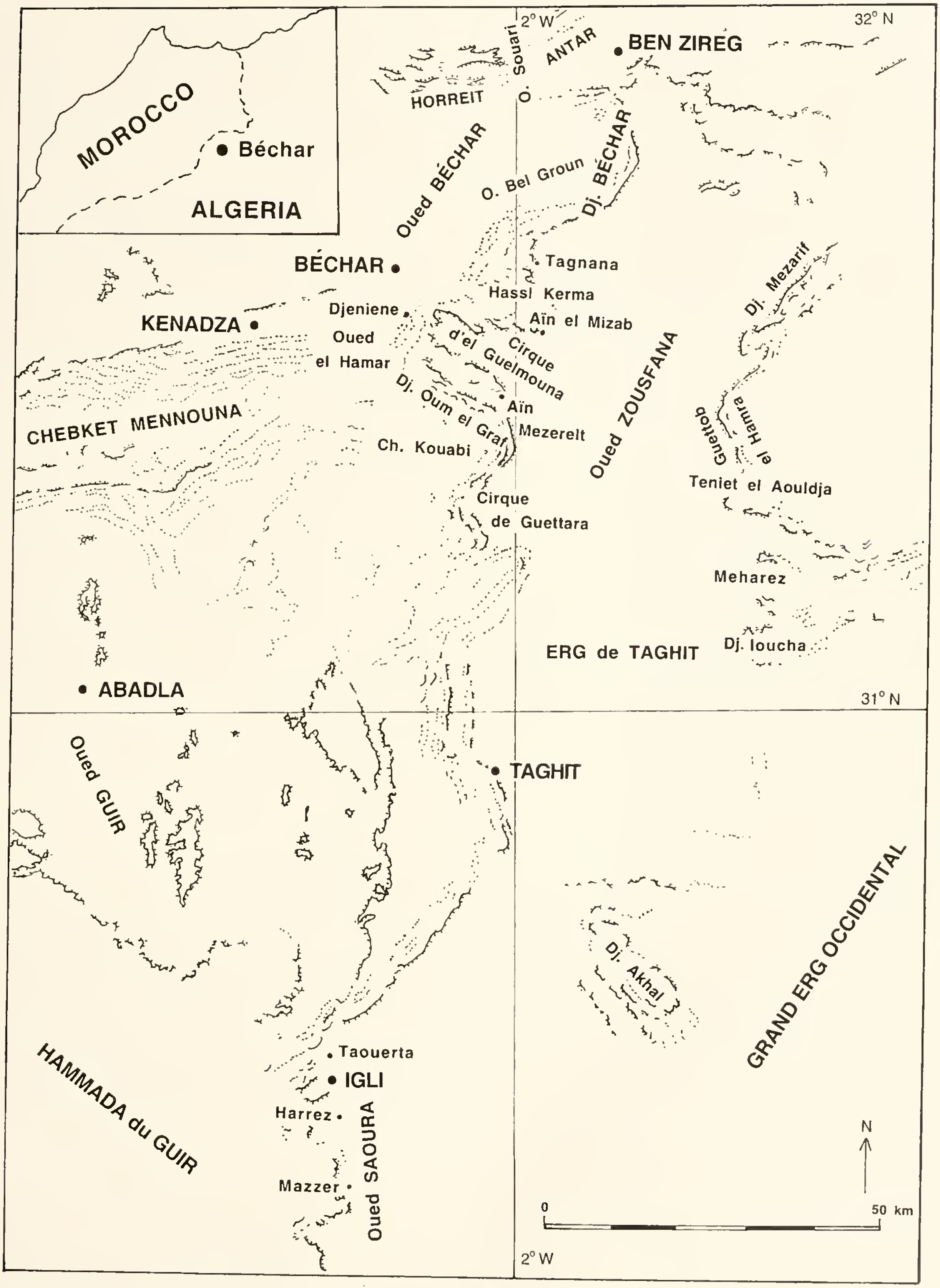
ACKNOWLEDGMENTS

The loan of specimens collected by C. Pareyn, M. Legrand-Blain, and C. Winkler Prins is kindly acknowledged. Specimens are housed in the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands. Washington State University granted professional leave to GDW when this study was initiated. Webster gratefully acknowledges the use of facilities and office space provided by the Department of Geology, Trinity College, Dublin, Ireland. Research support from the National Science Foundation and Kansas Geological Survey is gratefully recognized by CGM. The reviews of W. Ausich and T. Kammer are gratefully acknowledged.

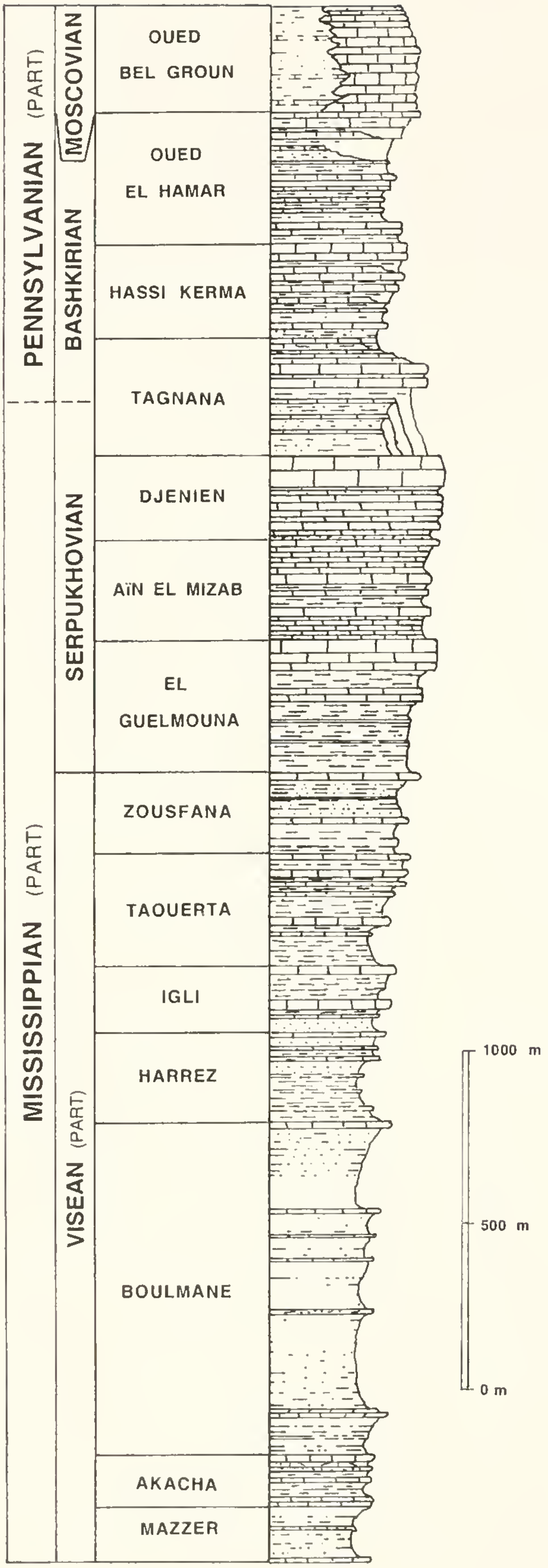
FAUNAL SIGNIFICANCE AND COMPARISONS

Echinoderms are recognized from 18 stratigraphic horizons, members, or formations of Viséan into Moscovian age in the Béchar Basin (Text-fig. 2). Collections from each of these horizons are referred to herein as a fauna. In some collections all specimens came from a single bed or surface, whereas others came from more than one bed or stratigraphic layer within a narrow stratigraphic interval. Locality information cited for each species is given as stated on original field or collection labels with the specimens from each of the three collections.

Most specimens are free of matrix, which precludes some interpretations of depositional and environmental relationships. The few crowns and partial crowns in the collections may reflect localized conditions of low current activity, rapid burial, or lack of scavenging prior to burial. Most specimens show varying degrees of wind abrasion and minor surface solution, reflecting the weathering conditions of the desert environs. Most specimens are unbroken cups and thecae, some of which are slightly distorted or crushed from compaction. The condition of all of these specimens is considered the result of taphonomic loss of arms and stem prior to burial and suggests some specimens may have been transported short distances or were exposed to currents and scavengers for short periods of time prior to burial. A few specimens have encrusting organisms on them, clearly reflecting exposure for some time prior to final burial. The lack of sets of arms, holdfasts,



Text-figure 1.—Map of the Béchar Basin showing named topographic features of echinoderm collecting localities (modified after Lemosquet and Pareyn *in* Weyant, 1985).



and abundant pluricolumnals in the collections might provide additional support for minor distances of transport or sorting with transport unless their absence reflects collection bias, which is a real possibility for columnals which are often considered to have little paleontological utility.

The extent of collection bias is uncertain. It is considered a strong factor concerning the lack of columnals, however, because it is uncommon to find cups and thecae without associated columnals or pluricolumnals. Until the Algerian area is more accessible for recollection and study, questions concerning collection bias with sedimentary and environmental relationships remain unanswered.

Each of the 18 faunas listed (See Appendix, p. 70) is followed by comments on the diversity, dominance, and comparisons to equivalent faunas. It should be noted that none of these faunas compares with the large diversity of some time-equivalent faunas from Scotland (Wright, 1950–1960) and the United States (Bassler and Moodey, 1943). Stratigraphic information is insufficient to determine the exact horizon from which a few of the specimens were collected. These specimens are indicated by an asterisk (*) and are included in all of the faunas in which they might have been found. Columnal taxa are preceded by the symbol o. Numbers in brackets following each taxon are the number of specimens. The faunas are discussed in order of oldest to youngest (Text-fig. 2).

Akacha Formation (Viséan)

Koryschisma saharae (Breimer and Macurda, 1972) [1]
Ectocrinus rouchi (Delpey, 1941) n. comb. [11]
Barycrinidae? indeterminate [5]
Balearocrinus pareyni n. sp. [1]
Cromyocrinid? indeterminate [1]
Cladid indeterminate 3 [1]
Sagenocrinid indeterminate 2 [1]

The fauna of the Akacha Formation is moderately diverse for its small size. It is dominated taxonomically by cladids (four species); however the most abundant taxon recovered is the camerate *Ectocrinus rouchi* n. comb. (11 specimens). Unfortunately, preservation of four specimens precludes generic identification; however, three of the four can be assigned to a family or order. Although specimens of *Koryschisma*

←

Text-figure 2.—Stratigraphic column of the crinoid-bearing parts of the Mississippian and Pennsylvanian strata of the Béchar Basin area. Standard lithologic symbols used for limestone, sandstone and shales. Section modified after Pareyn (1961) and Lemosquet and Pareyn *in* Weyant (1985). For member subdivisions of the Zousfana through Oued el Hamar formations see appendix.

saharae were not included in specimens studied, one specimen from the Akacha Formation was reported by Breimer and Macurda (1972) from the Pareyn collection. This is the oldest occurrence of *K. saharae*, also known from the Aïn Mezerelt and Aïn el Mizab members, ranging from the late Viséan into the early Serpukhovian. The genus is also known from the Kinderhookian (Tn2) of Montana in the western part of the United States (Sprinkle, 1973), from whence *K. saharae* was apparently derived.

Ectocrinus rouchi and *Balearocrinus pareyni* n. sp. are related to equivalent-age species in England and Spain, respectively. Barycrinids have been reported from the Devonian (Emsian) of Spain, the Mississippian (Osagean and Meramecian) of North America (Moore and Teichert, 1978), and the Tournaisian of England (Wright, 1942). Pentameric columnals assigned to *Barycrinus* sp. were reported from the Chadian of England by Donovan and Veltcamp (1990).

Cromyocrinids are most abundant in the Pennsylvanian, but Viséan taxa have been reported from the Mississippian of Russia, Spain, England (Moore and Teichert, 1978), and the United States (Kammer and Ausich, 1993). Sagenocrinids are known from Mississippian faunas of Europe and North America but usually in small numbers. Thus, the Akacha fauna has affinity with North American and European faunas, more with the latter. It differs from most middle Viséan faunas by the small number of camerate taxa but reflects the increasing dominance of the cladids over the camerates throughout the Mississippian.

Zousfana Formation

Aïn Guettara Member (Late Viséan)

Actinocrinitid indet. 2 [1]

The single specimen of an actinocrinitid in the Aïn Guettara Member may reflect an isolated preservation. The specimen is probably from the top of the Aïn Guettara Member from the limestone overlying the sandstones. Actinocrinitids were at their acme during the late Tournaisian and Viséan.

El Guelmouna Formation

Aïn Mezerelt Member (Serpukhovian)

Koryschisma saharae (Breimer and Macurda, 1972) [3]
Rhodocrinites sp. [1]
Ectocrinus mezereltensis n. sp. [9]
Ectocrinus redactus n. sp. [1]
Actinocrinites becharensis n. sp. [1]
Actinocrinites combinatus n. sp. [1]
Platycrinites reouienensis n. sp. [2]
Synbathocrinus sp. [1]
Zeacrinitid? indeterminate 2 [1]

Pareyn (1961) recognized a vast meadow of crinoids dominated by camerates in the Aïn Mezerelt Member in exposures in the El Guelmouna Basin. He reported (p. 72) five species of camerates, differing from our identifications. We assume that the taxa listed, but not illustrated, by Pareyn are included within the species we have identified from his collections based on the stratigraphic information. In addition, Pareyn (p. 89) listed six taxa from the El Guelmouna Formation at the cliffs of Aïn Tagnana. Stratigraphic information with two of the specimens Pareyn listed as *Synbathocrinus* nov. sp. and *Zeacrinites* nov. sp., here identified as *Synbathocrinus* sp. and Zeacrinitid? indeterminate, indicates they are from the Aïn Mezerelt Member, where we have included them.

The Aïn Mezerelt Member fauna has a strongly cosmopolitan composition. It contains four equatorial-belt cosmopolitan genera, which are considered by us to have had wide ecologic tolerance limits. *Actinocrinites*, *Platycrinites*, *Rhodocrinites*, and *Synbathocrinus* were cosmopolitan in the equatorial belt during the Tournaisian and Viséan. Camerates dominate the fauna of the Aïn Mezerelt Member. *Rhodocrinites* sp. probably was derived from Western Saharan Devonian or Moroccan Viséan species and is related to Scottish, Russian, Chinese, and United States Tournaisian and Viséan species. The two species of *Ectocrinus* are derived from *E. rouchi* and closely related to English and Irish species. The species of *Actinocrinites* and *Platycrinites* are related closely to English, Scottish, and North American species. Although zeacrinitids are known from the Viséan of England and Scotland (Bather, 1916), most are known from the United States where they reached their diversity acme during the Pennsylvanian.

El Guelmouna Member (Early Serpukhovian)

Pleurocrinus glomerosus n. sp. [8]
Cosmetocrinus? sp. [2]
Dicromyocrinus vastus n. sp. [19]
Ureocrinus commus n. sp. [1]

The El Guelmouna Member fauna is dominated by cladids. This may be a reflection of a high clay content in the living environment as the El Guelmouna Member consists of claystones in the lower half and dolomite in the upper half. Pareyn (1961, p. 89) listed two cladids, *Phanocrinus* nov. sp. and *Aphelecrinus* or *Fifeocrinus* sp., from the El Guelmouna Member. We identify these specimens as *Cosmetocrinus*? sp. and *Ureocrinus commus* n. sp., respectively. Pareyn (1961, p. 89) also listed two flexible crinoids for the El Guelmouna Member; however no flexibles were in his collections for our study from the El Guelmouna Member. The El Guelmouna Member contains the oldest known occurrence of *Dicromyocrinus*, extending the range downward from the Morrowan into the Serpukhovian.

Aïn El Mizab Formation

El Harrada Member (Early Serpukhovian)

Ectocrinus sp. [1]
Mooreocrinus glomerosus n. sp. [2]
Zeacrinitid indeterminate 1 [2]

With two cladids and one camerate, the El Harrada Member fauna is similar at the subclass level to the El Guelmouna Member fauna and is another low-diversity fauna. The El Harrada Member is oolitic in the middle and yields crinoid remains in the thinner bedded lower and upper parts (Pareyn, 1961). Pareyn (1961, p. 89) listed *Amphoracrinus* nov. sp. from the El Harrada Member from the cliffs of Aïn Tagnana. We identify the specimen as *Ectocrinus* sp. The El Harrada Member contains the oldest recognized occurrence of *Mooreocrinus*, extending the range downward from the Morrowan into the Serpukhovian.

Aïn El Mizab Member (Middle Serpukhovian)

Ampullacrinus tritubulus n. gen., n. sp. [1]
Palaechinus sp. [1]

The echinoderm fauna of the Aïn el Mizab Member is small. *Ampullacrinus tritubulus* also occurs in the upper part of the Djenien Formation. This is the lowest occurrence of *Ampullacrinus*.

Mouizeb El Atchane Member (Middle Serpukhovian)

Koryschisma saharae (Breimer and Macurda, 1972) [3]
Megaliocrinus? sp. [1]
Platycrinites aouidjaensis n. sp. [2]
Scytalocrinus sp. [2]
Dicromyocrinus vastus n. sp. [1]
Mooreocrinus glomerosus n. sp. [2]
Ampullacrinus marieae n. gen., n. sp. [4]

The Mouizeb el Atchane Member fauna is a mixed fauna of moderate diversity. Cladids taxonomically outnumber the camerates four to two. It contains the youngest occurrence of *Koryschisma saharae*. *Megaliocrinus* is known from this fauna and from some Spanish middle late Namurian faunas (reported as *Iberocrinus* by Sieverts-Doreck, 1951, and referred to *Megaliocrinus* by Strimple, 1976). The greater abundance of cladids again reflects their increasing diversity in the late Mississippian and a high clay content in the sediments. Pareyn (1961) reported crinoids occurring in the uppermost thicker bed of the Mouizeb el Atchane Member. Specifically, he (p. 76) reported three crinoid taxa. The camerate, listed as *Amphoracrinus* nov. sp. A, we identify as *Megaliocrinus*? sp. The cladids, listed as *Phanerocrinus* [*sic*] nov. sp. and Cf. *Fifeocrinus tielensis*, we identify respectively as *Scytalocrinus* sp. and *Ampullacrinus marieae* n. gen. n. sp.

Djenien Formation

Hid El Kef Member (Late Serpukhovian)

**Platycrinites aouidjaensis* n. sp. [1]

The faunas of the Hid el Kef Member, boundary beds of the Hid el Kef and Djenien members, and the undesignated part of the Djenien Member are perhaps isolated occurrences. Pareyn (1961) reported crinoids from the green shales of the Hid el Kef Member. The importance of these faunas is the occurrence of *Hydriocrinus*? *confusus* n. sp. in the boundary beds of the Hid El Kef and Djenien members and *Paianocrinus*? *carinatus* n. sp. in the Djenien Member (undesignated). Although the generic assignments are questioned, as explained in the systematics, these forms represent taxa not recognized in any of the other Algerian faunas. They provide significant paleobiogeographic information and provide new evolutionary lineage links.

Boundary Beds of Hid El Kef and Djenien Members (Late Serpukhovian)

Hydriocrinus? *confusus* n. sp. [1]
See comments under Hid el Kef Member above.

Djenien Member (Undesignated) (Late Serpukhovian)

**Paianocrinus*? carinatus n. sp. [1]
See comments under Hid el Kef Member above.

Upper Part of Djenien Member (Late Serpukhovian)

Actinocrinitid? indet. 5 [1]
Platycrinites djihaniensis n. sp. [2]
Platycrinites cf. *P. djihaniensis* n. sp. [4]
Platycrinites sp. 2 [3]
Ampullacrinus tritubulus n. gen., n. sp. [2]
**Paianocrinus*? *carinatus* n. sp [1]
Cibolocrinus africanus Strimple and Pareyn, 1982 [3]
Amphicrinus formosus n. sp. [2]

Pareyn (1961) reported crinoids occurring in thin dark detrital beds that are interbedded with massive white limestones. At the generic level, the fauna from the upper part of the Djenien Member contains two camerates, one cladid, and two flexibles. This is an unusual faunal assemblage in the late Serpukhovian, as most faunas of this age are dominated by cladids with minor numbers of camerates, and even fewer flexibles (Bassler and Moodey, 1943; Webster, unpublished compilations). Most late Serpukhovian diverse echinoderm faunas are known from North America such as the Glen Dean Formation (Bassler and Moodey, 1943), Pitkin Formation (Strimple, 1951a, 1978), Bangor Limestone and Monteagle Formation (Burdick and Strimple, 1983), and Sloans Valley Member of the Pennington Formation (Chestnut and Ettensohn, 1988), among others. The few late Serpukhovian crinoids reported from Russia and Europe are often single-taxon occurrences. Cromyocrinids are rare in North American faunas of late Serpukhovian age, whereas scytalocrinid genera generally dominate the cladid-dominated faunas. This upper part of the Djenien fauna is more like Meramecian faunas of North America, which have higher camerate diversity with cladids and rare, but fairly ubiquitous, flexibles.

Tagnana Formation
(Late Serpukhovian–Early Bashkirian)

Hebohenocrinus quasipatellus n. gen., n. sp. [1]
Dicromyocrinus vastus n. sp. [2]

One dendrocrinid and one cladid are insufficient to evaluate the Tagnana fauna with more than broad generalizations. *Hebohenocrinus quasipatellus* n. gen., n. sp. is an endemic taxon questionably assigned to the Mastigocrinidae. The continuation of the cromyocrinids in the fauna is a carryover from older faunas. The exact horizon from which the crinoids are derived is not specified, but they are from the interbedded shales and limestones of the upper half of the formation. The Serpukhovian–Bashkirian boundary occurs within the middle of the Tagana Formation. Therefore, the age of this fauna is earliest Bashkirian.

Hassi Kerma Formation

Lower Part of Hassi Kerma Formation
(Early Bashkirian)

Dicromyocrinus? sp. [7]
Cladid indeterminate 2 [3]
ø*Floricyclus* cf. *F. angustimargo* Moore and Jeffords, 1968 [1]
ø*Plummeranteris*? sp. [1]
Taxocrinid indeterminate [1]
Sagenocrinid indeterminate 1 [5]

The fauna from the lower part of the Hassi Kerma Formation is mostly disarticulated cup ossicles, columnals, and fragmentary cups. This fauna is distinctive in the absence of camerates and the near codominance of flexibles and cladids. The continuation of the cromyocrinids corresponds with their common occurrence in Pennsylvanian faunas in North America (Webster, 1981) and presence in 14 of the 18 faunas recognized herein. This collection and that from the upper part of the Hassi Kerma Formation are the only two containing abundant disarticulated ossicles, including columnals. It is not known if this is a result of taphonomy, collecting bias, or both.

Upper Part of Hassi Kerma Formation
(Early Bashkirian)

Aacocrinus algeriaensis n. sp. [5]
Aacocrinus algeriaensis? [2]
Blairocrinus grafensis n. sp. [1]
Actinocrinitid indet. 4 [5]
Platycrinites hamarensis n. sp. [1]
Platycrinites sp. 3 [1]
Platycrinites sp. 4 [2]
Platycrinites sp. 5 [2]
Dicromyocrinus catillus n. sp. [1]
Mathericrinus wallacei n. comb.[1]
Cladid indeterminate 2 [3]
Cladid indeterminate 4 [2]
Cladid indeterminate 5 [1]
Cladid indeterminate 6 [1]
Cladid indeterminate 7 [4]
ø*Plummeranteris*? sp. [1]
øColumnal undesignated [1]
Amphicrinus prinsi n. sp. [7]
Crinoid Indeterminate 1 [1]
Crinoid Indeterminate 2 [2]
Crinoids Indeterminate [17]

Although the list of taxa for the fauna from the upper part of the Hassi Kerma Formation is the largest of the Algerian faunas, it cannot be considered to be a true count of the number or diversity of taxa recognized. Two or three of the indeterminate taxa may be from a single taxon, *Platycrinites* sp. 3, 4, and 5 may be parts of one or two species, and some of the columnal taxa may belong to one of the other taxa listed.

The estimated composition of this fauna, occurring in limestones, is four camerates, six to eight cladids, and one flexible. The large number of camerates in a Bashkirian fauna is unusual. Most Bashkirian faunas worldwide either lack camerates or have only platycrinitid columnals, which are often not reported. The occurrence of *Aacocrinus* is of particular significance because it extends the range of the genus upward from the Early Carboniferous (Osagean) into the Late Carboniferous. *Blairocrinus* is also of significance because this is only the second reported occurrence of the genus in the Late Carboniferous, the other from Desmoinesian strata of Japan (Hashimoto, 2001).

Oued el Hamar Formation

Lower Part of Oued El Hamar Formation
(Late Bashkirian)

**Pimlicocrinus octobrachiatus* n. sp. [8]
Pimlicocrinus sp. [1]
**Platycrinites hamarensis* n. sp. [4]
Mathericrinus wallacei n. comb. [28]
**Archaeocidaris* sp. [2]

Three of the taxa listed may belong in the upper part of the Oued el Hamar Formation, which contains a much larger fauna. If all of the identified taxa belong here, the crinoid fauna is camerate-dominated with an associated cromyocrinid and echinoid.

Upper Part of Lower Part of Oued El Hamar Formation (Late Bashkirian)

**Pimlicocrinus octobrachiatus* n. sp. [8]
Actinocrinitid indeterminate 1 [2]

All of the small number of taxa are camerates. Actinocrinitid indeterminate 1 may not be from this horizon, but we are uncertain in which part of the Oued el Hamar Formation it may have been found.

Upper Part Of Oued El Hamar Formation (Late Bashkirian)

Sampsonocrinus cheguigaensis n. sp. [74]
**Pimlicocrinus octobrachiatus* n. sp. [8]
Actinocrinitid indeterminate 3 [1]
**Platycrinites hamarensis* n. sp. [5]
Platycrinites sp. [1]
Pleurocrinus folliculus n. sp. 2 [3]
Eucladocrinus? asymmetricus n. sp. [8]
Eucladocrinus? sp. [2]
Mathericrinus wallacei n. comb. [28]
Cladid indeterminate 1 [1]
**Archaeocidaris* sp. [2]

Even without the three questionable occurrences this fauna is dominated at the generic level by camerates. This may suggest, however, that the questionable occurrences are from this interval. As noted above this is atypical of known Bashkirian faunas, and many of the same comments can be made about this fauna as that of the upper part of the Hassi Kerman Formation. The fauna occurs in a clay-dominated sequence of interbedded claystones and thin limestones. These lithologies are generally cladid dominated. Of particular importance in this fauna is the occurrence of *Sampsonocrinus* and *Eucladocrinus*. This is an upward extension into the Bashkirian of their previously recorded ranges from the Kinderhookian and Osagean.

Oued Bel Groun Formation (Moscovian)

Platycrinites? sp. [1]
Dicromyocrinus? invaginatus n. sp. [5]
Metacromyocrinus? sp. [1]
Flexible indeterminate [1]

The Oued Bel Groun fauna is the youngest known Paleozoic echinoderm fauna from Algeria. It is dominated by cromyocrinids, a group reaching their diversity acme during the early and middle Late Carboniferous. The occurrence of a platycrinitid in the fauna is not unexpected since platycrinitids, although rare, are found in the equatorial belt worldwide throughout the Late Carboniferous (Bowsher and Strimple, 1986).

FAUNAL SUMMARY

Several generalizations may be made when comparing the various Algerian faunas to time-correlative faunas worldwide. The Algerian faunas provide considerable new interpretations regarding evolution and paleobiogeographic distributions of some taxa.

With the exception of *Koryschisma saharae*, *Ectocrinus rouchi* n. comb., *Mathericrinus wallacei* n. comb., *Cibolocrinus africanus*, and ø*Floricyclus* cf. *F. angustimargo*, all named species in the Algerian faunas are new species. With the exception of *Rhodocrinites*, *Ectocrinus* (as *Amphoracrinus*), *Actinocrinites* (as *Actinocrinus*), *Platycrinites* (as *Platycrinus*), *Pleurocrinus*, *Cibolocrinus*, and *Archaeocidaris* this is the first report of *Megaliocrinus*, *Aacocrinus*, *Sampsonocrinus*, *Blairocrinus*, *Pimlicocrinus*, *Eucladocrinus*, *Synbathocrinus*, *Hebohenocrinus* n. gen., Balearocrinus, *Scytalocrinus*, *Ampullacrinus* n. gen., *Hydriocrinus*, *Cosmetocrinus*, *Dicromyocrinus*, *Mooreocrinus*, *Metacromyocrinus*, *Mathericrinus*, *Paianocrinus*, *Amphicrinus*, ø*Floricyclus*, ø*Plummeranteris*, and *Palaechinus*, from North Africa, extending geographic ranges for various genera from Europe, North America, Russia, China, Australia, and Japan.

The stratigraphic ranges are extended downward into the Serpukhovian for *Hydriocrinus*, *Dicromyocrinus*, and *Mooreocrinus*. *Hydriocrinus* was previously known from Desmoinesian into Virgilian strata. *Dicromyocrinus* and *Mooreocrinus* were previously known from Morrowan through Desmoinesian strata. Stratigraphic ranges are extended upward into the Bashkirian for *Ectocrinus*, *Aacocrinus*, *Sampsonocrinus*, and *Eucladocrinus*. The upper range of all of these genera was previously recognized as Viséan.

Four species in the Algerian faunas are reported from more than one horizon. *Koryschisma saharae* ranges from the Akacha Formation into the Mouizeb el Atchane Member (Viséan–Serpukhovian). *Dicromyocrinus vastus* n. sp. occurs in the El Guelmouna Formation, Mouizeb el Atchane Member, and boundary beds of the Hid el Kef Member and Djenien Member (all Serpukhovian). *Platycrinites aouidjaensis* n. sp. occurs in the Mouizeb el Atchane and Hid el Kef members (both Serpukhovian). *Ampullacrinus tritubulus* n. gen. n. sp. occurs in the Aïn el Mizab and Djenien formations (both Serpukhovian).

Actinocrinitids and platycrinitids were exceedingly abundant during the Mississippian of Europe and North America, as shown on the distribution lists compiled by Bassler and Moodey (1943) and more recently reported in China (Chen and Yao, 1993) and Australia (Lindley, 1979, 1988; Webster and Jell, 1999a). Actinocrinitids and platycrinitids were essentially equatorial-belt cosmopolitan taxa during the Mississippian. Platycrinitids, although they became less common, continued as equatorial cosmopolitan taxa through the Pennsylvanian and into the Permian, whereas the actinocrinitids were restricted to the Tethys during this time. Actinocrinitids have been reported in Japan (Hashimoto, 2001) and Iran (Webster *et al.*, 2001) from the Early Pennsylvanian (Morrowan or Bashkirian). Although their occurrence in Algeria expands their paleogeographic distribution within the Tethys and explains where they continued to evolve during the Early Pennsylvanian before their presence in the Permian of Timor (Wanner, 1916, 1924, 1937) and Late Permian extinction, a large time gap still exists between these Early Pennsylvanian and Permian occurrences. The actinocrinitids must have been somewhere during this time, but where remains to be discovered.

Disparid crinoids are minor elements of the Algerian faunas, occurring in two of the oldest three faunas. Cladid crinoids taxonomically dominate the fauna from the Akacha Formation, but do not occur in abundance. *Balearocrinus* is also known from the island of Minorca in the Mediterranean and appears to be a western Tethys endemic of Viséan age. The dendrocrinid *Hebohenocrinus* n. gen. may be an early Bashkirian western Tethys endemic.

Cromyocrinids dominate the cladids in the Algerian faunas. The occurrences of cromyocrinids in most of the Algerian faunas, with the downward extension of the ranges of *Dicromyocrinus*, *Mathericrinus*, and *Mooreocrinus*, suggest that major evolution was occurring in this clade in northern Africa during the Serpukhovian. Although cromyocrinids are present in the Viséan and Serpukhovian in Europe and North America, often they are relatively insignificant in numbers and diversity. Their greatest diversity and abundance are in the Pennsylvanian of North America (Webster, 1981).

Scytalocrinacids are the second most common cladid in the Algerian faunas, but they do not occur in abundance and are restricted to the Serpukhovian faunas. Some of the indeterminate crinoids in the upper part of the Hassi Kerman Formation may be scytalocrinids. Recognition of a cladid crown with three entoneural canals shows that evolution of entoneural canals occurred in more than one clade, and by itself, is not a diagnostic character of the articulates. The occurrence of the pirasocrinacid *Paianocrinus*? *carinatus* n. sp. possibly extends the geographic range of the genus from North America; whereas the occurrences of two zeacrinitids in the late Viséan Aïn Mezerelt Member and the early Serpukhovian El Harrada Member show relationship with both European and North American faunas.

Flexible crinoids are generally few in number and low in diversity, occurring in five of the 18 faunas of Algeria. Of particular significance is the occurrence of *Cibolocrinus* in the late Serpukhovian part of the Djenien Formation as reported by Strimple and Pareyn (1982), the oldest record of this genus. *Cibolocrinus* apparently spread from Algeria into North America, where it is known from several species during the Late Carboniferous and Early Permian. It reached its acme during the Permian, and is known from various shelf basins along the southeast (especially Timor), western, and northern margins of the Tethys, as well as Bolivia (Webster, 2003). This is the first record of *Amphicrinus* from the Serpukhovian. It was recognized previously in the Viséan of Scotland and Russia and the Morrowan and Desmoinesian of the United States (Webster, 2003).

Archaeocidarid spines and interambulacral plates are common elements in many Late Paleozoic faunas, whereas coronas seldom are preserved. The preservation of a partial corona suggests rapid burial of the specimen.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Generic and specific concepts followed herein are based on morphologic characters used in the *Treatise* (Moore and Teichert, 1978). Crinoid species are more variable than was realized by most researchers in the nineteenth and first half of the twentieth century. Where large populations are available for study, characters such as the number of arms, disposition of the anal plates, and degree of ornamentation are found to vary considerably (see, for example, Ausich and Sevastopulo 2001; Lane 1963; Wright 1927). A character that is commonly variable in one clade, however, is not necessarily so in another. Where a large number of specimens were available in this study, as, for example, in *Ectocrinus*, it was possible to assess intraspecific versus interspecific variation. In the majority of taxa, however, large populations were not available. New species erected, however, are sufficiently distinct morphologically from previously described congeneric species that it is unlikely that they will be found to be junior synonyms. The delimitation of supraspecific taxonomic categories in crinoids in the past has not been consistent, and many examples of polyphyletic and paraphyletic groupings are evident in the *Treatise*. In this study, we have tried to ensure that genera are monophyletic clades. The characters that serve to differentiate genera vary from clade to clade.

TERMINOLOGY

Crinoid terminology follows Ubaghs *et al. in* Moore and Teichert (1978), with modifications by Webster (1974) and Webster and Lane (1987). Blastoid terminology follows the *Treatise* (Moore, 1967), as modified by Breimer and Macurda (1972). Columnal noditaxis formulae are after Webster (1974), and measurement and curvature teminology are after Webster and Jell (1999a).

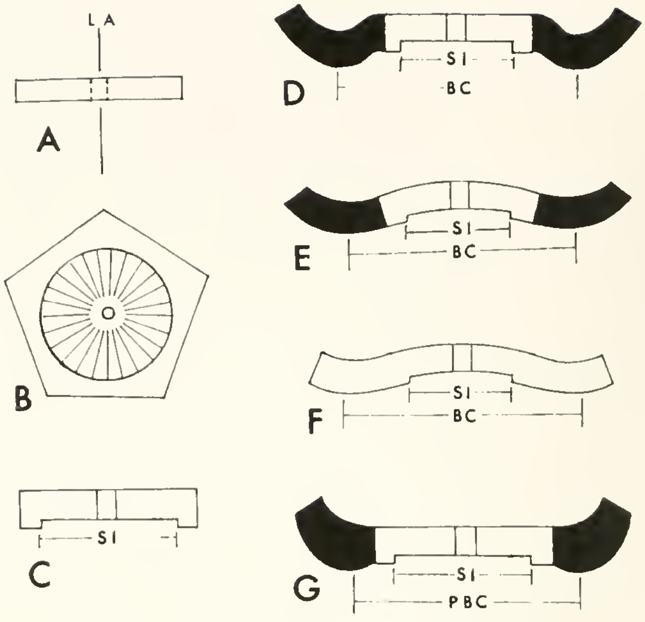
Basal Cup and Proximal Stem

The terms stem impression, basal concavity, and basal invagination have been used interchangeably and indiscriminantly by various authors in the past. For uniformity of description, we propose and apply the following terminology when describing the base of the cup (Text-fig. 3).

Horizontal infrabasal or basal circlet.—forms a planar fused (one single plate) or articulated (two to five plates) plate at the base of the cup normal to the linear axis of the crinoid, irrespective of the living orientation of the animal (Text-fig. 3A). There is no flexure in the plate(s) although the exterior surface distal to the stem facet may contain elevated or depressed ornamentation.

Stem facet.—is the circular or polygonal attachment scar formed where the stem attaches to the base of the cup. Stem facet refers only to the configuration of the attachment scar, which may or may not be horizontal and may or may not have a central depression (Text-fig. 3B). The stem facet may be flush with the external surface of the cup (usually the infrabasal or basal circlet) or, more commonly, at the base of an impression. Stem facet is distinct from articular facet. Articular facet is applied to the proximal and distal articular surfaces of columnals, but these are easily distinguished in context, and usually referred to as columnal facets.

Stem impression.—is the depression on the external surface of the cup (usually the infrabasal or basal circlet) formed by an inset of the proximal columnal into the cup with or without any flexure of the cup plate(s) (Text-fig. 3C). The stem impression may be filled by part or all of the proximal columnal and may become deeper with growth of the plates. Often the proximal columnal is preserved attached to the cup and when in a basal concavity may be difficult to recognize without having a cross-section of the specimen cutting through the stem facet.



Text-figure 3.—Diagrams of base of cup demonstrating plate relationship of stem impression, and basal concavity or invagination. Symbols and abbreviations: Basal plates in black; LA—linear axis, SI—stem impression, BC—basal concavity, PBC—pseudobasal concavity. A. Orientation of linear axis of crinoid and "horizontal" infrabasal or basal circlet. Living organism may tilt to a great angle laterally or even hang upside down. Linear axis may curve laterally in one or both directions distally from circlet. Centrally positioned axial canal dashed. B. Exterior surface of fused infrabasal or basal circlet showing stem facet and central axial canal. C. Cross-section through axial canal of horizontal infrabasal or basal circlet with stem impression on exterior surface. D. Cross-section through axial canal of part of crinoid cup with horizontal infrabasal circlet with stem impression at base of basal concavity or invagination. Note the downward flexure in the proximal part and recurving upward flexure in the distal part of the basals (in black). E. Cross-section through axial canal of part of crinoid cup with downflaring infrabasal circlet with stem impression (SI) at base of basal concavity (BC) or invagination. The basals (in black) are recurved. F. Cross-section through axial canal of an infrabasal circlet. Infrabasals downflaring proximally and extend beyond the basal plane recurving distally flaring upward and are visible in lateral view. G. Cross-section through axial canal of horizontal infrabasal circlet with bulbous basals (in black) forming a pseudobasal concavity (PBC) or invagination. Note the lack of any downward flexure in the infrabasals or basals.

Basal concavity (= basal invagination).—is a distinct flexure of the base of the cup, usually the basal (Text-fig. 3D) or infrabasal (Text-fig. 3F) plates, producing an invagination or concavity at the base of the cup with the stem facet at the deepest part of the invagination. Distal from the deepest part of the invagination the basal or infrabasal plates recurve to form the basal part of the walls of the cup. The distal parts of the infrabasals and proximal parts of the basals may be downflared (Text-fig. 3E) to form the basal concavity in some crinoids. Rarely the proximal parts of the radials also are downflared, such as in some genera of the Zeacrinitidae. To avoid confusion, it is recommended that stem invagination not be used when discussing the cup, because invaginations sometimes occur on the stem, such as where cirri attach. These could be referred to as stem invaginations although they are more appropriately referred to as *cirral* or *cirrus invaginations*.

Pseudobasal concavity (= pseudobasal invagination).—is the concavity formed by externally inflated cup plates adjacent to the stem facet without any downward inflection of the interior surface of the inflated plates as observed in cross-section (Text-fig. 3G). In some instances, immature stages have a flat or upflared base. With growth, the plates become inflated and a pseudobasal concavity develops. Without an interior view of the stem facet, it is sometimes impossible to determine if a basal concavity or pseudobasal concavity exists.

Radial Facet Width

Terms to describe the relative width of the radial facet compared to the width of the radial are angustary, peneplenary, and plenary. Plenary has been accepted as the facet occupying the full width of the radial to the lateral suture with adjacent radials or anals. The use of peneplenary and angustary has been subjective and what one author might call angustary another would call peneplenary. The *Treatise* (Moore and Teichert, 1978, pp. 231, 232) defined angustary as "very much narrower than width of plate," and peneplenary "occupying most but not all of distal extremity of plate, leaving nonarticular surfaces (generally narrow) next to sutures at plate margins." In order to standardize the meaning of these two terms, we propose that angustary be defined as occupying 70% or less of the radial width at the distal ends of the lateral suture of the radial with adjacent plates. Peneplenary is defined as occupying greater than 70% but less than 100% of the width of the radial at the distal ends of the lateral suture with adjacent plates.

Cladid Anals

Cladid anals have been referred to as radianal, anal X, and right-tube plate by most crinoid workers since the early 1900s. Prior to that time a number of nomenclature systems were used by various authors. Webster *et al.* (2003) used primanal, secundanal, and tertanal respectively for the cladid anal plates. Webster and Maples (2003) noted that the use of anal X is often a misnomer and recommended following the usage of Webster *et al.* (2003). That recommendation is followed herein.

CLASSIFICATION

Problems within higher level classifications of Paleozoic crinoids have been discussed by numerous authors over the past 20 years, as briefly summarized by Webster (1997) and McIntosh (2001). Currently the classification is undergoing critical review by several crinoid workers, some of who have proposed different classifications (*e.g.*, Simms and Sevastopulo, 1993; Ausich, 1998a). Modification of these classifications was proposed to include Paleozoic articulates by Webster and Jell (1999b). Undoubtedly there will be additional modifications within the next few years, especially within the Inadunata, a subclass that was discarded by both Simms and Sevastopulo (1993) and Ausich (1998b). Also, there will be considerable change in the classification of crinoids currently in the Suborder Poteriocrinina, which may be polyphyletic and was discarded by McIntosh (2001) and Webster (2003). Webster (1997) discussed some of the problems within the Poteriocrinina and considered the Family Poteriocrinitidae to be derived from the cyathocrinitids, whereas McIntosh (2001) considered the Poteriocrinitidae to be derived from the dendrocrinids.

REPOSITORY

All specimens are reposited in the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands, under six-digit numbers preceded by RGM, except as noted under *Cibolocrinus africanus*.

Subphylum **CRINOZOA** Matsumoto, 1929

Class **BLASTOIDEA** Say, 1825

Order **FISSICULATA** Jaekel, 1918

Family **PHAENOSCHISMATIDAE** Etheridge and Carpenter, 1886

Genus **KORYSCHISMA** Sprinkle and Gutschick, 1990

Koryschisma saharae (Breimer and Macurda), 1972
Plate 3, figures 15, 16

Pentremites sp. Pareyn, 1961, p. 223–224.

Phaenoschisma? *saharae* Breimer and Macurda, 1972, p. 18–20, 387, pl. 5, figs. 4, 5, 10; Macurda, 1983, p. 61–65, pl. 14, figs. 1–13, table 21.

Koryschisma saharae (Breimer and Macurda, 1972). Sprinkle and Gutschick, 1990, p. 120.

Diagnosis.—Theca large, elongate conical, L/W averages 1.71, pelvis much longer than vault, V/P averages 0.23, pelvic angle averages 38°; deltoid crests low to medium, hypodeltoid large, other deltoids appear confined to ambulacral sinuses; ambulacra nearly linear, lancet making up about ¼ of width; 5–9 hydrospire slits per group, number reduced by ⅓ on anal side; subdued secondary deposits at tip of basals.

Remarks.—The original description of *Koryschisma saharae* by Breimer and Macurda (1972) was based on three specimens collected by Pareyn from the undifferentiated Akacha and Mazzer formations, Mississippian (late Viséan, P2) at Djebel Ioucha (two specimens), and from the top of the El Guelmouna For-

Table 1.– -Measurements in mm for *Koryschisma saharae.*

	Spec. no. (RGM)		
	361 151	361 150	361 152
Length	24.5	19.4	16.63
Width	16.8	15.1	10.9
Vault	5.65	5.9	5.65
Pelvis	18.85	13.5	10.98
Pelvic angle	36	38	36
Length/width	1.46	1.28	1.52
Vault/pelvis	0.3	0.44	0.51

mation, Mississippian (early Serpukhovian, E1) at El Guelmouna (one specimen). Both localities are southeast of Béchar in northwestern Algeria. These specimens are not well preserved, particularly in the critical oral and anal areas, making generic assignment questionable. As a part of the discussion of these specimens, Breimer and Macurda (1972, p. 20) stated that "... if there is an epi- and hypodeltoid, this most closely resembles a new Lower Mississippian genus being described from Montana by James Sprinkle and Raymond Gutschick. They will re-assign it to their genus." Macurda (1983) provided a more complete description of the species based on eight additional specimens from the same localities that were much better preserved. Sprinkle and Gutschick (1990) erected *Koryschisma* for their material from Montana and reassigned the Algerian specimens to *Koryschisma saharae.* There is no indication that they had additional Algerian material to examine.

We conclude that the specimens described in this collection are conspecific with *Koryschisma saharae* even though they are somewhat wider relative to length than indicated in the revised diagnosis of Sprinkle and Gutschick (1990) and have a somewhat longer vault (Table 1). We will not repeat the detailed description of the species from Macurda (1983) because our specimens fit well within the parameters given there for *Koryschisma saharae.* Although the current specimens are generally well preserved, each is missing the hypodeltoid. The lateral margins of the ambulacral sinuses are not preserved well enough to determine the number of hydrospire slits.

Breimer and Macurda (1972) reported *Koryschisma saharae* from the Akacha-Mazzer Formation of late Viséan age and the Mouizeb el Atchane Member of middle early Serpukhovian age. The occurrence in the Aïn Mezerelt Member of earliest Serpukhovian age fills part of the gap between the earlier reported occurrences.

Koryschisma is known from the Kinderhookian (early Tournaisian) part of the Lodgepole Formation, Montana, and the Osagean (late Tournaisian) Lake Valley Formation, New Mexico, in western North America (Sprinkle and Gutschick, 1990). Its occurrence in the late Viséan and early Serpukhovian of northern Africa reflects migration into the western Tethys during the Early Mississippian.

Material.—Three specimens: RGM 361 150 (illustrated), RGM 361 151, and RGM 361 152 from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (Serpukhovian, E1, Pareyn, 1961), at Mouïzeb Reouïen, Legrand-Blain collection.

Class **CRINOIDEA** J. S. Miller, 1821

Subclass **CAMERATA** Wachsmuth and Springer, 1885

Order **DIPLOBATHRIDA** Moore and Laudon, 1943

Superfamily **RHODOCRINITACEA** Roemer, 1855

Family **RHODOCRINITIDAE** Roemer, 1855

Genus **RHODOCRINITES** J. S. Miller, 1821

Rhodocrinites sp.

Plate 1, figures 1–3.

Description.—Theca globose, exposed length 15 mm, width 21 mm, widest at distal ends of first primibrachial, walls slightly inclined distally, rounded stellate ornament, ray ridges not present, deep apical pits, all plates very tumid. Infrabasals confined to deep basal concavity, not exposed. Basals 5, large, hexagonal, length 5 mm (estimated), width 4.9 mm, form base of cup, recurved, proximal end in basal concavity, distal ends upflared. Radials 5, septagonal, equidimensional 4.9 mm, outflared. Primanal in line of radials; anal series 1-3-4-2+-?. Interray series begins in line of radials; series 1-2-3-3-?. First primibrachial hexagonal. Second primibrachial pentagonal, axillary, isotomous branching. Stem circular in transverse section, heteromorphic; noditaxis N3231323 minimal. Columnals short, symplectial articulation; latus convex; lumen pentalobate.

Remarks.—The globose shape of the specimen suggests that it may represent a new species. It is one of the few forms with deep apical pits, such as the truncate-cone shaped *Rhodocrinites kirbyi* (Wachsmuth and Springer, 1889) and *Rhodocrinites* sp. (Arendt, 2002, pl. 1, fig. 1), the latter also of Serpukhovian age. The specimen is well preserved but lacks the free arms. The distal base of the fixed arms, tegmen, and anal opening are not exposed, precluding its use as a holotype. Webster (1997) noted that *Rhodocrinites,* which reached its acme during the Osagean of North America and late Tournaisian of Europe, is in need of review.

Material.—One specimen RGM 361 153, Aïn Mezerelt Member, El Guelmouna Formation, Mississippian

(Serpukhovian, E1), at Mouïzeb Reouïen, Pareyn collection.

Order **MONOBATHRIDA** Moore and Laudon, 1943

Suborder **COMPSOCRININA** Ubaghs *in* Moore and Teichert, 1978

Superfamily **PERIECHOCRINACEA** Bronn, 1849

Family **PARAGARICOCRINIDAE** Moore and Laudon, 1942

Genus **MEGALIOCRINUS** Moore and Laudon, 1942

Megaliocrinus? sp.

Plate 1, figure 13

Amphoracrinus nov. sp. A Pareyn, 1961, p. 76.

Description.—Partial theca with calyx plates poorly preserved, numerous ungrouped arm openings, and numerous bulbous tegmen plates leading to terminal large central plate.

Remarks.—The cup is not preserved and the tegmen is crushed inward on the opposite side. The preserved part of the specimen is similar to *Megaliocrinus aplatus* Moore and Laudon (1942) from the Morrowan (Early Pennsylvanian) of North America. The two rows of larger distal tegmen plates below the terminal plates on this specimen, however, distinguish it from *M. aplatus*. Provisionally this extends the range of the genus downward into the Mississippian. The genus is also known from the Early Pennsylvanian (Bashkirian) of Spain (Strimple, 1976).

Material.—One partial theca (RGM 361 175) from the Mississippian (Serpukhovian, E2; Pareyn, 1961) Mouizeb el Atchane Member of the Aïn el Mizab Formation, at Mader el Mahjib, synclinal bed 14, Pareyn collection.

Family **AMPHORACRINIDAE** Bather, 1899

Emended diagnosis.—Actinocrinoid-like crinoids possessing five large oral plates at the tegmen summit, having the anal opening on a short anal tube or obliquely oriented beneath the large posterior oral plate, and commonly with meshwork ornamenation on calyx plates.

Remarks.—The families Amphoracrinidae and Actinocrinitidae are in need of systematic reevaluation. Currently, the Family Amphoracrinidae contains three genera: *Amphoracrinus*, *Ectocrinus*, and *Pimlicocrinus*. The main features that distinguish *Pimlicocrinus* from the other two genera are an extremely low calyx to tegmen length ratio (as opposed to longer calyx to tegmen length ratios in the other genera), the absence of five large oral plates at the tegmen summit (as opposed to presence of five large orals at the summits of the tegmens in the other genera), and the presence of a central to subcentral anal opening at the tegmen summit (as opposed to an anal opening at the end of a laterally directed anal tube positioned beneath the large posterior oral plate in the other genera).

We consider that *Pimlicocrinus* is more closely related to actinocrinitids than to amphoracrinids. Because the arms are grouped rather strongly on our specimens of *Pimlicocrinus*, which also is the case for the specimens of *Pimlicocrinus* figured by Wright (1955), and following the classificatory key to subfamilies and genera of the Actinocrinitidae presented in Webster and Lane (1987), we here remove *Pimlicocrinus* from the Amphoracrinidae and place it within the Subfamily Actinocrinitinae, Family Actinocrinitidae.

In addition to *Amphoracrinus* and *Ectocrinus*, two genera that were erected since publication of the *Treatise* (Moore and Teichert, 1978), *Ancalocrinus* and *Displodocrinus* Webster and Lane (1987) possess large spinose orals at the tegmen summit and an obliquely directed anal opening. *Ancalocrinus* was placed in the family Actinocrinitidae and *Displodocrinus* was placed in the Sunwaptacrinidae. Based on their shared characters with the two other genera of amphoracrinids, however, we here remove *Ancalocrinus* from the Family Actinocrinitidae and *Displodocrinus* from the Family Sunwaptacrinidae and place them both within the Family Amphoracrinidae. These changes in the family Amphoracrinidae now restrict its range to the Mississippian (Tournaisian, Viséan, and Serpukhovian) of North America, Europe, southwest China, and North Africa.

Genus **ECTOCRINUS** Wright, 1955

Remarks.—Wright (1955) discussed the early recognition of *Amphoracrinus*, noted the previous recognition of *A. gilbertsoni* (Miller *in* Phillips, 1836) as the type species by Wachsmuth and Springer (1897), established the neotype for *A. gilbertsoni*, and erected *Ectocrinus*. Although he did not specify the generic differences between the two genera, his description of *Ectocrinus* mentions that the tegmen has very steep or concave sides and the cup has a more inflated bowl shape. All three species that Wright (1955) assigned to *Ectocrinus* (*E. olla*, *E. expansus*, and *E. macneanensis*) are distinguished from *Amphoracrinus* by the concave sides of the tegmen, a more inflated cup, and the presence of five very large orals with projecting transverse ridges at the summit of the tegmen. The extreme development of the orals (large blade-like transverse protrusions ending in three short rounded nodes) also occurs on *A. anthodeus* Chen and Yao (1993), which we assign to *Ectocrinus*. One could argue that the morphologic differences between *Amphoracrinus* and *Ectocrinus* are insignificant for generic recognition because *Amphoracrinus* also has 5 large orals at the summit. In *Amphoracrinus*, however, the orals tend to be smaller, commonly are very bulbous or have rounded protrusions, and lack the transverse ridge. Currently the 17 species assigned to *Amphoracrinus* (Bassler and Moodey, 1943; Wright, 1955; Webster and Lane, 1987; Chen and Yao, 1993) are known from northwestern Europe, North America, and China. *Ectocrinus* probably evolved from *Amphoracrinus* by modification of the orals and, including those below, currently has seven species assigned to it from England, Ireland, Morocco, Algeria, and China.

Ectocrinus rouchi (Delpey, 1941), new combination
Plate 1, figures 4–12

Amphoracrinus rouchi Delpey, 1941, p. 217, figs. 4–8. Termier and Termier, 1950, p. 83, pl. 208, figs. 37–41; Webster, 1973, p. 51.

Description.—Theca turbinate, tegmen shorter than calyx, all plates with fine anastomosing ridge ornament forming irregular meshwork pattern, sutures impressed, pentalobate in oral view, may be slightly wider on posterior. Calyx medium high to wide bowl-shaped, sides weakly convex, base truncated for stem attachment. Basal circlet formed by 3 subequal plates, proximally horizontal, distally upflared at approximately 50°, visible in lateral view. Radials 5, hexagonal (A, C, and D) or septagonal (B and E) if adjoining 2 basals, slightly wider than long to equidimensional, outflared at approximately 50°, straight to slightly convex longitudinally, gently convex transversely. Radial facet plenary. Primanal hexagonal, slightly longer than wide, slightly smaller than radials, in line with radials; anitaxis 1-2-3-3-tegmen. Primibrachials 2; first primibrachial hexagonal, widening to base shoulder facets; second primibrachial pentagonal, axillary, much wider than long, straight to gently convex longitudinally; both primibrachials gently convex transversely, upflaring more steeply than radials. First and second secundibrachials fixed; second secundibrachials biserial, arms free above. Ambulacral openings 2 per ray, elongate, separated by narrow elongate ambulacral plate adjoining two central mutually adjacent second secundibrachials. Tegmen highly inflated, sides slightly concave, capped by 5 large orals, summit concave, plates slightly to moderately bulbous. Posterior oral largest, adjoining other 4 in a semicircle. Orals bear upward-flared sharply angular transverse ridge along midline, commonly lost by breakage. Ambulacral plates adjacent and above openings small, numerous, irregular, grade into slightly larger plates below large orals. Interambulacral plates of intermediate size, irregular up to large orals. Anal opening on distal side of anal tube formed of small irregular plates, directed upward inside rounded lip terminating tube. Transverse medial ridge on posterior oral forms shield above anal opening. Stem facet round, slightly impressed, crenularium very narrow along wide areola, axial canal broadly pentalobate. Distal arms and stem unknown. Measurements given in Table 2.

Table 2.—Measurements in mm for *Ectocrinus rouchi* n. comb.

	Spec. no. (RGM)		
	361 154	361 155	361 156
Thecal length	37.8	32	45
Thecal width	30.4	30.2	38 (max.)
Diameter basal circlet	12	9.3	13
Basal length	6.1	4.5	6.4
Basal width	9.0	6.9	10
Radial length	7.8	6	8.4
Radial width	10.1	7.3	0.5
Primanal length	8.2	6	9.6
Primanal width	7.5	5.6	9.0
First primibrach length	5.4	5.1	6.4
First primibrach width	8.0	6.7	8.2
Second primibrach length	4.5	4	5.3
Second primibrach width	7.3	6.5	7.3
Anal oral length	6.2 (approx.)	5.9	7.7
Anal oral width	9.3 (approx.)	8.4	9.5
Diameter stem facet	6.6	6.8	6.6

Remarks.—*Ectocrinus rouchi* (Delpey, 1941) was described from upper Viséan strata of Morocco. The original figures (Delpey, 1941, unnumbered plate figs. 4–8) are fine sketches and show a fine granular ornament. Delpey (1941, p. 217), however, described the ornament as "L'ornementation des plaques est guillochée, souvent avec un centre, mais ne forme jamais d'étoile," which we interpret as "The ornamentation is a window-like meshwork, often with a center, but without radiating ridges." This is a meshwork ornament which is present on *Amphoracrinus gilbertsoni* (Miller *in* Phillips, 1836) as illustrated by Wright (1955, pl. 49, figs. 12, 13) and on *Ectocrinus olla* (M'Coy, 1851) as illustrated by Wright (1955, pl. 52, figs. 1, 10). *Ectocrinus rouchi* has a considerably longer vase-shaped cup than the Irish species *E. macneeanensis* Wright (1955) or the two English species, *E. olla* and *E. expansus* Wright (1955), all of which have relatively shorter more globose-shaped cups.

Most specimens of *E. rouchi* are slightly to moderately distorted and part of the theca may be lost by weathering. Variation in shape of the primibrachials is particularly noteworthy among these specimens (Table 3). In addition, rarely there is a single axillary primibrachial in one ray (RGM 361 156). Abnormalities are noted on two specimens. Specimen RGM 361 154 has

Table 3.—Number of sides of primibrachial plates of *Ectocrinus rouchi*. Axillary primibrachials followed by capital A.

Spec. no. (RGM)	A ray	B ray	C ray	D ray	E ray
361 154	6	6	6	6	4
361 155	?	6	5	6	?
361 156	4	4	6 A	4	4
361 157	6	5	6	?	?
361 158	5	4	4	?	?
361 159	6	6	?	?	4
361 160	6	6	6	?	6
361 161	6	5	6	?	?
361 162	6	6	6	6	?

an abnormal E ray. It appears to have been damaged and in the process of regeneration of the proximal secundibrachials at the time of death or it was not regenerated (Pl. 1, fig. 5). Specimen RGM 361 157 has aberrant growth with extreme shortening of the D ray in the tegmen, which resulted in arm openings very high on the tegmen (Pl. 1, fig. 11). This is interpreted as the living organism having grown against an unknown object and the arm openings were unable to become free at the normal position.

Specimen RGM 361 163—rays uncertain, one primibrachial quadrangular, one pentagonal, one hexagonal, others unknown.

Specimen RGM 361 164—specimen too fractured, rays uncertain.

Material.—Eleven specimens: Four figured specimens RGM 361 154, RGM 361 155, RGM 361 157, and RGM 361 158 and seven unfigured specimens RGM 361 156, and RGM 361 159 through RGM 361 164, all from the undifferentiated Akacha and Mazzer formations (Pareyn, 1961), at Couverture au Djebel loucha of late Viséan, very late P1 (Pareyn, 1961); Pareyn Collection. Specimens RGM 361 154–RGM 361 156 and RGM 361 158 are from a slightly lower stratigraphic level than all others.

Ectocrinus mezereltensis, new species
Plate 2, figures 1–12; Plate 3, figures 7–14

Diagnosis.—Distinguished by one or more of the following features: tegmen approximately equal to calyx length but variable, tegmen with slightly convex to mostly concave sides, coarser nodose to anastomosing ornament, or narrower transverse ridges on five large orals.

Description.—Theca turbinate, tegmen approximately same length as calyx varying from slightly less to a little greater length, all plates with coarse granulose to anastomosing ridge ornament, pentalobate in oral view, widest on posterior. Calyx wide bowl-shaped, sides vary from slightly concave to straight to weakly convex, base truncated for stem attachment. Basal circlet tripartite, formed by 3 subequal plates, proximally horizontal, distally outflared, visible in lateral view. Radials 5, hexagonal (A, C, and D) or heptagonal (B and E) if adjoining 2 basals, slightly wider than long to equidimensional, outflared at approximately 45°, straight to slightly concave longitudinally, gently convex transversely. Radial facet plenary. Primanal hexagonal, slightly longer than wide, slightly smaller than radials, in line with radials; anitaxis 1-2-3-4-tegmen. Primibrachials 2; first primibrachial quadrate, pentagonal, or hexagonal widening to base shoulder facets, shape dependent on contacts with first interprimibrachials, quadrate none, pentagonal 1, hexagonal 2; proximal and distal sutures convex outward giving pseudohexagonal or puffy quadrate form; second primibrachial pentagonal, axillary, wider than long, straight to gently convex longitudinally, moderately convex transversely, outflaring at same angle as radials to more upflaring. First secundibrachial fixed; second secundibrachials biserial, arms free above. Ambulacral openings 2 per ray, elongate, separated by narrow elongate ambulacral plate adjoining 2 central mutually adjacent second secundibrachials. Tegmen highly inflated, sides slightly concave to slightly convex, capped by 5 large orals. Posterior oral largest adjoined by all others. Orals bear upward-flared transverse ridge slightly distal of midline, often lost by breakage. Ambulacral plates adjacent and above ambulacral openings small, numerous, irregular up to large central plate followed by 2 rows of intermediate size interlocking staggered plates up to large orals. Interambulacral plates of intermediate size, irregular up to large orals. Anal opening on protruded interambulacral series of small plates, directed laterally or obliquely upward. Stem transversely round, heteromorphic proximally; noditaxis N1 minimal. Columnals very short, latus angular or rounded; crenularium very narrow along wide areola; lumen large, broadly pentalobate. Distal arms and stem unknown. Measurements given in Table 4.

Remarks.—*Ectocrinus mezereltensis* n. sp. differs from *E. rouchi* by having nodose to anastomosing ornament that is coarser than that of any of the three species recognized by Wright (1955). The transverse ridge of *E. mezereltensis* is much smaller than the plate-like protrusions on *E. anthodeus* (Chen and Yao, 1993).

Variation is noted in the relative length of the tegmen, width of the posterior interray, number and arrangement of the ambulacral plates, relative size of plates immediately below the orals, and concavity of the tegmen summit of *E. mezereltensis*. As in *E. rouchi*, considerable variation occurs in the shape of the

Table 4.—Measurements in mm for *Ectocrinus mezereltensis* n. sp.

	Type			
	Holotype	Paratype 1	Paratype 2	Paratype 3
	Spec. No. (RGM)			
	361 165	361 166	361 167	361 168
Thecal length	37.4	20.9	28.7	35.5
Thecal width (maximum)	40.3	20	26.6	32.5
Diameter basal circlet	10.1	5.1	8	10.5
Basal length	5.6	3.3	4	5
Basal width	8.1	5	6.7	7.6
Radial length	7	3.1	4.3	6.0
Radial width	8.6	5.4	6.4	8.2
Primanal length	6.7	3.6	5.1	6.1
Primanal width	6.1	3.3	4.5	6.1
First primibrachial length	6.8	2.2	3.6	4.5
First primibrachial width	7.6	4.1	5.5	7.5
Second primibrachial length	2.3	2.6	5	5
Second primibrachial width	4.5	6.6	8.5	7.2
Anal oral length	7.5	5	4.9	7.5
Anal oral width	8.5	5.5	7.5	7.4
Diameter proximal columnal	3.5	5.5	6.5	

first primibrachials of *E. mezereltensis* (Table 5) and rarely there is an axillary single primibrachial in one ray.

Material.—Nine specimens: Holotype RGM 361 165, six paratypes RGM 361 166–RGM 361 171, and two mentioned specimens (RGM 361 172, RGM 361 173). All specimens from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (early Serpukhovian, E1; Pareyn, 1961), at Mouïzeb Reouïen; Pareyn collection.

Etymology.—Named for the Aïn Mezerelt Formation.

Ectocrinus redactus, new species

Plate 3, figures 1–4

Diagnosis.—Distinguished by having most rays with single primibrachial axillary, relatively shorter calyx length, and the loss of intermediate-size plates between the small ambulacrals and the larger distal ambulacrals below the large orals at the tegmen summit.

Table 5.—Number of sides of primibrachial plates of *Ectocrinus mezereltensis*. Axillary primibrachials followed by capital A.

Spec. no. (RGM)	A ray	B ray	C ray	D ray	E ray
361 165	6	6	6	6	7 A
361 167	4	4	5	5	5
361 168	5	5	6	6	5
361 169	4	4	5	4	4
361 170	6	6	6	6	5
361 171	6	6	5	6	4 A
361 172	6	6	6	6	6
361 173	5	?	?	5	4

Description.—Theca turbinate, length 21.6 mm, width 21.3 mm, tegmen approximately same length as calyx, all plates with medium granulose to anastomosing ridge ornament, pentalobate in oral view. Calyx wide bowl-shaped, length 10.4 mm, width 18.5 mm, sides vary from slightly concave to weakly convex, base truncated for stem attachment. Basal circlet tripartite, diameter 7.8 mm, formed by 3 subequal plates, proximally horizontal, distally outflared, visible in lateral view. Radials 5, hexagonal (A, C, and D) or heptagonal (B and E) if adjoining 2 basals, wider (7.3 mm) than long (5.2 mm) to equidimensional, A ray widest, narrower toward anal, outflared at approximately 45°, straight to slightly concave longitudinally, gently convex transversely. Radial facet plenary. Primanal hexagonal, slightly longer than wide, slightly smaller than radials, in line with radials; anitaxis 1-2-3-tegmen. Single primibrachial axillary, hexagonal or heptagonal, shape dependent on contacts with second interprimibrachials; C ray with 2 primibrachials, first pentagonal, axillary second hexagonal. Interprimibrachials large, series 1–2-tegmen. Secundibrachials 2, fixed; arms free above. Ambulacral openings 2 per ray, elongate, separated by narrow elongate ambulacral plate adjoining two central mutually adjacent second secundibrachials. Tegmen highly inflated, sides slightly concave to slightly convex, capped by 5 large orals. Posterior oral largest adjoined by all others. Orals bear upward-flared transverse ridge distal of midline, commonly lost by breakage. Ambulacral plates adjacent and above ambulacral openings small, numerous, irregular up to large central plate followed by single larger plate below large orals. Interambulacral plates of intermediate size, 2 rows interlocking up to large orals. Anal opening on protruded interambulacral series of small plates, directed obliquely upward, incomplete. Stem facet transversely round, diameter 4.5 mm, crenularium very narrow along wide areola; lumen large, broadly pentalobate. Distal arms and stem unknown.

Remarks.—*Ectocrinus redactus* n. sp. was derived from *E. rouchi* or *E. mezereltensis* by reduction of the primibrachials to a single axillary primibrachial in most rays. As noted in the descriptions, both *E. rouchi* and *E. mezereltensis* have considerable variability in the number of primibrachials (mostly two, but sometimes one), and *E. redactus* approaches the condition of a single primibrachial in all rays. Perhaps more important is the loss of intermediate-size plates between the small ambulacrals and the larger distal ambulacrals below the large orals at the tegmen summit of *E. redactus*. This results in *E. redactus* having a relatively shorter calyx length.

Second secundibrachials of the holotype are lost by weathering or breakage on all rays, but facets for their attachment to the tegmen plates are present on the plates along the sides of the ambulacral openings. The narrow intersecundibrachial plate is preserved in two rays.

Material.—Holotype, RGM 361 174, from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (early Serpukhovian, E1), at Mouïzeb Reouïen; Pareyn collection.

Etymology.—*redactus*, Latin, meaning reduced, which refers to the reduced number of primibrachials.

Ectocrinus? sp.

Plate 3, figures 5, 6

Remarks.—A fragmentary infrabasal circlet (two large, one small infrabasal plates) and partial basal circlet with three columnals has very fine granular to vermiform ornament. It is questionably assigned to *Ectocrinus*, lacking the proximal arm plates and tegmen needed for unquestioned generic assignment.

Material.—Figured specimen (RGM 361 350) from the El Harrada Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E1), Cirque de Tagnana (Oued Narkla); Pareyn collection.

Family **ACTINOCRINITIDAE** Austin and Austin, 1842

Subfamily **ACTINOCRINITINAE** Ubaghs *in* Moore and Teichert, 1978

Genus **ACTINOCRINITES** J. S. Miller, 1821

Remarks.—The stratigraphic range of *Actinocrinites* is Middle Devonian to Permian (Webster, 2003). The acme of the genus is in the Tournaisian, where it is cosmopolitan in the equatorial belt. Discovery of the Algerian Serpukhovian species fills a gap in the previously recognized range. *Actinocrinites* is currently unknown in the Pennsylvanian and known only from the Permian of Timor and Australia.

Actinocrinites becharensis, new species

Plate 3, figures 17–20

Diagnosis.—Distinguished by the combination of cup equal to tegmen length, lesser degree of arm protrusion, smaller number of arms, and enlarged bulbous ornament on proximal half of radials.

Description.—Theca turbinate, length 34.1 mm (incomplete), width 32.6 mm; calyx medium bowl-shaped, length 15.9 mm, width 17.5 mm; tegmen conical with slightly excentric anal tube; fixed arms grouped, brachial lobes protruded; pentalobate in oral view; strongly inflated along E ray from base of cup to tegmen summit. Basal circlet 8.2 mm diameter, formed of 3 subequal plates with stem facet impression proximally surrounded by basal flange, distally upflared with tips projecting slightly beyond basal flange. Radials 5, hexagonal in contact with 2 basals (B and E), pentagonal in contact with 1 basal (A, C, and D), upflared, wider than long; radial facet plenary, concave exterior suture. Primanal hexagonal, equidimensional (4.7 mm), in line of radials; anitaxis1-2-3-3-3-tegmen plates. First primibrachial hexagonal where in contact with 2 interprimibrachials, pentagonal where in contact with 1 interprimibrachial (C ray only), length 4.7 mm, width 7 mm, gently convex longitudinally and transversely. Second primibrachial axillary, heptagonal, length 5.3 mm, width 5.8 mm. Axillary secundibrachial heptagonal or octagonal. Two tertibrachials fixed, arms free above, second tertibrachial on outer half of ray axillary. Arms flare with first secundibrachial, 6 arms per ray where free. Interprimibrachial series 1-2-3-3-tegmen plates. Intersecundibrachial series 1–2-tegmen plates. Intertertibrachial series 1-1-2- or 1-2-2-tegmen plates. Tegmen plates medium size, with central node irregularly along center of ambulacral plates. Interambulacral plates lack nodes. Ornament on cup plates enlarged bulbous area on proximal half of radial leading to broadly rounded ray ridges extending onto tertibrachials. Finer ornament of anastomosing ridges on cup and tegmen plates, most strongly developed at top cup to base tegmen. Anal tube excentric, incomplete, extending at least 4.4 mm above tegmen summit. Stem facet round in outline, 6.2 mm diameter, axial canal pentalobate. Distal arms and stem not preserved.

Remarks.—Late Tournaisian and Viséan species of *Actinocrinites* have relatively long cups, most considerably longer than the tegmen, giving the specimen a long turbinate appearance with straight to concave cup walls; the arms are strongly grouped and widely protruded; and the ornament varies from rounded nodose to coarse nodose to ray ridge. These contrast markedly to the inflated convex walls, cup length equal to tegmen length, and less protruded bunched arms of *A. becharensis* n. sp.

Material.—Holotype, RGM 361 176, is from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (early Serpukhovian, E1; Pareyn, 1961), from Mouïzeb Reouïen; Pareyn collection.

Etymology.—The species name refers to the region in which the specimen was found.

Actinocrinites combinatus, new species

Plate 4, figures 6–9

Diagnosis.—Distinguished by one or a combination of some of the following features: cup equal to tegmen length, strongly protruded grouped arms, eight arms at thecal rim, and elongated nodose ornament.

Description.—Theca spindle-shaped, length 21.7 mm (incomplete), width 30.3 mm; calyx medium bowl-shaped, length 15.4 mm, width 23.3 mm; tegmen inverted medium bowl shape, excentric anal tube of unknown length; fixed arms grouped, brachial lobes strongly protruded; pentalobate in oral view. Calyx ornament coarse nodes elongated to form ray ridges from base radials onto tertibrachials, inverted V ridges from base radials to first interprimibrachials, and flange around proximal edge of basal circlet. Basal circlet 6.6 mm diameter, formed of 3 subequal plates with horizontal? stem facet proximally, distally upflared with tips not visible in lateral view obscured by flange on radials. Radials 5, hexagonal in contact with 2 basals (B and E), pentagonal in contact with 1 basal (A, C, and D), upflared, wider (6.1 mm) than long (4.3 mm); radial facet plenary, concave exterior suture. Primanal hexagonal, slightly longer (4.4 mm) than wide (4.1 mm), in line of radials; anitaxis1-2-3-5-3-tegmen plates. First primibrachial hexagonal where in contact with 2 interprimibrachials, pentagonal where in contact with 1 interprimibrachial, quadrangular if not in contact with interprimibrachials, length 4.6 mm, width 6.3 mm, strongly convex longitudinally and transversely. Second primibrachial axillary, pentagonal, hexagonal or heptagonal depending on contacts with interprimibrachials, length 4.7 mm, width 6 mm. Axillary secundibrachial pentagonal or hexagonal depending on contacts with primibrachials, flares outward. Tertibrachials 2 or 3, second tertibrachial on outer half ray axillary, third tertibrachial axillary on inner half ray. Arms flare with first secundibrachial, 8 arms per ray where free. Interprimibrachial series 1-2-2-3 or 4-tegmen plates. Tegmen plates small, numerous, tumid or with coarse central node. Anal tube excentric, extending above tegmen summit unknown distance. Proximal columnals round in transverse section, 5.2 mm diameter, heteromorphic, noditaxis N1 minimal. Columnals with roundly convex latus, subpentagonal lumen, symplectial articulation. Axial canal pentalobate. Distal arms and stem not preserved.

Remarks.—The calyx ornament and number of arms at the thecal rim distinguishes *Actinocrinites becharensis* n. sp. (six arms per ray at tegmen ring) from *A. combinatus* n. sp. (much coarser cup ornament and eight arms per ray at tegmen ring). Both *A. becharensis* and *A. combinatus* may have evolved from a form similar to *A. subpulchellus* Miller and Gurley (1896), an Osagean form from the Burlington Limestone of Iowa. The ornamentation is similar to that of *A. becharensis* n. sp., but the calyx of *A. subpulchellus* has the elongate appearance of most late Tournaisian and Viséan actinocrinitids.

Material.—Holotype, RGM 361 177 from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (early Serpukhovian, E1), at Mouïzeb Reouïen; Pareyn collection.

Etymology.—From the Latin *combino* referring to the combination of morphologic characters which distinguish the species.

Genus **AACOCRINUS** Bowsher, 1955

Aacocrinus algeriaensis, new species

Plate 4, figures 1–5

Diagnosis.—Distinguished by the combinaion of a medium bowl-shaped calyx, four arms per ray at thecal rim, reduced fixed interbrachials, and longer tegmen.

Description.—Calyx medium bowl-shaped, wider than high to nearly equidimensional, pentalobate in oral view, walls convex, brachial lobes sharply extended in lateral view, flaring out on axillary secundibrachials, widely flared with tertibrachials, 4 arms per ray at thecal rim. Stellate ornamentation aligned along rays with secondary ridges to center of interbrachials, on all cup plates, extending minimally to proximal tertibrachial. Tegmen inflated, plates bulbous. Basals 3, equal in size, sutures nearly ankylosed, form gently upflared base, truncated by circular stem impression. Radials 5, hexagonal, wider than long, moderately convex transversely and longitudinally, largest plates in calyx. First primibrachial wider than long, quadrangular, rounded sides, moderately convex transversely and longitudinally. Primibrachial 2 axillary, pentagonal, wider than long, moderately convex transversely, gently convex becoming moderately concave longitudinally. Secundibrachial axillary, heptagonal, wider than long, fixed in brachial lobe, widely out-

Table 6.—Measurements in mm for *Aacocrinus algeriaensis* n. sp.:

	Type		
	Holotype	Paratype 1	Paratype 2
		Spec. no. (RGM)	
	361 178	361 169	361 180
Calyx height (less anal tube)	17.9	15.7	16.2
Calyx width	21.8	19.7	20.1
Basal circlet diameter	7.9	5	7
Basal length	4.6	2.1	3.1
Basal width	5.4	4	(est.) 4.9 (est.)
Radial length	5.8	4.2	3.9
Radial width	7.2	5.7	6.7
Primibrachial 1 length	3.2	2.9	2.5
Primibrachial 1 width	4.9	4.5	4.6
Primibrachial 2 length	2.7	2.6	2.8
Primibrachial 2 width	5.1	5.2	5.2
Secundibrachial length	2.9	2.4	3
Secundibrachial width	3.2	3	3.6
Primanal length	6	4.1	5
Primanal width	5.2	3.5	4.5
Interbrachial length	6.2	5	4.3
Interbrachial width	5.3	4.5	4.3
Stem impression diameter		2	

flared, convex transversely, concave longitudinally. Outer tertibrachial 1 nearly equidimensional, larger than wider than long inner tertibrachial 1, both fixed in brachial lobe, outflared widely; 4 arms per ray at thecal rim. Primanal narrower and in line with radials, slightly longer than wide. Anitaxis series 1-2-3-2, plates longer than wide, decrease in longitudinal convexity distally, third series in line with arm lobes. Interbrachial series 1–2, with interbrachial 2 in line with arm lobes; interbrachial 1 large, longer than wide, octagonal, widest at apices with primibrachials 1 and 2, moderately convex transversely and longitudinally. Tegmen strongly arched, plates numerous, 50 to 60, size small to medium, moderate to pronounced central bulbous elevation on each plate. Anal opening protruded, surrounded by 7 to 9 small bulbous plates bearing facets for higher circlet of plates forming short anal tube. Measurements given in Table 6.

Remarks.—There is variation in the relative length of the theca to the tegmen, amount of tegmen arching, and number and arrangement of tegmen plates among the five specimens of *Aacocrinus algeriaensis* n. sp. Preservation of all specimens is only moderate as weathering processes have etched the surface destroying much of the ornamentation and stem facets. Specimens show numerous fractures following rhombohedral cleavage planes.

Aacocrinus algeriaensis belongs to the lineage of *Aacocrinus* that has four arms per ray at the thecal rim, such as *A. chouteauensis* (S.A. Miller, 1891b) or *A. tetradactylus* Brower, 1967. It is an advanced form of the genus showing reduction of the number of interbrachial plates in the theca, from five to three, and a relatively shorter calyx and longer tegmen.

This is the youngest known occurrence of *Aacocrinus*. It is the first report of the genus from Northern Africa. The genus attained its acme during the Kinderhookian of North America. It has also been reported from the Tournaisian or Viséan of Australia (Webster and Jell, 1999a) and the Osagean of North America (Brower, 1967; Webster and Lane, 1987).

Material.—Five specimens: Holotype, RGM 361 178, and paratypes 1–4, RGM 361 179–RGM 361 182 from the upper part of the Hassi Kerma Formation, Pennsylvanian (middle Bashkirian), at Oglat Hamia; Legrand-Blain collection.

Etymology.—Named for Algeria.

Aacocrinus algeriaensis?

Remarks.—Two globose internal molds show the outlines for the same plate arrangement of the theca as described for *Aacocrinus algeriaensis* except the anitaxis is 1-2-4-2. This is probably intraspecific variation. The molds show the four ambulacral tracks merging into two immediately inside the tegmen then continuing along the roof of the tegmen merging toward the mouth at a central junction next to the anus. The anus would have protruded above the mouth, probably as a short anal tube or projection on the tegmen. Unfortunately the number and arrangement of tegmen plates are unknown. Because of this, plus the lack of all calyx plates to determine ornamentation, the spec-

Table 7.—Measurements in mm for *Sampsonocrinus cheguigaensis* n. sp.

	Type		
	Holotype	Paratype 1	Paratype 2
	Spec. no. (RGM)		
	361 185	361 186	361 187
Thecal length	15.5	14.4	12.6
Thecal width	23.6	21.2	17.8
Calyx length	9.0	8.1	8.8
Calyx width	17.0	14.2	13.3
Diameter basal circlet	5.0	5.2	4.4
Radial length	3.4	4.1	3.4
Radial width	5.7	5.7	4.5
First primibrachial length	2.7	2.1	1.9
First primibrachial width	5.1	4.6	3.3
Second primibrachial length	2.2	2.0	1.5
Second primibrachial width	3.6	3.5	2.5
Primanal length	4.6	4	3.4
Primanal width	4.1	3.5	3.1
Diameter stem impression	3.3	2.0	2.7

imens are questionably referred to *Aacocrinus algeriaensis.*

Material.—Two specimens, RGM 361 183 and RGM 361 184, from the upper part of the Hassi Kerma Formation, Pennsylvanian (middle Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Genus SAMPSONOCRINUS Miller and Gurley, 1895

Sampsonocrinus cheguigaensis, new species

Plate 5, figures 1–19; Plate 6, figures 1–15

Diagnosis.—Distinguished by flaring with axillary secundibrachial and tegmen formed of many small nodose plates.

Description.—Theca small, globose, arms strongly grouped, protruded, pentalobate in oral view. Cup bowl-shaped, wider than long, sharp multiple ridge stellate ornament of ray ridges, circular rings around radial circlet and primibrachial circlet extending across interprimibrachials, and diagonal ridges from radials across interprimibrachials and anals. Basal circlet flat proximally, distal tips upflared, visible in side view; formed of 3 subequal plates, with thickened ridge surrounding stem facet. Radials 5, wider than long, outflared at 45°, gently convex longitudinally and transversely; A, C, and D pentagonal with 1 suture with basal plate; B and E hexagonal with 2 sutures with 2 basal plates. Primanal longer than wide, gently convex longitudinally and transversely; anitaxis 1–2–3 to 5 (4 most common)-tegmen plates. First primibrachial wider than long, quadrangular to hexagonal depending on contacts with interprimibrachials laterally, rarely axillary. Axillary second primibrachial wider than long, pentagonal to heptagonal depending on contacts with interprimibrachials on distal shoulders and contact with intersecundibrachial. Axillary secundibrachials wider than long, normally hexagonal adjoining one interprimibrachial on both sides, rarely pentagonal not adjoining an interprimibrachial on one side, outflaring. Interprimibrachial series 1–2-variable number of tegmen plates; first interprimibrachial large, approximately equidimensional, hexagonal. Intertertibrachial elongate, slender, adjoining 2 tegmen ambulacrals distally. Tegmen moderately arched, plates very tumid, tumidity increasing distally; ambulacrals small, numerous at ambulacral opening, increase in size distally; interambulacrals with single large plate in line of thecal rim followed by 3 smaller and then 2 to 4 larger plates distally. Vertically directed anal opening excentric, surrounded by 6 or 7 very tumid to nodose plates. Stem impression circular; facet with wide crenularium, narrow areola, wide pentalobate axial canal. Measurements given in Table 7.

Remarks.—Variation is noted among the 74 specimens of *Sampsonocrinus cheguigaensis* n. sp. in the amount of inflation of the tegmen from less than half to more than half the thecal length. A predominance of quadrangular and pentagonal primibrachials occurs in the higher cups, whereas hexagonal primibrachials predominate in lower cups as is normal for other species of *Sampsonocrinus.* Cups of *S. cheguigaensis* are rarely composed of primibrachial plates all of one shape. Quadrangular and hexagonal plates do not occur in the same cup. Cup length is controlled primarily by the relative lengths of the first interprimibrachial and first primibrachial plates. Another morphologic feature that may control cup length in some of the actinocrinoids is the position of flaring of the arms.

which is consistently at the axillary secundibrachials on *S. cheguigaensis*. In older species of the genus the fixed arms in the cup begin to flare with the axillary primibrachial. The numerous small plates of the tegmen also distinguish *S. cheguigaensis* from other species.

The axillary first primibrachial occurs in the A ray on specimen RGM 361 196, the B ray on specimen RGM 361 197, and the C ray on specimen RGM 361 193. Because these are collections and not populations it is uncertain if these are abnormal specimens or if they reflect genetic variability within the species.

The number of free arms at the tegmen ring varies from four to six. Specimens from Foum ech Cheguiga and Teniet Aissa ben Azzi consistently have six arms, whereas specimens from Chebket Mennouna are variable. It is uncertain if the variation is the result of loss by weathering, growth stage, or actual number of free arms at the tegmen ring. Where six arms are present, the fifth and sixth arms are developed along the outer half of each half ray and first appear as small impressions of the ambulacral tract in the plates along the sides of the brachial plates. These subordinate ambulacral tracts appear to join the main ambulacral tracts above the impression within the axillary brachial.

The 48 specimens from north of Chebket Mennouna are not as well preserved as those from Foum ech Cheguiga or Teniet Aissa ben Azzi. Stellate ray ornament on the Foum ech Cheguiga and Teniet Aissa ben Azzi specimens is obvious, whereas that on the Chebket Mennouna is vague on a few, and obliterated on most, specimens. This is interpreted as a taphonomic difference among the three collections. The best preservation of the ornament on the Chebket Mennouna specimens is commonly in relatively sheltered areas around the flared brachials, but variation is noted on the degree of sharpness of the ornament among the specimens. Based on this, the Chebket Mennouna specimens apparently remained at the sediment-water interface for a greater length of time than those from Foum ech Cheguiga or Teniet Aissa ben Azzi.

This is the first report of *Sampsonocrinus* from the late Bashkirian and the first known from northern Africa. The genus previously was reported from the Kinderhookian and Osagean of North America, late Tournaisian of England, late Tournaisian and early Viséan of Ireland, and ?Viséan of Australia. The European species have been assigned to a new genus *Thinocrinus* by Ausich and Sevastopulo (2001).

Material.—Seventy four specimens, all from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian) in age; Pareyn collection. Holotype, RGM 361 185, Paratypes 1–7, RGM 361 186–RGM 361 192, mentioned specimen RGM 361 193, and two lots (RGM 361 194, 2 specimens; RGM 361 195, 8 specimens) from Foum ech Cheguiga. Two mentioned specimens (RGM 361 196, RGM 361 197), three listed specimens (RGM 361 198–RGM 361 200), one figured specimen (RGM 361 201), plus 42 specimens (lot RGM 361 202) are all from north of Chebket Mennouna. Two specimens (lot RGM 361 203) are from south of Teniet Aissa ben Azzi. Five specimens (RGM 361 204) are probably from Foum ech Cheguiga.

Etymology.—The species name refers to Foum ech Cheguiga where the type specimens were found.

Genus **BLAIROCRINUS** S.A. Miller, 1891a

Remarks.—*Blairocrinus* is known from North America, represented by a Kinderhookian species (*B. trijugis* S.A. Miller, 1891a) and an undesignated Osagean specimen (*B.* sp. Lane and Dubar, 1983) and from Japan by a Desmoinesian specimen questionably referred to the genus (*B.?* sp. Hashimoto, 2001). Lane *et al.* (1997) reported the genus *Blairocrinus* from Late Devonian (Famennian) rocks in northwestern China. Waters *et al.* (2003) reexamined this material and noted that the first primibrachials were either pentagonal or hexagonal. In both cases, however, the primibrachials appeared quadrangular because the pentagonal or hexagonal shape was created by very small truncations of the distal corners for contact with interbrachial plates. Consequently, Waters *et al.* (2003) placed the specimen in *Actinocrinites*. This is the first report of the genus from the Early Pennsylvanian.

Blairocrinus grafensis, new species

Plate 4, figures 13–15

Diagnosis.—Distinguished by a much wider calyx and tumid rather than nodose or spinose tegmen plates.

Description.—Theca ovoid, much wider (31.4 mm) than long (19.7 mm), tegmen arched as much above thecal rim as medium bowl-shaped calyx length below rim, pentalobate in oral view. Basal circlet flat, 6.5 mm diameter, formed of 3 subequal plates, not visible in lateral view. Radials 5, wider (7.8 mm) than long (5.5 mm), hexagonal where in contact with 1 basal or heptagonal where in contact with 2 basals, widely outflared, barely visible in lateral view. Primanal hexagonal, length 5.9 mm, width 5.1 mm, in line of radials; anitaxis 1-2-3-tegmen plates. Primibrachials 2; first primibrachial quadrangular, wider (6 mm) than long (4.5 mm); second primibrachial axillary, wider (6.9 mm) than long (3.5 mm), hexagonal where in contact with 2 interprimibrachials or heptagonal where in contact with 3 interprimibrachials. Secundibrachial axillary, wider than long, normally pentagonal, hexagonal if in contact with 3 interbrachials. First tertibrachial on outer half of half ray axillary; second tertibrachial on inner half of half ray nonaxillary. Arms free above second tertibrachial, 8 arms per ray at tegmen ring. Interprimibrachial series 1–2-tegmen. Intersecundibrachial slender, elongate. Tegmen plates tumid; ambulacral plates very small and numerous above ambulacral openings increasing to medium size distally; interambulacral plates very small above interprimibrachials increasing to medium size distally; excentric anal opening on anal tube of indeterminate length at tegmen summit. Axial canal pentalobate. Stem and distal arms unknown.

Remarks.—The calyx of *Blairocrinus grafensis* n. sp. is inflated in the C ray, and the tegmen is inflated in the posterior, giving the specimen an asymmetrical, unbalanced appearance. Solution weathering has destroyed plate ornament except along the thecal rim. Ambulacral openings of the eight arms at the tegmen ring are preserved only on the D ray. In lateral view the ambulacral openings appear to alternate in size (small-intermediate-small-large) from the outer to inner part of the half ray (Plate 4, figure 13). Branching occurs along both sides of the outer arms of each half ray above the secundibrachials. It is unknown if the largest ambulacral opening on the inner arm of the tertibrachials and the intermediate-sized ambulacral opening on the outer part of the same half ray represent the coalesced ambulacral tracts of one or more distal branchings within the free arms leading to these openings or if they simply are larger than the other arms of that half ray at the tegmen ring. It is also unknown if the size of the openings corresponds to the relative number of distal branchings. The calyx is much wider, and the tegmen is not nodose or spinose and much shorter in *B. grafensis* than that of the only other species *B. trijugis* Miller, 1891a, from the Mississippian (Osagean) of North America.

Material.—Holotype RGM 361 205 from the upper part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian, R; Pareyn, 1961), from south of Teniet Oum el Graf; Pareyn collection.

Etymology.—The species name refers to Teniet Oum el Graf where the specimen was found.

Genus **PIMLICOCRINUS** Wright, 1943

Pimlicocrinus octobrachiatus, new species
Plate 7, figures 1–11

Diagnosis.—Distinguished by eight arms where free and coarse nodes on distal tegmen plates.

Description.—Theca medium size, pear-shaped in lateral view, pentalobate in basal or oral view with strongly grouped arms projecting horizontally; tegmen highly inflated with central anal opening on anal tube of unknown length at summit. Calyx discoid to shallow, wide bowl shape, all plates strongly inflated with stellate ornament with apical pits. Basal circlet tripartite, 3 subequal plates, proximally bearing circular stem facet, horizontal to slightly upflared distally. Radials 5, pentagonal (A, D, C) or hexagonal (B, E), wider than long, subhorizontal to weakly upflared, D radial more equidimensional. Primanal hexagonal, approximately equidimensional, in radial circlet; anal series 1-2-5-tegmen plates. Primibrachials 2; first primibrachial wider than long, rectangular, pentagonal, or hexagonal, may be in contact on distal shoulders with 1 or 2 interprimibrachial plates; second primibrachial wider than long, axillary, pentagonal, hexagonal, or heptagonal, laterally in contact with 1 or 2 interprimibrachials. Tertibrachials 1 per ray, axillary, wider than long, normally pentagonal, hexagonal if intertertibrachial present. First quartibrachial nonaxillary in inner half of ray, axillary in outer half of ray. Second quartibrachial axillary in inner half of ray. Arms 8 per ray, projecting horizontally to slightly downflaring, free above branchings on second quartibrachial. Interprimibrachial plates large, series 1–2-tegmen. Single intertertibrachial not common, very small. Tegmen tapers distally; plates increase in size distally, very tumid or with very coarse nodes on all distal plates. Ambulacral plates above ambulacral openings small, increasing in size distally; ambulacral plates smaller than interambulacral plates proximally, forming rounded covering above arm bases. Tegmen summit capped by 6 or 7 larger plates followed by smaller plates forming anal tube. Proximal columnal circular in transverse section, narrow crenularium and areola, wide lumen round, rounded latus. Free arms and distal stem unknown. Measurements given in Table 8.

Remarks.—*Pimlicocrinus octobrachiatus* n. sp. differs from the three English species (Wright, 1955) and the three Chinese species (Chen and Yao, 1993) by having coarser nodes on the distal tegmen plates and eight arms where free. In addition, the shape of the theca differs from that of some of the species. The theca is relatively higher in *P. octobrachiatus* than in *P. latus* Wright, 1955. *Pimlicocrinus* has been reported from the Tournaisian of England (Wright, 1955) and China (Chen and Yao, 1993), Pennsylvanian (Namurian and Moscovian) of Spain (Breimer, 1962), and Moscovian of Morocco (*fide* Breimer, 1962, p. 82).

Preservation of the specimens is good to poor. Ornamentation commonly has been modified or destroyed, presumably by solution and abrasion processes. The tips of the fixed arms rarely are preserved beyond the tertibrachials.

Material.—Eight specimens from the Pennsylvanian (upper Bashkirian) Oued el Hamar Formation; Pareyn collection. Holotype (RGM 361 206), paratype 2

Table 8.—Measurements in mm for *Pimlicocrinus octobrachiatus* n. sp.

	Type		
	Holotype	Paratype 1	Paratype 2
		Spec. no. (RGM)	
	361 206	361 207	361 208
Thecal length	23	21.5	26
Thecal width (maximum)	28.7	29.2	35.9
Tegmen length (incomplete)	16.8	13.6	16.4
Diameter basal circlet	6.1	7.3	7.4
Radial length	3.7	4.1	5.4
Radial width	6.6	6.6	8.2
First primibrachial length	3	3	4.2
First primibrachial width	5.5	6	6.4
Primanal length	4.6	4.8	5.1
Primanal width	4.3	4.8	5
Diameter proximal columnal		4.1	

(RGM 361 208), paratype 4 (RGM 361 210), and specimen (RGM 361 211) are from the north flank of Chebket Mennouna. Paratypes 1 (RGM 361 207) and two specimens (lot RGM 361 212) are from southwest of Djebel Horreit. Paratype 3 (RGM 361 209) is from south of Teniet Aissa ben Azzi.

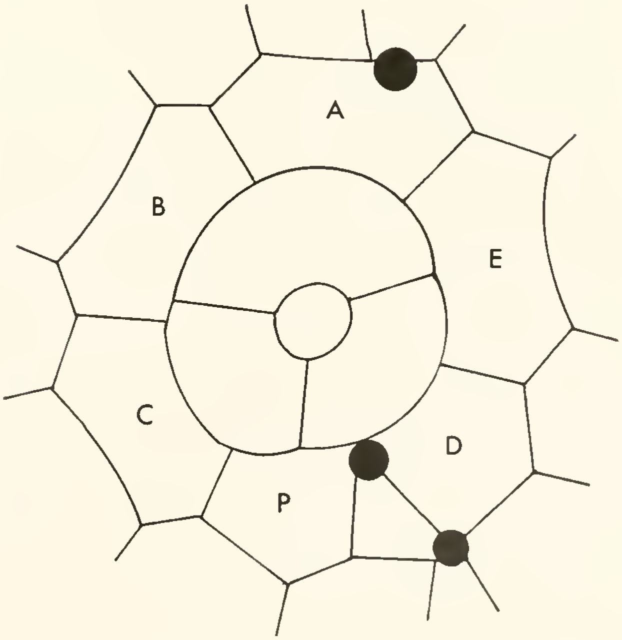
Etymology.—*Octobrachiatus*, Greek, refers to eight arms where free.

Pimlicocrinus sp.

Plate 7, figures 18, 19

Description.—Calyx medium size, 23 mm long (incomplete), 26.7 mm wide, pear-shaped in lateral view, pentalobate in basal or oral view with weakly grouped arms. Calyx discoid, subhorizontal, sutures deeply impressed, all plates strongly tumid. Basal circlet small, 7.4 mm diameter, subhorizontal, with 1.7 mm circular invagination for stem attachment. Basals 3, subequal, length 3.2 mm, width 4.9 mm. Radials 5, wider (5.9 mm) than long (2.9 mm), hexagonal, slightly elevated above basal circlet; D radial more equidimensional. Primanal in radial circlet, pentagonal, length 3.2 mm, width 3.6 mm; anal series 1-2-5-tegmen. Primibrachials 2; first primibrachial hexagonal, second primibrachial hexagonal or heptagonal depending on number of interray plates in contact. First secundibrachial wider than long, nonaxillary. Second secundibrachial wider than long, normally nonaxillary, may be axillary in anterior half of D ray. Arms 4 per ray where free, minimum 20 total, project downward slightly at base of free arms. Tegmen highly inflated, tapering distally; all plates bulbous, bearing coarse nodose ornament; ambulacral plates elevated above intervening interambulacral areas. Anal opening probably central at distal end of tegmen, not preserved. Free arms and stem not preserved.

Remarks.—There are three small circular borings, each 2 mm diameter, of an unknown organism on the calyx of *Pimlicocrinus* sp. (Text-fig. 4; Pl. 7, fig. 19). One is at the junction of the D radial, primanal, and basal circlet and may have resulted in deformation of the D radial. The second boring is between the D radial and first primibrachial toward the anal side. A third boring is between the A radial and the first primibrachial toward the E ray side. All borings are filled with matrix, and it is uncertain if they completely penetrate the plates or not. All are located at plate sutures, one



Text-figure 4.—Plate diagram of lower part of calyx of *Pimlicocrinus* sp. showing location of drill holes. Central stem impression surrounded by tripartite basal circlet. A ray at top. Radials—A through E, primanal—P, drill holes—black circles.

a triple junction, and suggest selection of the boring site was made by the boring organism at points of weakness of the calyx. All of these sites were well below the anal opening and made while the crinoid was living. Baumiller (1990) documented gastropod drilling of crinoid tegmens. Although he did not specifically note that the drilling occurred at triple junctions, it would appear that most of the drillings he illustrated were situated at plate junctions, mostly triple junctions. Donovan (1991) illustrated a cup of *Synbathocrinus conicus* from the Mississippian of England with a boring site at a triple junction, which resulted in a deformation of the cup. He suggested that this site was located in a protected position, well elevated, and up current. We agree that the boring site would have been up current in an elevated position, but it depends upon the living orientation of the crinoid as to how direct the exposure was within the current.

The calyx lacks parts of A and E rays above the base of the arms and the distal part of the tegmen. Abrasion has obliterated most of the ornament on the cup and the tegmen. The four arms per ray distinguish *Pimlicocrinus* sp. from the eight arms per ray of *P. octobrachiatus*. This is not thought to be a growth stage difference because comparable and smaller specimens of *P. octobrachiatus* have eight arms per ray.

Material.—Figured specimen RGM 290 871 is from the Pennsylvanian (upper Bashkirian) Oued El Hamar Formation, lower member limestone above level ML176 at Mouizeb El Atchane, 300 m north of Béchar; Winkler Prins collection.

Actinocrinitids indeterminate

Remarks.—Several specimens of actinocrinitids are similar to *Sampsonocrinus*, but are incomplete or so poorly preserved that they are unidentifiable with certainty below the family level. They are mentioned for completeness of the fauna.

Actinocrinitid indeterminate 1

Remarks.—Two unfigured weathered thecae (lot RGM 361 213) with nodose tegmen plates similar to those of *Sampsonocrinus* are from the Oued el Hamar Formation, southwest of Djebel Horreit; Pareyn collection.

Actinocrinitid indeterminate 2

Plate 4, figure 12

Remarks.—One partial calyx (RGM 361 214) lacking the D ray plates and most plates of the thecal rim, possibly belonging to *Sampsonocrinus*, is from the Chabet Kerkour Formation (= Aïn Guettara Member) at Iaouerta, southwest of Djebel Horreit; Pareyn collection.

Actinocrinitid indeterminate 3

Plate 4, figures 10, 11

Remarks.—One abnormal partial theca, lacking the D ray and anal interray, has a small narrow extra plate in the B ray of the basal circlet, two primibrachials, an axillary secundibrachial, an axillary tertibrachial on the outer half ray, and two nonaxillary tertibrachials on the inner half ray. The arms flare with the axillary second primibrachial and are free above second tertibrachial or first quartibrachical. There are six arms per ray where free and the tegmen plates are all tumid to nodose. The tegmen is approximately the same length as the calyx. It is possibly a *Sampsonocrinus*. The specimen (RGM 361 251) is from the upper part of the Oued el Hamar Formation, Pennsylvanian (Bashkirian), at Foum ech Cheguiga; Pareyn collection.

Actinocrinitid indeterminate 4

Plate 7, figures 12–17

Remarks.—Five tegmen fragments, perhaps from the same specimen, consist of numerous small variable-sized bulbous to blunt-spined polygonal plates. The largest specimen (RGM 361 216) formed less than $\frac{1}{5}$ of the tegmen and is formed by more than 50 plates. One specimen (RGM 361 220) has several very small elevated ambulacral plates along one edge that are the outflared thecal rim plates immediately above the ambulacral openings of one ray. Two specimens (RGM 361 216, RGM 361 218) lack the very small ambulacral plates, but have the converging smooth ambulacra trackways on the interior. Specimen RGM 361 217 has three plates along one edge that bordered the anal opening, which would have been ventrally directed and projected as an anal tube of undetermined length.

These tegmen fragments are much larger and have higher bulbous to spinous surfaces than those of *Aacocrinus algeriaensis*. The tegmen would have contained many more plates than that of *A. algeriaensis*. Features preserved in these fragments show general morphology common to the aacocrinids and actinocrinids, thus they are conservatively referred to the actinocrinitids.

Material.—Five fragmentary specimens, RGM 361 216–RGM 361 220, from the upper part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Actinocrinitid? indeterminate 5

Remarks.—One tripartite basal circlet, 3.9 mm long, 9.6 mm diameter, has irregular anastomosing ridge ornament surrounding the stem facet, has a pentalobate axial canal, and retains the proximal and part of the second columnal.

Material.—Basal circlet, RGM 361 221, from the top of the Djenien Formation, Late Mississippian (Serpukhovian, E2), at Chebket Djihani; Pareyn collection.

Suborder **GLYPTOCRININA** Moore, 1952

Superfamily **PLATYCRINITACEA** Austin and Austin, 1842

Family **PLATYCRINITIDAE** Austin and Austin, 1842

Genus **PLATYCRINITES** J. S. Miller, 1821

Remarks.—Approximately 175 named species, based on cups and crowns, currently are assigned to *Platycrinites* (Webster, 2003). All Silurian and most Devonian species assigned to the genus were judged not to belong to *Platycrinites* but were not reassigned (see Lane *et al.*, 2001). Slightly over 100 species of *Platycrinites* are of Tournaisian and early Viséan age, with most reported from North America (70 species) and Europe (23 species), followed by China (6 species), Australia (1 species), and Japan (1 species). Even though some of the North American and European Tournaisian and Viséan species are probably synonyms, this time interval represents the acme of the genus. During this acme, *Platycrinites* was a cosmopolitan equatorial-belt taxon occurring between a maximum of 40° S (Australian block) to 30° N (northern part of the North American block), based on paleogeographic reconstructions of Scotese and McKerrow (1990).

From the late Viséan through the Guadalupian only 14 named species have been reported world wide, with 10 of these between the Mississippian (late Viséan) and Pennsylvanian (late Bashkirian) from North America (6 species), Scotland (2 species), Russia (1 species), and Morocco (1 species). Permian species are known from Canada (1 species), Russia (1 species), Australia (1 species), and Timor (1 species). A number of unnamed species based on cups, crowns, and columnals have been reported from this same time interval from these same areas. An excellent review of the columnals assigned to *Platyplateium* Moore and Jeffords, 1968, and *Platycrinites* for this time interval was given by Bowsher and Strimple (1986).

Species of *Platycrinites* from Algeria occur in five horizons from the basal part of the Late Mississippian (Serpukhovian) into Pennsylvanian (basal Bashkirian) strata. Thus they provide significant new information about the genus during a time interval when relatively few species are known elsewhere. The species are considered part of an evolutionary lineage that probably evolved from one of the Tournaisian or Viséan taxa of *Platycrinites* with nodose ornament illustrated by Wright (1956), such as *P. granulatus* Miller, 1821, and *P. striatus* Miller, 1821, from Tournaisian strata of Ireland, or from one of the numerous spinose or nodose species illustrated by Wachsmuth and Springer (1897), such as *P. hemisphericus* (Meek and Worthen, 1865), *P. nodostriatus* (Wachsmuth and Springer, 1897), *P. pocilliformis* (Hall, 1858), *P. spinifer* (Wachsmuth and Springer, 1897), *P. spinifer elongatus* (Washsmuth and Springer, 1897), and *P. verrucosus* (White, 1865), among others, from North America.

Nodes, anastomosing coalesced nodes, and ridge ornament on the cups of Carboniferous species of *Platycrinites* show an extreme range of development, including a few aligned nodes (*P. parvinodus* (Hall, 1861)), many aligned nodes (*P. pocilliformis* (Hall, 1858)), many aligned granules (*P. ornogranulus* (McChesney, 1860)), aligned very coarse nodes to blunt spines (*P. verrucosus* (White, 1865)), aligned to anastomosing coalesced nodes (*P. saffordi* (Hall, 1858)), parallel ridges (*P. regalis* (Hall, 1861)), and more. Several patterns within this wide range of ornament development are obvious with only a cursory scanning of the specimens. Multiple types of patterns may occur on a single specimen. These patterns include a variety of types at specific locations on the cup that we interpret to represent morphologic development by the crinoid to thwart platyceratid gastropods or other unwanted organisms from crawling up the stem and across the cup before reaching the base of the arms or the tegmen. Each type is described here, followed by an interpretation for its position.

1. Aligned nodes to ridges around stem attachment: obstruct or discourage organisms from crawling onto the cup.
2. Aligned nodes to ridges radially across the basal circlet from the stem facet to distal edge in interray position: obstruct or discourage organisms from crawling along the interray onto the radials and then onto the tegmen.
3. Aligned nodes to ridges radially across the basal circlet from the stem facet to distal edge in line of ray axes: obstruct organisms from crawling along the ray axes onto the radials and then to the base of the arms.
4. Aligned nodes, ridge, or parallel rows of ridges between stem facet and distal edge or along distal edge of basal circlet: obstruct organisms from crawling onto the radials and thence onto the tegmen or reaching the base of the arms.
5. Aligned nodes to ridges radially along the lateral edges of the radial: obstruct organisms from crawling across the radial to reach the tegmen.
6. Aligned nodes to ridges radially along the axes

of the radial from the proximal edge to the base of the arms: obstruct organisms from crawling across the radial to reach the base of the arms.

7. Aligned nodes, ridge, or parallel rows of ridges along proximal edge to base of arms: obstruct organisms from crawling across the radial to reach the base of the arms.

8. Aligned nodes or ridge forming inverted V from base of radial facet to proximal apices of radials: obstruct organisms from crawling onto the radials and thence onto the tegmen or reaching the base of the arms. This ornament may continue onto the basal circlet.

9. Aligned nodes or ridge along proximal side of radial facet: obstruct organisms from obtaining access to tissue of base of arm.

10. Aligned nodes or ridge along distal edge of radials lateral of facet: obstruct organisms crawling across radial onto tegmen.

11. Radially aligned nodes or ridge on first interambulacral: obstruct organisms crawling across plate onto tegmen.

Nodes or short spines on tegmen plates and the development of anal tubes also are interpreted as obstructions to organisms trying to crawl across and settling on the tegmen. Development of spines on columnals would have been an additional deterent to organisms crawling along or attaching to the stem. Similar node and ridge ornament is found in some of the other genera of the platycrinitids, such as *Eucladocrinus* and *Plemnocrinus*, and probably served the same purposes. The development of nodose plates and stellate ridge ornament among some genera of the glyptocrinids, melocrinitids, rhodocrinitids, coelocrinids, acrocrinids, batocrinids, and actinocrinitids is considered to have served the same purposes as was node development. Genera within each of these taxonomic groups with platyceratids still attached to the calyx have been reported by several authors (Keyes, 1888; Clarke, 1921; Bowsher, 1955a; Yakovlev, 1956, among others). In the Viséan as most of the camerates declined, the platyceratids adapted to living on the cromyocrinids, and continued to do so into the Permian. In the Late Carboniferous the cromycrinids developed nodose ornament similar to that of the more nodose platycrinitids.

Platycrinites reouienensis, new species

Plate 8, figures 1–8

Diagnosis.—Distinguished from non-Algerian Mississippian and Permian species by the combination of the globose theca, tegmen moderately arched, cup bowl-shaped, basal circlet shallow bowl, walls subvertical, radial facets elongate horseshoe-shaped on radial platform, single axillary primibrachial, and anal opening projecting obliquely. Distinguished from other Algerian species by the coarse nodose ornament forming an inverted-V pattern from radial facet to basal-radial apices, aligned along lateral sides of radials, and a few irregular nodes along the proximal part of the radials.

Description.—Theca globose, medium size, length 13.6 mm (crushed inward and laterally), width 16 mm (average). Cup bowl-shaped, length 10.9 mm, width 16 mm (average), walls subvertical, sutures slightly impressed. Basal circlet shallow bowl, 10.5 mm diameter, formed of 3 plates, 2 larger of equal size, smaller in EA interray; proximal tips downflared below stem facet in shallow impression or basal concavity, distally upflared forming 3.5 mm of cup length; with coarse nodes aligned along interrays and less aligned along distal sides of plates. Radials 5, 8.3 mm long, 8.6 mm wide, widest at distal end of interradial sutures, moderately convex longitudinally and transversely; ornamented with coarse nodes forming inverted V from radial facet to basal-radial apices, aligned along lateral sides of radials, and a few irregular nodes along the proximal part of radials. Radial facet angustary, narrow, elongate, horseshoe-shaped, on slight radial platform, subvertical to slightly upward projecting. Single primibrachial axillary, overlapped laterally by first secundibrachials. Arms unknown, minimum 2 per ray. Tegmen crushed, proximal plates bulbous, distal plates with very coarse nodes; ambulacral plates small adjacent to ambulacral openings, distally become larger; interambulacrals with single large plate followed by 3 smaller plates and medium to larger plates distally. Anal opening separated from radials minimally by single row of small plates, may have had short anal tube. Opening projecting obliquely well below radial summit. Stem facet circular, 2 mm diameter, concave. Axial canal weathered, probably pentalobate.

Remarks.—The tegmen is crushed, with plates of the anterior side doubled against one another and projected over the AB interray on the holotype (RGM 361 222) of *Platycrinites reouienensis* n. sp. Before crushing, the tegmen would have been moderately arched, approximately half the height of the cup. The cup is only slightly distorted with the A radial extended outward. C- and D-ray primibrachials are weathered, and only two are preserved. Small facets on the outer edges of the radial facets are for the outer parts of first secundibrachials. A small holdfast is attached to the posterior side of the radial facet of the E radial. The paratype (RGM 361 223) is uncrushed and shows the large tegmen plates of the moderately inflated tegmen but lacks the plates around the anal opening. Although the specimen is abraded and the nodes on the radials are greatly subdued, it still shows the same pattern as that of the holotype.

Arrangement of the nodose ornamentation of *Platycrinites reouienensis* is similar to, but specimens lack the keels present on, *P. faberi* (Miller, 1889), a Late Mississippian (Meramecian or Chesterian) form from North America. The disarticulated cup plates identified as *P. spinifer elongatus* Wachsmuth and Springer, 1897, by Termier and Termier (1950) from the Viséan of Morroco may have been the progenitor of the younger Algerian species of *Platycrinites* described herein. The Moroccan specimens are not considered conspecific because they have less spinose tegmen plates, finer nodes, and a longer basal circlet than the holotype figured by Wachsmuth and Springer (1897, pl. 67, fig. 7). The Morocco specimens have a longer (*i.e.*, more highly arched) tegmen than the Algerian specimens.

Material.—Two specimens: Holotype, RGM 361 222, (CP52.27b) from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (Serpukhovian, early E1), at Moïzeb Reouïen; Pareyn collection. Paratype, RGM 361 223, from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (Serpukhovian, early E1), at El Aouidja; Legrand-Blain collection.

Etymology.—Named for the locality where the specimen was found, Moïzeb Reouïen.

Platycrinites aouidjaensis, new species
Plate 8, figures 20, 21

?*Platycrinus spinifer elongatus* (Wachsmuth and Springer, 1897). Termier and Termier, 1950, p. 86, pl. 226, figs. 36–37.

Diagnosis.—Distinguished from non-Algerian Mississippian and Permian species by the combination of the globose theca, tegmen flat, cup bowl-shaped, sutures flush, basal circlet medium bowl, walls subvertical, radial facets elongate horseshoe-shaped on radial platform, single axillary primibrachial, and anal opening projecting subvertical. Distinguished from other Algerian species by the combination of the irregularly spaced coarse nodose ornament, which may form a poorly developed inverted-V pattern from radial facet to basal-radial apices, a ring of nodes surrrounding the stem facet, and a flat tegmen.

Description.—Theca globose, large, length 22.2 mm (distal apex not exposed), width 24.6 mm, pentagonal in basal view. Cup medium bowl-shaped, length 17.7 mm, width 24.6 mm, base truncated for stem attachment, distal half of walls subvertical, sutures flush. Basal circlet medium bowl, 16.9 mm diameter, 7.6 mm length, plates fused, proximal tips subhorizontal for stem attachment, distally upflared at approximately 45°; with coarse nodes aligned along midline of interrays, ringed around stem facet, and some irregular. Radials 5, 6.5 mm long, 8.2 mm wide, widest at distal end of interradial sutures, moderately convex longitudinally and transversely; ornamented with coarse nodes irregularly spaced to forming poorly developed inverted Vs radiating from the radial facets to the basal radial apices. Radial facet angustary, narrow, elongate, horseshoe-shaped, on slight radial platform, subvertical to slightly upward projecting, laterally bear small facets for ends of first secundibrachials. Arms unknown, minimum 4 per ray. Tegmen flat, one-fourth length of cup, plates large with coarse nodes; ambulacral plates small adjacent to ambulacral openings, distally larger; interambulacrals with single large plate followed by 3 smaller (but large) node-bearing plates distally. Inflated anal area affecting subjacent radials, visible in basal view as obvious bulge in CD interray. Anal opening separated from radials minimally by single row of small plates, on anal tube of indeterminate length; opening projecting subvertical below radial summit near rim of tegmen. Stem facet circular, 4.8 mm diameter, concave areola.

Remarks.—The holotype (RGM 361 224) of *Platycrinites aouidjaensis* n. sp. is well preserved, with matrix covering most of the tegmen. The paratype (RGM 361 225), similarly preserved, has lost the basal circlet and proximal parts of some radials but shows the anal opening. A single radial (RGM 361 226) assigned to *P. aouidjaensis* shows the proximal ends of four ambulacral grooves on the interior and retains the triangular-shaped axillary primibrachial and axillary single secundibrachials. The facets for the tertibrachials on the outer half of the ray are much smaller than those for the tertibrachials on the inner half of the ray, perhaps implying that the inner ones branch again. If so, there would be six arms per ray.

Platycrinites aouidjaensis is distinguished from *P. reouienensis* by the flat rather than moderately arched tegmen, medium rather than shallow bowl-shaped basal circlet, poorly developed inverted-V nodes rather than aligned nodes on the radials, presence of a ring of nodes around the stem facet, and flush sutures.

Material.—Three specimens. The holotype (RGM 361 224, measured specimen) is from the Mouïzeb el Atchane Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E2), from Teniet el Aouidja. The paratype (RGM 361 225) was found between the Djenien and El Guelmouna formations, probably from the Mouïzeb el Atchane Member of the Aïn el Mizab Formation, Mississippian (Serpukhovian, E2), from Teniet el Aouidja. A partial radial (RGM 361 226) is from the Mouïzeb el Atchane Member of the Aïn el Mizab Formation, Mississippian (Serpukhovian, E2), from the ravine at Djenien. All Pareyn collection.

Etymology.—Named for the locality where the specimens were found, Teniet el Aouidja.

Platycrinites djihaniensis, new species

Plate 8, figures 14–19

Diagnosis.—Distinguished from non-Algerian Mississippian and Permian species by the combination of the globose calyx, tegmen low flat, cup bowl-shaped, basal circlet shallow bowl, walls subvertical, radial facets elongate horseshoe-shaped on radial platform, single axillary primibrachial, and anal opening projecting obliquely. Distinguished from other Algerian species by the combination of coarse nodose ornament forming inverted V from radial facet to basal-radial apices, aligned nodes along lateral sides of radials, nodes forming an inverted T below the radial facet along the ray axis, and anal opening projecting obliquely.

Description.—Theca globose, small, length 14.6 mm, width 16.3 mm, base flat, tegmen low flat, circular in oral view. Cup bowl-shaped, length 19.4 mm, width 16.3 mm, walls subvertical at top, sutures slightly impressed. Basal circlet fused, shallow bowl, 11.4 mm diameter, length 3.1 mm, with coarse nodes aligned along interrays, ringing stem facet and forming a T in central part of each ray. Radials 5, 8 mm long, 8.8 mm wide, widest at distal end of interradial sutures, moderately convex longitudinally and transversely; ornamented with coarse nodes forming inverted V from radial facet to basal-radial apices, aligned along lateral sides of radials, and forming an inverted T below the radial facet along the ray axis. Radial facet angustary, narrow, elongate, horseshoe-shaped, upward projecting 20° above horizontal; with single axillary primibrachial overlapped laterally by first secundibrachial. Arms unknown, minimum 2 per ray. Tegmen low, flat topped, plates with very coarse nodes to short spines; ambulacral plates small adjacent to ambulacral openings, distally become larger; interambulacrals with single large plate followed by 2 or 3 smaller plates and larger plates distally. Anal opening separated from radials by single large interambulacral followed by minimum of 1 row of small plates, may have had short anal tube, with opening projecting vertically. Stem facet circular, 2.9 mm diameter, shallowly concave, wide crenularium and areola, pentalobate axial canal.

Remarks.—*Platycrinites reouienensis, P. aouidjaensis,* and *P. djihaniensis* n. sp. are closely related. *Platycrinites aouidjaensis* and *P. djihaniensis* probably are derived from *P. reouienensis* by flattening of the tegmen, increased development of the nodose ornament, and slight differences in plate sizes and arrangement leading to the anal opening. The radial facets of *P. djihaniensis* are considerably more upflaring than those of *P. reouienensis* and *P. aouidjaensis,* whereas the basal circlet is relatively longer, and the pentagonal outline in oral view is best developed on *P. aouidjaensis.* The nodose ornamentation of the tegmen of *P. reouienensis, P. aouidjaensis,* and *P. djihaniensis* separates them from the bulbous ornament of the tegmen of *P. hamarensis* n. sp.

Material.—Two specimens: holotype (RGM 361 227) and paratype (RGM 362 228) are from the top of the Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani; Pareyn collection.

Etymology.—Named for the locality where the specimens were found, Chebket Djihani.

Platycrinites cf. **P. djihaniensis**

Plate 8, figures 11–13

Remarks.—One fused partial basal circlet, one nearly complete radial, and two partial radials have the same basic nodose ornamentation pattern as *P. djihaniensis,* except the nodes are much more numerous between the interray aligned nodes forming triangles within triangles on the basal circlet and radials, the radial facets are relatively narrower with respect to the width of the radial, and the basal circlet is more upflaring. These specimens may represent a variant of *P. djihaniensis* or a different species. Because the tegmen is unknown, all specimens are disarticulated, and most are fragmentary, they are referred to *P. djihaniensis.*

Material.—Four specimens, a partial basal circlet (RGM 361 229), 1 nearly complete (RGM 361 230) and 2 partial radials (RGM 361 231, RGM 361 232), from the top of the Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani; Pareyn collection.

Platycrinites hamarensis, new species

Plate 9, figures 15–22

Diagnosis.—Distinguished from non-Algerian Mississippian and Permian species by the combination of the globose calyx, tegmen moderately arched, cup bowl-shaped, basal circlet very shallow bowl, walls subvertical, sutures impressed, radial facets wide horseshoe-shaped, single axillary primibrachial, and anal opening projecting obliquely. Distinguished from other Algerian species by the combination of coarse irregular nodose and vermiform ornament.

Description.—Theca globose, large, length 17.1 mm, width 19.2 mm, tegmen moderately arched, pentagonal in oral view. Cup medium bowl-shaped, length 8.5 mm, width 15.8 mm, base very shallowly convex, walls subvertical, sutures strongly impressed, plates with broad coarse irregular nodose and vermiform ornament. Basal circlet fused or tripartite, very shallow bowl, 11.2 mm diameter, length 2.5 mm; base with shallow concavity, distal edges upflared, barely visible in side view; azygous basal in E-A interray. Radials 5, large, 10.1 mm long, 10.4 mm wide, widest at distal end of interradial sutures, gently convex longitudinally and transversely, ornament of low broad nodes. Radial facet angustary, wide, horseshoe-shaped, subvertical. Primibrachial small, axillary, triangular in exterior outline, moderately convex transversely, with low broad central node. First secundibrachials much wider than long, laterally extending beyond primibrachial to attach to radial. Second secundibrachial axillary. Minimum 4 arms per ray, free with first secundibrachial. Tegmen plates with very bulbous centers; ambulacral plates small adjacent to ambulacral openings, distally become larger; interambulacrals with single plate followed by 2 or 3 smaller plates and larger plates distally. Anal interray has single large plate, larger than all other first interambulacrals, followed by 3 smaller plates at base of bulbous anal opening slightly above central tegmen summit. Anal opening projecting obliquely at 45°. Stem facet impressed, circular, small, 3.4 mm diameter, moderately concave.

Remarks.—The holotype (RGM 361 233) of *Platycrinites hamarensis* n. sp. lacks a part of the A radial and a small part of the basal circlet but has the protruded anal area. Paratype 1 (RGM 361 234) has a slightly flatter tegmen with more sharply defined ornamentation. Paratype 2 (RGM 361 235) is weathered and has lost part of the anal side of the theca. Paratype 3 (RGM 361 236) is partly embedded in matrix. A fifth specimen (RGM 361 237) is abraded and has a fragment of the basal circlet missing.

Platycrinites hamarensis is distinguished from *P. reouienensis*, *P. aouidjaensis*, and *P. djihaniensis* by its impressed sutures, coarse nodose and vermiform ornament, bulbous tegmen plates, and obliquely projecting bulged anal opening.

Material.—Five specimens. Holotype (RGM 361 233) and paratypes 1–3 (RGM 361 234–RGM 361 236) from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), north flank of Chebket Mennouna; Pareyn collection. Mentioned specimen (RGM 361 237) is from the Hassi Kerma Formation, Pennsylvanian (late Bashkirian), at Oglat Hamia; Legrand-Blain collection.

Etymology.—Named for the Oued el Hamar Formation.

Platycrinites sp. 1

Plate 9, figures 23, 24

Remarks.—A single specimen is referred to *Platycrinites* sp. 1. The specimen is of moderate size with a flat base, gently arched tegmen, outflaring cup walls, pentagonal in oral view, and has medium-coarse nodose ornament forming in three to five semi-aligned rows massed along the interray edges of the radials and single spine alignments below the radial facets. It is poorly preserved, and the radial facets and arm bases are not exposed. The combination of the above features allows recognition as a separate form, probably representing a new species. Lacking knowledge of the arms, it is left in open nomenclature and mentioned for faunal completeness.

Material.—Figured specimen (RGM 361 238) from the upper part of the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), from Foum ech Cheguiga; Pareyn collection.

Platycrinites sp. 2

Remarks.—Three partial radials are abraded or weathered, but still retain some nodes and aligned nodes or ridges. They are possibly variants of *P. djihaniensis*, but so fragmentary they are considered indeterminate.

Material.—Three partial radials (RGM 361 239), all from the top of the Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani; Pareyn collection.

Platycrinites sp. 3

Remarks.—Platycrinitid partial radial with primibrachial and first secundibrachials.

Material.—One partial radial (RGM 362 337), from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar; Winkler Prins collection.

Platycrinites sp. 4

Plate 8, figures 22, 23; Plate 17, figures 1, 2

Remarks.—A large tripartite basal circlet and a smaller fused basal circlet, both with irregular coarse-ridge ornament, are assigned to *Platycrinites*. The nearly circular stem facet is on a pedestal slightly below the exterior level of the circlet and is bordered by a round-based, narrow impressed trough. The irregular ornament is most prominent around the distal margin of the circlet. The small axial canal is pentalobate.

Material.—Two basal circlets (RGM 361 338; RGM 361 339) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar; Winkler Prins collection.

Platycrinites sp. 5
Plate 8, figures 9, 10

Remarks.—Two unornamented platycrinitid twist columnals (from segmented twist stems) with a denticulate fulcal ridge splitting into four finer ridges on distal ends (RGM 361 344).

Material.—Two columnals (RGM 361 344, RGM 361 351), from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar; Winkler Prins collection.

Platycrinites? sp.
Plate 9, figures 25–27

Description.—Calyx medium size, length 20.7 mm, width 23.4 mm, mushroom-shaped, pentagonal in oral view. Cup bowl-shaped, length 9.5 mm (estimated), width 19.5 mm, base shallowly invaginated, walls nearly vertical. Basal circlet tripartite, subhorizontal, 15.8 mm diameter, distal edges slightly upflaring, bearing circular 3.4 mm diameter stem facet. Basals 3, unequal. Radials 5, considerably wider (10.4 mm) than long (6.5 mm estimated), projecting slightly medially for horseshoe-shaped subvertical angustary radial facet, proximally with extended lip for basal-radial suture, internally proximal edges with concave-downward thickening projection to attach to thick distal edges of basals, shoulders extend distally well above radial facet. Radial facets deep. Single axillary primibrachial triangular exteriorly. Secundibrachials deep, short, strongly convex transversely, gently convex longitudinally, minimum of 2 per half ray, bear V-shaped ambulacral groove. First secundibrachial overlaps primibrachial to contact radial facet. Arms 10, minimum, project subhorizontally from radials. Tegmen strongly inflated, projecting laterally beyond radials, formed of numerous medium sized bulbous plates bearing coarse nodose ornament. Single interambulacral plate followed by 3 or 4 plates in tegmen. Anal opening not exposed. Stem facet bears narrow crenularium along outer edge.

Remarks.—The specimen is slightly distorted and cup plates are moderately to deeply abraded, especially along the basal-radial sutures. The assignment to *Platycrinites* is not certain because the anal series is not exposed. The tegmen is similar to that of *P. hamarensis*. Approximately age-equivalent loose radials and basals bearing similar thickenings of the proximal edges of the radials and distal edges of the basals are known from the northwestern part of the People's Republic of China (Lane *et al.*, 1996).

Material.—Figured specimen (RGM 290 857), from the Oued Bel Groun Formation, Moscovian, Bed M1 (Deleau, 1951), from Béchar-Djedid, immediately south of Béchar. Winkler Prins collection.

Genus **PLEUROCRINUS** Austin and Austin, 1843

Emended diagnosis.—A platycrinitid recognized as having five prominent orals, with each of the four smaller orals in contact with the larger central anal oral forming the summit of the tegmen with a variable small number of smaller interambulacral and ambulacral plates between them and the radials, and an anal opening directed laterally.

Remarks.—Genera of the Platycrinitidae commonly are recognized on the position or direction of the anal opening. An exception is *Eucladocrinus* Meek, 1872, recognized by having two main arm-bearing ramules in each ray. The excentric anal opening on *Platycrinites* is commonly on the side of the tegmen slightly above the radials but may occur much higher on the tegmen, with or without an anal tube. *Pleurocrinus* was defined on the presence of a laterally directed anal opening. Otherwise, it is indistinguishable from *Platycrinites*, from which it was derived. The significance of the position of the anal opening, plate structure surrounding it, and overall plate structure of the tegmen with respect to the anal opening is uncertain. Perhaps the position of the anal opening on the edge of the tegmen or on an anal tube was an evolutionary or ecophenotypic morphologic response to avoid being covered by platyceratid gastropods. This suggestion is supported by the absence of drill holes through the tegmen of crinoids with platyceratids positioned above the anal opening and the presence of drill holes through the tegmen with platyceratids attached but not above the anal opening (Lane, 1978; Baumiller, 1990).

All anal openings of *Platycrinites* and *Pleurocrinus* are excentric but the position between the radials and central linear axis is quite variable, sometimes showing variation within a single species. Species assigned to these two genera have a complete gradation from anal openings through the tegmen directly above the radials without intervening small plates, anal openings with small intervening plates, and openings separated from the radials by one or two larger plates with or without small intervening plates, anal openings well above the radials separated from the radials by a series of small to medium plates, to anal openings originating near the radials to well above the radials at the end of a short to lengthy anal tube. Except for one late Viséan species (*P. grandis* Wright, 1938), all other species currently assignable to *Pleurocrinus* are known from the Tournaisian and early Viséan of England, Ireland, and North America (Wright, 1956; Brower, 1970; among others) or the Permian of Timor (Wanner, 1916, 1937).

Review of the nearly 200 species currently assigned to *Platycrinites* and *Pleurocrinus* is beyond the scope of this study. One trend that we recognize, however, is in the number of tegmen plates, which tends to decrease throughout the late Paleozoic range of the Platycrinitidae, with the exception of *Oenochocrinus*, which is an early member with five large orals. Until revision of the Platycrinitidae is made, we recommend that *Pleurocrinus* be defined as having five prominent orals, with each of the four smaller orals in contact with the larger central anal oral forming the summit of the tegmen with a variable small number of smaller interambulacral and ambulacral plates between them and the radials. Five large orals in the tegmen also are present in *Neoplatycrinus* Wanner, 1916, *Oenochocrinus* Breimer, 1962, and *Plemnocrinus* Kirk, 1946, in the Platycrinitidae, as well as a number of camerate and cladid genera, all of which lack the intervening smaller plates or have a greatly reduced number of plates between the radials and the large orals.

It is highly probable that the laterally directed anal openings evolved repeatedly within the *Platycrinites* lineage during the late Paleozoic and that species assigned to *Pleurocrinus* are homeomorphs. This interpretation of *Pleurocrinus* may be supported by analysis of the stem. Devonian and earliest Carboniferous species of *Platycrinites* have a continuous twist stem, which gave rise to the segmented twist stem (Webster, 1997) in the Early Mississippian (Kinderhookian). Both types of stems coexisted until Late Mississippian (Chesterian) when the segmented twist stem prevailed. To our knowledge, all Pennsylvanian and Permian species of *Platycrinites* have the segmented twist stem and the continuous stem type is unknown even as disassociated columnals. The stem of *Pleurocrinus* is unknown except for the proximal-most one or two columnals, which are round to slightly elliptical, probably becoming elliptical distally as in *Platycrinites*. If the Pennsylvanian and Permian species of *Pleurocrinus* were shown to have the segmented twist columnal, it would suggest that the earlier and later species are homeomorphs, there was convergence in the columns, or *Pleurocrinus* species are a repeated variant of *Platycrinites*.

Pleurocrinus glomerosus, new species
Plate 9, figures 1–10

Diagnosis.—Distinguished by having unrounded V-shaped ambulacral grooves, inset radial facets, coarser ornament, and deeply inset sutures.

Description.—Calyx globose, small, length 12.9 mm, width 13 mm, widest slightly above tegmen base, ambulacral openings near midlength, all plates very tumid, sutures impressed, subpentalobate in oral view. Cup bowl-shaped, length 8 mm, width 12.8 mm, base flat, walls vertical, unweathered plates show coarse subdued fluted ridge ornament. Basal circlet discoid, 7.6 mm diameter, very gently upflared distally, bearing small (1.5 mm diameter) stem impression centrally. Basals 3, unequal, azygous in A-E interray, horizontal proximally, gently upflared distally. Radials 5, wider (7.2 mm) than long (5.4 mm), slightly convex longitudinally, moderately convex transversely, forming walls of cup. Radial facet angustary, inset slightly, subvertical, with deep V-shaped ambulacral groove. Single primibrachial axillary, small, triangular exterior, does not fill facet. First secundibrachials wider than long, extend beyond primibrachial to cover radial facet. Arms minimum 2 per ray, at least 10 in total, project horizontally from cup. Primanal large, length 3.5 mm, width 4 mm, adjoined distally by 2 large plates on each shoulder and shares 2 very small plates with larger plates. Anal opening directed obliquely upward, surrounded by 6 large plates and an inner row of 6 disconnected small plates, or variable number of smaller plates, which may form a double row as a rudimentary anal tube. Tegmen highly inflated with flattened summit, extending slightly beyond cup walls above ambulacral openings, with a central large posterior oral at summit surrounded by 6 large and 2 small (in anal interray) plates above large single interambulacral plate in each interray; ambulacral opening bordered by 2 small (1 mm or less) quadrangular plates, 1 to each side of arm mid-point with or without a central small diamond-shaped plate centrally located separating the oral side of the 2 ambulacral tracts joining at the base of the first secundibrachial. Stem and distal arms unknown.

Remarks.—*Pleurocrinus glomerosus* n. sp. is more like Tournaisian and Viséan (Wright, 1956) than Permian species (Wanner, 1916, 1937) assigned to the genus, in that the basal circlet is wide and nearly discoid. It differs from those forms by having a shallow basal invagination, and it differs from all described species in that the ambulacral grooves are unrounded V-shaped, the radial facets are inset, the ornament is coarser, and sutures are deeply inset.

Measurements were made on the holotype (RGM 361 240). All specimens show some degree of abrasion destroying most ornamentation. Paratype 1 (RGM 361 241) shows the primibrachial in two rays and first secundibrachials in one ray. All of the five non-type specimens (lot RGM 290 875) are broken, distorted, or partial calices.

Material.—Eight specimens: Holotype (RGM 361 240), two paratypes (RGM 361 241, RGM 361 242), and five other specimens (RGM 290 875) from the Mississippian (Serpukhovian, Pendleian), marly limestone above DZ12 of the El Guelmouna Formation at Djenien, east of Palmeraie de, before the pass, Béchar; Winkler Prins collection.

Etymology.—Latin meaning like a ball, round, and refers to the globose shape.

Pleurocrinus folliculus, new species
Plate 10, figures 1–8

Platycrinites tuberculatus Miller, J. S., 1821. Termier and Termier, 1950, p. 86, pl. 212, figs. 10, 11.
non *Pleurocrinus tuberculatus* Wright, 1938, p. 278, pl. 10, figs. 1–4.

Diagnosis.—Distinguished by elliptical ambulacral tracts and a greater number of small plates in the tegmen.

Description.—Theca globose, small, length 17 mm, width 17.7 mm, base flat, tegmen moderately arched, pentagonal in oral view. Cup medium flat-based bowl-shaped, length 10.4 mm, width 15.6 mm, walls subvertical, basal-radial sutures impressed, plates with broad coarse irregular nodose and vermiform ornament. Basal circlet fused or tripartite, discoid to very shallow bowl, 9.2 mm diameter, distal edges upflared, barely visible in side view; thickened ridge parallels distal edges; azygous basal in E-A interray. Radials 5, large, 6.4 mm long, 9.5 mm wide, widest at distal end of interradial sutures, straight longitudinally, gently convex transversely, thickest proximally forming ridge overhanging basal circlet. Radial facet angustary, wide, horseshoe-shaped, subvertical, at distal end of radial. Primibrachial small, axillary, triangular in exterior outline, moderately convex transversely. First secundibrachials much wider than long, laterally extending beyond primibrachial to attach to radial. Second secundibrachial, axillary; elliptical ambulacral tract of outer heterotomous arm much smaller than inner ambulacral tract. Tertibrachials 2, second axillary. Minimum 8 arms per ray, free with second secundibrachial. Tegmen inflated, gently arched; plates large, bearing central tumid node; 5 orals at tegmen summit, anal oral in semicirular contact with 4 others, separated from ambulacral opening by few small ambulacral and interambulacral plates. Anal interray has single row of plates above radials. Anal opening on side of tegmen, directed laterally. Stem facet circular, small, 2.4 mm diameter. Distal arms and stem unknown.

Remarks.—*Pleurocrinus folliculus* n. sp. is most closely related to, but differs from, *P. glomerosus* by having elliptical ambulacral tracts, and a greater number of small plates in the tegmen.

Material.—Three specimens: Holotype (RGM 361 243), paratype 1 (RGM 361 244), and paratype 2 (RGM 361 245) from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), at Foum ech Cheguiga; Pareyn collection.

Etymology.—Latin, meaning an inflated ball, referring to the inflated shape of the tegmen.

Genus **EUCLADOCRINUS** Meek, 1872

Eucladocrinus? asymmetricus, new species
Plate 10, figures 9–12

Diagnosis.—Distinguished by four arms per ray and robust size.

Description.—Theca globose, large, length 20.4 mm, width 27 mm, base concave, tegmen low flat to very gently arched, elevated above ambulacral openings, pentagonal in oral view. Cup medium bowl-shaped, length 12.6 mm, width 25.1 mm, walls subvertical, trough along basal-radial sutures. Basal circlet fused, discoid to very shallow bowl, 16.4 mm diameter, length 2.5 mm; base concave with shallow concavity, distal edges upflared, barely visible in side view. Radials 5, large, 11 mm long, 14.1 mm wide, widest at distal end of interradial sutures, gently convex longitudinally and transversely, ornament of low broad nodes. Radial facet angustary, wide, horseshoe-shaped, subvertical; shows 3 facets, single axillary primibrachial overlapped laterally by first secundibrachials. Primibrachial small, triangular in exterior outline, with rounded transverse ridge. First secundibrachials much wider than long, laterally attach to radial, with rounded transverse ridge. Second secundibrachial not preserved, axillary. Minimum 4 arms per ray, free with first secundibrachial. Tegmen low, flat to slightly arched; plates large with very coarse bulbous to nodose centers; ambulacral plates small adjacent to ambulacral openings, distally become larger; interambulacrals with single large plate followed by 2 or 3 smaller plates and larger plates distally. Anal opening separated from radials by single large interambulacral followed by minimum of double row of small plates, projecting vertically. Stem facet circular, large, moderately concave, very narrow crenularium, wide areola; axial canal small, probably pentalobate.

Remarks.—*Eucladocrinus? asymmetricus* n. sp. is distinguished by its robust size and concave basal circlet. Measurements were taken on the holotype (RGM 361 246). The concave base has an asymmetry with a greater declivity at the distal ends, commonly greatest in the D-E interray area. One specimen (RGM 361 253) has the greater declivity in the CD interray. These cups are remarkably similar to that of *E. pleurovimenus* (White, 1862) as illustrated by Wachsmuth and Springer (1897, pl. 74, fig. 1). The generic assignment is tentative because *Eucladocrinus* has two large rami in each ray giving off pinnulate ramuli distally. It is assumed that the four ambulacral openings on *E.? asymmetricus* represent the proximal ends of four rami or arms; it may represent a new genus.

All specimens are solution- and abrasion-weathered and have lost most ornament. Paratype 1 (RGM 361 247) retains a small part of the broad nodes on one radial, shows the development of the proximal end of the two small ambulacral openings on the outer sides of each half ray in two rays, and retains part of the stem facet morphology. The bulbous tegmen plates are best preserved on paratype 2 (RGM 361 248) and paratype 3 (RGM 361 249). Specimen RGM 361 252 retains the stem facet and is abnormal, as the E and A radials are fused into one large armless plate. Specimen RGM 361 253 has an inflated cup, with more strongly rounded walls, a more bowl-shaped cup, and greatest declivity in the CD interray; features we consider to reflect intraspecific variation.

Material.—Eight specimens: Holotype (RGM 361 246), four paratypes (RGM 361 247–RGM 361 250), listed specimen (RGM 361 251), and mentioned specimen (RGM 361 252) from the Oued el Hamar Formaton, Pennsylvanian (late Bashkirian), southwest of Djebel Horreit. Mentioned specimen (RGM 361 253) from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), from the north flank of Chebket Mennouna. All Pareyn collection.

Etymology.—From the Greek *asymmetros*, referring to the asymmetry of the basal circlet.

Eucladocrinus? sp.

Remarks.—Two specimens are tentatively assigned to *Eucladocrinus*? sp. These specimens are similar to *E.? asymmetricus* n. sp., but have gently rounded basal circlets. It is uncertain if they represent variation or a separate species. Both specimens are weathered, poorly preserved, and unsuitable to serve as types.

Material.—Two mentioned specimens (RGM 361 254) from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), southwest of Djebel Horreit; Pareyn collection.

Subclass **DISPARIDA** Moore and Laudon 1943

Remarks.—Recent studies of the higher level classification of the Crinoidea have resulted in major reallocation of several taxa above the superfamily level (Simms and Sevastopulo, 1993; Ausich, 1997, 1998a). One change with which most echinoderm workers are in agreement is dropping of the Subclass Inadunata because taxa within it are considered polyphyletic.

Superfamily **BELEMNOCRINACEA** S. A. Miller, 1883

Family **SYNBATHOCRINIDAE** S. A. Miller, 1889

Genus **SYNBATHOCRINUS** Phillips, 1836

Synbathocrinus sp.

Plate 9, figures 11–14

Description.—Cup conical, wider (13.4 mm) than high (8.2 mm), base truncated, walls gently convex becoming concave below radial facets. Basal circlet wider (8.4 mm) than high (2.3 mm), forms lower ⅓ of cup. Basals 3, 2 equal, 1 azygous in anal interray, horizontal proximally, steeply upflared distally. Radials 5, wider (7.3 mm) than long (6.4 mm), widest just below radial summit, gently convex transversely, gently convex becoming concave distally longitudinally or gently convex longitudinally. Radial facets plenary, upflaring adorally. Transverse ridge narrow, low, extends full width of facet. Outer ligament pit narrow, moderately deep, 0.5 facet width. Narrow transverse ridges and grooves along transverse ridge from ends of ligament pit to distal termination. Outer margin narrow. Muscle areas triangular with gently arched medial areas bordered by shallow grooves adoral of transverse ridge and along narrow V-shaped ambulacral groove. No inner ligament pit. Anal notch wider (3.1 mm) than deep (0.9 mm), almost entirely on C radial. Stem facet circular, 4.1 mm diameter, impressed in basal circlet.

Remarks.—*Synbathocrinus* is a long-ranging cosmopolitan crinoid, most common in the Mississippian (Kinderhookian and Osagean) of North America and Tournaisian of Europe (Kesling and Smith, 1963). There are a few records from the late Viséan of Ireland (Waters and Sevastopulo, 1984) and the Serpukhovian (E2) of the Pyrenees (Delvolvé *et al.*, 1996). All Pennsylvanian species are known from North America (Strimple, 1938; Strimple *et al.*, 1971; Strimple, 1975a; Burdick and Strimple, 1983) and have low bowl-shaped cups with convex radials. Although *Synbathocrinus* sp. may represent a new species, no name is designated because the surface is etched. Ornamentation, if developed, is not preserved, and a better specimen is needed to serve as holotype.

Material.—Figured cup (RGM 361 255) from the Aïn Mezerelt Member, El Guelmouna Formation at El Aouidja, summit El Hamar, Mississippian (Serpukhovian, E1); Legrand-Blain collection.

Subclass **CLADIDA** Moore and Laudon, 1943

Remarks.—The Order Cladida was elevated to subclass status by Simms and Sevastopulo (1993), a proposal that was accepted by Ausich (1997, 1998b), but not by all authors (Webster, 1997; Webster and Houck, 1998; Webster and Hafley *in* Webster *et al.*, 1999).

Ausich (1998b) recognized the cladid orders Cyathocrinida and Dendrocrinida, but suggested that the relationships of the poteriocrines (Suborder Poteriocrinina of the *Treatise*, Moore and Teichert, 1978) needed additional study, with which we concur.

Order **CYATHOCRINIDA** Moore and Laudon, 1943

Suborder **CYATHOCRININA** Bather, 1899

Superfamily **CYATHOCRINITACEA** Bassler, 1938

Family **BARYCRINIDAE** Jaekel, 1918

Remarks.—McIntosh (1984) transferred *Barycrinus* to the Botryocrinidae noting that both had a small primanal and larger secundanal. This was accepted by Kammer (2000) and Gahn and Kammer (2002). Although we agree that barycrinids may be more closely related to the dendrocrinids than the cyathocrinitids, we do not agree that *Barycrinus* belongs in the Botryocrinidae, because *Barycrinus* has a pentameric stem and *Botryocrinus ramnossius* Angelin, 1878, the type species, has a holomeric stem. Also, *Barycrinus* has more advanced radial facets with a transverse ridge and other secondary grooves and ridges radiating from the central pit whereas *Botryocrinus* has smooth radial facets lacking other morphologic features. The *Treatise* (Moore and Teichert, 1978) noted that pentameric stems are developed in some species of *Botryocrinus*. The significance of the pentameric stem, anal plates, and morphology of the radial facets within the cyathocrinitids and dendrocrinids needs detailed analysis, beyond the scope of this study. We would suggest, however, that the results of such an investigation may result in a much greater shuffling of the genera and families within the cyathocrinitids and dendrocrinids.

Barycrinidae? indeterminate

Plate 10, figures 13–17

Description.—Cup moderately large, ?bowl-shaped, all plates with sharp stellate ridge ornament extending across plate boundaries and medium granular ornament. Infrabasals 5?, large, distal tips upflared, visible in lateral view. Basals large, length 11.9 mm, width 11 mm, hexagonal (posterior basal heptagonal), gently convex longitudinally and transversely. Radials large, length 12.8, width 15.5, moderately convex longitudinally and transversely, incurving distally. Radial facet angustary, 8.7 mm wide, concave, horseshoe-shaped, subvertical to slightly upflared; transverse ridge formed by double row of anastomosing ridges; outer marginal ridge of short adorally directed ridges and grooves; outer ligament furrow wide; muscle areas large, narrowing adorally; ambulacral groove deep V-shaped with extended slit at base of V. Anals 2; large primanal rectangular; larger secundanal pentagonal, on posterior basal, extending above radial summit. Column circular in transverse section, diameter 8.9 mm, heteromorphic; noditaxis N3231323. Columnals with wide crenularium, pentalobate lumen.

Remarks.—The description of Barycrinidae? indeterminate is based on disarticulated plates or parts of cups as follows: one radial, one fragment of a large radial; one cup fragment of one radial, two basals, and the distal tip of an infrabasal plate; one cup fragment of three basals, three radials, and two anal plates; and an associated loose pluricolumnal.

Classification of the material is uncertain. The two anals and radial facets are similar to those in the barycrinids (*sensu* Moore and Teichert, 1978). The primanal is rectangular, however, it is much larger than typical in the barycrinids or botryocrinids, which have a primanal much smaller than the secundanal. Unfortunately, the tegmen and arms of this specimen are unknown leaving additional uncertainty concerning the classification. The ornament and radial facets are similar to those found in some taxa of the Poteriocrinitidae. The column is holomeric unlike the pentameric column of *Barycrinus*. The radial facets have a transverse ridge, an intermediate development in the evolution of the radial facet morphology of the early cladids.

Material.—Five specimens: Two partial cups (RGM 361 256, RGM 361 257), one radial (RGM 361 258), one partial radial (RGM 361 259) and one pluricolumnal (RGM 361 260) from the Akacha-Mazzer Formation, unit 13 (Pareyn, 1961), Mississippian (late Viséan), at Djebel Ioucha; Pareyn collection.

Order **DENDROCRINIDA** Bather, 1899

Suborder **DENDROCRININA** Bather, 1899

Superfamily **MASTIGOCRINACEA** Jaekel, 1918

?Family **MASTIGOCRINIDAE** Jaekel, 1918

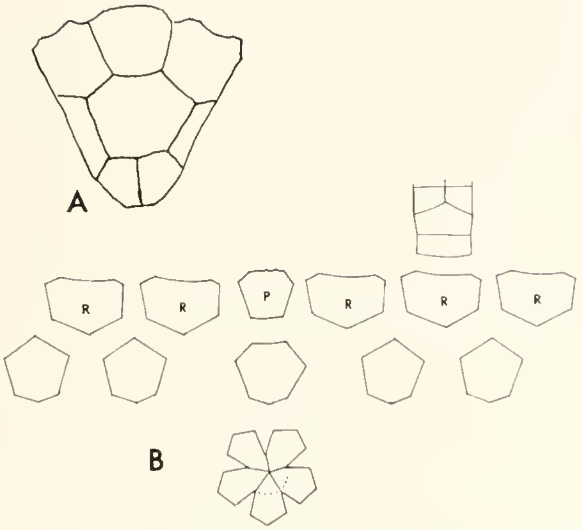
Genus **HEBOHENOCRINUS**, new genus

Type species.—*Hebohenocrinus quasipatellus* new genus, new species, here designated.

Diagnosis.—Cup medium asymmetrical cone-shaped, small; microscopic granular ornament on cup and primibrachials; 5 infrabasals, basals, and radials strongly upflared; radial facets peneplenary; interradial notches narrow; 1 anal mostly within cup, distally with 4 facets; ?single primibrachial axillary, isotomous branching widely flaring; stem facet horizontal, pentagonal, axial canal circular.

Description.—As for the type species.

Remarks.—Suprageneric classification of this specimen is problematic. The cone-shaped cup is a primitive feature. The peneplenary radial facets and pentag-



Text-figure 5.—A. *Hebohenocrinus quasipatellus* n. gen. and sp., posterior view, holotype RGM 361 262, ×4.3. B. Plate diagram of *Hebohenocrinus* n. gen. based on holotype: R—radial, P—primanal.

onal stem are intermediate evolutionary features in the cladids. Branching on the first primibrachial in at least one ray and presence of a single anal are advanced features (Text-fig. 5). The morphologic features of the steeply inwardly inclined thin radial facets relates them to the cladids. However, the transverse ridge is nondenticulate, whereas most cladids have denticulate transverse ridges. Most high-cone cladids have much thicker radial facets that are shallowly inclined inward, subhorizontal, or inclined outward. The genus is questionably assigned to the Mastigocrinidae based on the primitive cup features but considered an advanced form based on the intermediate and advanced features.

Etymology.—From the Greek *hebos*, meaning at the threshold of manhood, and *henos*, meaning old or former, in reference to the advanced and primitive characters of the specimen, combined with *krinon*, meaning sea lily.

Hebohenocrinus quasipatellus, new species

Plate 11, figures 5–7; Text-figure 5

Diagnosis.—As for the genus.

Description.—Cup medium asymmetrical cone-shaped, longest on posterior side, small, length 6 mm, width at radial summit 7 mm, plates thin, with microscopic granular ornament. Infrabasals 5, dart-shaped, length 1.8 mm, width 1.8 mm, strongly upflaring distally, gently convex longitudinally and transversely. Basals 5, hexagonal, except posterior basal heptagonal, length 2.8 mm, width 2.6 mm, slightly concave longitudinally, gently convex transversely. Radials 5, wider (3.4 mm) than long (2.4 mm), strongly upflared, gently convex longitudinally and transversely, distal edge scalloped. Radial facets peneplenary, thin, slightly concave transversely, lens-shaped external of transverse ridge, thickest centrally; transverse ridge not denticulate; outer marginal area moderately wide, with moderately deep ligament pit; medium-sized muscle areas slope steeply inward and downward. Interradial notches narrow. Single anal 2.7 mm long, 2.4 mm wide, distal tip slightly above radial summit, distally with 4 small facets. May be 1 or 2 primibrachials, horseshoe-shaped in transverse section, slightly concave longitudinally, strongly convex transversely, bearing microscopic granular ornament as on cup. Isotomous branching widely flaring. More distal arms, tegmen, and stem unknown. Stem facet horizontal on infrabasal circlet, pentagonal, 1 mm in diameter; axial canal circular.

Remarks.—All plates of *Hebohenocrinus quasipatellus* n. sp. have been replaced by iron oxides. Some of the proximal brachials, including at least one nonaxillary and three axillary primibrachials, are dislocated, but preserved within the cup. The nonaxillary primibrachial is slightly dislocated from the B radial into the interior of the cup with an axillary primibrachial dislocated to its left. The B ray apparently had two primibrachials. The other two axillary primibrachials have no associated nonaxillary primibrachials in association. There are two secundibrachals dislocated into the interior of the cup. There was probably a minimum of ten arms total.

Material.—Holotype (RGM 361 262) probably from between the Hassi Kerma and Djenien formations (Tagnana Formation), Mississippian (late Serpukhovian, E2), Tiberbatine Anticline, east side of Oued Guir; Pareyn collection.

Etymology.—From the Latin *quasi*, meaning appearing as if, and *patella*, meaning small dish, and refers to the patelloid process-like appearance of the radial facets in lateral view.

Family **POTERIOCRINITIDAE** Austin and Austin, 1842

As used in the *Treatise* (Moore and Teichert, 1978), the Suborder Poteriocrinina (of Order Cladida) includes several superfamilies in addition to the Poteriocrinitacea. The poteriocrinids were separated from the other cladids based on the presence of pinnules. Webster and Hafley (*in* Webster *et al.*, 1999) did not accept the development of pinnules as a justifiable character for classification at the level of suborder, pointing out that pinnules have evolved repeatedly in various groups of crinoids during the Paleozoic. They recommended that the Cupressocrinitidae be removed from the poteriocrinids and placed under the Gasterocomacea of the Cyathocrinina. Webster and Jell

(1999b) recognized the Order Ampelocrinida of the Subclass Articulata as including some genera of the Ampelocrinidae and Cymbiocrinidae, the families Corythocrinidae and Calceolispongiidae, and some unclassified poteriocrinid genera. These changes removed a number of genera from the poteriocrinids. In addition, there have been several reallocations of genera and families within the Poteriocrinina since publication of the *Treatise* (Moore and Teichert, 1978).

We recommend abandonment of the Suborder Poteriocrinina, because we believe that the origin of the Poteriocrinitidae is from the Cyathocrinina on the evidence of the morphology of the radial facets and structure of the cup, arms, and tegmen. The origin of the superfamilies Rhenocrinacea and Scytalocrinacea is through the Dendrocrinina, on the evidence of the morphology of the radial facet and structure of the tegmen and arms. Other superfamilies within the Poteriocrinina (*Treatise* usage) also are believed to be derived from either the Cyathocrinina or Dendrocrinina and require study beyond the scope of this paper for proper reallocation. Taxa described and discussed herein are assigned to poteriocrinine families as used in the *Treatise*, but are not considered poteriocrinids unless assigned to the Family Poteriocrinitidae.

Genus **BALEAROCRINUS** Bourrouilh and Termier, 1973

Remarks.—The primibrachials of *Balearocrinus* are quite distinctive. They are exceedingly short and the syzygial articulation leaves them firmly interlocked on the radial. Proximal primibrachials may be partially fixed to the radials. In the illustrations of Bourrouilh and Termier (1973, pl. 27, fig. 4; fig. 3, no. D) it is apparent that the first primibrachial is overlapped laterally by the second and perhaps higher primibrachials on the E-ray radial (right side of figure). On the A-ray radial (center radial, pl. 11, fig. 15) the first primibrachial is tapering on the lateral ends and is overlapped by the second primibrachial near or at the radial margin. The primibrachials on the B radial (left side of figure) also taper toward the lateral end but extend to the end of the facet. Additional evidence of the overlapping of the first primibrachial by the second primibrachial is present on the illustrations of the brachials by Bourrouilh and Termier (1973, pl. 28, figs. 1–3). The crenularium of the brachial of their figure 3 terminates along the sides without reaching horizontal radiations (*i.e.*, less than a hemisphere). We interpret this as a first primibrachial facet, whereas the facets shown on their figures 1 and 2 radiate in a complete hemisphere, which we interpret as facets on distal brachials. We consider the narrow first primibrachial being overlapped by the second primibrachial to be an important morphologic character of the genus but are uncertain how variable this feature is within the genus. These radial facets are related to the angustary radial facets of *Poteriocrinites* and the peneplenary radial facets of *Rhabdocrinus*, neither of which have the first primibrachial overlapped laterally by the second primibrachial. The short brachials of *Rhabdocrinus* with radiating crenularia are very similar to those of *Balearocrinus*, but the latter lacks the interprimibrachials of the former.

Balearocrinus pareyni, new species

Plate 11, figures 13–15

Cf. *Rhabdocrinus scotocarbonarius* (Wright, 1937). Pareyn, 1961, p. 223.

Diagnosis.—Cup high conical, truncated base, plates smooth, very shallow apical pits, 3 anals in primitive position; plenary radial facets concave, slope outward; primibrachials very short, first primibrachial overlapped laterally by second primibrachial; crenularium on outer margin of brachials and anals; proximal columnals round, heteromorphic, N1 noditaxis, syzygial articulation.

Description.—Cup high conical, 18.5 mm long, 14.9 mm wide (minimum), 18.5 mm wide (maximum), 16.7 mm (average), truncated base, shallow apical pits, plates smooth. Infrabasals 5; proximal half covered by proximal columnal, probably horizontal; visible distal half strongly upflared, length 5.5 mm, width 7.3 mm. Basals 5, slightly longer (9 mm) than wide (7.8 mm), hexagonal (except posterior heptagonal), straight to faintly concave longitudinally, gently convex transversely. Radials 5, equidimensional (7.9 mm), strongly upflared, straight longitudinally, gently convex transversely. Radial facets plenary, concave, strongly rounded outer rim, slope outward. Anals 3, primitive position. Primanal largest, 6.6 mm long, 6.1 mm wide, pentagonal, supporting third anal distally. Secundanal pentagonal, 6.4 mm long, 6.1 mm wide, distal tip at radial summit. Tertanal equidimensional, 4.7 mm, distal tip above radial summit. Tube plate above tertanal with externally radiating crenularium of fine culmina and crenellae. Primibrachials very short, uniserial, strongly rounded externally, 3 commonly retained in cup, bear externally radiating crenularium as on tube plate, syzygial articulation; first primibrachial overlapped laterally by second primibrachial. Second primibrachial tapers on lateral edges, reaching end of radial facet. Distal arms and tegmen unknown. Proximal columnals transversely elliptical, long axis 8.6 mm, short axis 7.8 mm, 8.2 mm average, heteromorphic, noditaxis N1, syzygial articulation.

Remarks.—*Balearocrinus pareyni* n. sp. has a taller cup and narrower first primibrachials than *B. breimeri* reported from Viséan strata of Minorca (Bourrouilh and Termier, 1973) and *B. cantabricus* from the late Viséan of the Cantabrian Mountains, northern Spain (Herbig, 1982, 1994). This is the first report of the genus from northern Africa.

The specimen is crushed slightly, normal to the A ray-posterior plane of symmetry. Attached proximal columnals are considered originally to have been round transversely and distorted to the elliptical shape by compaction.

Material.—Holotype (RGM 361 261) from the Mazzer Formation, Mississippian (late Viséan), Mader el Mahjib syncline, bed 13; Pareyn collection.

Etymology.—Named for C. Pareyn who found the specimen.

Superfamily **SCYTALOCRINACEA** Moore and Laudon, 1943

Family **SCYTALOCRINIDAE** Moore and Laudon, 1943

Genus **SCYTALOCRINUS** Wachsmuth and Springer, 1880

Scytalocrinus sp.
Plate 11, figure 16

Phanerocrinus nov. sp. Pareyn, 1961, p. 76 [*sic*].

Description.—Cup truncated medium cone, length 8.7 mm, width 16.6 mm (average), medium granular oranment on all plates including secundibrachials. Infrabasal circlet with basal concavity, diameter 7.6 mm, proximally horizontal, distal tips weakly upflared, barely visible in lateral view; infrabasals 5. Basals 5, slightly wider (7.1 mm) than long (6.1 mm), hexagonal (CD basal may be heptagonal if in contact with secundianal), gently convex longitudinally and transversely, form lower half of cup wall. Radials 5, much wider (10.6 mm) than long (6.6 mm), pentagonal, gently outflaring, slightly convex longitudinally, moderately convex transversely. Radial facet plenary. Anals 3, primitive to slightly advanced arrangement. Radianal largest, pentagonal or hexagonal, either underlies both secundanal and tertanal or abuts secundanal and underlying tertanal. Secundanal mostly in cup, in line of radials. Tertanal proximal half in cup. Axillary single primibrachial widest at base, constricted medially, strongly convex transversely, concave longitudinally. First secundibrachials widest at base, narrowing distally, slightly cuneate, concave longitudinally, moderately convex transversely. Stem facet round, 2.6 mm diameter, wide crenularium, no areola, circular axial canal.

Remarks.—Both specimens of *Scytalocrinus* sp. are distorted through compaction with the one specimen with proximal brachials of three rays preserved partly enclosed in matrix and positioned above the oral surface of the more completely exposed cup of the other specimen. The shape of the distal brachials and the distal branching patterns are unknown.

These specimens closely resemble *S. robustus* (Hall, 1861) in cup shape and structure, but differ by the presence of granular ornament. Ornamentation is not common in species assigned to *Scytalocrinus* (most species are described as having smooth plates or lacking ornamentation). *Scytalocrinus disparilis* (Miller and Gurley, 1890) was described as having smooth or granular plates and *S. cantonensis* (Miller and Gurley, 1890) was illustrated (pl. 8, figs. 3, 4) as having granular ornamentation, but the ornamentation was not mentioned in the description. *Scytalocrinus seafieldensis* (Wright, 1948) was described as having smooth or very finely frosted plates. Webster (1997) recognized three clades within *Scytalocrinus* based principally on the shape of the brachials. Because the distal brachials of these specimens are unknown they are left in open nomenclature, but are thought to represent a new species.

Material.—Two specimens (RGM 361 263) from the base of Mouizeb el Atchane Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E2), at Gadet Sedra; Pareyn collection.

Genus **HYDRIOCRINUS** Trautschold, 1867

Hydriocrinus? confusus, new species
Plate 11, figures 1–4

Diagnosis.—Distinguished by more elongate primibrachials, an advanced primitive anal condition with the secundanal not in contact with the posterior basal, and a round stem.

Description.—Cup elongate vase-shaped, length 8.4 mm, width 5.8 mm, widest slightly below distal end of basals, surface ornament of microscopic granules. Infrabasals 5, dart-shaped widening distally, visible length 3 mm, width 2.1 mm, straight longitudinally, gently convex transversely. Basals 5, large, length 3.7 mm, width 2.1 mm, hexagonal, moderately convex longitudinally and transversely, inflaring gently distally. Radials 5, large, length 3.1 mm, width 3.6 mm, pentagonal, gently outflaring proximally, inflaring distally, gently convex transversely. Radial facets plenary, slope inward moderately, bear transverse ridge, sharp outer marginal ridge, moderately deep outer ligament pit, and deep wide muscle areas. Anals 3. Primanal hexagonal, in contact with C radial, BC (narrowly) and CD basals, D radial, secundanal, and tertanal. Secundanal pentagonal, distal tip slightly above radial summit adjoined by 2 tube plates, tertanal, primanal, and D radial. Tertanal hexagonal, distal half above radial summit, adjoined distally by 2 tube plates, one in common with secundanal. E ray primibrachial elongate, nonaxillary, strongly rounded transversely, slight hour-glass shape. Axillary C and D ray primibrachials much shorter (2 mm) than E ray primibrachial (3.2 mm). Secundibrachial on anal side of D ray primibrachial slightly cuneate. More distal brachials and tegmen unknown. Proximal columnals transversely round, tapering from 2.1 mm diameter at infrabasal facet to 2 mm on distal end of second columnal. Columnal facet with crenularium and areola of equal width; lumen shape unknown.

Remarks.—The single specimen of *Hydriocrinus? confusus* n. sp. is replaced with iron oxides and uncrushed. The anals are in a slightly advanced primitive condition with the secundanal not in contact with the posterior basal.

The small size and vase shape of the cup are similar to *Hydriocrinus pusillus* Trautschold, 1867, reported from the Moscovian of Russia. *Hydriocrinus*, however, has a pentagonal stem, relatively short medially constricted primibrachials, rectilinear brachials, and arms that branch at least twice in some rays. It is uncertain from the original description and illustrations of *Hydriocrinus* if all the primibrachials are the same length and if all are axillary. The two primibrachials of *H.? confusus* are constricted medially, but relatively much longer than those of *H. pusillus* Trautschold. The only single secundibrachial preserved on *H.? confusus* is slightly cuneate. Also, the round stem of *H.? confusus* is in contrast to the pentagonal stem of *H. pusillus*. *Hydriocrinus? confusus* with the slightly advanced position of the anals occurs stratigraphically earlier (Serpukhovian) than *H. pusillus*, a Moscovian form, in which the anals are in the primitive position with the secundanal in contact with the posterior basal.

Comparison of *Hydriocrinus? confusus* with other Carboniferous species assigned to the genus led us to question the generic assignment of each. In discussions with other crinoid workers, it was suggested that all Devonian and Early Carboniferous species assigned to *Hydriocrinus* actually belong to other genera (N. G. Lane, personal communication). The partially exposed cup of *H. mjassoedowae* Yakovlev (1926) has a more bowl shape, impressed sutures, and a round stem facet. It is not considered a *Hydriocrinus*. Two species, *H. lorraineae* Strimple and Watkins (1969) and *H. turbinatus* Strimple (1971), have conical-shaped cups, 10 arms, isotomous branching on the axillary primibrachial, cuneate brachials, and pentagonal stems with round lumens. These two species are considered to belong to the same genus but not to *Hydriocrinus*. The second set of arms (Strimple and Watkins, 1969, pl. 34, figs. 6, 7) assigned to *H. lorraineae* have much more cuneate brachials and are not from the same species. The dorsal cup of *H. acehillensis* Pabian and Strimple (1985) is a conical cup, possibly belonging to the same genus as *H. lorraineae* and *H. turbinatus*. Their description states that the specimen has three anals, as shown in the posterior view of the cup (Pabian and Strimple, 1985, fig. 25i), however the oral view (fig. 25k) shows a specimen with six radial facets and no anals. It appears that two different specimens are illustrated, but the description and remarks are based on a single specimen. Another dorsal cup, *H.? rosei* Moore and Plummer, 1938, referred to *Phacelocrinus* by Strimple (1971), was considered to be the progenitor of *Hydriocrinus* in North America by Strimple and Watkins (1969) and Pabian and Strimple (1985). This specimen has an asymmetrical conical cup, considerably larger than *Hydriocrinus* cups, and probably belongs to a scytalocrinid, perhaps *Hypselocrinus* or *Phacelocrinus*.

The anal structure of *Melbacrinus* has been considered to be comparable to that of *Hydriocrinus* (Strimple, 1971). The lower conical cup, elongate primibrachials, and round stem of *Melbacrinus*, however, are quite distinct. The elongate primibrachials and round stem are comparable to those of *H.? confusus*, but the cup shapes differentiate these two genera.

Material.—Holotype (RGM 361 264) from a horizon between the Hid el Kef and Djenien members, Djenien Formation, Mississippian (Serpukhovian, E2), north of Djebel Arlal; Pareyn collection.

Etymology.—From the Latin *confusio* meaning mixture, disorder.

Family **AMPULLACRINIDAE**, new family

Type genus.—*Ampullacrinus* n. gen.

Diagnosis.—Crown slender elongate, cup medium bowl or globe shape, shallow basal concavity, radial facets plenary, 3 anals in primitive position with secundanal in contact with posterior basal, arms 10, branching isotomously on single primibrachial, 3 entoneural canals in brachials, advanced articular facets with transverse ridges on all proximal brachials, brachials slightly cuneate, proximal columnals round to weakly pentagonal, axial canal pentalobate.

Remarks.—Sevastopulo and Keegan (1980) reported the discovery of triple aboral nerve canals, in an isolated brachial from the Mississippian (late Viséan) Charlestown Main Limestone of Scotland, when describing a technique to study stereom structure of fossil crinoids. *Ampullacrinus* is the first report of the triple canals in an articulated partial crown. If it did not have the three entoneural canals in the brachials, *Ampullacrinus* would be considered a scytalocrinid. Entoneural canals and advanced articular facets on the brachials are two features of *Ampullacrinus* shared with the articulates.

Entoneural canals evolved several times in crinoids. They are present in crotalocrinids, euspirocrinids, some codiacrinids, gasterocomacids, encrinids, and the articulates as illustrated in the *Treatise* (Moore and Teichert, 1978, among others). Except for the articulates and encrinids, all of these groups became extinct in the Paleozoic. The encrinids became extinct in the Triassic. Crotalocrinids, euspirocrinids, codiacrinids, and gasterocomacids lack advanced articular facets on the brachials, except at arm divisions, and have a single entoneural canal (Moore and Teichert, 1978). The articulates have two entoneural canals and advanced articular facets on the brachials (Webster and Jell, 1999b). The encrinid *Chelocrinus* has two entoneural canals and have advanced articular facets on the uniserial brachials, and two entoneural canals on the distal biserial brachials (Hagdorn, 1982).

Webster and Jell (1999b) considered the synapomorphic feature that defines the Articulata to be the development of syzygial brachial pairs in the arms. *Ampullacrinus* lacks the distal parts of the arms beyond the ninth secundibrachial. There is no indication of development of syzygial brachial pairs within the nine secundibrachials. Syzygial brachial pairs are not developed in *Corythocrinus* or *Archaeoisocrinus* until the fourth secundibrachial, and *Chlidonocrinus* is defined in Moore and Teichert (1978, p. T674) as having "Arms branching more than twice, some with syzygial paired brachials." This latter statement implies either that not all arms have syzygial paired brachials or that some species of *Chlidonocrinus* do not have syzygial paired brachials. Those species lacking syzygial paired brachials may be improperly assigned to *Chlidonocrinus*.

Development of the articular facets on brachials other than axillary brachials and their distal counterparts is considered an important morphologic character of the ampelocrinids, demonstrating that they are primitive articulates. In some instances preservation of articulated arms or recrystalliation could easily mask the small entoneural canals, but the articular facets may be less affected. Thus, the development of, or combination of, any one or more of the three synapomorphic features, two entoneural canals, syzygial brachial pairs, or articular facets on brachials other than axillary brachials, should be used for recognition of Paleozoic articulates.

Logocrinus Goldring (1923) was considered the progenitor of the articulate crinoids based on the presence of syzygial paired brachials by Webster and Hafley (*in* Webster *et al.*, 1999). This includes *L. geniculatus* Goldring, 1923, *L. infundibuliformis* Goldring, 1923, *L. kopfi* (Goldring, 1946) *L. brandoni* Sigler *et al.*, 1971, and ?*L. conicus* Kesling, 1968. The arms of *L. conicus* are unknown above the primibrachials, thus it is questionably assigned to the genus. The arm fragment with syzygially paired brachials, identified as *Charientocrinus ithacensis* by Goldring (1923, pl. 53, fig. 3), belongs to *L. geniculatus* or *L. infundibuliformis*. *Logocrinus* lacks entoneural canals (George McIntosh, personal communication, December 2000). *Logocrinus* probably evolved from an early glossocrinid and is herein questionably referred to the Family Corythocrinidae but may be the progenitor of the primitive articulates. Including *Logocrinus*, the Corythocrinidae ranges from Givetian to the Sakmarian-Artinskian boundary.

Ampullacrinus is specifically excluded from the primitive articulates because it lacks syzygial paired brachials and has three entoneural canals. *Ampullacrinus* is probably derived from a scytalocrinid with development of the three entoneural canals. This is another instance of polymorphic evolution of entoneural canals not in the lineage of the articulates. Hagdorn (1995) reported that encrinids were derived (Encrinidae, Traumatocrinidae, and Ainigmacrinidae) from a proto-articulate crinoid. Because encrinids lack syzygial paired brachials they are excluded from the articulate lineage. Encrinids are a separate example of evolutionary development of entoneural canals from an unspecified late Paleozoic cladid, perhaps like *Aesiocrinus* or one of the scytalocrinids with two primibrachials. Their evolution included loss of the anals, development of biserial brachials distally, articulation facets with transverse ridges on proximal brachials minimally, and entoneural canals.

AMPULLACRINUS, new genus
Text-figure 6 E

Type species.—*Ampullacrinus marieae* n. gen., new species, here designated.

Diagnosis.—As for the family.

Description.—As for *Ampullacrinus marieae*, new species.

Remarks.—Without the presence of the muscular and ligamentary facets and the entoneural canals, visible only on the brachial facets, this taxon would be assigned to *Scytalocrinus* on the basis of the cup and arm morphology.

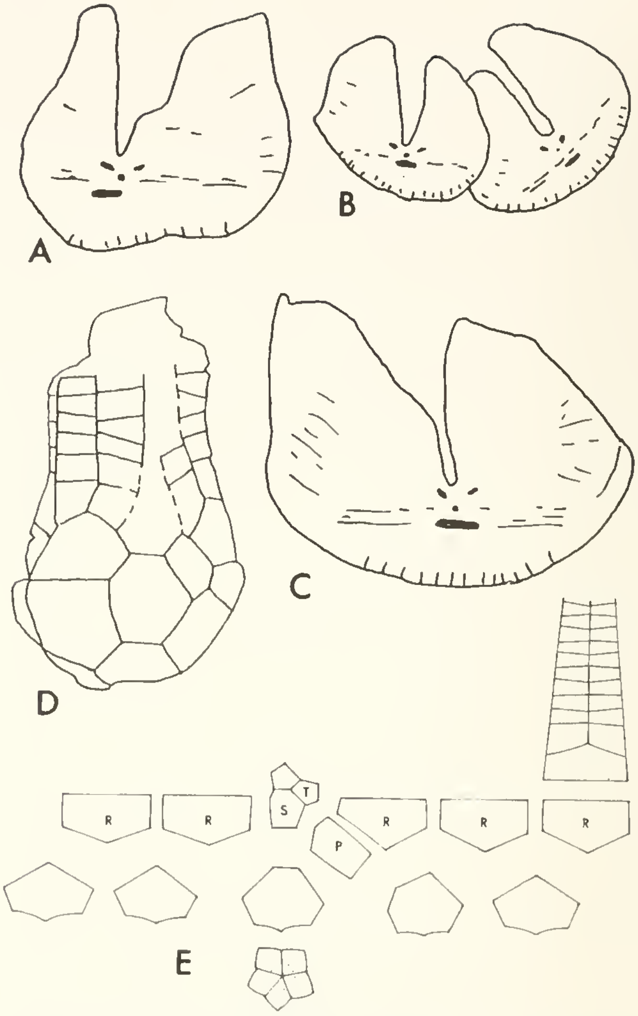
Etymology.—From the Latin, *ampulla*, meaning flask and refers to an irregular flask-like shape of the enclosed crown.

Ampullacrinus marieae, new species
Plate 12, figures 1–10; Text-figure 6 B–E

Cf. *Fifeocrinus tielensis* (Wright, 1936). Pareyn, 1961, p. 76.

Diagnosis.—Distinguished by having a medium bowl-shaped cup, very fine granular ornament grading into vermiform and aligned granules, and a weakly pentagonal stem.

Description.—Cup medium bowl shape, wider than long, widest at radial summit, sutures flush, not impressed, very fine granular grading into vermiform and aligned ornamentation. Infrabasal circlet subhorizontal, 6.1 mm diameter. Infrabasals 5, dart-shaped, slightly longer than wide, distal tips visible in lateral view, proximal ends downflaring in shallow basal concavity. Basals 5, wider than long, gently convex transversely and longitudinally. Radials 5, largest plates in cup, wider than long, gently convex transversely and longitudinally. Radial facets plenary; transverse ridge narrow, sharp crested; outer ligament pit ⅓ length transverse ridge, deep, slopes under ridge; outer marginal ridge with transverse ridges and grooves across facet; outer margin shelf moderately wide centrally, crescent-shape; muscle areas not exposed. Anals 3, large, in primitive position. Primanal largest, oblique position, adjoined by C radial, BC and CD basals, secundanal and tertanal. Secundanal elongate, distal half above radial summit. Primibrachials wider than long, strongly convex transversely, gently convex longitudinally, axillary; primibrachials unequal in length, A longest, C and D second longest, B and E shortest. First secundibrachials wider than long, strongly convex transversely, straight longitudinally. Arms 2 per ray, 10 total if no branching above primibrachials. Brachials strongly rounded transversely, straight longitudinally, slightly cuneate. Brachial facets symmetrical to slightly asymmetrical, bear nondenticulate transverse ridge, medium depth ligament pit, denticulate outer marginal ridge, and narrow outer ligament furrow; muscle areas large, transversely irregularly ridged, separated from transverse ridge by wide, coarsely crenulate articular fields along lateral sides and admedial smooth interareas; intermuscular furrow shallow, lacking recognizable central pit. Three small entoneural canals (Text-fig. 6); central canal medial between transverse ridge and intermuscular furrow; 2 elliptical lateral canals diverging adorally to central canal along aboral end of intermuscular furrow. Stem facet weakly pentagonal; axial canal pentagonal; crenularium with 4 to 6 coarse crenula (longest centrally) per infrabasal. Proximal 2 columnals weakly pentagonal, heteromorphic; latus rounded; minimum N1 noditaxis. Measurements given in Table 9.



Text-figure 6.—A–C. Camera-lucida drawings of brachial facet of *Ampullacrinus* showing three entoneural canals. A. *Ampullacrinus tritubulus* n. gen., n. sp. Distal facet of second secundibrachial, right side of A ray. Paratype 2, RGM 361 335, ×23. B. *Ampullacrinus mariea* n. gen., n. sp. Distal facets of first secundibrachials, E ray. Paratype 2, RGM 361 329, ×7.5. C. *Ampullacrinus mariea* n. gen., n. sp. Distal facet of third or fourth secundibrachial, left side of A ray. Paratype 2, RGM 361 329, ×12. D. *Ampullacrinus marieae* n. gen. and sp., posterior view, holotype RGM 361 330, ×2.2. E. Plate diagram of *Ampullacrinus* n. gen. based on holotype and paratypes of *A. marieae* n. sp.; R—radial, P—primanal, S—secundanal, T—tertanal.

Remarks.—The holotype of *Ampullacrinus marieae* n. sp. is crushed with elongation in the A ray-posterior axis, has some chipping of cup plates, has up to 10 secundibrachials preserved, and shows the entoneural canals and brachial facets. The cup of paratype 1 is not crushed, lacks the D radial, has crushed arms, and retains the first and part of the second columnals; it also retains up to the third secundibrachial. Paratype 2 (RGM 361 329) is crushed with elongation normal to the A ray-posterior axis, has up to the third secundibrachial preserved, and retains the best preservation of

Table 9.—Measurements in mm for *Ampullacrinus mariea* n. gen., n. sp.

	Type		
	Paratype 2	Holotype	Paratype 1
	Spec. no. (RGM)		
	361 329	361 330	361 331
Specimen length	19.1	23.2	17.6
Cup length	8.5	7.5	7.5
Cup width maximum	17.8	16.5	18.6
Cup width minimum	12.0	14.1	18.0
Cup width average	14.9	15.3	18.3
IBB length	2.9	3	3.5
IBB width	2.6	3	3.5
BB length	5.2	4.9	6.2
BB width	5.8	5.4	6.7
RR length	5.3	5.5	6.4
RR width	8.1	8.4	10.4
Primanal length	5.6	5.9	6.8
Primanal width	4	4.5	4.7
Secundanal length	5	4.2	4.8
Secundanal width	3.7	4.3	4.5
Primibrachial length	5.2	4.2	5
Primibrachial width	8.4	7.4	8.4
1st secundibrachial length	3.2	2.8	3.2
1st secundibrachial width	4.5	3.5	3.9
Diameter stem facet	2.7 avg.	2.1	
Diameter proximal columnal			3.1

the entoneural canals and articular facets of the brachials. Paratype 3 is crushed with elongation in the E-A interray-C ray axis, has crushed arms retaining up to the second secundibrachial, and has four solution-etched proximal columnals.

Material.—Four specimens from the Mouizeb el Atchane Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E2). Paratype 2 (RGM 361 329) from Djebel Béchar; Legrand-Blain collection. Holotype and paratype 1 (RGM 361 330; RGM 361 331) from the ravine at Mouizeb el Atchane and paratype (RGM 361 332) from Ravine de Djenien; Pareyn collection.

Etymology.—Named for Marie Legrand-Blain who found one of the specimens.

Ampullacrinus tritubulus, new species
Plate 11, figures 17–23; Text-figure 6 A

Diagnosis.—Distinguished by having a medium globe-shaped cup, fine granular and anastomosing ornament, and a round stem.

Description.—Cup medium globe shape, length 5.8 mm, width 14.8 mm (average), shallow basal concavity, plates slightly inflated, sutures lightly impressed, fine granular and anastomosing ornament. Infrabasal circlet pentagonal, shallowly invaginated, 5.3 mm diameter. Infrabasals not visible in lateral view. Basals 5, AB, DE, and EA hexagonal, BC and CD heptagonal for adjoining anals, length 5.3 mm, width 5.2 mm, moderately convex longitudinally and transversely, outflaring forming lower half of cup wall. Radials 5, pentagonal, wider (8.1 mm) than long (4.4 mm), moderately convex longitudinally and transversely, slightly outflaring distally. Radial facet plenary, sloping outward slightly. Anals 3, in primitive position. Primanal largest, length 4.5 mm, width 4 mm, pentagonal, abutting secundanal, supporting tertanal. Secundanal hexagonal, directly above posterior basal, slightly less than half extending above radial summit. Tertanal smallest, hexagonal, slightly more than half extending above radial summit. Single primibrachials axillary, wider (7.6 mm) than long (4.2 mm estimate). Brachials strongly rounded transversely, straight longitudinally, slightly cuneate. Brachial facets symmetrical to slightly asymmetrical, bear nondenticulate transverse ridge, medium depth ligament pit, denticulate outer marginal ridge, and narrow outer ligament furrow; muscle areas large, transversely irregularly ridged, separated from transverse ridge by wide, coarsely crenulate articular fields along lateral sides and admedial smooth interareas; intermuscular furrow shallow, lacking recognizable central pit. Three small entoneural canals; central circular canal medial between transverse ridge and intermuscular furrow; two elliptical lateral canals diverging adorally to central canal along aboral end of intermuscular furrow. Branching isotomous, 2 arms per ray, 10 arms total if no distal branching. Secun-

Table 10.—Measurements in mm for *Cosmetocrinus*? sp.

	Spec. no. (RGM)	
	290 874	361 265
Cup length	5.5	7.3 (crushed)
Cup width	6.5	9.6 max., 5.3 min., 7.4 avg.
Infrabasal length	1.9 (est.)	2.1
Infrabasal width	1.9	2
Basal length	2.6	3.2
Basal width	2.5	2.7
Radial length	2.4	3
Radial width	3.2	3.7
Primibrachial length	3.4	3.5
Primibracbial width	2.8	3.8
Diameter proximal columnal or impression	1.5	2.6

dibrachials much wider than long, moderately cuneate. Proximal stem round, heteromorphic; minimum N1 noditaxis; lumen pentalobate.

Remarks.—The cup of the holotype (RGM 361 333) of *Ampullacrinus tritubulus* n. sp. is slightly crushed normal to the A ray-posterior plane of symmetry. Distal parts of the arms are not preserved except for a fragment of one arm retained among the arm bases. The infrabasal circlet is not preserved. Paratype 1 (RGM 361 334) retains the basal circlet (which is crushed inward slightly), the D and E radials are broken with parts missing, the arms are not preserved, and the abraded proximal stem is attached. Paratype 2 (RGM 361 335) lacks the infrabasal and basal circlets and retains proximal parts of all arms up to the third secundibrachial.

Without the arms showing the entoneural canals, *Ampullacrinus tritubulus* has some resemblance to *Mooreocrinus*. The cup has a closely similar shape and may bear similar ornamentation. It differs, however, by having much thinner plates, less impressed sutures, and lacking the stitched appearance along the sutures typical of most cromyocrinids. *Ampullacrinus tritubulus* differs from *A. marieae* by having coarser ornament, a medium globe-shaped cup, and a round stem.

Material.—Three specimens: Holotype (RGM 361 333) from the base of the Aïn el Mizab Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E1), from Foum es Sba. Paratype 1 (RGM 361 334) from the top of the Djenien Member, Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani. Paratype 2 (RGM 361 335) from the Djenien Member, Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani. All Pareyn collection.

Etymology.—From the Latin *tri*, meaning three, and *tubus*, meaning pipe or tube, and referring to the three entoneural canals.

Family **APHELECRINIDAE** Strimple, 1967

Genus **COSMETOCRINUS** Kirk, 1941

Cosmetocrinus? sp.

Plate 11, figures 8–12

Description.—Cup small, high cone-shaped, unornamented. Infrabasals 5, equidimensional to slightly longer than wide, proximal end horizontal for stem facet, distal three-fourths upflared, visible in lateral view, forming basal one-fourth of cup, moderately convex transversely. Basals 5, slightly longer than wide, straight longitudinally, moderately convex transversely, AB, DE, and EA hexagonal, BC and CD septagonal in contact with anals. Radials 5, shorter than long, straight longitudinally, moderately convex transversely, outflaring, maximum width at base of very narrow interradial notch. Radial facets peneplenary, slightly outset, subhorizontal. Radial-primibrachial suture gaping. Anals 3, normal position. Primanal and secundanal approximately same size. Primanal pentagonal elongate. Secundanal hexagonal, extending slightly above radial summit. Anal series continues as two parallel columns of stacked polygonal plates in base of slender anal tube. Single primibrachials axillary in all rays, isotomous branching. Brachials strongly rounded transversely, straight to slightly concave longitudinally, hourglass-shaped. Proximal secundibrachials shorter than primibrachials, shape similar to primibrachials, cuneate. Arms 10 in preserved portion. Proximal columnal round transversely, lumen subpentalobate. Measurements given in Table 10.

Remarks.—These two partial crowns are tentatively assigned to *Cosmetocrinus* because they have very narrow interradial notches, that are essentially concealed by the outset radial facets. Interradial notches are not known in any species of *Cosmetocrinus*. The primibrachials are of differing lengths, with the B ray longest on both specimens. Differing lengths of the primibrachials is a feature common to *Cosmetocrinus*

Table 11.—Measurements in mm for *Dicromyocrinus vastus* n. sp.

	Type				
	Holotype	Paratype 1	Paratype 2	Paratype 3	Paratype 4
	Spec. no. (RGM)				
	361 266	361 267	361 268	361 269	361 270
Crown length (incomplete)	17.4	10.8			
Cup length	8.8	5.7	13.5	10.9	7.9
Cup width	15	10.8	6.5	5.4	14.6
Diameter infrabasal circlet	6.2	4.3	6.9	4.8	6.8
Basal length	5.4	3.7	4.8	3.2	5.6
Basal width	5.7	4	5.3	4.5	6.3
Radial length	5.7	3.5	5.2	3.3	6
Radial width	8.3	5.3	7.5	5.8	8
Primanal length	5.3	3.4	4.2	3.5	4.1
Primanal width	3.6	2.6	4	3.2	3.4
Primibrachial length	3.8		6		
Primibrachial width	7.6		4.1		
Stem facet diameter			2.8	1.4	
Proximal columnal diam.	2.5	1.8			7.4

and several other genera of the cladids. The small conical cup is also known among a few genera of the Scytalocrinidae, but none has interradial notches and the brachials are quite long, branching on primibrachial two or higher.

Material.—Two specimens (RGM 290 874, RGM 361 265) from marly limestone above DZ12 of the El Guelmouna Member, El Guelmouna Formation, Mississippian (Serpukhovian, E1), at Djenien, east of Palmeraie de, before the pass, Béchar; Winkler Prins collection.

Superfamily **CROMYOCRINACEA** Bather, 1890

Family **CROMYOCRINIDAE** Bather, 1890

Genus **DICROMYOCRINUS** Jaekel, 1918

Dicromyocrinus vastus, new species

Plate 12, figures 11–21; Plate 17, figures 25, 26

Diagnosis.—Distinguished by the medium-sized ornamentation, lesser degree of suture impression, tertanal in contact with primanal, and a slightly upflaring infrabasal circlet.

Description.—Crown small, cylindrical with arm girdle in proximal part of secundibrachials. Cup medium bowl- to globe-shaped, incurving at distal tips of radials, base subhorizontal to shallow basal invagination; all cup plates and proximal brachials bear medium granular to vermiform ornament; apical pits shallow, sutures weakly to moderately impressed. Infrabasal circlet horizontal proximally, downcurving to horizontal medially, gently upcurved distally. Infrabasals 5, dart-shaped, widest at basal plane, distal tips barely visible in lateral view. Basals 5, large, slightly wider than long, AB, DE, and EA hexagonal, BC and CD heptagonal to accomodate adjoining anals, moderately convex longitudinally and transversely, outflaring proximally, subvertical distally, form lower half of cup wall. Radials 5, much wider than long, widest slightly below radial summit, moderately convex longitudinally and transversely, incurving distally, form upper half of cup wall. C radial with shortened side adjacent to anal series; C and D radials not as wide as A, B, and E radials. Radial facet plenary, sloping outward slightly, with wide outer ligament area, moderately deep ligament pit, straight transverse ridge nearly plenary, wide muscle areas. Anals 3, primitive to intermediate advanced position; primanal largest, pentagonal, oblique, in contact with C radial, BC and DC basals or CD basal only, secundanal, and tertanal; secundanal hexagonal, directly above CD basal, one-third above radial summit; tertanal smallest, hexagonal, slightly less than half above radial summit. Single primibrachial axillary in all rays, much wider than long, moderately convex transversely, longitudinally convex proximally becoming concave distally, moderate gape with radial. Branching isotomous, 2 arms per ray, 10 arms total unless additional branching distally. Proximal columnals circular transversely, heteromorphic. Noditaxis at least N212. Lumen pentalobate. Crenularium narrow, on outer half of facet. Measurements given in Table 11.

Remarks.—Weathering apparently has destroyed much of the ornament on the cup plates of most specimens of *Dicromyocrinus vastus* n. sp. leaving an abraded surface with remnants of median coarse nodose and anastomosing ridge ornament. The ornamentation is intermediate in size between the fine and coarse clades recognized by Webster (1981). It is most similar to that of *D. medius* Moore and Strimple (1973). These two species differ in the lesser degree of suture impression, the tertanal is in contact with the primanal, and the infrabasal circlet is slightly upflared in *D. vastus*, whereas the sutures are deeply impressed, the tertanal is not in contact with the primanal, and the infrabasal circlet is horizontal to slightly impressed in *D. medius*. It is distinguished from other species of the genus by the medium-sized ornamentation, not being as coarse as in *D. granularis* Easton (1962) from Lower Pennsylvanian strata from North America. The ornament is coarser and the base flatter in *D. vastus* than in *D.? papillatus* Worthen (1882) from Upper Mississippian strata of the Illinois Basin, North America. The medium bowl-shaped cup of *D. vastus* is an intermediate form between the more primitive high-bowl or medium-globe shape of *D. catillus* n. sp. and the advanced low-bowl shape of *D. ?invaginatus* n. sp., although it occurs stratigraphically below both species. The arm girdle or constriction of the arms above the radials in the enclosed position (Webster and Lane, 1967) is a common morphologic feature of most cromyocrinids and some other late Paleozoic cladids and articulates (Webster and Jell, 1999b).

Dicromyocrinus vastus belongs to the more primitive group of the genus with a rounded base but shows a slightly advanced condition with a shallow basal invagination involving the proximal parts of the infrabasal circlet and variation in the anals. The anals show variation from the normal primitive oblique to slightly advanced position with the primanal not in contact with the BC basal and the distal tip nearly at the radial summit. Variation in the anals is common in other genera of the cromyocrinids, such as *Ulocrinus* as illustrated by Wright (1927).

Preservation of the specimens differs with the formation. The two cups from a horizon between the Hassi Kerma Formation and Djenien Member are uncrushed, replaced with iron oxide, and have a shiny to dull ferruginous brown appearance. Specimens from the El Guelmouna Member are partial crowns (lacking the arms above the proximal secundibrachial or two), abraded, solution etched, slightly distorted from compaction, and weather a dull gray to gray-brown. The cup from the Mouizeb el Atchane Member is uncrushed, retains two primibrachials, is abraded, and weathers a polished light gray-tan. The species ranges through the Serpukhovian.

Material.—Twenty-two specimens. Holotype (RGM 361 266), paratype 1 (RGM 361 267), paratype 5 (RGM 361 271), paratype 6 (RGM 361 272), and 15 other specimens (lot RGM 290 876) from the marly limestone above DZ12 of the El Guelmouna Member, El Guelmouna Formation, Mississippian (Serpukhovian, E1), at Djenien, east of Palmeraie de, before the pass, Béchar; Winkler Prins collection. Paratypes 2 and 3 (RGM 361 268; RGM 361 269) found between the Hassi Kerma Formation and Djenien Formation (Tagnana Formation?), Mississippian (Serpukhovian, E2), Tiberbatine Anticline, east side of Oued Guir; Pareyn collection. Paratype 4 (RGM 361 270) from the Mouizeb el Atchane Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E2), at Djebel Arlal; Legrand-Blain collection.

Etymology.—From the Latin *vastus*, meaning desolate or vast, in reference to the region wherein the specimens were found.

Dicromyocrinus catillus, new species
Plate 13, figures 10–12

Diagnosis.—Distinguished by the combination of low bowl shape and fine anastomosing ornament.

Description.—Cup low bowl-shaped, width (16.3 mm) more than twice height (6.8 mm), widest at basal apices, very shallow basal invagination, walls incurved at radial summit, sutures impressed, all plates ornamented with fine low anastomosing irregular ridges. Infrabasal circlet 8.1 mm diameter, subhorizontal, not visible in lateral view. Infrabasals 5, slightly wider (4.0 mm) than long (3.8 mm). Basals 5, wider (7.9 mm) than long (5.7 mm), strongly convex transversely and longitudinally, horizontal proximally, vertical distally. Radials 5, width 8.4 mm, length 4.9 mm, strongly convex transversely and longitudinally, widest between apices of basals. Radial facets plenary, subhorizontal, deep, abraded. Anals 3, in primitive arrangement. Primanal largest, 5.8 mm long, 3.9 mm wide, in oblique position, pentagonal, adjoins C radial, BC and CD basals, secundanal and tertanal. Secundanal elongate, 4.5 mm long, 2.6 mm wide, distal half extends above radial summit. Stem impression circular, 2.5 mm diameter; lumen pentagonal.

Remarks.—The cup of *Dicromyocrinus catillus* n. sp. has been slightly distorted normal to the plane of symmetry, giving it a slightly lop-sided appearance in lateral view. Weathering has obliterated the fine details of the articular facets, which had a transverse ridge, outer ligament pit, and inner muscle areas. Vermiform ornament is not the coarse nodose ornament normally developed on *Dicromyocrinus* (Webster, 1981). This specimen belongs to the low-bowl lineage of *Dicromyocrinus*, which evolved from the high-bowl form. The low bowl combined with the fine anastomosing ornament distinguishes *D. catillus* from all other species of the genus.

Material.—Holotype (RGM 361 273), from the upper part of the Hassi Kerma Formation, Pennsylvanian

(Bashkirian), at Oglat Hamia; Legrand-Blain collection.

Etymology.—From the Latin *catillus*, meaning bowl, in reference to the shape of the cup.

Dicromyocrinus? invaginatus, new species

Plate 13, figures 13–16; Plate 17, figures 9–14

Diagnosis.—Distinguished by the combination of the moderate to deep basal invagination and coarse nodose ornament.

Description.—Cup medium flat-bottomed bowl-shaped, incurved slightly at distal tips of radials, moderate to deep basal invagination; all cup plates bear coarse nodose ornament; apical pits moderate, sutures moderately impressed. Infrabasal circlet horizontal proximally, forming vertical walls of invagination medially, slightly outflaring distally, all within basal invagination. Infrabasals 5, dart-shaped, not visible in lateral view. Basals 5, equidimensional, hexagonal or septagonal (BC and CD basals only) where in contact with anals, strongly convex longitudinally, moderately convex transversely, proximal tip in basal invagination, medially form base of cup recurving upward and outflaring distally forming lower half of cup wall. Radials 5, much wider than long, widest very slightly below radial summit, moderately convex longitudinally and transversely, incurving slightly distally, form upper half of cup wall. C radial with shortened side adjacent to anal series; C and D radials not as wide as A, B, and E radials. Radial facet plenary, wide outer ligament area, moderately deep ligament pit, straight transverse ridge, wide muscle areas. Anals 3, primitive or slightly advanced position; primanal largest, hexagonal, oblique, in contact with C radial, BC and CD basals, D radial, secundanal, and supports tertanal; secundanal pentagonal, directly above but not in contact with CD basal, more than half above radial summit, if hexagonal in contact with CD basal; tertanal smallest, pentagonal, two-thirds above radial summit. Arms unknown. Stem facet circular, crenularium half radius. Measurements given in Table 12.

Remarks.—The generic assignment of *Dicromyocrinus*? *invaginatus* n. sp. is tentative because specimens have a moderate to deep basal invagination that includes the proximal ends of the basals. As recognized by Webster (1981), *Dicromyocrinus* may have a slightly upflared or slightly invaginated base. No species assigned to the genus has a moderate to deep basal invagination. None of the other cromyocrinids in the Late Carboniferous with three anals and a moderate to deep basal invagination has ornament. The moderate to deep basal invagination is an advanced evolutionary character. If all of these specimens had two anals, they would possibly be assigned to *Ethelocrinus*, which has a shallow to moderately deep invagination. Variation in the position of the anals suggests mosaic evolution was occurring within *D.*? *invaginatus*: three specimens show the primitive position with the secundanal in contact with and directly above the CD basal, whereas two specimens show the slightly advanced position with the secundanal directly above, not in contact with the CD basal. The arms are unknown on the specimen, which is another reason to question the generic assignment, because *Dicromyocrinus* has 10 uniserial arms and *Ethelocrinus* has 16 to 18 biserial arms (Webster, 1981). With future collecting we would not be surprised to see specimens found with three anals and 16 to 18 biserial arms.

Table 12.—Measurements in mm for *Dicromyocrinus*? *invaginatus* n. sp.

	Type	
	Holotype	Paratype 1
	Spec. no. (RGM)	
	361 281	361 282
Cup length	8.7	8.2
Cup width	19.0	16.9
Diameter infrabasal circlet	5	4
Basal length	7.6	6.2
Basal width	8.3	6.2
Radial length	6.4	5.8
Radial width	10	9.2
Diameter stem facet	2	0.9
Length basal invagination	1	1.6

Both *Dicromyocrinus* and *Ethelocrinus* have similar ornament. *Dicromyocrinus* may be divided into two clades based on fine or coarse ornament. These specimens belong to the coarse ornament clade of *Dicromyocrinus* as recognized by Webster (1981).

All specimens are dorsal cups, lacking the arms and stem, and most ornament has been lost by abrasion or solution. The holotype (RGM 361 281) and one of the non-type (RGM 290 858) specimens have one radial missing. The smallest specimen (RGM 290 856) lacks the anals and three radials.

Material.—Five specimens: Holotype (RGM 361 281) and paratypes 1 and 2 (RGM 361 282, RGM 361 283) and two other specimens (RGM 290 856, RGM 290 858) from the Oued Bel Groun Formation, Pennsylvanian (Moscovian), Bed M1 (Deleau, 1951), from Béchar-Djerid, immediately south of Béchar; Winkler Prins collection.

Etymology.—From the Latin *in*, into, and *vagina*, sheath, and refers to the basal invagination.

Dicromyocrinus? sp.

Plate 13, figures 1–5

Remarks.—One disarticulated radial (RGM 361 274, 7.3 mm long, 12.0 mm wide), two BC basals

(RGM 361 275, 14.2 mm long, 19.8 mm wide; RGM 361 276, 11.4 mm long, 14.3 mm wide), three non-BC basals (RGM 361 277, 11 mm long, 13.0 mm wide; RGM 361 278, 12.2 mm long, 15.4 mm wide; RGM 361 279, 11.1 mm long, 12.7 mm wide), and one partial infrabasal circlet (RGM 361 280, 15.6 mm in diameter); all bearing fine granular ornament that grades into a vermiform ornament are tentatively referred to *Dicromyocrinus*, based on several criteria. The basals and radials are convex transversely and longitudinally. Radials are widest at the basal apices, narrow upward and wedge inward with plenary radial facets, as on *Aaglaocrinus*, *Dicromyocrinus*, and other cromyocrinids. The infrabasal circlet is upflared gently distally and was barely visible in lateral view, based on the curvature of the basals and radials. Three anals are in the cup in primitive arrangement, which is shown by the presence of an extra facet for the primanal articulation on the two BC basals positioned between the radial-tertanal facet, within the radial circlet, and the BC-CD basals suture below. The radial facets are plenary, subhorizontal, and deep. The transverse ridge is narrow and plenary; the outer ligament pit is shallow, narrow, and 0.7 length of transverse ridge. The outer ligament ridges are narrow, sharp crested, and divided by a narrow shallow furrow. The muscle areas are wide with furrows adoral to the transverse ridge. The stem facet is round (5.5 mm diameter) and has a pentalobate lumen. Based on the above features the cup would have had a medium globe shape. This fits the primitive lineage of *Dicromyocrinus* with a convex base.

Material.—Seven specimens: One radial (RGM 361 274), two BC basals (RGM 361 275, RGM 361 276), three non-BC basals (RGM 361 277–RGM 361 279), and one infrabasal circlet (RGM 361 280) from the lower part of Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Genus **MOOREOCRINUS** Wright and Strimple, 1945

Mooreocrinus glomerosus, new species

Plate 13, figures 17–26

Diagnosis.—Distinguished by the combination of less impressed sutures and lower cup with more rounded base.

Description.—Cup medium bowl-shaped, wider (15.0 mm average) than long (8.5 mm), base flat to shallow basal invagination, sutures flush to slightly impressed, base walls rounded, distal walls vertical, no ornamentation. Infrabasal circlet subhorizontal with shallow central invagination, 6.1 mm diameter, central stem impression moderately deep. Infrabasals 5, dart-shaped, slightly longer (2.9 mm) than wide (2.6 mm), not visible in lateral view, downflaring proximally, horizontal distally. Basals 5, wider (5.8 mm) than long (5.2 mm), gently convex transversely and longitudinally. Radials 5, largest plates in cup, 8.1 mm wide, 5.3 mm long, gently convex transversely and longitudinally. Radial facets plenary; transverse ridge narrow, sharp crested; outer ligament pit ⅓ length transverse ridge, deep, slopes under ridge; outer marginal ridge with transverse ridges and grooves across facet; outer margin shelf moderately wide centrally, crescent-shaped; muscle areas not exposed. Anals large, in primitive position. Primanal largest, 5.6 mm long, 4.0 mm wide, oblique position, adjoined by C radial, BC and CD basals, secundanal, and tertanal. Secundanal elongate, 5 mm long, 3.7 mm wide, distal half above radial summit. Axillary primibrachial wider (8.4 mm) than long (5.2 mm), strongly convex transversely, gently convex longitudinally; primibrachials unequal in length, A longest, C and D second longest, B and E shortest. First secundibrachial wider (4.5 mm) than long (3.2 mm), strongly convex transversely, straight longitudinally. Arms 2 per ray, 10 in total if no branching occurs above primibrachial. Stem round, 2.7 mm (average) diameter; lumen pentagonal. Columnals heteromorphic, noditaxis N1 at least; latus rounded.

Remarks.—The holotype (RGM 361 284) of *Mooreocrinus glomerosus* n. sp. is distorted slightly and retains parts of the D, E, and A ray arms up to the sixth secundibrachial as well as the proximal columnal. Paratype 1 (RGM 361 285) is a cup with the E, A, and B ray primibrachials and one of the first secundibrachials in the E and A rays. In addition it retains the proximal three columnals. Paratype 2 (RGM 361 286) is a crushed partial crown with distorted proximal parts of the arms and three proximal columnals. Paratype 3 (RGM 361 287) is a ferruginous-replaced cup.

Mooreocrinus glomerosus lacks the moderately to deeply impressed sutures of *M. mendesi* (Lane, 1964), *M. wilburni* Strimple and Watkins (1969) and *M. geminatus* (Trautschold, 1867). It is most similar to *M. magdalenensis* Strimple, 1975b, but has a relatively lower cup and more rounded base with less of the basals in the vertical cup walls.

This is the first report of *Mooreocrinus* from the Mississippian. It is also the first report of the genus from North Africa.

Material.—Four specimens: Holotype (RGM 361 284) and paratype 3 (RGM 361 287), from the El Harrada Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E1), at Cirque de Tagnana (Ued Narkla); paratypes 1 and 2, (RGM 361 285, RGM 361 286) from the Mouizeb el Atchane Member, Aïn el Mizab

Formation, Mississippian (Serpukhovian, E2), at Ravine de Djenien; Pareyn collection.

Etymology.—Latin, meaning like a ball, referring to the bowl-shaped cup.

Genus **METACROMYOCRINUS** Strimple, 1961

Metacromyocrinus? sp.

Plate 15, figures 1–4

Description.—Cup globose, small, length 6.2 mm, width 9.0, all plates with vermiform ornament; apical depressions shallow, deeper at radial-basal apices than basal-infrabasal apices. Infrabasals 5, dart-shaped, length 3.2 mm, width 2.4 mm, gently convex longitudinally and transversely, proximally bear 1.2 mm shallow invagination for stem attachment, distally upflared, visible in lateral view. Basals 5, moderately large, length 3.9 mm, width 4.3 mm, hexagonal, except BC and CD basals septagonal in contact with anals, moderately convex longitudinally and transversely, form maximum width of cup. Radials 5, nearly twice as wide as long, length 3.7 mm, width 4.9 mm, narrowing distally, moderately convex longitudinally and transversely, incurved distally. Radial facets plenary, slope gently inward. Anals 3, normal position; primanal elongate pentagonal, length 3.7 mm, width 1.9 mm, supporting tertanal on left upper shoulder. Secundanal directly above posterior basal, length 2.6 mm, width 1.6 mm, distal half above radial summit. Stem and arms unknown.

Remarks.—The cup of *Metacromyocrinus*? sp. is abraded but still shows vestiges of the vermiform ornament. The arms, tegmen, and stem are not preserved. Although this is probably a new species, preservation precludes using the specimen for a holotype. It is tentatively assigned to the genus, because of the preservation.

Material.—Figured specimen (RGM 290 860) from the Oued Bel Groun Formation, Pennsylvanian (early Moscovian), bed M13 (Deleau, 1951), east? of Oglad Hamia, Kenadza; Winkler Prins collection.

Genus **MATHERICRINUS** Webster, 1981

Remarks.—Termier and Termier (1950) described *Parulocrinus wallacei* recognizing variation in the cup shape and questioned whether it should be assigned to *Ulocrinus* or *Parulocrinus*. Webster (1981) recognized variation in the cup shape from globose to an elongate urn as is common in *Mathericrinus*, *Parulocrinus*, and *Ulocrinus*. Furthermore, some species assigned to each of these three genera show variation in the number of anals from three to two. These three genera are differentiated by ornamentation on cup plates in *Mathericrinus*, the other two genera lacking ornamentation, and *Ulocrinus* having 10 arms while *Parulocrinus* has 14 to 18 arms. Some species that have been assigned to each of these genera are based on cups, lacking the arms, so that their generic assignments are uncertain, especially for the unornamented species. *Mathericrinus* ranges from the Early to Middle Pennsylvanian and is known from the United States and China. *Ulocrinus* ranges from Middle into early Late Pennsylvanian and is known only from the United States. *Parulocrinus* ranges from Middle Pennsylvanian into Early Permian and is known from the United States and Brazil (Webster, 2003).

Mathericrinus wallacei (Termier and Termier, 1950), new combination

Plate 13, figures 6–9; Plate 14, figures 1–24

Parulocrinus wallacei Termier and Termier, 1950, pp. 100–101, pl. 217, figs. 5–14, 17, 18; pl. 222, figs. 6–8, ?14–22.

Diagnosis.—Distinguished by fine granular to aligned granular and anastomosing ornament.

Description.—Cup flat based medium bowl to elongate urn shape, widest at basal apices, fine granular to aligned granular and anastomosing ornament, may have secondary ornament of 2 or 3 narrow ridges restricted to distal parts of plates aligned with corresponding ridges on adjacent plates but never extending across the central part of the plates, sutures slightly to moderately impressed, plates slightly inflated. Infrabasal circlet relatively large, horizontal proximally, weakly to moderately upflared distally. Infrabasal plates 5, dart shaped, distal tips not visible to barely to obviously visible in lateral view. Basals 5, large, form lower half of cup wall, moderately convex longitudinally and transversely, proximally may be horizontal forming part of base of cup or outflaring forming base of wall, distally vertical; BC basal heptagonal for contact with primanal on upper left shoulder, all other basals hexagonal. Radials 5, large, wider than long, widest between basal apices, moderately convex longitudinally, moderately convex transversely, vertical to slightly inflared distally. Radial facet plenary, slopes inward slightly. Radial facet deep, inner part of outer ligament furrow and outer ligament ridge denticulate; ligament pit shallow; transverse ridge denticulate on lateral two-thirds; wide triangular muscle areas slope downward toward intermuscular furrow; central pit trifurcate at transverse ridge. Anals 2 or 3, variable positioning, in slightly (tertanal barely in contact with primanal) to strongly advanced (tertanal not in contact with primanal, virtually out of cup) primitive condition. Primanal largest; normally pentagonal in contact with C radial, BC and CD basals, secundanal, and tertanal; quadrangular when not in contact with tertanal. Secundanal longer than wide, narrow suture with CD

Table 13.—Measurements in mm for *Mathericrinus wallacei* n. comb.

	Spec. no. (RGM)				
	361 291	361 288	361 289	361 290	316 292
Cup length	9.1	10.1	12.3	13.3	14.4
Cup width	17.5	15	13.5	19.3	21.3
Diameter infrabasal circlet	7.8	7.3	7.8	9.7	11
Basal length	6.7	7	6.5	8.7	9.1
Basal width	8.2	7.4	7	10	11.3
Radial length	5.5	8	5.4	7.3	8.9
Radial width	9.2	5.2	6.7	10	11.4
Primanal length	5.6	5.6	6	7.7	7.8
Primanal width	4.7	4	3.6	5	5.9
Stem facet diameter	2.2	2.5	2.7	2	4.1

basal, distal ¼ above radial summit. Tertanal smallest, narrow suture with primanal when in contact, otherwise V-shaped proximally, widening distally, mostly to entirely above radial summit. Stem facet slightly impressed, circular, wide crenularium, no areola, pentalobate axial canal. Arms and stem unknown. Measurements given in Table 13.

Remarks.—The presence of fine granular to aligned granular and anastomosing ornament distinguishes *Mathericrinus wallacei* n. comb. from other species assigned to the genus, all of which have different types of ornament. Ornamentation is commonly weathered and completely to mostly lost on specimens of *M. wallacei.* Those specimens with the ornament preserved, however, have variation in the degree of development or lack of the secondary ridges passing across plate boundaries. On several specimens weathering has accentuated the aligned ridges extending onto adjacent plates and suturing along plate boundaries. Fracturing along rhombohedral cleavage planes resulted in the loss of parts of some plates on a few specimens. *Mathericrinus wallacei* is most similar to *M. percultus*, which has radial ridge ornament, lacking granular ornament.

Parulocrinus wallacei is transferred to *Mathericrinus* because the cup is ornamented; *Parulocrinus* lacks ornamentation. Loose cup plates assigned to *P. wallacei* by Termier and Termier (1950, pl. 22, figs. 14–22) are tentatively assigned to *M. wallacei.* In particular the radials illustrated in figures 16, 19 and 21 may belong to three different taxa, based on drawings of the radial facet. No type was designated by the Termiers and we have been unable to locate the original figured specimens. Without seeing the original specimens we are unwilling to designate a lectotype. If the Termier specimens are lost, one of the specimens designated 1 to 6 below could be designated a neotype. The above diagnosis and description are given because the brief comments given in the original description are inadequate to define the species.

Variation in the cup shape of *Mathericrinus wallacei* ranges from a flat-based medium bowl (RGM 361 292) with the infrabasal circlet confined to the base to a higher medium globe (RGM 361 288) with the infrabasal circlet gently to moderately upflared and visible in lateral view. Maximum width of the cup shifts from the radial summit or slightly below on the medium-bowl cups to the proximal tip of the radials on the globe-shaped cups. The medium bowl cups are very similar in shape to cups of *Dicromyocrinus.* These cups are assigned to *M. wallacei* because cups with intermediate shape and bearing the same ornamentation and anals variation are present in the collections.

Although the anals are closely similar, they show progressive elimination of the tertanal from the cup, with most specimens having the tertanal resting on the primanal, rarely widely (RGM 361 289; RGM 361 293), commonly narrowly (RGM 361 291; RGM 361 292). The most advanced forms have the tertanal nearly out of the cup (RGM 361 288; RGM 361 290), not in contact with the primanal, and some could almost be considered to have two anals in the cup because only the proximal tip is below the radial summit.

Material.—Twenty-nine specimens. All specimens except specimen 5 are from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), Pareyn collection. Specimen 1 (RGM 361 288), specimen 2 (RGM 361 289), specimen 6 (RGM 361 293), specimen 7 (RGM 361 294) one listed specimen (RGM 361 295), one specimen (RGM 361 298), three specimens (RGM 361 300), two specimens (RGM 361 301), and three specimens (RGM 361 302) from the upper part of Oued el Hamar Formation, Foum ech Cheguiga. Specimen 3 (RGM 361 290) from an undesignated part of the Oued el Hamar Formation, at Chebket Khouabi. Specimen 4 (RGM 361 291), two specimens (RGM 361 299) and five specimens (RGM 361 304) from undesignated part of the Oued el Hamar Formation, south of Teniet Aissa ben Azzi. Specimen 5 (RGM 361 292) from the upper part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Oglat Hamia; Legrand-Blain collection. Specimen 8 (RGM 361 296), specimen 9 (RGM 361 297), and three specimens (RGM 361 303) from an undesignated part of the Oued el Hamar Formation, on the north flank of Chebket Mennouna.

Genus **UREOCRINUS** Wright and Strimple, 1945

Type species.—*Ureocrinus bockschii* Geinitz, 1846.

Remarks.—The shapes of species of *Ureocrinus* range from globose to high globe or vase, with the majority of species being a medium globe. The high-globe or vase shape is similar to the high-cone shape of *Hydriocrinus*. Differences in arm structure and anal arrangement, however, are sufficient to distinguish these taxa. Lane *et al.* (2001) removed all Devonian species from *Hydriocrinus*. See remarks under *Hydriocrinus? confusus* for comments on the Late Carboniferous species of the genus.

Ureocrinus commus, new species
Plate 15, figures 9–13

Diagnosis.—Distinguished by the presence of granular to vermiform ornament.

Description.—Cup high vase-shaped, base narrow, widest at lowermost tips of radials, distal tips of radials incurved; length 14.8 mm; width 10.7 mm minimum, 12.1 mm maximum, 11.5 mm average; all plates with granular to vermiform ornament tending to discontinuous to continuous ridges parallel to sides of plates giving appearance of growth rings. Infrabasals large, longer (7.3 mm) than wide (4.2 mm), dart-shaped, straight longitudinally, moderately convex transversely; proximal tips horizontal forming base of cup, covered by proximal columnals; distal ¾ upflared, forming basal ¼ of cup; C ray infrabasal slighly wider (5.4 mm) than others. Basals 5, longer (7.5 mm) than wide (6.6 mm), moderately convex longitudinally and transversely, 4 hexagonal, 3 with 2 equal upper edges; CD basal hexagonal with elongated upper right shoulder in full contact with longest edge of primanal, slightly longer than all basals except BC basal; BC basal heptagonal, in full contact on upper left shoulder with short edge of radianal, slightly longer than all other basals. Radials 5, slightly convex longitudinally, moderately convex transversely; A and E wider (6.2 mm) than long (5.5 mm), B and C about as wide as long, D slightly longer than wide; posterior sides of C and D radials project slightly higher than, and bottoms of radials not as low as, other radials to accommodate cup anals. C radial hexagonal, all others pentagonal, narrowing slightly distally. Radial facets poorly preserved, plenary, outer margin slightly convex, transverse ridge straight. Anals 3. Radianal largest, hexagonal, length 5.3 mm, width 3.9 mm. Secundanal small, length uncertain, width 2.2 mm, situated in notch on left shoulder of primanal and right shoulder of D radial, projecting above radial summit. Tertanal pentagonal, not preserved, space smaller than secundanal, above primanal, projecting above radial summit. Proximal columnal subpentagonal, diameter 3.2 mm, crenulate latus, lumen weakly pentalobate, crenularium narrow, approximately ⅓ radius of facet. Arms and tegmen not preserved.

Remarks.—The cup of *Ureocrinus commus* n. sp. is well preserved and compares most closely in shape with *U. doliolus* (Wright, 1936). It differs from all species of *Ureocrinus*, however, by having ornamentation. Parts of two primibrachials, lacking the exterior surfaces, are in the oral cavity. Their position suggests that there were gapes along the radial-primibrachial suture.

Material.—Holotype (RGM 290 873) from marly limestone above DZ12, El Guelmouna Member, El Guelmouna Formation, Mississippian (Serpukhovian, E1), at Djenien, east of Palmeraie de, before the pass, Béchar; Winkler Prins collection.

Etymology.—From the Greek *kommos* meaning ornamentation.

Cromyocrinid? indeterminate
Plate 15, figure 19

Description.—Partial cup, medium cone shape, large (minimum 17 mm long, 27 mm wide); sutures impressed, stitched, plates thick. Infrabasal circlet (5 plates), large (18.2 mm diameter); deep round basal invagination. Distally infrabasals form cup base and walls, visible in lateral view. Basals very wide, outflaring. Radials large, outflaring, facets plenary. Anals uncertain, minimum 2 in cup, probably 3, in primitive position. Stem and arms unknown.

Remarks.—The fractured and slightly distorted cup of this indeterminate cromyocrinid? is embedded in dark red calcareous shale. The impressed stitched sutures and thick plates suggest relationship with the cromyocrinids. Most cromyocrinids have bowl- instead of cone-shaped cups, and most do not have a deep basal invagination. This specimen may represent a new genus but is of insufficient quality to serve as a holotype.

Material.—One cup (RGM 361 305) from the Mazzer Formation, Mississippian (late Viséan), Mader El Madjid (syncline bed 13, Pareyn, 1961); Pareyn collection.

Superfamily **PIRASOCRINACEA** Moore and Laudon 1943

Family **LAUDONOCRINIDAE** Moore and Strimple, 1973

Genus **PAIANOCRINUS** Strimple, 1951b

Paianocrinus? carinatus, new species

Plate 15, figures 16–18

Diagnosis.—Distinguished by isotomous arm branching.

Description.—Crown elongate (53.6 mm long), flared medially (35.6 mm wide, average), flattened along C-E rays, more than 40 arms. Cup low bowl-shaped, 6.9 mm high, 16.4 mm wide (average), base faintly convex, walls widely flared. Infrabasal circlet small, 5.5 mm diameter, horizontal to faintly upflared. Infrabasals 5, small, 3.6 mm wide, covered proximally by proximal columnal. Basals 5, small, 4.3 mm long, 5.0 mm wide, gently convex transversely, straight longitudinally. Radials 5, dominant plate in cup, 5.4 mm long, 8.7 mm wide, gently convex transversely, straight longitudinally. Radial facets peneplenary, with short narrow deep outer ligament pit and narrow outer margin, remainder not exposed. Anals 3, in primitive oblique position. Primanal equidimensional, 4.2 mm wide and long (may be partly eroded on proximal end); secundanal largest, elongate, 4.7 mm long, 4.1 mm wide, distal half above radial summit; tertanal smallest, proximal ⅓ below radial summit. Primibrachials wider (8.2 mm) than long (6.6 mm), moderately convex transversely, gently convex longitudinally, variable height with A ray shortest, C and D rays longest, all axillary. First secundibrachials wider (5.2 mm) than long (3.2 mm), strongly convex transversely, straight longitudinally. All higher brachials wider than long, strongly convex or angular transversely. All brachials rectilinear, above secundibrachials bear medial ridge which may grade into a very short blunt spine on distal end. All branchings isotomous on single primibrachial, secundibrachials 3 to 5, tertibrachials 4 or 5, quartibrachial 8. Last branching in E ray only, may be abnormal. Normally 8 arms per ray, 41 total. Tegmen unknown. Stem facet round, 3.8 mm diameter; axial canal pentagonal.

Remarks.—Width of the radial facet varies with almost plenary (least peneplenary) facets of the A and B rays, more peneplenary E ray, and most peneplenary D ray of *Paianocrinus*? *carinatus* n. sp. The C-ray radial is not preserved. Variation in relative width of the radial facets on a single specimen is highly unusual. Generally only slight variation is observed among specimens of the same species. All arm branching is isotomous except in the E ray. The last branching in the E ray is endotomous, occurring only on the adanal side of the adanal half ray. It is possible that this is an abnormal branching or repair of an injury.

Classification of this crown is difficult because the cup has affinity with the Laudonocrinidae (possessing peneplenary radial facets, low bowl shape, and three anals); however, all arm branching except in the E ray is isotomous (the laudonocrinids have exotomous branching after the first branchial). The brachials resemble those of *Exocrinus* Strimple, 1949, but that genus has plenary radial facets.

We assign *P.*? *carinatus* to the genus *Paianocrinus* only tentatively because the shape of the brachials is quite different and is perhaps of generic significance. The brachials of *P. durus* are thinly rectilinear (wider than long) and broadly convex transversely. Axillary brachials are strongly tumid, bearing distinct protuberances, with the primibrachials bearing short blunt spines. The rectilinear brachials of *P.*? *carinatus* are relatively longer and bear an angular longitudinal median ridge. Axillary brachials lack the protuberance or short spine. The brachials of *P. aptus* are similar to, but lack the strong tumidity and short spines of *P. durus*.

The family description for the Laudonocrinidae by Moore *et al.* (*in* Moore and Teichert, 1978) stated that the arms are endotomous. The arms, however, are known for only three (*Anchicrinus*, *Paianocrinus*, *Schistocrinus*) of the six genera assigned to the family. Under the diagnosis of *Paianocrinus*, the arms are listed (*ibid.*) as isotomous. Either the diagnosis of the family needs revision, or *Paianocrinus* does not belong in the family. The cup of *Paianocrinus* fits the diagnosis for the Laudonocrinidae, but there is no recognized family that matches both cup and arm morphology.

We believe that there are major taxonomic problems within several families of the "poteriocrinines" that involve the arm structure. Genera of the Laudonocrinidae whose arm structure is known are included within the taxa in need of reevaluation. Because this problem is beyond the scope of this report, we tentatively leave *Paianocrinus* in the Laudonocrinidae. *Paianocrinus* has been reported from Chesterian (Late Mississippian) strata of North America (Strimple, 1951b; Burdick and Strimple, 1983).

Material.—One crown, holotype (RGM 361 306), from the basal part of the Djenien Member, Djenien Formation, Mississippian (early Serpukhovian, E2), at Djebel Béchar; Legrand-Blain collection.

Etymology.—From the Latin *carina*, meaning keel or ridge, referring to the longitudinal ridge along brachials.

Superfamily **ZEACRINITACEA** Bassler and Moodey, 1943

Family **ZEACRINITIDAE** Bassler and Moodey, 1943

Zeacrinitidae indeterminate 1

Plate 17, figures 32–35

Description.—Cup discoid, 4.3 mm long to end radial facets, 22.2 mm wide; deep (2.5 mm) basal invagination 10.2 mm wide; all cup plates with proximal ends in basal invagination. Infrabasals fused, confined to top of basal invagination, covered by proximal columnal externally. Basals 5, strongly convex longitudinally, concave transversely, longer than wide, distal tips in basal plane to barely upturned; posterior basal slightly longer, truncated distally for reception of second anal. Radials 5, 6.3 mm long, 11.4 mm wide, strongly convex longitudinally, moderately convex transversely, widely outflared. Radial facet plenary, slope outward at 45°; outer marginal ridge sharp, bounded internally by moderately deep narrow vermiform-covered outer ligament furrow; outer ligament pit narrow, deep, approximately ⅓ facet width; transverse ridge full width of facet, vermiform surface, widening toward center, then narrowing across center of outer ligament pit; muscle areas deep, wide, with ridge wider and higher toward center of facet; no central pit, area built up into an oval high continuing as a low intermuscular ridge admedially rather than intermuscular furrow. Anals 3, primitive position. Primanal pentagonal, adjoining C radial, BC and CD basals, second and third anals. Second anal hexagonal, longer than wide, distal half extends above radial summit. Tertanal smallest, approximately equidimensional, distal half extending above radial summit. Arms unknown. Stem facet indicates stem round transversely with narrow crenularium. Axial canal round.

Remarks.—The cups of the three genera *Zeacrinites, Alcimocrinus,* and *Parazeacrinites* of the Zeacrinitidae are indistinguishable from one another. Differences in arm width and number in combination with the tegmen shape are the characters used to distinguish these genera. Unfortunately, the Algerian specimens of Zeacrinitidae indeterminate 1 lack the arms and cannot be assigned to a genus. The specimens, which are of the same size and show the interiors, may represent a new species.

Material.—Two specimens: Figured specimen (RGM 361 307) and unfigured cup (RGM 361 308) are from the El Harrada Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E1), Cirque de Tagnana (Oued Narkla); Pareyn collection.

Zeacrinitidae? indeterminate 2

Plate 15, figure 14

Description.—Crown elongate, 52.5 mm long (incomplete), 31.1 mm wide (average), crushed along bilateral symmetry plane, more than 40 arms, bearing large tegmen. Cup mostly lost. Radials 5, wider (11.1 mm) than long (6.1 mm), gently convex transversely, faintly convex to straight longitudinally, radial facet plenary, not exposed. Anals 3, large, in primitive arrangement. Primanal pentagonal, 7.1 mm long, 6.1 mm wide, positioned oblique, adjoined by C radial, BC and CD basals, secundanal and tertanal, gently convex longitudinally and transversely. Secundanal longer (6.6 mm) than wide (6.0 mm), distal ⅔ above radial summit. Anal interarea wide with large plates continuing exposure to tertibrach 2. Primibrachial wider (6.2 mm) than long (4.0 mm), gently convex longtudinally and transversely, axillary. Secundibrachial 1 wider (7.4 mm) than long (5.9 mm), moderately convex transversely, straight to gently concave longitudinally. Secundibrachial 2 axillary. Tertibrachials through quinquibrachials generally rectilinear, some slightly cuneate, wider than long proximally becoming more equidimensional distally. All branching isotomous with last branching endotomous; branching on tertibrachial 3 or 4, quartibrachial 4 or 5; 6 arms per half ray, 12 per ray, 60 total if branching is the same in all rays. Tegmen plates hexagonal, bulbous center, interconnecting stellate ridges between all plates; shape expanding distally, top not preserved.

Remarks.—The infrabasals and basals are not preserved and weathering has destroyed much of the surface ornamentation of the partial crown of Zeacrinitidae? indeterminate 2. Classification of the specimen is provisional. Most genera assigned to the Zeacrinitidae have large anal plates, a wide anal interarea, endotomous branching on all branchings after the first, a large elongate tegmen that expands into a mushroom shape distally (where known), and thin cuneate brachials. This specimen has the large anal plates and wide anal interarea, but the endotomous branching does not commence until the third branching. The elongate tegmen of unknown termination may have continued to expand into a mushroom shape. The rectilinear brachials are not typical of most genera assigned to the zeacrinitids but are known on *Zeacrinites,* which has a mushroom-shaped tegmen (Moore and Teichert, 1978). A taxonomic review of the Zeacrinitidae is needed to resolve the significance of the numerous differences in arm types among the genera assigned to the family.

Material.—One partial crown (RGM 361 309) from the Aïn Mezerelt Member, El Guelmouna Formation, Mississippian (Serpukhovian, E1) at El Aouidja, summit El Hamar 1; Legrand-Blain collection.

Cladid indeterminate 1
Plate 17, figures 27–28

Description.—Partial cup, lacking C radial and anals; cup medium bowl shape, base shallow basal concavity, fine granular grading into vermiform and aligned ornamentation; plates slightly inflated. Distal tips of infrabasals horizontal, forming base of cup; basals and radials slightly outflaring. Radial facet plenary, moderately deep; transverse ridge denticulate, outer ligament furrow wide, moderately deep; ligament pit deep; muscle areas wide, upflaring distally. Facets on BC and CD basals indicate 3 anals in primitive position. Stem facet roundly pentagonal, impressed; lumen pentalobate.

Remarks.—At first glance, this specimen of cladid indeterminate 1 is similar to some cromyocrinids. It lacks the sutured intracup facets of the cromyocrinids, however, and no cromyocrinid has a proximal roundly pentagonal stem. The cup is also similar to several genera of the scytalocrinids. Lacking the stem and arms, the specimen is not suitable to serve as a holotype and is left in open nomenclature.

Material.—One partial cup (RGM 361 310) from the upper part of the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), at Foum ech Cheguiga; Pareyn collection.

Cladid indeterminate 2
Plate 15, figures 5–8

Description.—Infrabasal circlet 4 plates, 3 small, 1 large, steeply upflared, slightly concave longitudinally, 19.4 mm diameter, base truncated, stem facet round (7.4 mm diameter); lumen roundly pentalobate, large (3 mm diameter). Columnals circular in transverse section; latus straight, smooth; symplectial articulation. Articulum full width of columnal; crenularium ¼ radius; culmina short, coarse, may branch on distal tip. Areola wide, diameter ¾ columnal diameter, slightly concave to flat, margins recessed sharply. Perilumen very narrow at outer edge of lumen lobes, wide between lobes; surface nodose where narrow, nodose to irregular culmina where wide. Lumen large, half columnal diameter, roundly pentalobate; jugula extended inward, moderately sharply pointed. Noditaxis pattern N1, alternating nodals and internodals.

Remarks.—The infrabasal circlet and two of the pluricolumanls of cladid indeterminate 2 are weathered and etched. Ornamentation, if initially present, is lost on the infrabasal circlet, and plates are relatively thin. The stem facet matches the articulum of the pluricolumnals; thus the specimens are considered to belong to the same species. One holdfast segment judged to belong with these pluricolumnals has the same articular facet with noditaxis pattern of N1 and two to five cirri on each nodal. The diameter of the holdfast (4.3 mm) is smaller than that of any of the other pluricolumnals (7.9 to 12.3 mm diameter). The specimen may represent a stem that tapers distally, it could be a branchlet of a holdfast, or it may be from an immature specimen.

The columnals could be assigned to *Floricyclus*, a genus reported from the Middle Mississippian (Osagean) to Late Pennsylvanian (Virgilian) of North America (Moore and Jeffords, 1968), the Tournaisian-Moscovian of Russia (Yeltyschewa and Polyarnaya, 1975; Chernova and Stukalina, 1989), and the Viséan of Poland (Gluchowski, 1981). Chernova and Stukalina (1989) also recognized a Late Devonian species from Kazakhstan and a Carboniferous species from Mongolia and China.

The Algerian specimens possibly belong to a blothrocrinid such as *Moscovicrinus* or *Nebraskacrinus*, both of which have large steeply upflaring infrabasal circlets. *Nebraskacrinus* also has a pentastellate lumen.

Material.—Six specimens: One infrabasal circlet (RGM 361 311) and one holdfast segment (RGM 361 312) are from the upper part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; and four pluricolumnals RGM 361 313; lot of three specimens (RGM 361 314) from the lower part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; all Legrand-Blain collection.

Cladid indeterminate 3

Remarks.—A moderately large partial cup consisting of two radials, part of a third radial, one basal, and part of a second basal would have had a bowl shape. All plates bear densely spaced, wavy-aligned, medium-coarse, granular ornament, which may grade into short anastomosing ridges. Sutures are impressed and subhorizontal; radial facets are plenary. The ornament differs from all other ornamented taxa described herein by its medium size and dense occurrence on all plates. The cup belongs to an indeterminate cladid and is listed for faunal completeness.

Material.—Partial cup (RGM 361 351) from upper part of the Akacha-Mazzer formations, Ioucha 18, Mississippian (late Viséan), southeast of Cirque du Meharez el Kébir; Pareyn collection.

Cladid indeterminate 4
Plate 17, figures 5–8

Remarks.—A medium-sized basal and radial with nodose to vermiform ornament is strongly convex transversely and longitudinally. The cup probably would have been bowl shaped with a basal impression. The basal is encrusted and the nodose ornament is nearly completely lost as a result of solution. This ornament is very similar to, but coarser and more vermiform than, that of *Dicromyocrinus*? sp. These specimens probably belong to a cromyocrinid.

Material.—One basal and one radial (RGM 361 342) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Cladid indeterminate 5

Remarks.—Cladid indeterminate 5 is a small thin-plated basal with granular to vermiform ornament.

Material.—One basal (RGM 290 862) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Cladid indeterminate 6

Plate 17, figures 15–16

Remarks.—Cladid indeterminate 6 is represented by a large (16 mm wide, 9.7 mm long) pentagonal radial with fine vermiform ornament and an externally rounded peneplenary facet.

Material.—One radial (RGM 361 345) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Cladid indeterminate 7

Plate 17, figures 3, 4

Remarks.—Cladid indeterminate 7 is represented by three small radials (1 mm wide, 5.3 mm long) and one axillary first primibrachial. All plates are deep, strongly rounded transversely, and the radial facet is peneplenary. The exterior surface of the radials is solution etched and the primibrachial retains a small amount of fine vermiform ornament along one side.

Material.—Three radials and one primibrachial (RGM 361 346) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Subclass **FLEXIBILIA** Zittel, 1895

Order **TAXOCRINIDA** Springer, 1913

Taxocrinid indeterminate

Plate 16, figure 4

Description.—Infrabasal and basal circlet relatively thick plated, gently upflared with projected CD basal for reception of primanal. Stem impression round, large (8.9 mm diameter), covering infrabasal circlet and proximal ⅔ of basals. Lumen pentalobate.

Remarks.—Flexible crinoids are not common in most Pennsylvanian crinoid faunas. Three Pennsylvanian taxocrinids (*Synerocrinus*, *Enascocrinus*, *Euonychocrinus*), however, have stem facets covering most of the basals as on this specimen of taxocrinid indeterminate. Unfortunately, the lack of a more complete specimen prevents generic identification.

Material.—One basal circlet (RGM 361 317) from the lower part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Order **SAGENOCRINIDA** Springer, 1913

Superfamily **LECANOCRINACEA** Springer, 1913

Family **MESPILOCRINIDAE** Jaekel, 1918

Genus **CIBOLOCRINUS** Weller, 1909

Cibolocrinus africanus Strimple and Pareyn, 1982

Cibolocrinus africanus Strimple and Pareyn, 1982, p. 231, fig. 2.

Remarks.—*Cibolocrinus africanus* is based on three moderately well-preserved crowns showing the arms (Strimple and Pareyn, 1982). The genus is known from the Mississippian (Serpukhovian) of Algeria; Pennsylvanian (Morrowan) of the United States; Permian (Artinskian) of the Ural Mountains, southwestern United States, and Bolivia; Permian (Wordian) of Sicily; and uncertain Permian horizons in Timor.

Material.—Holotype and two paratypes 70.1147 E2, top of Djenien Formation, Mississippian (Serpukhovian, E1), Chebket Djihani; Pareyn collection.

Superfamily **SAGENOCRINITACEA** Roemer, 1854

Family **EURYOCRINIDAE** Moore and Strimple, 1973

Genus **AMPHICRINUS** Springer, 1906

Amphicrinus formosus, new species

Plate 16, figures 11–15

Diagnosis.—Distinguished by the combination of the stem covering the infrabasals and proximal parts of the basals, no ornament, and fewer plates in the interray series.

Description.—Crown ovoid bowl-shaped, medium size, length 30.3 mm, width 25.2 mm minimum, 40.8 mm maximum, 33 mm average, plates thick, no ornament. Cup very low bowl. Infrabasals covered by proximal columnal. Basals 5, small, distal tips project slightly beyond proximal columnal; posterior basal truncated distally for reception of primanal, extends above radial summit. Radials 5, 2.8 mm long, 6.8 mm wide, gently convex longitudinally and transversely, heptagonal, adjoin interray plates on distal shoulders; radial facets plenary, concave transversely. Anals series 1-?. Primibrachials 2, much wider than long, gently convex longitudinally and transversely. First primibrachial 3.7 mm long, 6.7 mm wide; axillary second primibrachial 3.5 mm long, 7.6 mm wide. Interray series variable, 1–2–1 or 1–1–1. Secundibrachials 3 or 4 in each half ray. A ray 3 and 4, B ray unknown, C ray 4 and 4, D and E rays 3 and 3. Intrasecundibrachial series variable, 1, 1–1, or 1–2–1. Number of tertibrachials varies from 4 to 8, most commonly 6. One additional branching of quartibrachial 7–11. First 2 branchings isotomous, third branching isotomous or heterotomous, fourth branching heterotomous. Arms incurl distally, free but closely abutting. Patelloid process poorly developed on secundibrachials, well developed on tertibrachials and higher. Proximal columnal elliptical transversely from crushing, 6.5 by 7.4 mm. Proximal columnals very short, symplectial articulation.

Remarks.—The holotype of *Amphicrinus formosus* n. sp. lacks the proximal part of the B ray and is crushed along the A-B interray-D ray plane, with the primanal tilted on edge and other anals covered if present. The paratype is a partial set of arms.

The specimens are assigned to *Amphicrinus* because they have two primibrachials, interprimibrachials do not touch the basals, intrasecundibrachials are present in small number, and the distal arm branching tends toward heterotomous. *Amphicrinus formosus* differs from *A. scoticus* Springer *in* Wright (1914) and *A. tuberculatus* Yakovlev (1961) (typographical error as *A. luberculatus* Yakolev [1961]), both of which have the stem completely covering the infrabasals, basals, and proximal tips of the radials. Also, *A. formosus* has fewer interray plates than *A. scoticus*, and *A. tuberculatus* has fine granular ornament. *Amphicrinus carbonarius* Springer (1920) is based on an imperfect crown with the cup and proximal brachials dislocated and jumbled together. Specimens from the same formation or laterally coeval strata as the holotype and identified as *A. carbonarius* by Laudon (1937) and Strimple (1962) are better preserved partial crowns showing the proximal stem completely covering the infrabasals, basals, and proximal tips of the radials. Also, there are many more plates in the anal and interray series than in *A. formosus*.

Two other species, *A. divergens* Strimple (1940a) and *A. simplex* Strimple (1940b), both from the Pennsylvanian, are based on partial crowns with only the cup, primibrachials, and proximal secundibrachials preserved. In these species the number of plates in the anal, interray, and intersecundibrachial series are uncertain, as are arm branching patterns. The proximal columnal does not cover the distal tips of the basals in either species, suggesting relationship with *A. formosus*.

Material.—Two specimens: Holotype (RGM 361 318) and paratype (RGM 361 319) from the top of the Djenien Formation, Mississippian (Serpukhovian, E2), at Chebket Djihani; Pareyn collection.

Etymology.—Latin, meaning beautifully formed.

Amphicrinus prinsi, new species

Plate 16, figures 7–10

Metichthyocrinus sp. Termier and Termier, 1950, p. 92, pl. 218, figs. 46–52.

Diagnosis.—Distinguished by the patelloid process developing higher in the secundibrachials, intersecundibrachials in contact with the first secundibrachials, five tertibrachials, and asymmetrical first tertibrachials.

Description.—Crown ovoid bowl-shaped, medium size (estimated 40 to 50 mm diameter), plates thick, exceedingly fine granular to vermiform ornament poorly preserved. Cup very low bowl. Infrabasals 3, very small, covered by proximal columnal. Basals 5, small, distal tips project slightly beyond proximal columnal; posterior basal truncated distally for reception of primanal. Radials 5, 3.8 mm long, 6.4 mm wide, gently convex longitudinally and transversely, heptagonal, adjoin interray plates on distal shoulders; radial facets plenary, concave transversely. Anals series 1-2-1-1-1-1. Primibrachials 2, much wider than long, gently convex longitudinally and transversely. First primibrachial 3 mm long, 5.5 mm wide; axillary second primibrachial 3.7 mm long, 8.7 mm wide. Interray series variable, 1-2-1-1, 1-2-1-1-1, or 2-2-2-1-1-1. Secundibrachials 3 in each half ray in 4 rays preserved. Intrasecundibrachial series 1–1. Number of tertibrachials varies from 4 to 7, most commonly 6. One additional branching of quartibrachial 6 in one arm fragment preserved. First two branchings isotomous, third branching isotomous or heterotomous, fourth branching heterotomous. Patelloid process poorly developed on secundibrachials, well developed on tertibrachials and higher. Proximal columnal round transversely, 7.3 mm diameter; lumen quinquestellate.

Remarks.—The seven specimens of *Amphicrinus prinsi* n. sp. are two partial crowns and five partial calyx/arm pieces, all showing exterior and interior surfaces. Two partial distorted crowns, holotype (RGM 361 320) and paratype 1 (RGM 361 321), were found in two pieces and reconstructed by gluing. The holotype retains the anal series, part of the proximal columnal, and the very small tripartite infrabasals, which are visible on the interior. Paratype 4 (RGM 361 324) has distal isotomous arm branching. The internal surface of most specimens shows the original boxwork stereom structure of the ossicles. Variation in the number of interray plates and intrasecundibrachials is noted from the interior to the exterior where some paired plates appear to be fused. Description of the species is based on the composite information from the five types.

Amphicrinus prinsi n. sp. is similar to *A. formosus* and likely derived from it. They differ in several morphologic features. The patelloid process is more obvious and first appears lower in the arms of *A. formosus* than *A. prinsi.* Intersecundibrachials and the stem facet are smaller in *A. formosus.* Not all intersecundibrachials are in contact with the first secundibrachial in *A. formosus,* whereas they are well developed in *A. prinsi.* The number of tertibrachials ranges from five to eight in *A. formosus* and is consistently five where known in *A. prinsi.* First tertibrachials are asymmetrical in only the C ray in *A. formosus,* whereas in *A. prinsi* all preserved rays show marked asymmetry of first tertibrachials with the outer ray half larger than the inner ray half.

Material.—Seven specimens: Holotype (RGM 361 320) and paratypes 1–4 (RGM 361 321–RGM 361 324) and two partial sets of arms (RGM 290 863) are from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar; Winkler Prins collection.

Etymology.—Named for C. Winkler Prins, who found the specimens.

Sagenocrinid indeterminate 1

Plate 16, figures 1–3

Description.—Based on 2 radials and 3 basals, plates relatively thin (2.5 mm thick), but large, bearing medium-coarse sharply-pointed granular ornament grading into short sharp-crested irregular ridge ornament along proximal edges of plates; formed large bowl-shaped cup with flat or shallow basal invagination, vertical walls, slight impressions or dimples at basal-radial apices, unknown number of anals. Basal, radial and basal-radial facets have shallow excavations for ligamentary articulation and denticulate edges. Basals wider than long, averaging 15.7 mm wide and 11.9 mm long, gently convex transversely, moderately convex longitudinally. Radials wider than long (17.4 mm wide, 10.9 mm long; 18.0 mm wide, 11.7 mm long), gently convex transversely and longitudinally. Radial facets peneplenary, slightly protruded on exterior of radial. Transverse ridge sharp-crested, not quite full width of facet; outer ligament pit moderately deep with sharp-crested outer ridge. Inner side of transverse ridge has fine vermiform surface for ligament attachment. Lateral ends of transverse ridge to the end of radial facet bear short coarse ridges and grooves normal to ridge. Ligament pit shallow.

Remarks.—The plates of sagenocrinid indeterminate 1 are disarticulated, with two of the basals distorted and the third weathered. These plates may have belonged to a single specimen and, probably, represent a mespilocrinid, such as *Cibolocrinus.*

Material.—Five specimens, two radials, three basals: Figured radial (RGM 361 325), figured basal (RGM 361 326), and one radial and two basals (lot RGM 361 327) from the lower part of the Hassi Kerma Fomation, Pennsylvanian (early Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Sagenocrinid indeterminate 2

Remarks.—A fragmentary cup consists of the infrabasal circlet, parts of two radials, and 18 distorted proximal columnals. The cup would have been a moderately large bowl with a large basal impression including all of the infrabasals and proximal parts of the basals. Plates are thin and lack ornament. The stem is heteromorphic, and the round proximal columnals are very thin with a narrow crenularium and moderately large pentalobate lumen. The specimen is probably an indeterminate mespilocrinid.

Material.—Partial cup (RGM 361 352) from upper part of the Akacha-Mazzer formations, Ioucha 18, Mississippian (late Viséan), southeast of Cirque du Meharez el Kébir; Pareyn Collection.

Flexible indeterminate

Plate 16, figures 5, 6

Description.—Infrabasal? or basal circlet? large, 15.6 mm by 14.8 mm widths, low, shallow bowl-shaped with shallow basal indentation for 4.9 mm diameter circular stem impression, formed by three plates. One of two nearly equal larger plates extended on end of mutual sutures to upwardly incurved moderately sharp point, presumably in anal interray. Azygous plate in EA interray. Ornament of radiating ridges and grooves on distal half of all plates. Edges of plates with irregular vermiform facet structure on inner half and moderately deep rounded groove along outer half covered by extended lip of outermost surface of plate.

Remarks.—An indeterminate flexible specimen shows no trace of smaller plates within the tripartite structure, typical of the infrabasal plate of many flexible crinoids. The sharply extended end of the one larger plate, however, is shaped like the posterior basal of many flexibles and the plate facets are typical of many flexibles. Fused basals are unknown in the flexibles and the azygous plate is normally in the C ray position. It is uncertain if this is an infrabasal plate with an extended end on the one plate, an advanced flexible having lost the infrabasals with the basals beginning to fuse, an abnormal infrabasal circlet, or an abnormal specimen.

Material.—Figured specimen (RGM 361 328) from the Oued Bel Groun Formation, Pennsylvanian (Moscovian), Bed M1 (Deleau, 1951), from Béchar-Djerid, immediately south of Béchar; Winkler Prins collection.

Crinoidea unclassified

Remarks.—Disarticulated and fragmentary ossicles from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, include a variety of unidentifiable specimens. These specimens show that the crinoid fauna of the Hassi Kerman Formation may be two to three times more diverse than that represented by identified taxa. Caution must be followed, however, in evaluating the diversity because it is likely that some of the individual specimens may be from different parts of a single taxon. For example, the platycrinitid radial and columnals, as well as one of the possible basal circlets, listed under *Platycrinites* spp. 2 to 5 could represent only one or two species. We believe that these indeterminate remains contain a minimum of one camerate and five cladids that are undescribed. Specimens are from the Winkler Prins collection.

Crinoid indeterminate 1

Plate 15, figure 15

Remarks.—One medium-sized partial cup shows only the exterior and is embedded in matrix. This specimen has a low bowl-shaped cup, tripartite infrabasal circlet consisting of two equally large plates and one small plate, a distally truncated posterior basal, and subvertical radials with plenary radial facets. It lacks the B and C radials and the anals. It is uncertain if the specimen had more than one anal. It is possibly a lecanocrinid.

Material.—(RGM 361 336) upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Crinoid indeterminate 2

Remarks.—Two small infrabasal circlets of five plates each and pentalobate axial canals, one (RGM 361 340) with a rounded ridge around the stem facet and the second (RGM 361 341) with an impressed stem facet. These two specimens may belong to different genera.

Material.—Two infrabasal circlets (RGM 361 340 and RGM 361 341) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Crinoids indeterminate

Remarks.—Assorted indeterminate tegmen plates, columnals, and other small ossicles (RGM 290 864) are from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Crinoid Columnals

Genus ØFLORICYCLUS Moore and Jeffords, 1968

ØFloricyclus cf. F. angustimargo Moore and Jeffords, 1968

Plate 17, figures 19, 20

Description.—Pluricolumnal of 2 columnals, 8.7 mm diameter, noditaxis N1 at least. Columnals circular in transverse section, latus straight, symplectial articulation. Articulum full width of columnal; crenularium narrow, $\frac{1}{11}$ columnal radius; culmina coarse, very short, unbranched. Areola wide, flat, recesses below crenularium and perilumen. Perilumen very narrow along lobes of lumen, wide between lobes, surface nodose. Lumen roundly pentalobate, diameter $\frac{1}{2}$ columnal diameter. Jugula large, rounded adaxial.

Remarks.—This pluricolumnal segment of *Floricyclus* cf. *F. angustimargo* is related to the segments assigned above to Cladid indeterminate 3. Major differences are the much shorter unbranched culmina, less-recessed areola, and rounded jugula on this specimen. It could represent a different section (more or less distal) of the column of Cladid indeterminate 3. The specimen differs from *F. angustimargo* by having a straight latus with less elongate and more rounded jugula. Moore and Jeffords (1968) reported *F. angustimargo* from the Middle Pennsylvanian (Desmoinesian) strata of Colorado.

Material.—Pluricolumnal (RGM 361 315) from the lower part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; Legrand-Blain collection.

Genus ØPLUMMERANTERIS Moore and Jeffords, 1968

ØPlummeranteris? sp.

Plate 17, figures 21–24

Description.—Nodal columnal circular in transverse section, latus very slightly convex. Articulum full width facet. Crenularium wide, $\frac{2}{5}$ radius. Culma full width crenularium, unbranched, no insertions, slight taper adaxial. Areola narrow, flat, recessed slightly below crenularium and perilumen. Perilumen narrow, nodose to irregular shaped nodes on surface. Lumen roundly floriform. Jugula short, rounded adaxial. Cirri facets aligned with lobes of lumen, slightly projected.

Remarks.—Moore and Jeffords (1968) defined *Plummeranteris* as having an articulum in which the broad crenularium extended to a weakly developed perilumen about a floriform lumen. Their illustration (pl. 24, fig. 13) of the facet of *P. sansaba*, however, shows a narrow areola. We tentatively assign two specimens to *Plummeranteris*, noting that they differ from *Floricyclus* by having a wide crenularium. They may belong to a cromyocrinid. *Plummeranteris* has been reported from the Middle Pennsylvanian of Texas (Moore and Jeffords, 1968).

Material.—Columnal (RGM 361 316) from the lower part of the Hassi Kerma Formation, Pennsylvanian (Bashkirian), at Djebel Béchar; Legrand-Blain collection. Columnal (RGM 361 343) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Columnal undesignated
Plate 17, figures 17, 18

Remarks.—A slender homomorphic pluricolumnal with a medium-width crenularium, unbranched culmina, narrow areola, and large round lumen is partly encrusted with a massive bryozoan that completely encircles part of the specimen. This implies that the bryozoan was attached to the stem while the crinoid was living. The articular facet is similar to *Cycloscaphus* Moore and Jeffords (1968), which was described as a heteromorphic taxon. It is unknown if the stem was homomorphic distally or proximally of the heteromorphic section.

Material.—Pluricolumnal (RGM 290 866) from the upper part of the Hassi Kerma Formation, limestone below level ML171, Pennsylvanian (Bashkirian), at Mouizeb El Atchane, 300 m north of the south gully, Béchar, Winkler Prins collection.

Subphylum **ECHINOZOA** Haeckel *in* Zittel, 1895
Class **ECHINOIDEA** Leske, 1778
Subclass **PERISCHOECHINOIDEA** M'Coy, 1849
Order **PALAECHINOIDA** Haeckel, 1866
Family **PALAECHINIDAE** M'Coy, 1849
Genus **PALAECHINUS** M'Coy, 1844
Palaechinus sp.
Plate 17, figure 31

Description.—Partial test medium size, 30.5 mm maximum dimension, 13.3 mm minimum, moderately convex, plates thick. Oculogenital ring monocyclic; genitals wider (3.1 mm) than long (2.5 mm), convex outer side, concave inner side, with 3 or 4 pores; oculars small, 1.7 mm long, 1.8 mm wide, narrowing toward periproct, with single pore. Ambulacral tracks narrow, straight, formed of 2 rows of interlocking plates, each bearing a double pore on the outer side; ambulacral plates much wider than long. Interambulacral areas much wider than ambulacral areas, formed of minimum of 6 rows of hexagonal plates increasing in size adorally.

Remarks.—This partial corona of *Palaechinus* sp. consists of three oculars and three genitals of the oculogenital ring and adoral parts of three ambulacral tracks and four interambulacral areas. One small fragmentary plate within the oculogenital ring probably was part of the periproct. All plates are strongly weathered and abraded, with loss of all traces of ornament and other morphologic features of the exterior surface. It is uncertain if the corona was fragmented by scavengers prior to burial or an artifact of weathering. *Palaechinus* is known from the Mississippian of Europe and North America.

Material.—Figured specimen (RGM 361 347) from the base of the Aïn el Mizab Member, Aïn el Mizab Formation, Mississippian (Serpukhovian, E1), at Foum es Sba; Pareyn collection.

Order **CIDAROIDA** Claus, 1880
Family **ARCHAEOCIDARIDAE** M'Coy, 1844
Genus **ARCHAEOCIDARIS** M'Coy, 1844
Archaeocidaris sp.
Plate 17, figures 29, 30

Description.—Interambulacral plate hexagonal, large, 10.5 × 9.4 mm, thin, nodose marginal rim; large central primary tubercle surrounded by scrobicular ring of small secondary tubercles around aureole. Fragment of approximately circular corticate spine shaft 23.6 mm long, 4.2 mm diameter; ornament of aligned nodes along 10 low linear ridges.

Remarks.—The interambulacral plate and fragment of a spine shaft of *Archaeocidaris* sp. are from the same locality, probably from the same species, and thus described together. The interambulacral plate has overgrowths of indeterminate organisms covering some of the scrobicular spines and has been abraded or subjected to solution weathering prior to burial. Ornament of the spine fragment shows little abrasion or solution weathering.

Material.—Two specimens: Interambulacral plate (RGM 361 348) and spine shaft (RGM 361 349) from the Oued el Hamar Formation, Pennsylvanian (late Bashkirian), south of Teniet Aissa ben Azzi; Pareyn collection.

REFERENCES CITED

Angelin, N.P.

1878. Iconographia crinoideorum in stratis Sueciae Siluricis fossilium. Samson and Wallin, Holmiae, 62 pp., 29 pls.

Arendt, Yu. A.

2002. Early Carboniferous echinoderms of the Moscow region. Paleontological Journal, vol. 36, Supplement 2, pp. 115–184.

Ausich, W.I.

1997. Calyx plate homologies and early evolutionary history of the Crinoidea. *In* Geobiology of echinoderms. J.A. Waters and C.G. Maples, *eds.*, The Paleontological Society Papers, no. 3, pp. 289–304.

1998a. Early phylogeny and subclass division of the Crinoidea (Phylum Echinodermata). Journal of Paleontology, vol. 72, pp. 499–510.

1998b. Phylogeny of Arenig to Caradoc crinoids (Phylum Echinodermata) and suprageneric classification of the Crinoidea. The University of Kansas Paleontological Contributions, n. s., vol. 9, 36 pp.

Ausich, W.I., and Sevastopulo, G.D.

2001. The Lower Carboniferous (Tournaisian) crinoids from Hook Head, County Wexford, Ireland. Monograph of the Palaeontolgraphical Society, Publication 617, 136 pp., 13 pls.

Austin, T.

1848. Observations on the Cystidea of M. Von Buch, and the Crinoidea generally. Geological Society of London, Quarterly Journal, vol. 4, pt. 1, pp. 291–294.

Austin, T., and Austin, T., Jr.

1842. XVIII.—Proposed arrangement of the Echinodermata, particularly as regards the Crinoidea, and a subdivision of the Class Adelostella (Echinidae). Annals and Magazine of Natural History, ser. 1, vol. 10, no. 63, pp. 106–113.

1843–1847. A monograph on recent and fossil Crinoidea, with figures and descriptions of some Recent and fossil allied genera. vol. 1, 2, pp. 1–32, pls. 1–4, (1843); vol. 3, pp. 33–48, pls. 5, 6 (1844); vol. 4, pp. 49–64, pls. 7, 8 (1845); vol. 5, pp. 65–80, pls. 9, 10 (1846); vol. 6–8, pp. 81–128, pls. 11–16 (1847); London and Bristol.

Bassler, R.S.

1938. Pelmatozoa Palaeozoica. *In* Fossilium catalogus, I: Animalia. Quenstedt, W., *ed.*, Part 83: W. Junk, s'Gravenhage, 194 pp.

Bassler, R.S., and Moodey, M.W.

1943. Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms. Geological Society of America Special Paper 45, 734 pp.

Bather, F.A.

1890. British fossil crinoids. II. The classification of the Inadunata. Annals and Magazine of Natural History, ser. 6, vol. 5, pp. 310–334, 373–388, 485–486, pls. 14, 15.

1899. A phylogenetic classification of the Pelmatozoa. British Association for the Advancement of Science, Report (1898), pp. 916–923.

1916. Notes on *Hydreionocrinus*. Transactions of the Geological Society of Edinburgh (1912), vol. 10, pt. 1, pp. 61–76, pl. 8.

Baumiller, T.K.

1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. Palaeontology, vol. 33, no. 3, pp. 743–748.

Bourrouilh, R., and Termier, G.

1973. *Balearocrinus breimeri*, Crinoïde nouveau du Viséen supérieur de Minorque (Baléares). Annales de la Société Géologique du Nord, vol. 93, no. 3, pp. 225–232, pls. 27, 28.

Bowsher, A.L.

1955a. Origin and adaptation of platyceratid gastropods. Mollusca, Article 5, University of Kansas Paleontological Contributions, pp. 1–11, 2 pls.

1955b. New genera of Mississippian camerate crinoids. Echinodermata, Article 1, University of Kansas Paleontological Contributions, pp. 1–23, 6 pls.

Bowsher, A.L., and Strimple, H.L.

1986. *Platycrinites* and associated crinoids from Pennsylvanian rocks of the Sacramento Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources Circular, vol. 197, pp. 1–37.

Breimer, A.

1962. A monograph on Spanish Paleozoic Crinoidea. Overdruk uit Leidse Geologische Mededelingen. Deel 27, 190 pp., 6 pls.

Breimer, A., and Macurda D.B., Jr.

1972. The phylogeny of the fissiculate blastoids. Verhandelingen der oninklijke Nederlandse Akademie van Wetenschappen, AfD. Natuurkunde, Eerste Reeks, Deel 26, no. 3, 390 pp.

Bronn, H.G.

1848–1849. Index palaeontologicus, unter Mitwirkung der Herren Prof. H. R. Göppert und H. von Meyer. Handbuch einer Geschichte der Natur, v. 5, Abt. 1, (1, 2), pt. 3, A. Nomenclator palaeontologicus; A–M, pp. 1–775; N–Z, pp. 776–1381, Stuttgart.

Brower, J.C.

1967. The actinocrinitid genera *Abactinocrinus, Aacocrinus* and *Blairocrinus*. Journal of Paleontology, vol. 41, pp. 675–705, pls. 75–78.

1970. Chapter 12, Crinoids. *In* E. D. McKee and R. C. Gutschick, History of the Redwall Limestone of Northern Arizona. Geological Society of America, Memoir 114 (1969), pp. 475–543, pls. 64–67.

Burdick, D.W., and Strimple, H.L.

1983. Genevievian and Chesterian crinoids of Alabama. Geological Survey of Alabama, Bulletin (1982), vol. 121, 277 pp.

Chen, Z-t., and Yao, J-h.

1993. Palaeozoic echinoderm fossils of western Yunnan, China. Beijing, Geological Publishing House, 102 pp.

Chernova, G.N., and Stukalina, G.A.

1989. K sistematike pozdnepaleozoickikh morskikh lilii semeistva Floricyclidae [On the systematics of the Late Paleozoic crinoids of the family Floricyclidae]. *In* Fossil and recent echinoderm researches [Problemy izucheniya iskopaemykh i sovremennykh iglokozhikh], D.L. Kalvo, *ed.*, Akademiya Nauk Estonskoi SSR, Tallinn, pp. 111–127, 3 pls. (In Russian).

Chestnut, D.R., and Ettensohn, F.R.

1988. Hombergian (Chesterian) echinoderm paleontology and paleoecology, south-central Kentucky. Bulletins of American Paleontology, vol. 95, 102 pp.

Clarke, J.M.

1921. Early parasitism of the snails upon the crinoids. *In* Organic dependence and disease: their origin and significance. New York State Museum, Bulletin (1919), nos. 221–222, pp. 64–78.

Claus, C.F.W.

1880. Gundzüge der Zoologie. 4th ed. Marburg and Leipzig, vol. 1, 821 pp., vol. 2, 522 pp.

Deleau, P.

1951. Contribution a l'étude du carbonifère des basins houillers du Sud-Oranais (Basins de Colomb-Bechar-Kénadza-Abadla-Sfaïa). Academy Science Paris C. R., vol. 232, no. 3, pp. 243–244.

Delpey, G.

1941. Crinoîdes du viséen superieur dans le pays de Skoura, au Maroc. Bulletin de la Société des Sciences Naturelles du Maroc, Rabat, vol. 19, pp. 214–220.

Delvolvé J.J., Babin, C., Gandl, J., Kullmann, J., Laveine, J.P., Legrand- Blain, M., Mackinney, F.K., Martinez Chacon, M.L., Perret, M.F., Schultze, P., Semenoff-Tian-Chansky, P., Sevastopulo, G.D., and Vachard, D.

1996. Carbonifère à facies Culm. *In* Synthèse géologique et géophysique des Pyrénées. A. Barnolas and J.C. Chiron, *eds.*, Tome 1. Cycle Hercynien. Edition B.R.G.M. Orléans and I.T.G.E., Madrid, pp. 303–338.

Donovan, S. K.

1991. Site selectivity of a Lower Carboniferous boring organism infesting a crinoid. Geological Journal, vol. 26, pp. 1–5.

Donovan, S.K., and Veltcamp, C.J.

1990. *Barycrinus* (Crinoidea) from the Lower Carboniferous of England. Journal of Paleontology, vol. 64, pp. 988–992.

Easton, W.H.

1962. Carboniferous formations and faunas of central Montana. U. S. Geological Survey, Professional Paper 348, 26 pp., 13 pls.

Etheridge, R., Jr., and Carpenter, P.H.

1886. Catalogue of the Blastoidea in the Geological Department of the British Museum (Natural History), with an account of the morpholgy and systematic position of the group, and a revision of the genera and species. British Museum Catalogue, London, 322 pp., 20 pls.

Gahn, F.J., and Kammer, T.W.

2002. The cladid crinoid *Barycrinus* from the Burlington Limestone (early Osagean) and the phylogenetics of the Mississippian botryocrinids. Journal of Paleontology, vol. 76, pp. 123–133.

Geinitz, H.B.

1846. Grundriss der Versteinerungskunde. Dresden und Leipzig, Arnoldische Buchhandlung, pp. 522–560, pls. 22, 23.

Gluchowski, E.

1981. Paleozoic crinoid columnals and pluricolumnals from Poland. Zeszyty Naukowe Akademii Gorniczo-Hutniczej, Geologia, vol. 7, no. 3, pp. 29–57, 5 pls.

Goldring, W.

1923. The Devonian crinoids of the state of New York. New York State Museum, Memoir 16, 670 pp., 60 pls.

1946. A new Lower Chemung crinoid. Bulletins of American Paleontology, vol. 31, no. 119, pp. 1–5, 1 pl.

Haeckel, E.H.

1866. Generelle morphologie der Organismen. Allgemeine grundzüge der Organischen formen-Wissenschaft, Mechanisch begründet durch die von Charles Darwin reformirte descendenztheorie. 2 vols, pls. G. Reimer, Berlin.

Hagdorn, H.

1982. *Chelocrinus schlotheimi* (Quendstedt) 1835 aus dem Oberen Muschelkalk (mo1, Anisium) von Nordwestdeutschland. Veröffentlichungen aus dem Naturkunde-Museum Bielefeld, vol. 4, pp. 5–33.

1995. Literaturbericht Triassic crinoids. Zentralblatt Geologie Paläontologie, Teil II, 1995, Heft 1/2, pp. 1–22.

Hall, J.

1858. Chapter 8. Palaeontology of Iowa. *In* J. Hall and J.D. Whitney, Report of the Geological Survey of the state of Iowa: Embracing the results of investigations made during portions of the years 1855, 56 & 57. vol. 1, part II; Palaeontology, pp. 473–724, 29 pls., index to Part II separately paginated, 3 pp.

1861. Descriptions of new species of Crinoidea from the Carboniferous rocks of the Mississippi valley. Journal of the Boston Society of Natural History, vol. 7, pp. 261–328.

Hashimoto, K.

2001. Pennsylvanian camerate crinoids from the Akiyoshi Limestone Group, southwest Japan. Bulletin of the Akiyoshidai Museum of Natural History no. 36, 16 pp., 5 pls.

Herbig, H-G.

1982. *Balearocrinus cantabricus* n. sp. (Crinoidea, Inadunata) aus dem Visé des Kantabrischen gebirges (Alba-Formation, Prov. León/NW-Spanien). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1982 (8), pp. 476–484.

1994. Remarks on the late Viséan crinoids from the Cantabrian mountains and Menorca (NW Spain and Balearic Islands). Revista Espanola de Paleontologia, vol. 9, pp. 24–28.

Jaekel, O.M.J.

1918. Phylogenie und System der Pelmatozoen. Paläeontogische Zeitschrift, Bd. 3, heft 1, 128 pp.

Kammer, T.W.

2001. Phenotypic bradytely in the *Costalocrinus-Barycrinus* lineage of Paleozoic cladid crinoids. Journal of Paleontology, vol. 75, pp. 383–389.

Kammer, T.W., and Ausich, W. I.

1993. Advanced cladid crinoids from the Middle Mississippian of the east-central United States: intermediate-grade calyces. Journal of Paleontology, vol. 67, pp. 614–639.

Kesling, R.V.

1968. *Logocrinus conicus*, a simple new Middle Devonian inadunate crinoid from Michigan. University of Michigan Contributions from Museum of Paleontology, vol. 22, pp. 163–167.

Kesling, R.V., and Smith, R.N.

1963. The crinoid *Synbathocrinus* in the Middle Devonian Traverse Group of Michigan. University of Michigan Contributions from Museum of Paleontology, v. 18, pp. 185–196.

Keyes, C.R.

1888. On the attachment of *Platyceras* to palaeocrinoids and its effects in modifying the form of the shell. American Philosophical Society, Proceedings and Transactions, vol. 25, no. 128, pp. 231–243.

Kirk, E.

1941. Four new genera of Mississippian Crinoidea Inadunata. Journal of Paleontology, vol. 15, pp. 81–88, pls. 17, 18.

1946. *Plemnocrinus*, a new crinoid genus from the Lower Mississippian. Journal of Paleontology, vol. 20, pp. 435–441, pls. 65, 66.

Lane, N.G.

1963. Meristic variation in the dorsal cup of monobathrid camerate crinoids. Journal of Paleontology, vol. 37, pp. 917–930.

1964. Inadunate crinoids from the Pennsylvanian of Brazil. Journal of Paleontology, vol. 38, pp. 362–366, pl. 57.

1978. Mutualistic relations of fossil crinoids. *In* Treatise on invertebrate paleontology. R.C. Moore and C. Teichert, *eds.*, Part T. Echinodermata 2(1). Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. T345–T347.

Lane, N.G., and DuBar, J.R.

1983. Progradation of the Borden delta: new evidence from crinoids. Journal of Paleontology, vol. 57, pp. 112–123.

Lane, N.G., Waters, J.A., Maples, C.G., Marcus, S.A., and Liao, Z.-T.

1996. A camerate-rich Late Carboniferous (Moscovian) crinoid fauna from volcanic conglomerate, Xinjiang, People's Republic of China. Journal of Paleontology, vol. 70, pp. 117–128.

Lane, N.G., Waters, J.A., and Maples, C.G.

1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian) Xinjiang-Uygur Autonomous Region, People's Republic of China. Journal of Paleontology, vol. 71, Memoir (Supplement to no. 2), pp. 1–43.

Lane, N.G., Maples, C.G., and Waters, J.A.

2001. Revision of Late Devonian (Famennian) and some Early Carboniferous (Tournaisian) crinoids and blastoids from the type Devonian area of North Devon. Palaeontology, vol. 44, pp. 1043–1080.

Laudon, L.R.

1937. New occurrence of the Upper Carboniferous crinoid genera *Amphicrinus* and *Synerocrinus*. Journal of Paleontology, vol. 11, pp. 706–708.

Legrand-Blain, M.

1967. Précisions sur la stratigraphie de la série des calcaires du Djebel Béchar (Namurien-Moscovien) à l'Est de Béchar (Algérie). Bulletin Société geologique France, vol. 7, no. 9, pp. 298–306.

Leske, N.G.

1778. Jacobi Theodori Klein naturalis dispositio echinodermatum. . . , edita et descriptionibus novisque inventis et synonomis auctorem aucta. Leipzig, 278 pp., 54 pls.

Lindley, I.D.

1979. An occurrence of the camerate crinoid genus *Eumorphocrinus* in the Early Carboniferous of New South Wales. Journal and Proceedings of the Royal Society of New South Wales, vol. 112, nos. 3–4, pp. 121–124.

1988. *Glaphyrocrinus*, a new camerate crinoid genus from the Lower Carboniferous of New South Wales. Alcheringa, vol. 12, pp. 129–136.

Macurda, D.B., Jr.

1983. Systematics of the fissiculate Blastoidea. Museum of Paleontology, The University of Michigan, Papers on Paleontology, no. 22, 291 pp.

Matsumoto, H.

1929. Outline of a classification of Echinodermata. Tohoku University Science Reports, series 2 (Geology), vol. 13, no. 2, pp. 27–33.

McChesney, J.H.

1860. Descriptions of new fossils from the Paleozoic rocks of the western states. Transactions of the Chicago Academy of Science, vol. 1, pp. 5–76 (1859).

McIntosh, G.C.

1984. Devonian cladid inadunate crinoids: Family Botryocrinidae Bather, 1899. Journal of Paleontology, vol. 58, pp. 1260–1281.

2001. Devonian cladid crinoids: Families Glossocrinidae Goldring, 1923, and Rutkowskicrinidae new family. Journal of Paleontology, vol. 75, pp. 783–807.

M'Coy, F.

1844. A synopsis of the characters of the Carboniferous Limestone fossils of Ireland. Dublin, University Press, 274 pp., 29 pls.

1849. On some new Palaeozoic Echinodermata. Annals and Magazine of Natural History, ser. 2, vol. 3, pp. 244–254.

1851–1855. British Palaeozoic Fossils, Part II. Palaeontology. *In* A. Sedgwick and F. M'Coy, A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils. Fasciculus 1, Radiata and Articulata (1851), pp. 116–122, pls. 1A–1G; Fasciculus 2 (1853), pp. 123–406; Fasciculus 3, Mollusca and Palaeozoic fishes (1855), pp. i–xcviii, 407–666, pls. 1–3k.

Meek, F.B.

1872. Preliminary list of the fossils collected by Dr. Hayden's exploring expedition of 1871, in Utah and Wyoming territories, with descriptions of a few new species. *In* F.V. Hayden, Preliminary report of the U. S. Geological Survey of Montana and portions of adjacent territories, Preliminary Report (fifth annual) (1871), pp. 373–377.

Meek, F.B., and Worthen, A.H.

1865. Descriptions of new crinoidea, etc. from the Carboniferous rocks of Illinois and some of the adjoining states. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 17, no. 3, pp. 155–167.

Miller, J.S.

1821. A natural history of the Crinoidea, or lily-shaped animals; with observations on the genera, *Asteria, Euryale, Comatula* and *Marsupites*. Bristol, England, Bryan & Co. 150 pp., numerous unnumbered plates.

Miller, S.A.

1883. The American Palaeozoic fossils: a catalogue of the genera and species, with names of authors, dates, places of publication, groups of books in which found, and the etymology and signification of the words, and an introduction devoted to the stratigraphical geology of the Palaeozoic rocks. 2d ed., Cincinnati, Ohio, the author. Echinodermata, pp. 247–334.

1889. North American geology and paleontology. Cincinnati, Western Methodist Book Concern, 664 pp.

1891a. Palaeontology: Advance sheets, Indiana Department of Geology and Natural Resources, 17th Annual Report, pp. 1–103, pls. 1–20.

1891b. North American geology and paleontology, first appendix. Cincinnati, Western Methodist Book Concern, pp. 665–718.

Miller, S.A., and Gurley, W.F.E.

1890. Description of some new genera and species of Echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri, and Iowa. Privately published, 59 pp., 10 pls.

1895. New and interesting species of Palaeozoic fossils. Illinois State Museum, Bulletin 7, 89 pp., 5 pls.

1896. New species of Echinodermata and a new crustacean from the Palaeozoic rocks. Illinois State Museum, Bulletin 10, 91 pp., 5 pls.

Moore, R.C.

1952. Evolution rates among crinoids. Journal of Paleontology, vol. 26, pp. 338–352.

Moore, R.C., *ed.*

1967. Treatise on Invertebrate Paleontology, Part S, Echinodermata 1. Geological Society of America and University of Kansas, 2 vols., 650 pp.

Moore, R.C., and Jeffords, R.M.

1968. Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. University of Kansas Paleontological Contributions, Echinodermata Article 9, pp. 1–86, 28 pls.

Moore, R.C., and Laudon, L.R.

1942. *Megaliocrinus*, a new camerate crinoid genus from the Morrow Series of northeastern Oklahoma. Denison University Bulletin, Journal of the Scientific Laboratories, vol. 37, pp. 67–76.

1943. Evolution and classification of Paleozoic crinoids. Geological Society of America, Special Paper 46, 151 pp.

Moore, R.C., and Plummer, F.B.

1938. Upper Carboniferous crinoids from the Morrow Subseries of Arkansas, Oklahoma and Texas. Denison University Bulletin, Journal of the Scientific Laboratories, vol. 32, pp. 209–314, pls. 12–16.

Moore, R.C., and Strimple, H.L.

1973. Lower Pennsylvanian (Morrowan) crinoids from Arkansas, Oklahoma, and Texas. University of Kansas Paleontological Contributions, Article 60, Echinodermata 12, 84 pp.

Moore, R.C., and Teichert, C., *eds.*

1978. Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea. Geological Society of America and University of Kansas, 3 vols., 1026 pp.

Pabian, R.K., and Strimple, H.L.

1985. Classification, paleoecology and biostratigraphy of crinoids from the Stull Shale (Late Pennsylvanian) of Nebraska, Kansas, and Iowa. University of Nebraska State Museum Bulletin, vol. 11, 81 pp.

Pareyn, C.

1961. Les massifs Carbonifères du Sahara Sud-Oranais. Publications du Centre de Recherches Sahariennes, Série Géologie, no. 1, vol. 1, pp. 1– 325, vol. 2, pp. 1–244, 28 pls.

Phillips, J.

1836. Illustrations of the geology of Yorkshire, or a description of the strata and organic remains. Pt. 2, The Mountain Limestone districts. 2d ed., London, John Murray, pp. 203–208, pls. 3, 4.

Pomel, N.A.

1885–1887. Paléontologie ou description des animaux fossiles de l'Algérie: Zoophytes. Alger, P. Fontana, vol. 2, no. 1, 79 pls. (1885); vol. 2, no. 2, pp. 1–3444 (1887)

Roemer, C.F.

1851–1856. Erste Periode, Kohlen-Gebirge. *In* Lethaea Geognostica, H.G. Bronn, 3d ed.: Stuttgart, E. Schweizerbart, vol. 2, pp. 1–788, 10 pls.

Say, T.

1825. On two genera and several species of Crinoidea. Zoological Journal, vol. 2, no. 7, pp. 311–315.

Scotese, C.R., and McKerrow, W.S.

1990. Revised world maps and introduction. *In* Palaeozoic palaeogeography and biogeography, C.R. Scotese and W.S. McKerrow, eds. The Geological Society Memoir no. 12, pp. 1–21.

Sevastopulo, G.D., and Keegan, J.B.

1980. A technique for revealing the stereom structure of fossil crinoids. Palaeontology, vol. 23, no. 4, pp. 749–756.

Sieverts-Doreck, H.

1951. Echinodermen aus dem spanischen Ober-Karbon. Palaontologiche Zeitschrift, vol. 24, pp. 104–119, 1 pl.

Sigler, J.P., White, D., and Kesling, R.V.

1971. *Logocrinus brandoni*, a new inadunate crinoid from the Middle Devonian Silica Shale of Ohio. University of Michigan Museum of Paleontology, Contributions, vol. 23, no. 13, pp. 213–220.

Simms, M.J., and Sevastopulo, G.D.

1993. The origin of articulate crinoids. Palaeontology, vol. 36, pp. 91–109.

Springer, F.

1906. Discovery of the disk of *Onychocrinus* and further remarks on the Crinoidea Flexibilia. Journal of Geology, vol. 14, pp. 467–523, pls. 4–7.

1913. Crinoidea. *In* Zittel, K.A. von, Text-book of paleontology (translated and edited by C.R. Eastman). 2d ed.: London, Macmillan & Co., Ltd., vol. 1, pp. 173–243.

1920. The Crinoidea Flexibilia. Smithsonian Institution Publication 2501, vol. 1, pp. 1–486, vol. 2, pls. A–C, 1–76.

Sprinkle, J.

1973. Morphology and evolution of blastozoan echinoderms. Harvard University Museum of Comparative Zoology, Special Publication, 283 pp., 43 pls.

Sprinkle, J., and Gutschick, R.C.

1990. Early Mississippian blastoids from western Montana. Bulletin of the Museum of Comparative Zoology, vol. 152, no. 3, pp. 89–166, 7 pls.

Strimple, H.L.

1938. A group of crinoids from the Pennsylvanian of northeastern Oklahoma. Private Publication, Bartlesville, Oklahoma, pp. 1–17, 2 pls.

1940a. Some new crinoid species from the Morrow Subseries. Bulletins of American Paleontology, vol. 25, no. 91, pp. 91–98.

1940b. Four new crinoid species from the Wewoka Formation. Bulletins of American Paleontology, vol. 25, no. 92, pp. 101–108.

1949. Crinoid studies: Part III, *Apographiocrinus arcuatus*, new species from the Missouri Series of Oklahoma; Part IV, *Exocrinus*, new genus from the Missouri Series of Oklahoma; Part V, *Allosocrinus*, a new crinoid genus from the Pennsylvanian of Oklahoma; Part VI, *Allagecrinus copani*, new species from the Pennsylvanian of Oklahoma; Part VII, New species of crinoids from southeastern Kansas. Bulletins of American Paleontology, vol. 32, no. 133, 42 pp.

1951a. New crinoids from the Pitkin of Oklahoma. Journal of the Washington Academy of Science, vol. 41, pp. 260–263.

1951b. New Carboniferous crinoids. Journal of Paleontology, vol. 25, pp. 669–676, pls. 98, 99.

1961. Late Desmoinesian crinoids. Oklahoma Geological Survey, Bulletin 93, 189 pp.

1962. Crinoids from the Oologah Formation. Oklahoma Geological Survey, Circular 60, pp. 1–75, 9 pls.

1967. Aphelecrinidae, a new family of inadunate crinoids. Oklahoma Geology Notes, vol. 27, pp. 81–85.

1971. The occurrence of *Hydriocrinus* in Oklahoma and Russia. *In* Fossil Crinoid Studies: University of Kansas Paleontological Contributions, Paper 56, pt. 3, pp. 16–18.

1975a. Middle Pennsylvanian (Atokan) crinoids from Oklahoma and Missouri. University of Kansas Paleontological Contributions, Paper 76, pp. 1–30.

1975b. A Morrowan crinoid fauna from the Hueco Mountains of Texas. Journal of Paleontology, vol. 49, pp. 702–705, 1 pl.

1976. Upper Carboniferous crinoids of northeast Spain. Neues

Jahrbuch für Geologie und Paläontologie, Monatshefte, vol. 10, pp. 630–640.

1978. Flexible crinoids from Pitkin Formation (Chesterian) of Oklahoma and Arkansas. Oklahoma Geology Notes, vol. 38, pp. 61–65.

Strimple, H.L., and Pareyn, C.

1982. *Cibolocrinus* from the Namurian of North Africa with notes on the genus. Journal of Paleontology, vol. 56, pp. 226–232.

Strimple, H.L., and Watkins, W.T.

1969. Carboniferous crinoids of Texas with stratigraphic implications. Palaeontographica Americana, vol. 6, no. 40, pp. 141–275, pls. 30–56.

Strimple, H.L., Allison, R.C., and Kline, G.L.

1971. Pennsylvanian crinoids from Alaska, Part 2. *In* Fossil crinoid studies: University of Kansas Paleontological Contributions, Paper 56, no. 2, pp. 9–15.

Termier, G., and Termier, H.

1950. Paléontologie Marocaine II. Invertébrés de l'Ère Primaire. 4. Annélides, Arthropodes, Echinodermes, Conularides et Graptolithes. Service Carte Géologique Maroc, Notes et Mémoires, vol. 79, no. 4, pp. 1–279, pls. 184–241.

Trautschold, H.

1867. Einige Crinoiden und andere Tierreste des jüngeren Bergkalks im Gouvernement Moskau. Bulletin de la Societie Imperial Naturalistes de Moscou, vol. 15, nos. 3–4, pp. 1–49, 5 pls.

Wachsmuth, C., and Springer, F.

1880–1886. Revision of the Palaeocrinoidea. Proceedings of the Academy of Natural Sciences of Philadelphia. Pt. I. The families Ichthyocrinidae and Cyathocrinidae (1880), pp. 226–378, pls. 15–17 (separate repaged pp. 1–153, pls. 1–3). Pt. II Family Sphaeroidocrinidae, with the sub-families Platycrinidae, Rhodocrinidae, and Actinocrinidae (1881), pp. 175–411, pls. 17–19 (separate repaged, pp. 1–237, pls. 17–19). Pt. III, Sec. 1. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions (1885), pp. 223–364, pls. 4–9 (separate repaged, pp. 1–138, pls. 4–9). Pt. III, Sec. 2. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions (1886), pp. 64–226 (separate repaged to continue with section 1, pp. 139–302).

1889. Discovery of the ventral structure of *Taxocrinus* and *Haplocrinus*, and consequent modifications in the classifications of the Crinoidea. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 40, pp. 337–363, pl. 18.

1897. The North American Crinoidea Camerata. Harvard College Museum of Comparative Zoology, Memoir, vol. 20, pp. 1–359; vol. 21, pp. 360–897; atlas, 83 pls.

Wanner, J.

1916. Die permischen Echinodermen von Timor, Teil. I. Paläontologie von Timor, pt. 6, no. 11, pp. 1–329, pls. 94–114. Stuttgart.

1924. Die permischen Krinoiden von Timor. Jaarbook van net Mijnwezen Nederlandes Oost-Indië, Verhandlungen (1921). Gedeelte, pt. 3, pp. 1–348, 22 pls.

1937. Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor, VIII–XIII. Palaeontographica, Supplement 4, IV Abteilungen, Abschnitt 1, 212 pp., 14 pls.

Waters, J.A., and Sevastopulo, G.D.

1984. The stratigraphical distribution and palaeoecology of Irish Lower Carboniferous blastoids. Irish Journal of Earth Sciences, vol.6, pp. 137–154.

Waters, J.A., Maples, C.G., Lane, N.G., Marcus, S., Liao, Z-T, Liu, L. Hou, H-F., and Wang, J-X.

2003. A quadrupling of Famennian pelmatozoan diversity: New Late Devonian blastoids and crinoids from northwest China. Journal of Paleontology, vol. 77, pp. 922–948.

Webster, G.D.

1973. Bibliography and index of Paleozoic crinoids, 1942–1968. Geological Society of America, Memoir 137, 341 pp.

1974. Crinoid pluricolumnal noditaxis patterns. Journal of Paleontology, vol. 48, pp. 1283–1288.

1981. New crinoids from the Naco Formation (Middle Pennsylvanian) of Arizona and a revision of the Family Cromyocrinidae. Journal of Paleontology, vol. 55, pp. 1176–1199.

1997. Lower Carboniferous echinoderms from northern Utah and western Wyoming. Utah Geological Survey Bulletin 128, Paleontology Series, vol. 1, 65 pp.

2003. Bibliography and index of Paleozoic crinoids, coronates, and hemistreptocrinoids, 1758–1999. Geological Society of America Special Paper 363, 2335 pp., Geological Society of America website.

Webster, G.D., and Houck, K.J.

1998. Middle Pennsylvanian, late Atokan–early Desmoinesian echinoderms from an intermontane basin, the Central Colorado Trough. Journal of Paleontology, vol. 72, pp. 1054–1072.

Webster, G.D., and Jell, P.A.

1999a. New Carboniferous crinoids from eastern Australia. Memoirs of the Queensland Museum, vol. 43, no. 1, pp. 237–278.

1999b. New Permian crinoids from eastern Australia. Memoirs of the Queensland Museum, vol. 43, no. 1, pp. 279–340.

Webster, G.D., and Lane, N.G.

1967. Additional Permian crinoids from southern Nevada. The University of Kansas Paleontological Contributions, Paper 27, 32 pp.

1987. Crinoids from the Anchor Limestone (Lower Mississippian) of the Monte Cristo Group, Southern Nevada. University of Kansas Paleontological Contributions, Paper 119, 55 pp.

Webster, G.D., and Maples, C.G.

2003. Cladid crinoid (Echinodermata) anal conditions and a terminology problem. Geological Society of America Abstracts with Program, vol. 35, no. 6.

Webster, G.D., Hafley, D.J., Blake, D.B., and Glass, A.

1999. Crinoids and stelleroids (Echinodermata) from the Broken Rib Member, Dyer Formation (Late Devonian, Famennian) of the White River Plateau, Colorado. Journal of Paleontology, vol. 73, pp. 461–486.

Webster, G.D., Maples, C., Mawson, R., and Dastanpour, M.

2003. A cladid-dominated Early Mississippian crinoid and conodont fauna from Kerman Province, Iran and revision of the glossocrinids and rhenocrinids. Journal of Paleontology, Memoir 60, supp. to vol. 77, no. 3, 35 pp.

Webster, G.D., Yazdi, M., Dastanpour, M., and Maples, C.

2001. Preliminary analysis of Devonian and Carboniferous crinoids and blastoids from Iran. Traveau de l'Institut Scientifique, Rabat, Série Géologie et Géographie Physique (2000), no. 20, pp. 108–115.

Weller, S.

1909. Description of a Permian crinoid fauna from Texas. Journal of Geology, vol. 17, pp. 623–635, 1 pl.

Weyant, M.
1985. North Africa. *In* The Carboniferous of the world II: Australia, Indian subcontinent, South Africa, South America, and North Africa, C. M. Diaz, *gen. ed.*, pp. 299–447.

White, C.A.
1865. Description of new species of fossils from the Devonian and Carboniferous rocks of the Mississippi Valley. Boston Society of Natural History Journal, vol. 9, pp. 8–33. (Preprint published in 1862).

Worthen, A.H.
1882. Descriptions of fifty-four new species of crinoids from the Lower Carboniferous limestones and Coal Measures of Illinois and Iowa. Illinois State Museum of Natural History, Bulletin, vol. 1, pp. 3–38.

Wright, J.
1914. On the occurrence of crinoids in the Lower Carboniferous limestones of Fife. Transactions of the Edinburgh Geological Society, vol. 10, pp. 148–163, pls. 18–21.
1927. Some variations in *Ulocrinus* and *Hydreionocrinus*. Geological Magazine, vol. 64, pp. 352–372.
1936. New Scottish Carboniferous crinoids. Geological Magazine, vol. 73, pp. 385–412, pl. 7–10.
1937. Scottish Carboniferous crinoids. Geological Magazine, vol. 74, pp. 385–411, pls. 13–16.
1938. Some British platycrinidae and descriptions of new species. Geological Magazine, vol. 75, pp. 266–287, pls. 8–11.
1942. New British Carbonifereous crinoids. Geological Magazine, vol. 79, pp. 269–283, pls. 9–12.
1943. *Pimlicocrinus* gen. n. and two new species of *Amphoracrinus* from the Carboniferous Limestone. Geological Magazine, vol. 80, pp. 81–94, pls. 3–6.
1948. *Scytalocrinus seafieldensis* sp. nov. and a rare *Ureocrinus* from the Carboniferous limestones of Fife; with notes on a blastoid and two crinoids from the Carboniferous limestone of the Clitheroe area. Geological Magazine, vol. 85, pp. 48–52, pl. 5.
1950–1960. The British Carboniferous Crinoidea. Palaeontographical Society, Monograph, vol. 1, pt. 1, pp. 1–24, pls. 1–7, 1950; vol. 1, pt. 2, pp. 25–46, pls. 8–12, 1951a; vol. 1, pt. 3, pp. 47–102, pls. 13–31, 1951b; vol. 1, pt. 4, pp. 103–148, pls. 32–40, 1952a; vol. 1, pt. 5, pp. 149–190, pls. 41–47, 1954; vol. 2, pt. 1, pp. 191–254, pls. 48–63, 1955a; vol. 2, pt. 2, pp. 255–272, pls. 64–67, 1955b; vol. 2, pt. 3, pp. 273–306, pls. 68–75, 1956; vol. 2, pt. 4, pp. 307–328, pls. 76–81, 1958; vol. 2, pt. 5, pp. 329–347, pls. A, B, 1960. London.

Wright, J. and Strimple, H. L.
1945. *Mooreocrinus* and *Ureocrinus* gen. nov., with notes on the family Cromyocrinidae. Geological Magazine, vol. 82, pp. 221–229, pl. 9.

Yakovlev, N.N.
1926. Ob anomaliyakh v stroenii chashchechki morskikh lilii [On the anomalies in the cup of the crinoids]. Ezhegodnik Russkogo Paleontologiches-kogo Obshchestva (1922–24), vol. 4, pp. 29–31 (In Russian).
1956. Organizm i sreda. Stati po paleoeckologii besnozvonochnykh 1913–1956 [Organisms and surroundings. Writings on paleoecology of invertebrates, 1913–1956]. Akademy Nauk SSSR, 140 pp. (In Russian).
1961. Morskie lilii iz nizhnego karbona Donbassa [Crinoids from the Lower Carboniferous of the Donetz Basin]. Geologicheskii Sbornik L'vovskogo Geologicheskogo Obshchestva, no. 7–8, pp. 417–420, 3 pls. (In Russian).

Yeltyschewa, R.S., and Polyarnaya, Zh. A.
1975. Crinoidea (Morskie lilii). V kn Paleontologicheskii Atlas Kamennourolnykh Otlozhenii Urala [Crinoidea (Sea lillies). *In* Paleontological atlas of the Carboniferous deposits of the Urals]. Trudy cinisterstvo Geol. SSSR Vsesoi Neftyanoi Nauchno-Issledovatelskii Geologorazvedochniyi Institut, vol. 383, pp. 204–207, 1 pl. (In Russian).

Zittel, K.A., von
1895. Grundzüge der Palaeontologie (Palaeozoologie). 1st edit, R. Oldenbourg, München, 971 pp.

Appendix.—Systematic list of taxa, giving number of specimens, stratigraphic horizon, and collector of each. P = Pareyn; M = Legrand-Blain; W = Winkler Prins. An asterisk (*) after the collector's name indicates uncertain of exact stratigraphic horizon. B = Breimer and Macurda who reported Pareyn specimens, which were not studied herein.

Series	Moscovian				Bashkirian				
Formation	Oued Bel Groun	Oued el Hamar		Hassi Kerma		Tagnana	Djenien		
Member		(upper)	(lower)	(upper)	(lower)		Djenien	Hid el Kef	Mouizab el Atchane
Koryschisma saharae (Breimer and Macurda, 1972) [3]									B
Rhodocrinites sp. [1]									
Megaliocrinus ? sp. [1]									P
Ectocrinus rouchi (Delpey, 1941) [3]									
Ectocrinus mezereltensis n sp. [9]									
Ectocrinus redactus n. sp. [9]									
Ectocrinus sp. [1]									
Actinocrinites becharensis n. sp. [1]									
Actinocrinites combinatus n. sp. [1]									
Aacocrinus algeriaensis n. sp. [5]				M					
Aacocrinus algeriaensis ? [2]				M					
Sampsonocrinus cheguigaensis n sp. [74]		P							
Blairocrinus grafensis n. sp. [1]				P					
Pimlicocrinus octobrachiatus n. sp. [8]		P*	P*						
Pimlicocrinus sp. [1]			W						
Actinocrinitid indeterminate 1 [2]		P							
Actinocrinitid indeterminate 2 [1]									
Actinocrinitid indeterminate 3 [1]		P							
Actinocrinitid indeterminate 4 [5]				M					
Actinocrinitid? indeterminate 5 [1]							P		
Platycrinites reouienensis n. sp. [2]									
Platycrinites aouidjaensis n. sp [3]								P	P
Platycrinites djihaniensis n. sp. [2]							P		
Platycrinites cf. *P. djihaniensis* n. sp. [4]							P		
Platycrinites hamarensis n. sp. [5]		M*	P*	M*					
Platycrinites sp. 1 [1]			P						
Platycrinites sp. 2 [3]							P		
Platycrinites sp. 3 [1]				W					
Platycrinites sp. 4 [2]				W					
Platycrinites sp. 5 [2]				W					
Platycrinites ? sp. [1]	W								
Pleurocrinus glomerosus n. sp. [8]									
Pleurocrinus folliculus n. sp. [3]		P*							
Eucladocrinus ? *asymmetricus* n. sp. [8]		P							
Eucladocrinus ? sp. [2]		P							
Synbathocrinus sp. [1]									
Barycrinidae indeterminate [5]									
Hebohenocrinus quasipatellus n. gen., n. sp. [1]						P			
Balearocrinus pareyni n. sp. [1]									
Scytalocrinus sp. [2]									P
Hydriocrinus ? *confusus* n. sp. [1]							P		
Ampullacrinus mariceae n. gen., n. sp. [4]									M, P
Ampullacrinus tritubulus n. gen., n. sp. [3]							P		
Cosmetocrinus ? sp. [2]									
Dicromyocrinus vastus n. sp. [22]						P			M
Dicromyocrinus catillus n. sp. [1]				M					
Dicromyocrinus ? *invaginatus* n. sp. [5]	W								
Dicromyocrinus ? sp. [7]					M				

Appendix.—Extended.

		Namurian				Viséan			(part)			
Ain el Mizab			El Guelmouna		Zousfana		Taouerta	Igli	Harrez	Boulmane	Akacha	Mazzer
Ain el Mizab	El Lefa	El Harrada	El Guelmouna	Ain Mezereit	Ourn el Graf	Ain Guettara						
				M							B	
				P								
											P	
				P								
				P								
		P										
				P								
				P								
						P						
				P, M								
				W								
				M								
												P
												P
P												
				W								
				W								

Appendix.—Continued.

Series	Moscovian			Bashkirian					
Formation	Oued Bel Groun	Qued el Hamar		Hassi Kerma		Tagnana	Djenien		
Member		(upper)	(lower)	(upper)	(lower)		Djenien	Hid el Kef	Mouizab el Atchane
Mooreocrinus glomerosus n. sp. [4]									P
Metacromyocrinus ? sp. [1]	W								
Mathericrinus wallacei n. comb. [29]		P	P	M					
Ureocrinus commus n. sp. [1]									
Cromyocrinid? indeterminate [1]									
Paianocrinus carinatus n. sp. [1]							M		
Zeacrinitid indeterminate 1 [2]									
Zeacrinitid? indeterminate 2 [1]									
Cladid indeterminate 1 [1]		P							
Cladid indeterminate 2 [6]				M	M				
Cladid indeterminate 3 [1]									
Cladid indeterminate 4 [2]				W					
Cladid indeterminate 5 [1]				W					
Caldid indeterminate 6 [1]				W					
Cladid indeterminate 7 [4]				W					
Taxocrinid indeterminate [1]					M				
Cibolocrinus africanus Strimple and Pareyn, 1982 [3]							P		
Amphicrinus formosus n. sp. [2]							P		
Amphicrinus prinsi n. sp. [7]				W					
Sagenocrinid indeterminate 1 [5]					M				
Sagenocrinid indeterminate 2 [1]									
Flexible indeterminate [1]	W								
Crinoid indeterminate 1 [1]				W					
Crinoid indeterminate 2 [2]				W					
Crinoids indeterminate [17]				W					
o*Floricyclus* cf. *F. angustimargo* Moore and Jeffords, 1968 [1]					M				
o*Plummeranteris* ? sp. [2]				M, W	M				
oColumnal undesignated [1]				W					
Palaechinus sp. [1]									
Archaeocidaris sp. [2]		P*	P*						

Appendix.—Extended continued.

Namurian						Viséan			(part)			
	Ain el Mizab		El Guelmouna		Zousfana		Taouerta	Igli	Harrez	Boulmane	Akacha	Mazzer
Ain el Mizab	El Lefa	El Harrada	El Guelmouna	Ain Mezereit	Oum el Graf	Ain Guettara						
			P									
				W								
												P
			P									
				M*								
												P
												P
P												

PLATES

EXPLANATION OF PLATE 1

Figure		Page
1–3.	***Rhodocinites*** sp. El Guelmouna Formation, Ain Mezereit Member	18
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4–8.	Oral, E ray (note plated over unregenerated arm opening), A ray, basal, and posterior views, ×1.6. RGM 361 154.	
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11–12.	C-D interray and oral views, ×1.5. RGM 361 157.	
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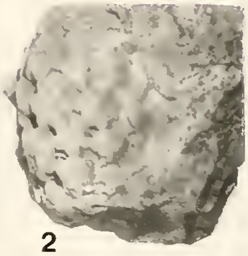
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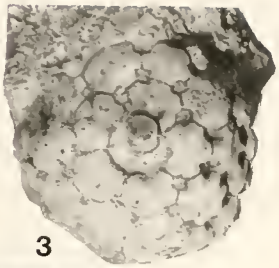
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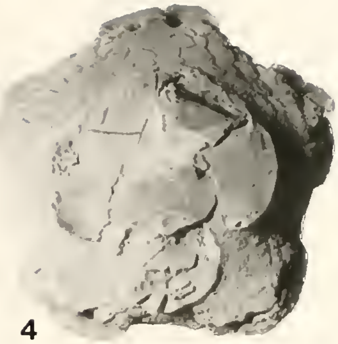
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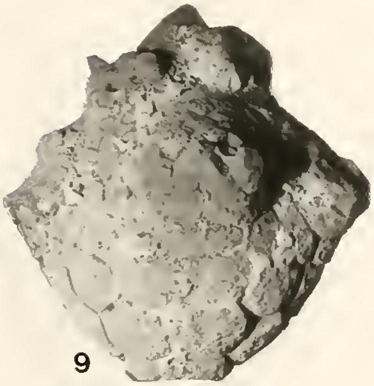
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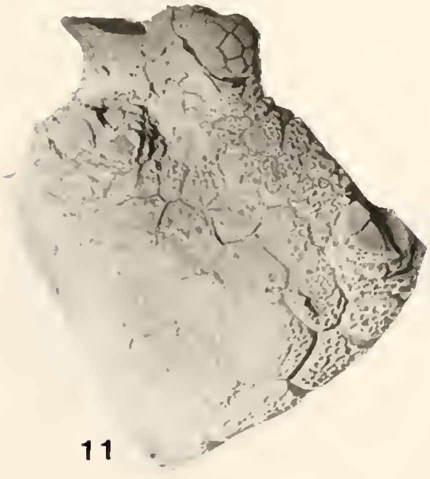
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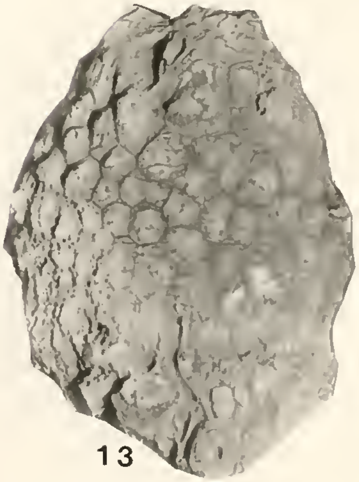
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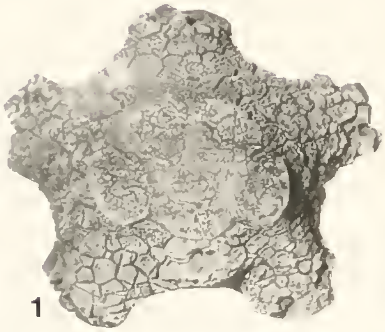
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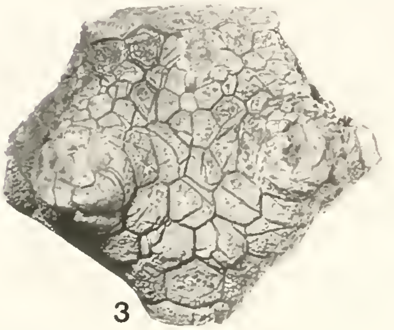
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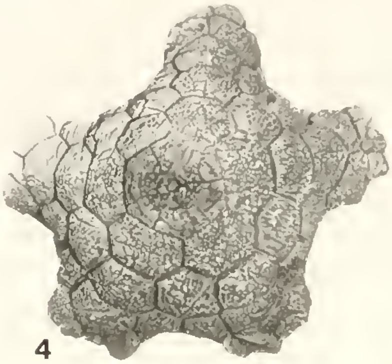
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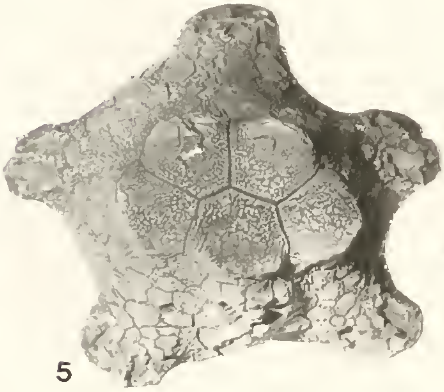
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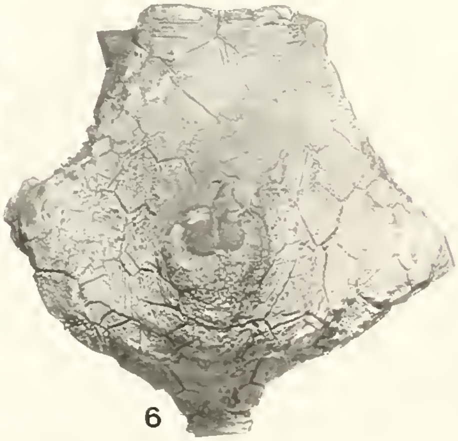
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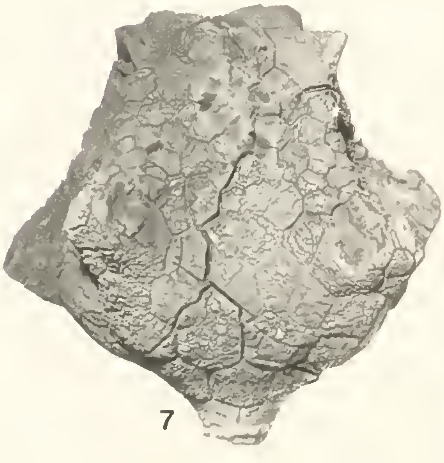
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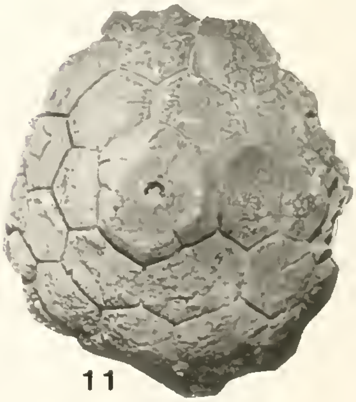
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15, 16.	***Koryschisma saharae*** (Breimer and Macurda, 1972). El Guelmouna Formation, Aïn Mezerelt Member 15, 16. Lateral and oral views, ×3. RGM 361 150.	17
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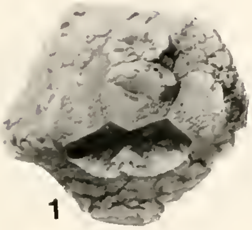
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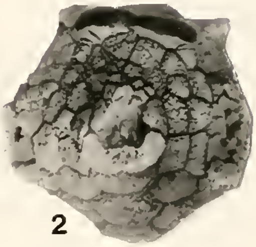
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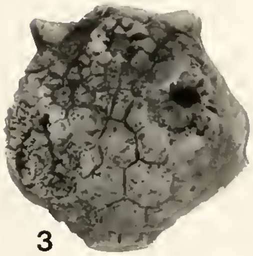
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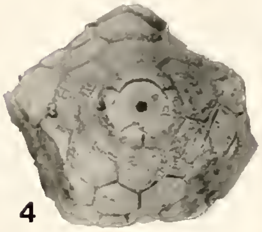
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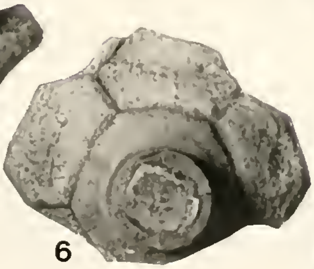
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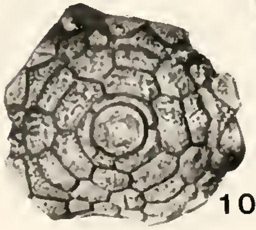
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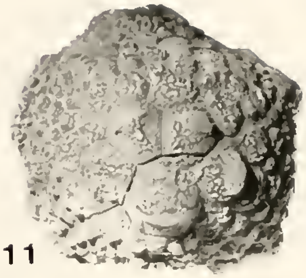
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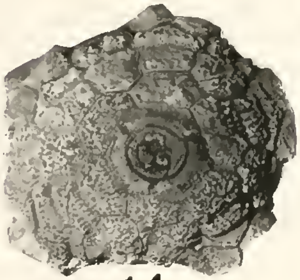
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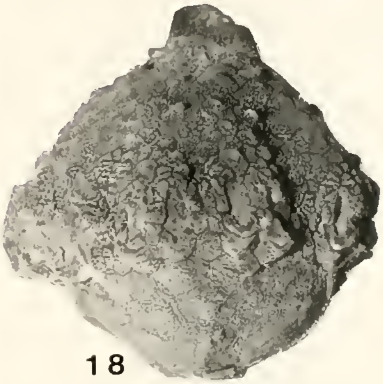
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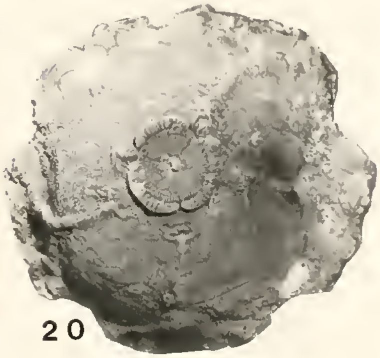
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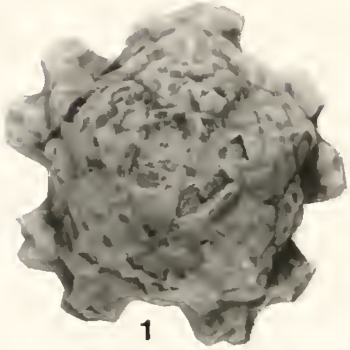
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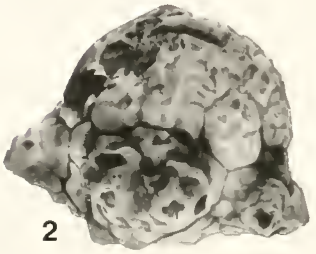
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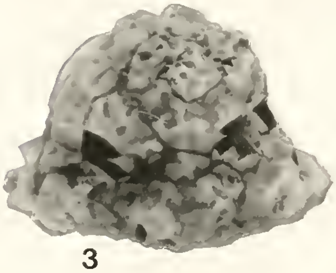
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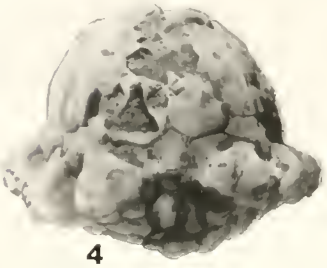
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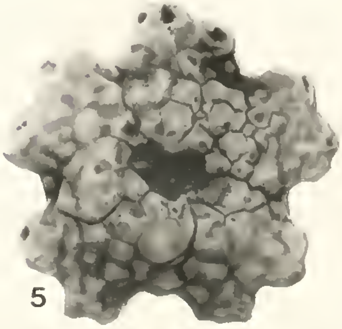
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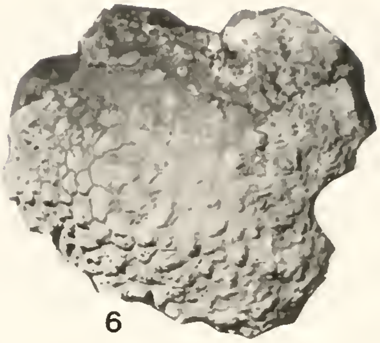
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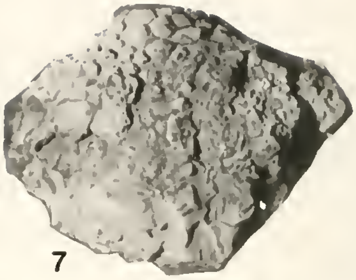
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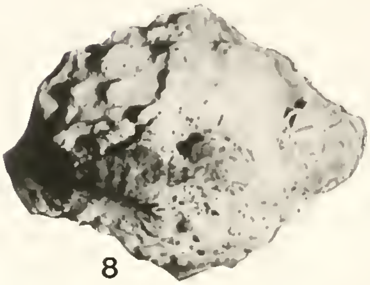
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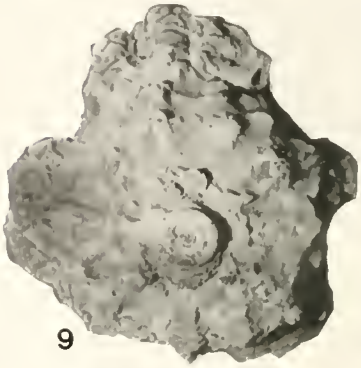
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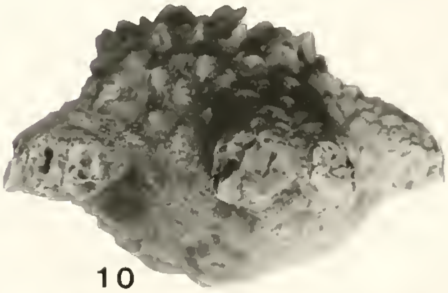
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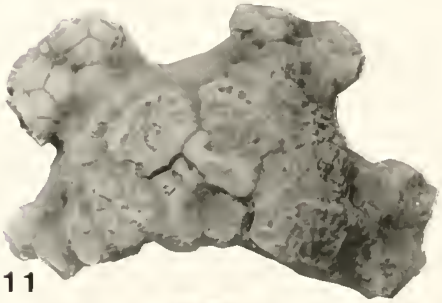
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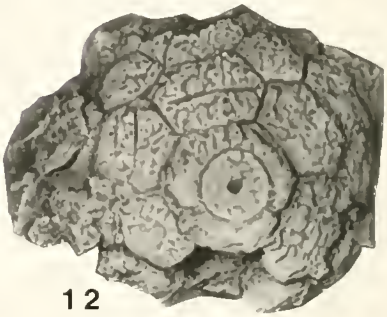
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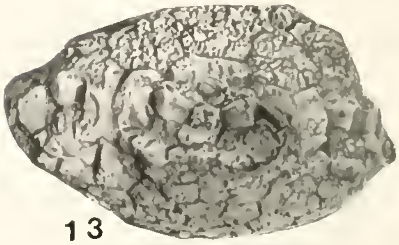
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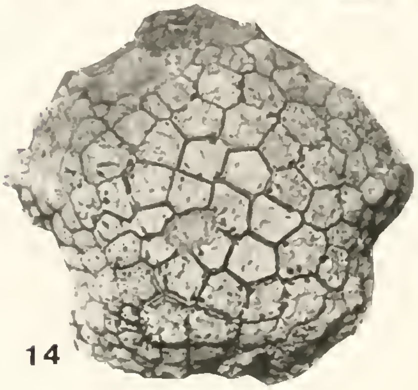
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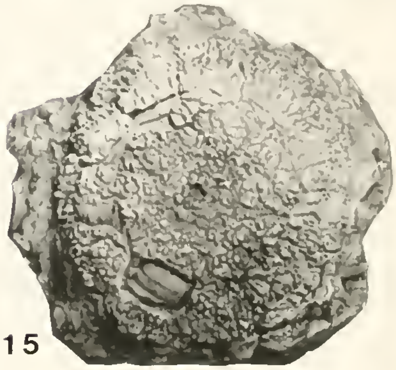
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EXPLANATION OF PLATE 4

Figure		Page
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EXPLANATION OF PLATE 5

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    13–15. A ray, posterior, and basal views, ×2. Holotype, RGM 361 185.
    16–19. Oral, A ray, posterior, and basal views, ×2.3. Paratype 1, RGM 361 186.


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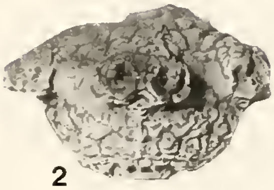
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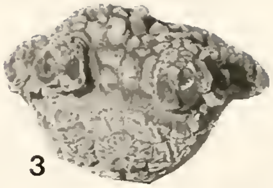
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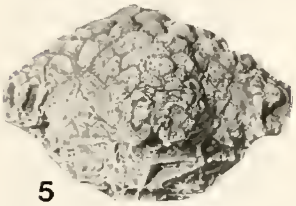
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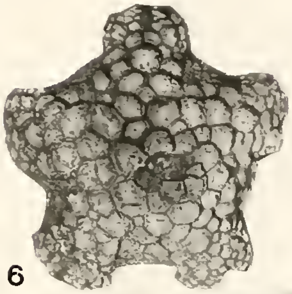
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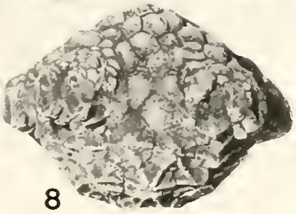
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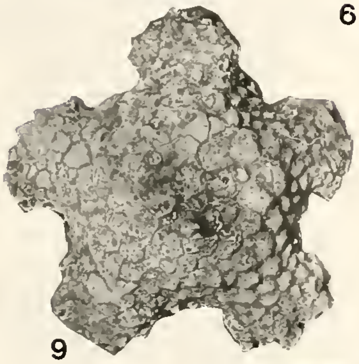
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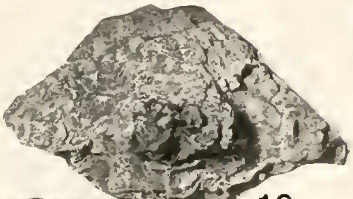
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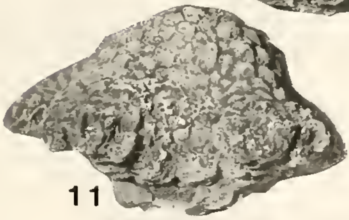
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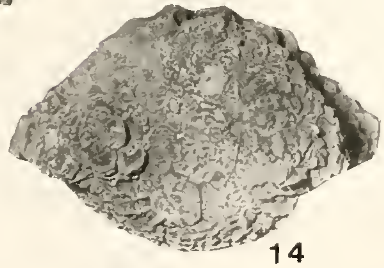
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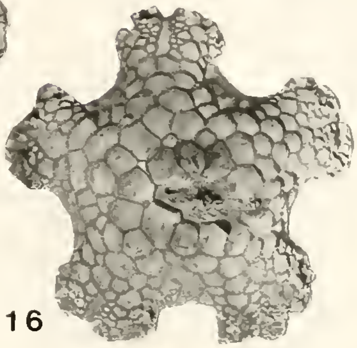
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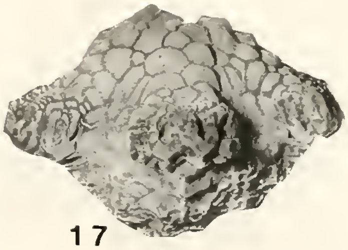
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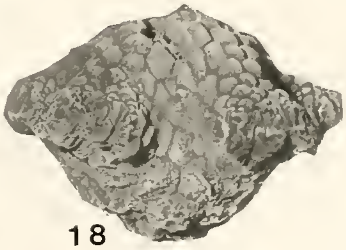
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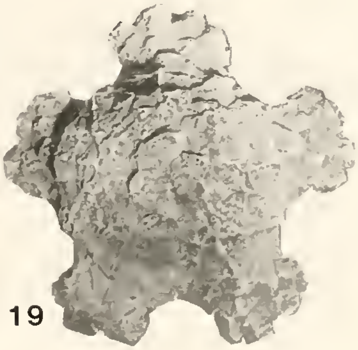
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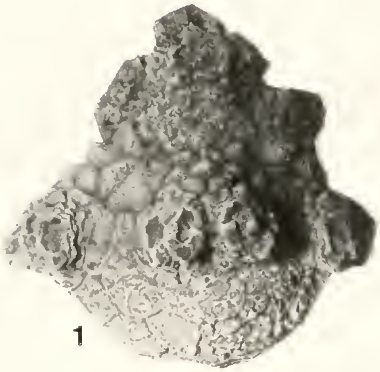
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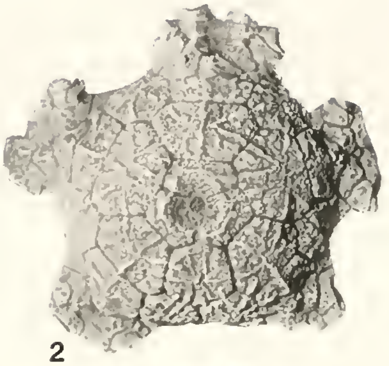
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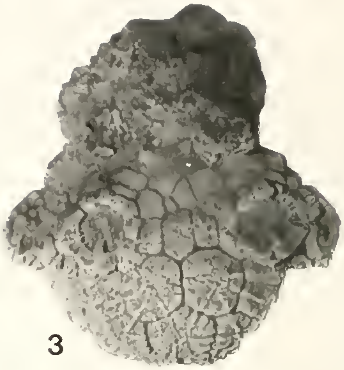
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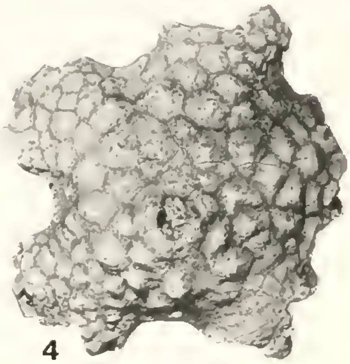
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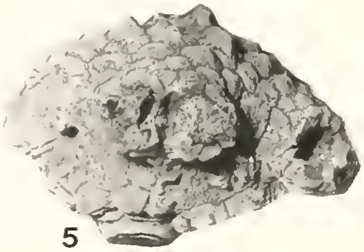
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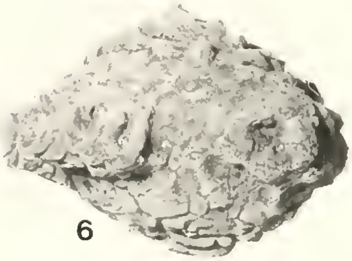
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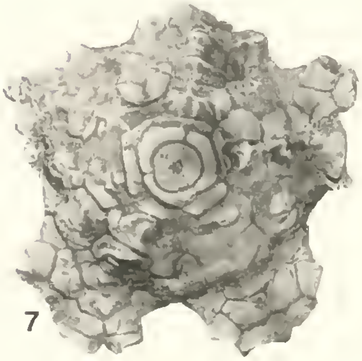
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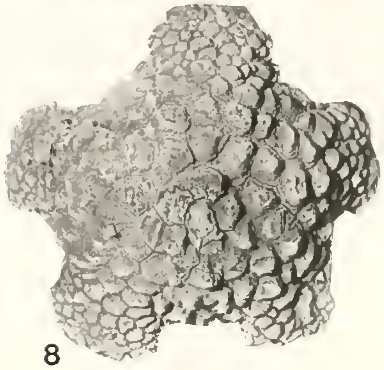
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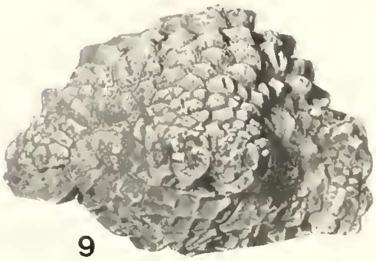
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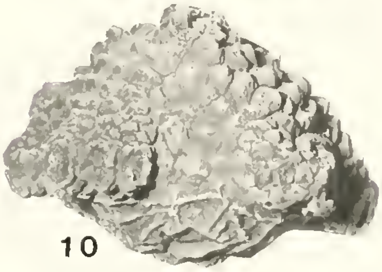
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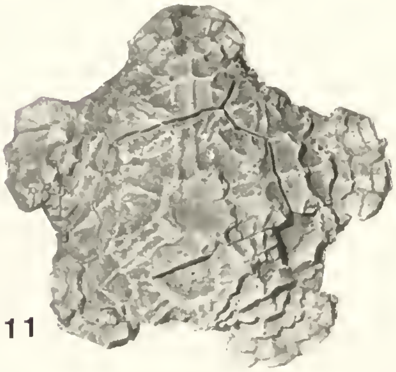
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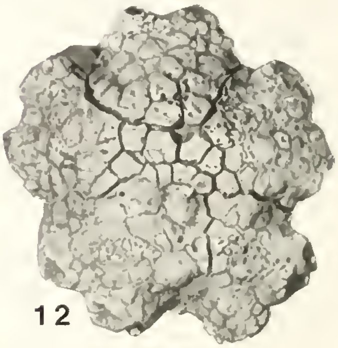
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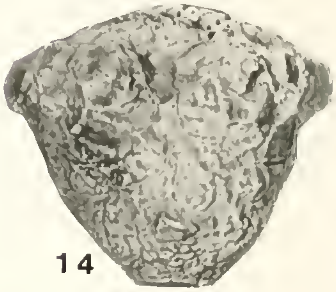
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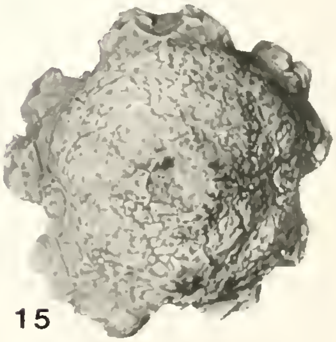
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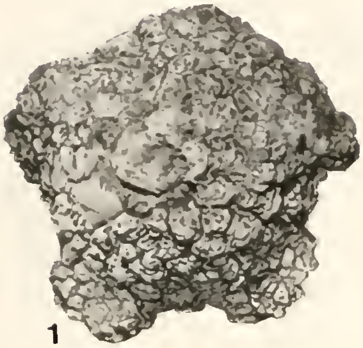
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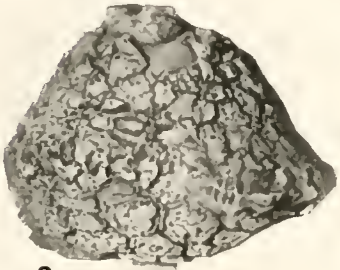
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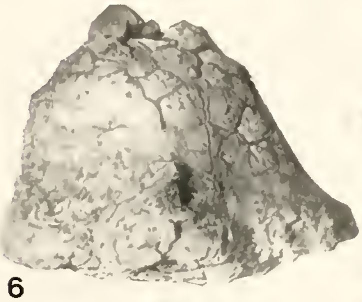
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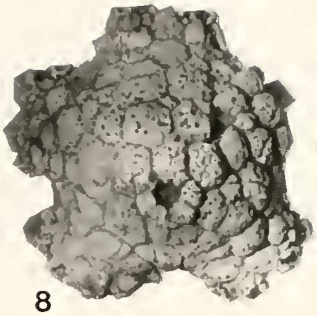
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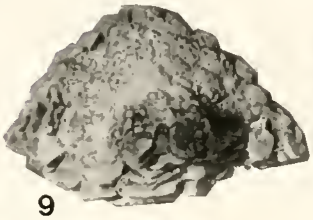
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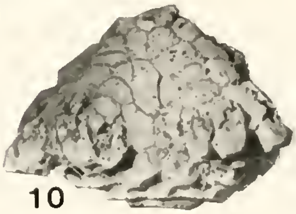
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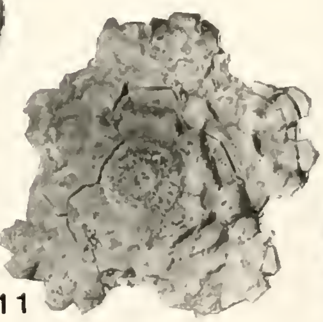
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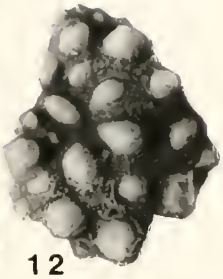
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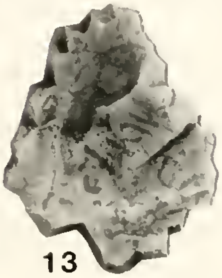
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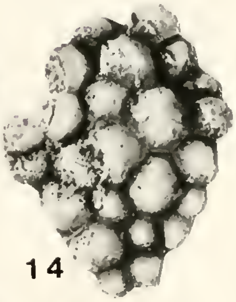
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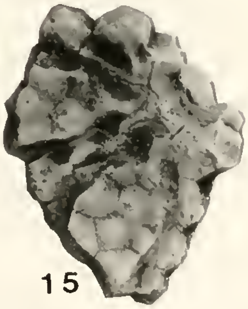
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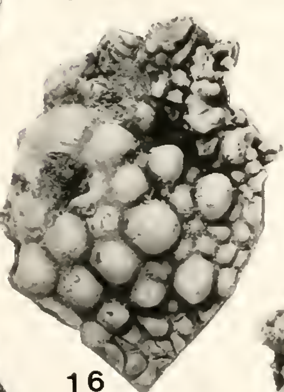
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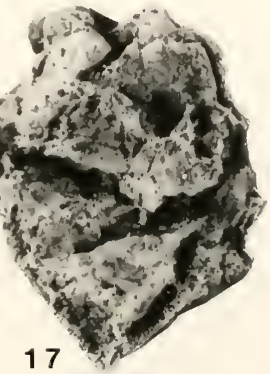
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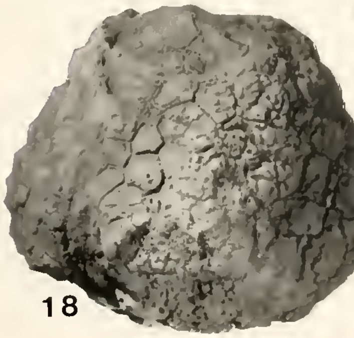
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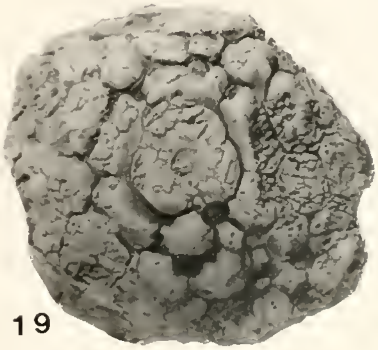
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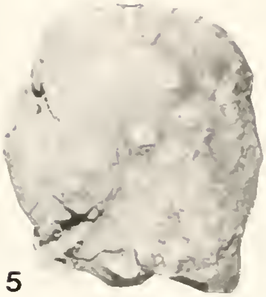
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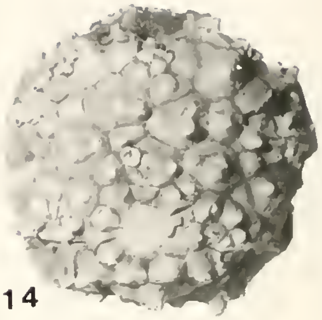
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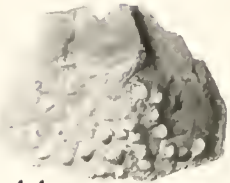
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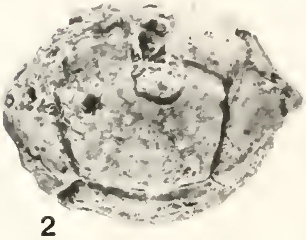
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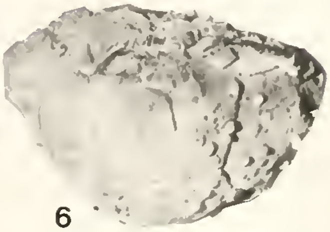
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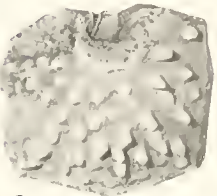
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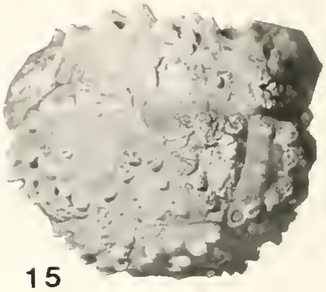
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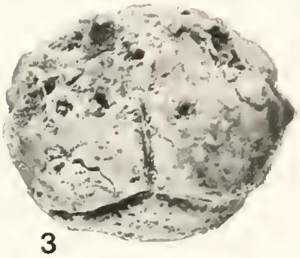
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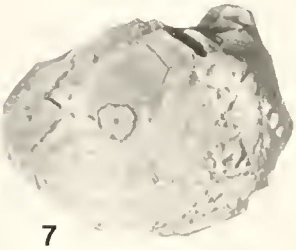
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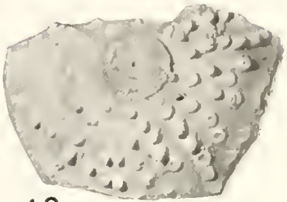
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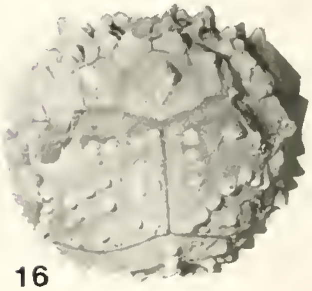
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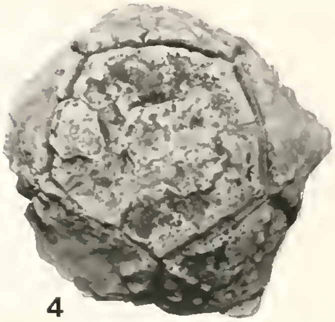
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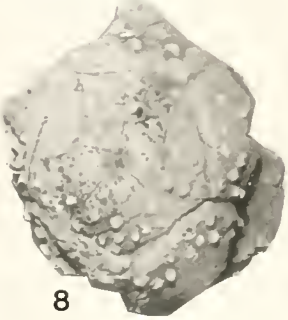
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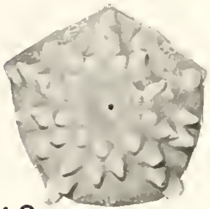
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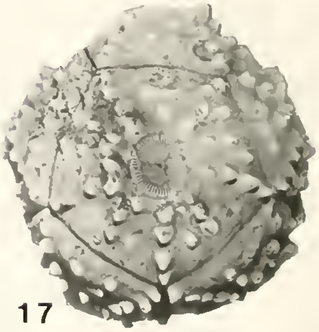
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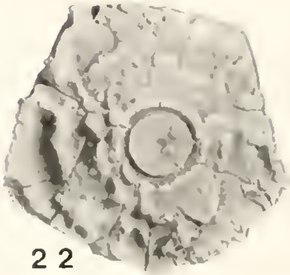
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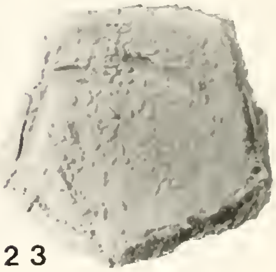
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EXPLANATION OF PLATE 8

Figure Page

1–8. ***Platycrinites reouienensis*** new species. El Guelmouna Formation, Aïn Mezerelt Member 32
1–4. Oral, A ray, posterior, and basal views, ×2.4. Paratype, RGM 361 223.
5–8. Oral, B ray, DE interray, and basal views, ×2.3. Holotype, RGM 361 222.

9, 10. ***Platycrinites*** sp. 5. Hassi Kerma Formation, Mouizeb El Atchane 36
9. Articular view of twist columnal, ×2. RGM 361 351.
10. Articular view of twist columnal, ×2. RGM 361 344.

11–13. ***Platycrinites*** cf. ***P. djihaniensis*** new species. Top of the Djenien Formation 34
11. External view, partial radial, ×2.5. RGM 361 232.
12. External view of nearly complete radial, ×2.5. RGM 361 230.
13. Basal view, partial basal circlet, ×2.5. RGM 361 229.

14–19. ***Platycrinites djihaniensis*** new species. Top of the Djenien Formation 34
14–17. Oral, A ray, posterior, and basal views, ×2.5. Holotype, RGM 361 227.
18, 19. External and internal views of basal circlet, ×2.6. Paratype, RGM 361 228.

20, 21. ***Platycrinites aouidjaensis*** new species. Ain el Mizab Formation, Mouïzeb el Atchane Member 33
20, 21. B ray and basal views, Holotype, RGM 361 224, ×1.6.

22, 23. ***Platycrinites*** sp. 4. Hassi Kerma Formation, Mouizeb el Atchane Member 35
22, 23. External and internal views of basal circlet, ×2. RGM 361 338.

EXPLANATION OF PLATE 9

Figure Page

1–10. ***Pleurocrinus glomerosus*** new species. El Guelmouna Formation 37
1–3. Oral, posterior, and basal views, ×2. Paratype 2, RGM 361 242.
4–6. Oral, E ray, and basal views, ×2. Paratype 1, RGM 361 241.
7–10. Oral, A ray, posterior, and basal views, ×2. Holotype, RGM 361 240.

11–14. ***Synbathocrinus*** sp. El Guelmouna Formation, Aïn Mezerelt Member 39
11–14. Oral, A ray, posterior, and basal views, ×2.5. RGM 361 255.

15–22. ***Platycrinites hamarensis*** new species. Oued el Hamar Formation 34
15–18. Oral, A ray, posterior, and basal views, ×2. Holotype, RGM 361 233.
19–22. Oral, A ray, posterior, and basal views, ×2.4. Paratype 1, RGM 361 234.

23, 24. ***Platycrinites*** sp. 1. Upper part of the Oued el Hamar Formation 35
23, 24. A ray and basal views, RGM 361 238, ×2.

25–27. ***Platycrinites***? sp. Oued Bel Groun Formation 36
25–27. Basal, oral, and BC interray views, RGM 290 857, ×2.


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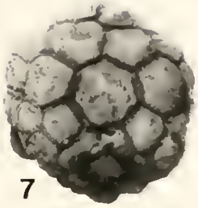
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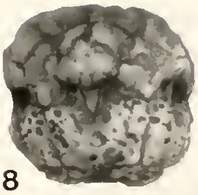
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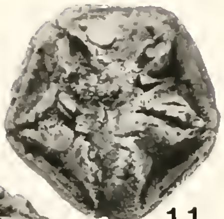
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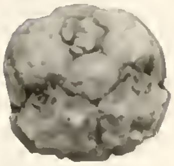
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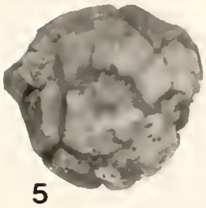
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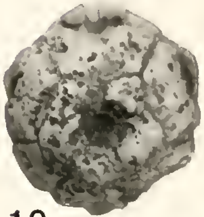
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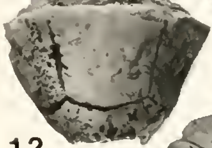
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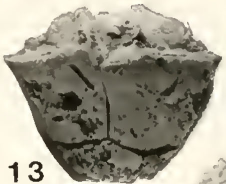
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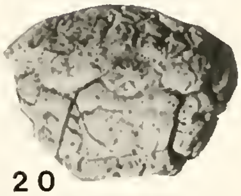
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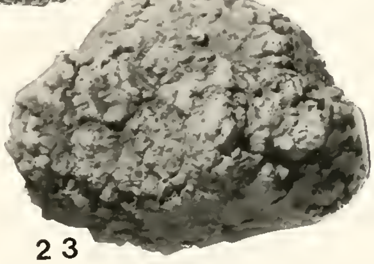
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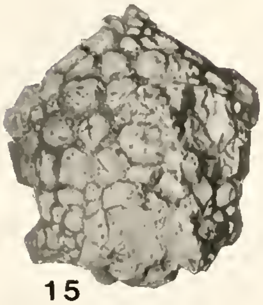
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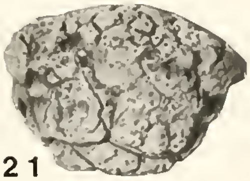
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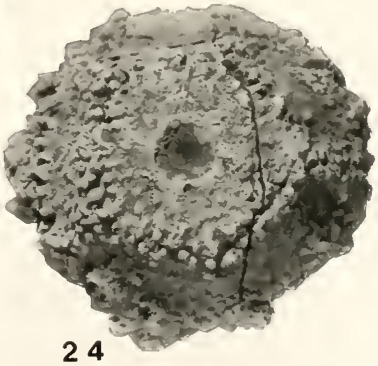
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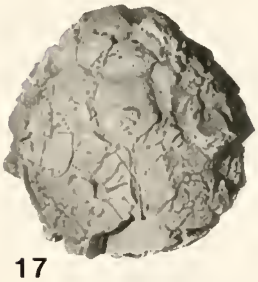
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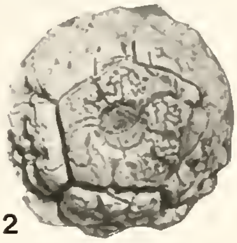
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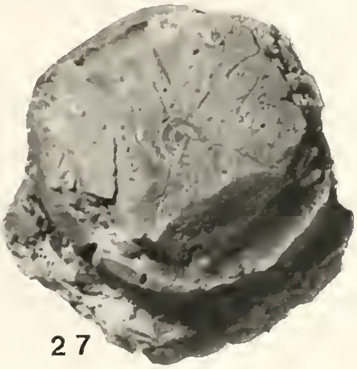
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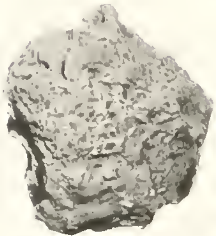
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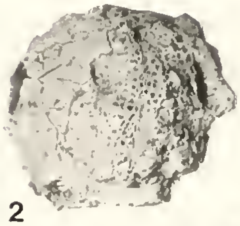
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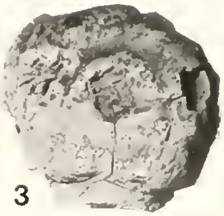
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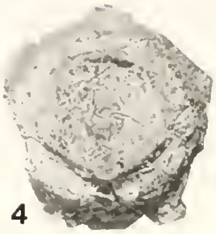
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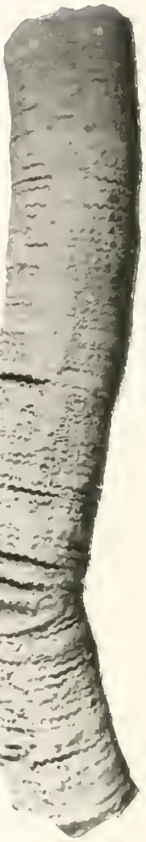
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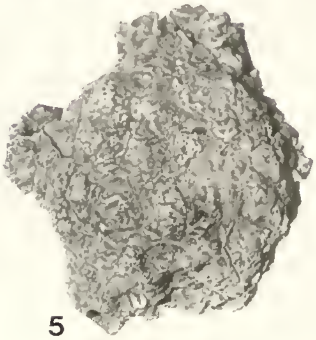
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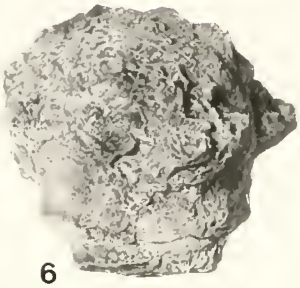
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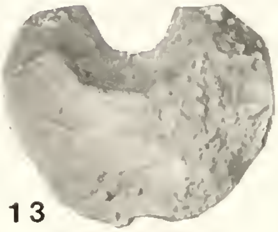
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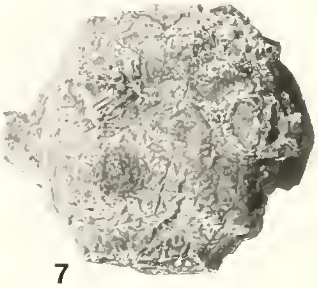
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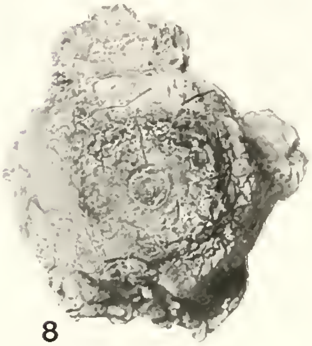
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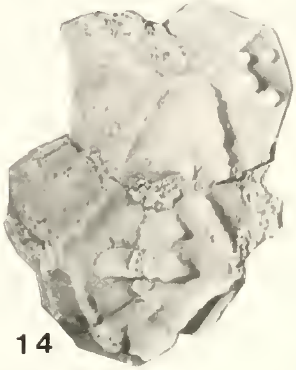
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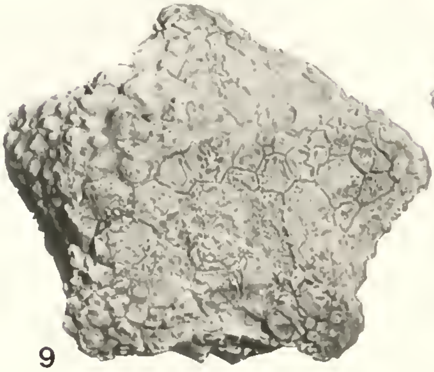
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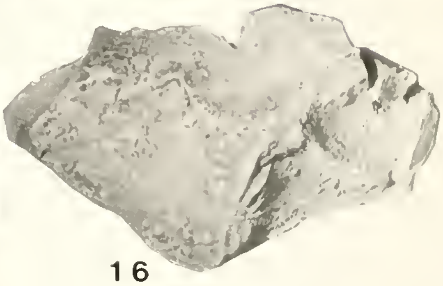
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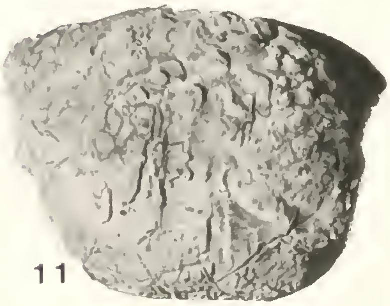
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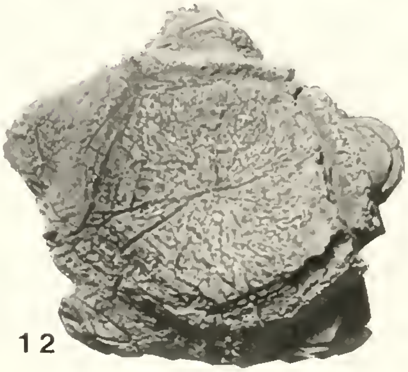
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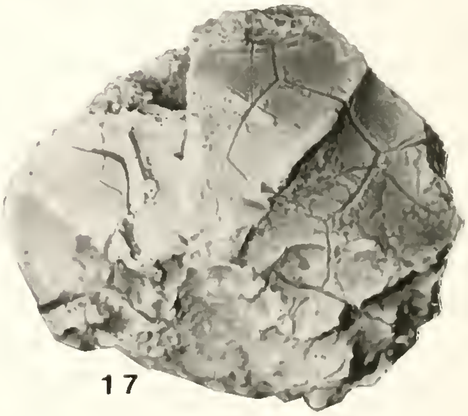
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1–8. ***Pleurocrinus folliculus*** new species. Oued el Hamar Formation . . . 38
  1–4. Oral, A ray, posterior, and basal views, ×2.6. Paratype 1, RGM 361 244.
  5–8. Oral, A ray, D-E interray, and basal views, ×2. Holotype, RGM 361 243.

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  9–12. Oral, B ray, posterior, and basal views, ×2. Holotype, RGM 361 246.

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  13. Exterior view of radial, ×2. RGM 361 258.
  14. Exterior view of a radial, two adjoined basals, and distal tip of an infrabasal, ×2. RGM 361 257.
  15. lateral view of columnal, ×2. RGM 361 260.
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  17. Anal view of partial cup, ×2. RGM 361 256.

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1–4. ***Hydriocrinus*? *confusus*** new species. Horizon between the Hid el Kef and Djenien members, Djenien Formation 43
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5–7. A ray, oral, and posterior views, ×3.7. Holotype, RGM 361 262.

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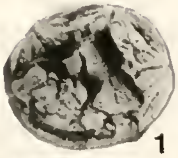
21–23. Oral, posterior, and basal views of partial crown, ×3.1; Djenien Formation, Djenien Member. Paratype 2, RGM 361 335.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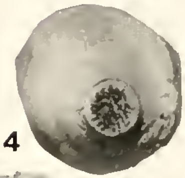
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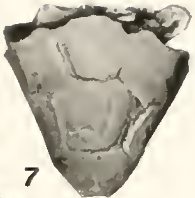
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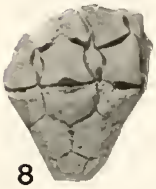
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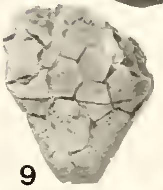
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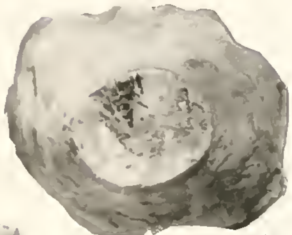
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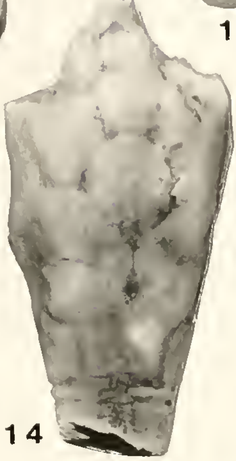
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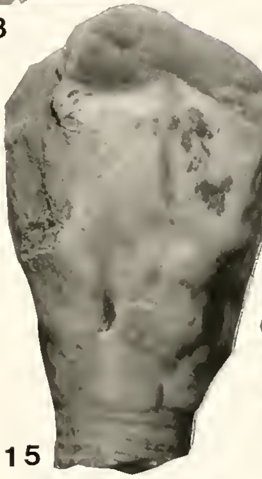
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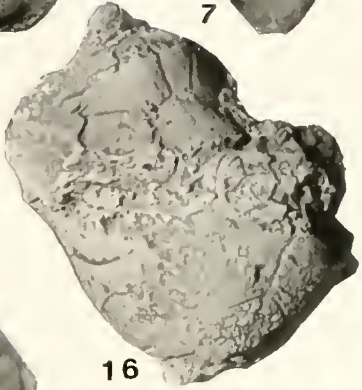
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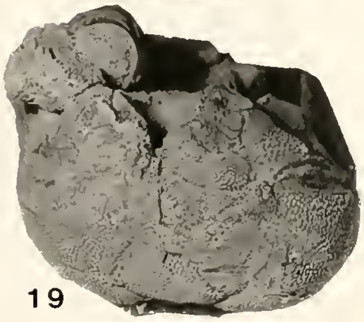
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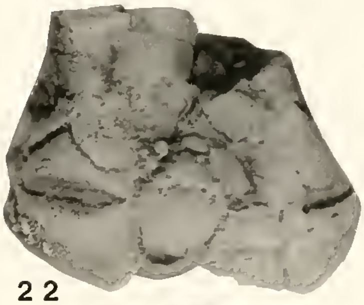
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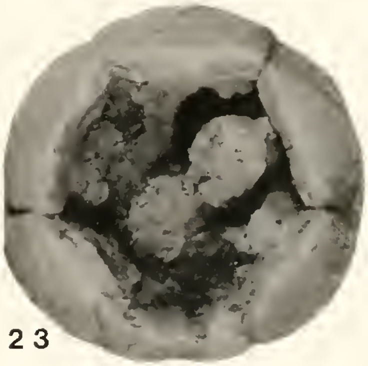
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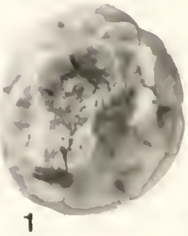
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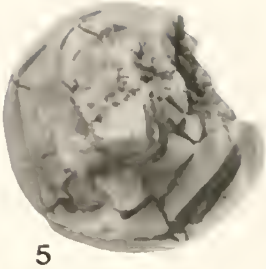
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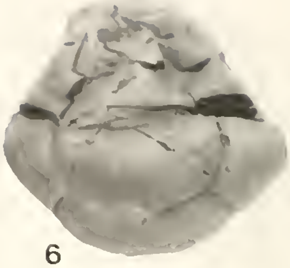
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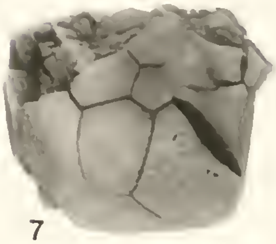
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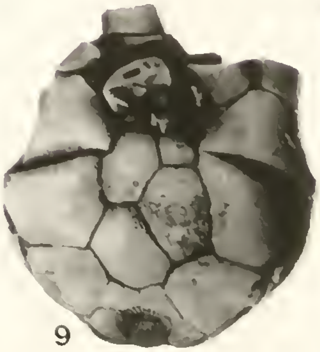
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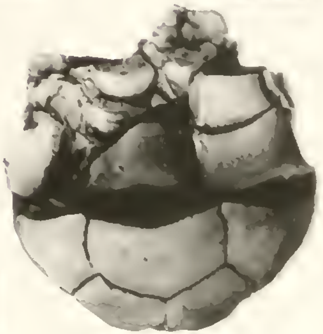
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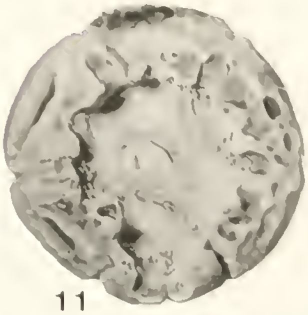
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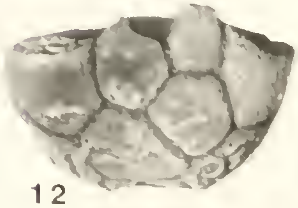
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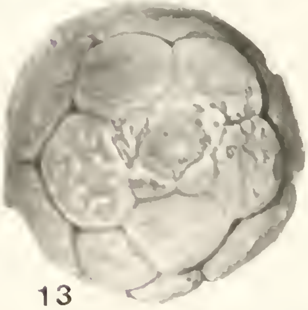
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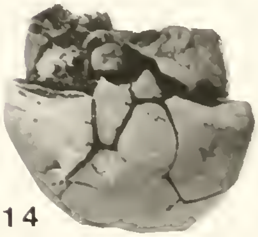
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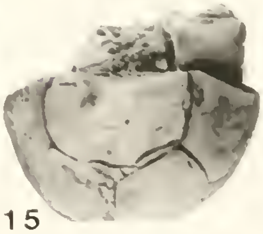
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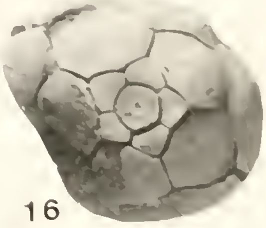
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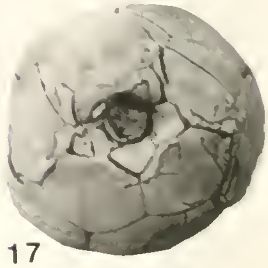
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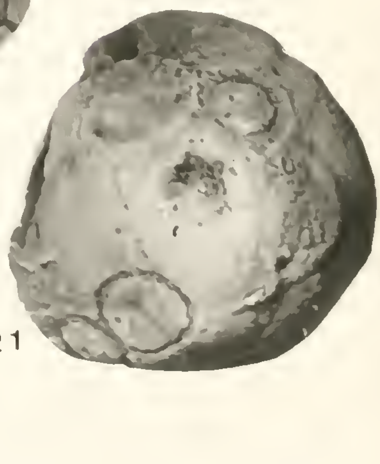
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1–10. ***Ampullacrinus marica*** new species. Ain el Mizab Formation, Mouizeb el Atchane Member 46
  1–4. Oral, basal, posterior, and A ray views of partial crown, ×3. Holotype, RGM 361 330.
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  17. Basal view, ×2.6. Paratype 6, RGM 361 272, El Guelmouna Formation, El Guelmouna Member.
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- 17–19. A ray, posterior, and basal views. ×2.4. Holotype, RGM 361 284, El Harrada Member, Ain el Mizab Formation.
- 20–23. Oral, A ray, posterior, and basal views, ×2.3. Paratype 1, RGM 361 285, Ain el Mizab Formation, Mouizeb el Atchane Member.
- 24–26. Oral, posterior, and basal views, ×3.6. Paratype 3, RGM 361 287, El Harrada Member, Ain el Mizab Formation.


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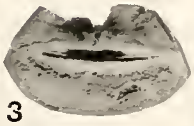
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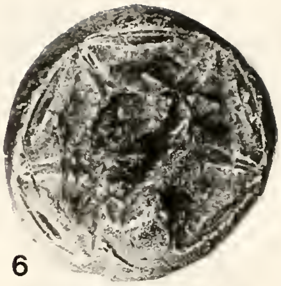
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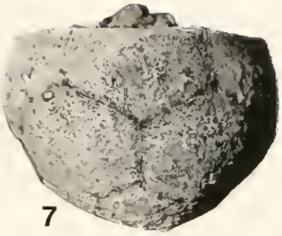
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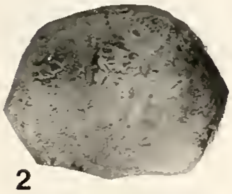
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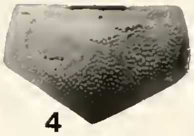
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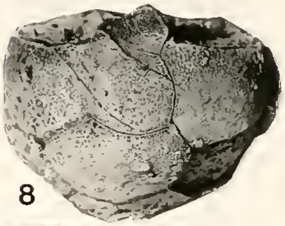
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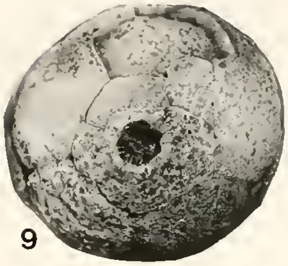
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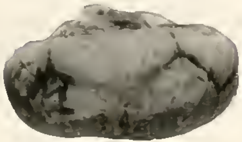
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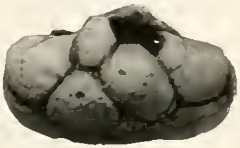
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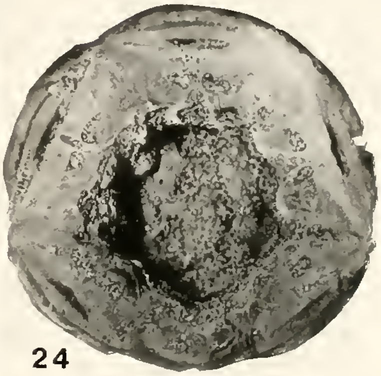
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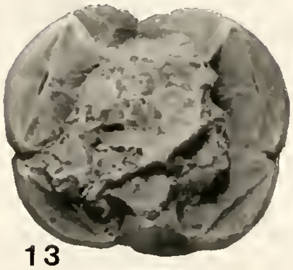
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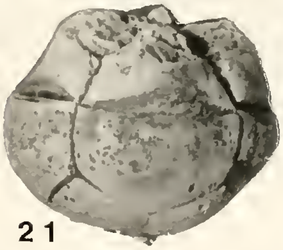
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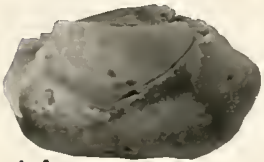
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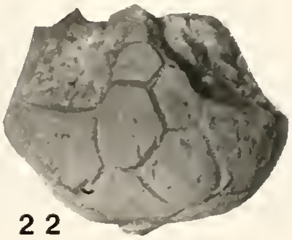
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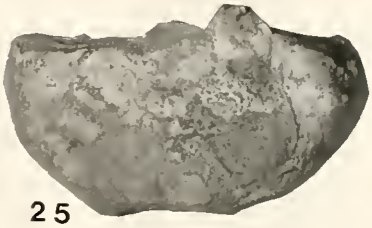
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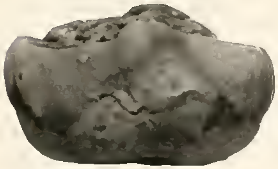
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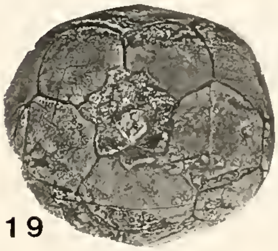
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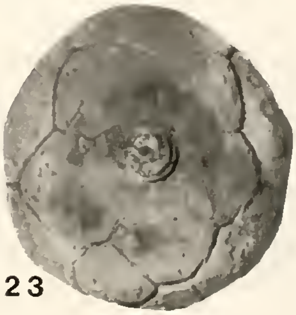
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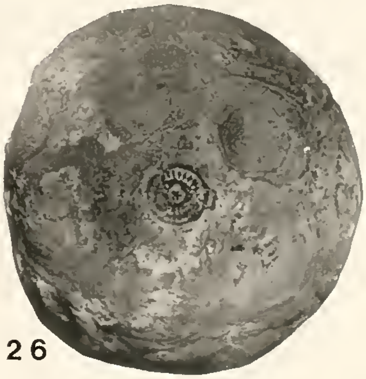
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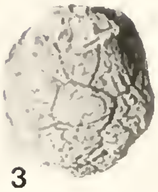
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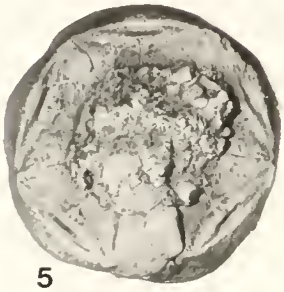
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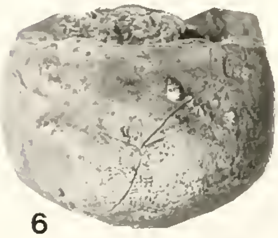
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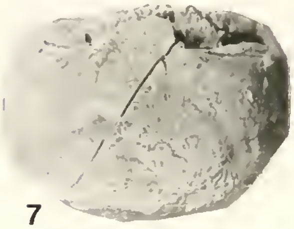
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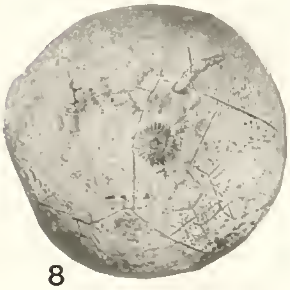
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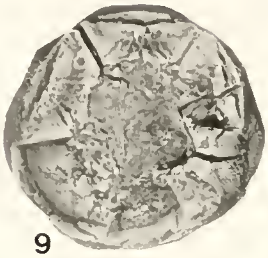
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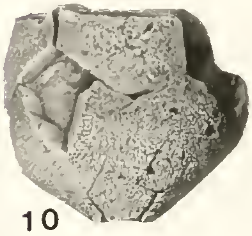
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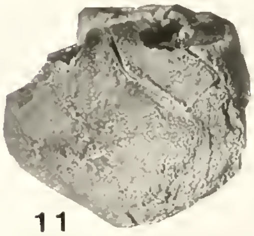
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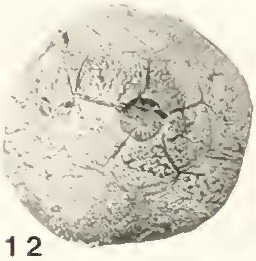
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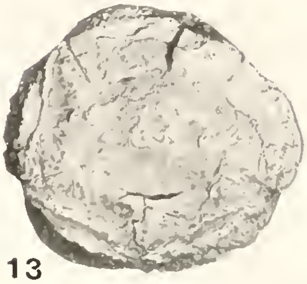
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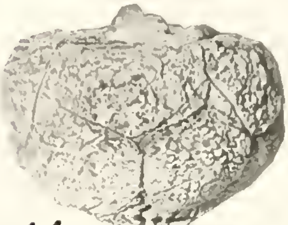
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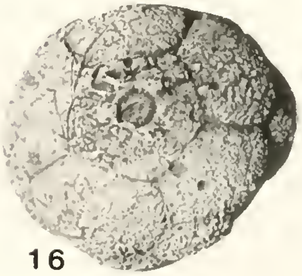
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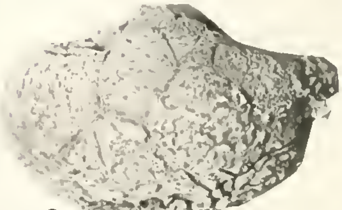
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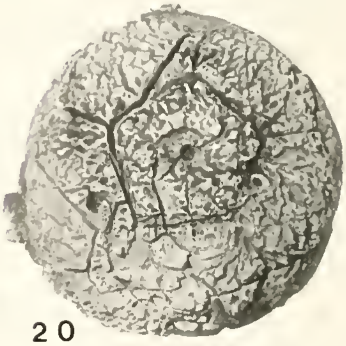
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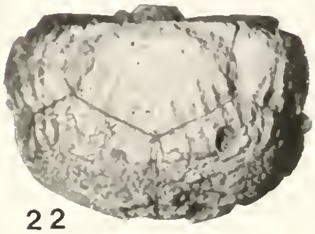
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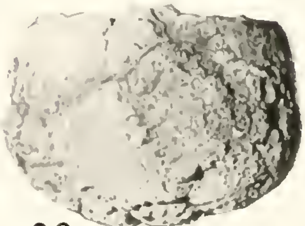
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EXPLANATION OF PLATE 14

Figure Page

1–24. ***Mathericrinus wallacei*** (Termier and Termier, 1950) new combination. Oued el Hamar Formation 53

- 1–4. Oral, A ray, posterior, and basal views, note urn shape and ridge ornament, ×1.6. Specimen 8, RGM 361 296.
- 5–8. Oral, A ray, posterior, and basal views, note fine granular ornament, ×, 2.5. Specimen 1, RGM 361 288.
- 9–12. Oral, A ray, posterior, and basal views, note extended urn shape, ×2.5. RGM 361 289, specimen 2.
- 13–16. Oral, A ray, posterior, and basal views, ×2.5. Specimen 7, RGM 361 294.
- 17–20. Oral, A ray, posterior, and basal views, note vermiform ornament and flat base, ×2.5. Specimen 4, RGM 361 291.
- 21–24. Oral, A ray, posterior, and basal views, note ridge ornament and globose form, ×2.4. Specimen 3, RGM 361 290.

EXPLANATION OF PLATE 15

Figure Page

1–4. ***Metacromyocrinus***? sp. Oued Bel Groun Formation 53
1–4. Oral, A ray, posterior, and basal views, ×3. RGM 290 860.

5–8. Cladid indeterminate 2. Hassi Kerma Formation 58
5. Lateral view of one holdfast segment of stem, ×2. RGM 361 312.
6, 7. Lateral and articular views of pluricolumnal, ×2. RGM 361 313.
8. Lateral view of infrabasal circlet, ×2. RGM 361 311.

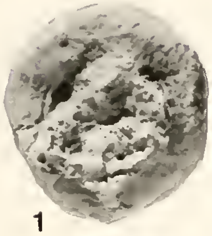
9–13. ***Ureocrinus conmus*** new species. El Guelmouna Formation, El Guelmouna Member 55
9–13. A ray, posterior, AB interray, and basal views, ×2; enlargement of AB basal for ornamentation detail, ×3. Holotype, RGM 290 873.

14. Zeacrinitidae? indeterminate 2. El Guelmouna Formation, Aïn Mezerelt Member 57
14. Posterior view of partial crown, ×1.5 or 2. RGM 361 309.

15. Crinoid indeterminate 1. Upper part of the Hassi Kerma Formation, limestone below level ML171, Bashkirian, at Mouizeb El Atchane, 300 m north of the south gully, Bechar 62
15. Partial cup, ×2. RGM 361 336.

16–18. ***Paianocrinus*? *carinatus*** new species. Basal part of the Djenien Member, Djenien Formation 56
16–18. Posterior, D ray, and A ray views, ×1.5. Holotype, RGM 361 306.

19. Cromyocrinid? indeterminate. Mazzer Formation 55
19. Basal view of partial cup, ×1.1. RGM 361 305.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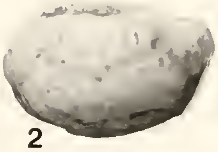
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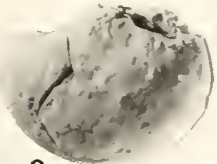
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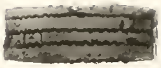
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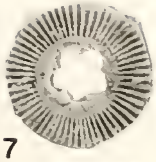
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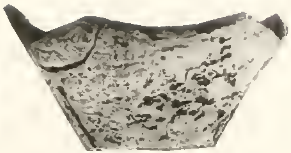
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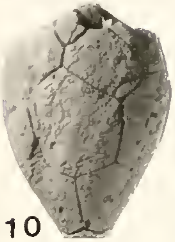
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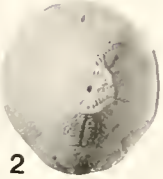
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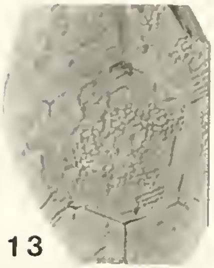
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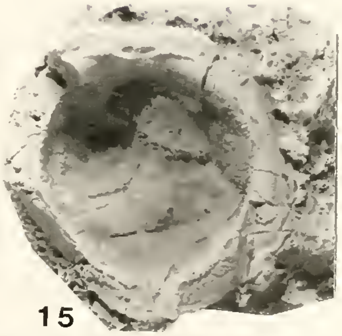
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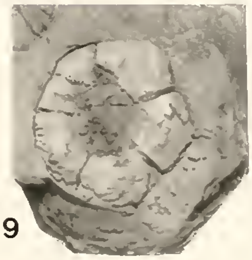
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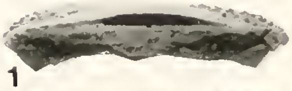
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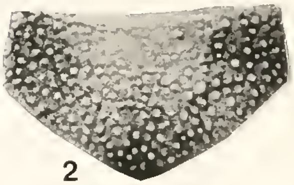
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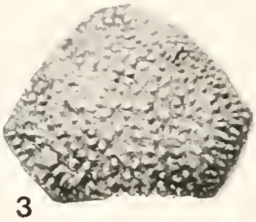
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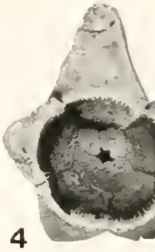
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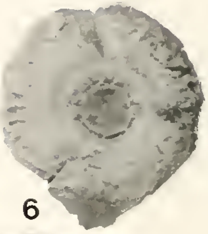
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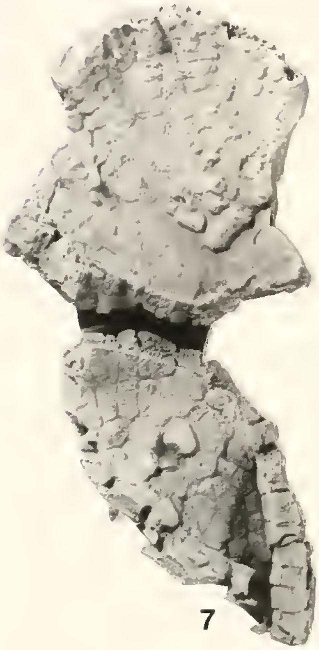
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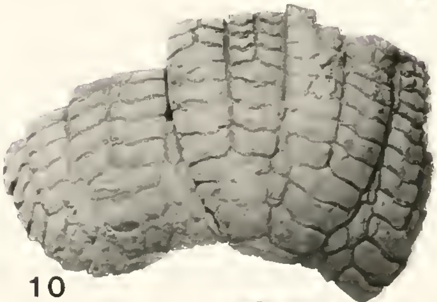
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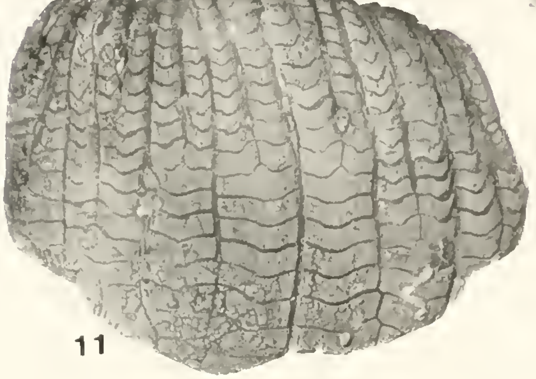
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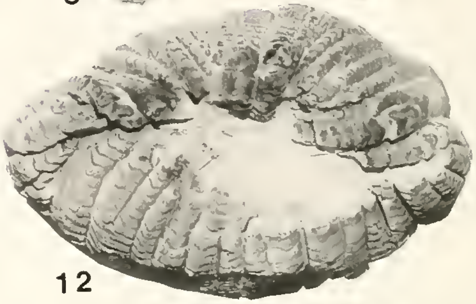
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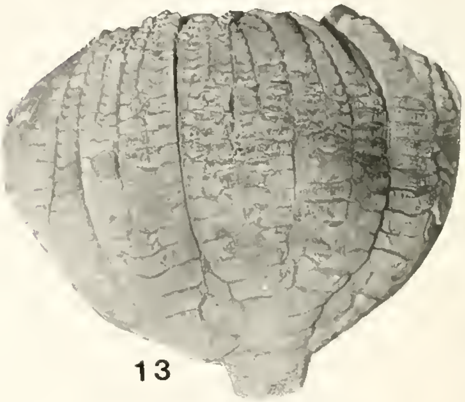
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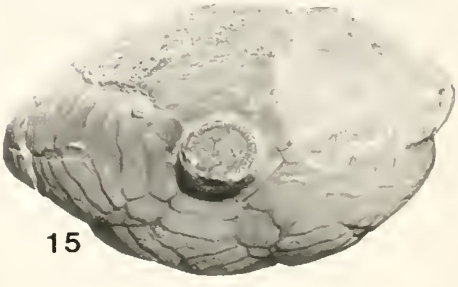
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EXPLANATION OF PLATE 16

Figure — Page

1–3. Sagenocrinid indeterminate 1. Lower part of the Hassi Kerma Formation 61
  1, 2. Oral and external views of radial, ×2.2. RGM 361 325.
  3. External view of basal, ×2.2. RGM 361 326.

4. Taxocrinid indeterminate. Lower part of the Hassi Kerma Formation 59
  4. External view of infrabasal and basal circlet, ×2.2. RGM 361 317.

5, 6. Flexible indeterminate. Oued Bel Groun Formation 61
  5, 6. Internal and external view of infrabasal circlet, ×2. RGM 361 328.

7–10. ***Amphicrinus prinsi*** new species Upper part of the Hassi Kerma Formation 60
  7, 8. Interior and exterior views of two halves of specimen splayed, A ray at top.
  9. Two halves enclosed as crushed in original preservation, ×1.5. Holotype, RGM 361 320.
  10. Exterior view of partial set of arms, ×1.5. Paratype 1, RGM 361 321.

11–15. ***Amphicrinus formosus*** new species. Top of the Djenien Formation 59
  11. Exterior view of partial set of arms, ×2.1. Paratype, RGM 361 319.
  12–15. Oral, E ray, CB interray, and basal views, ×1.5. Holotype, RGM 361 318.

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3, 4.	Cladid indeterminate 7. Upper part of the Hassi Kerma Formation 3. Lateral view of primibrachial; 4, lateral view of radial, ×2. RGM 361 346.	59
5–8.	Cladid indeterminate 4. Upper part of the Hassi Kerma Formation 5, 6. Articular and lateral views of radial; 7, 8, exterior and interior views of basal, ×2. RGM 361 342.	58
9–14.	***Dicromyocrinus*? *invaginatus*** new species. Oued Bel Groun Formation 9–11. B ray, posterior, and basal, views, ×2. Paratype 2, RGM 361 283. 12–14. E ray, posterior, and basal, views, ×2. Paratype 1, RGM 361 282.	51
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17, 18.	Columnal undesignated. Upper part of the Hassi Kerma Formation 17, 18. Articular and lateral views of pluricolumnal, ×2. RGM 290 866.	63
19, 20.	***Floricyclus*** cf. ***F. angustimargo*** Moore and Jeffords 1968. Lower part of the Hassi Kerma Formation 19, 20. Articular and lateral views, pluricolumnal, ×2.5. RGM 361 315.	62
21–24.	***Plummcranteris*?** sp. Hassi Kerma Formation 21, 22. Articular and lateral views, columnal, ×2.5. RGM 361 316. Lower part of Hassi Kerma Formation. 23, 24. Articular and lateral views, pluricolumnal, ×2. RGM 361 343. Upper part of Hassi Kerma Formation.	62
25, 26.	***Dicromyocrinus vastus*** new species. El Guelmouna Member, El Guelmouna Formation 25, 26. A ray and posterior views, ×2. Paratype 5, RGM 361 271.	49
27, 28.	Cladid indeterminate 1. Upper part of the Oued el Hamar Formation 27, 28. A ray and basal views of partial cup, ×2. RGM 361 310.	58
29, 30.	***Archaeocidaris*** sp. Oued el Hamar Formation 29. Lateral view, spine shaft, ×2. RGM 361 349. 30. External view of interambulacral plate, ×2. RGM 361 348.	63
31.	***Palaechinus*** sp. Base of the Ain el Mizab Member, Ain el Mizab Formation 31. External view of partial corona, ×2.1. RGM 361 347.	63
32–35.	Zeacrinitidae indeterminate 1. Ain el Mizab Formation, El Harrada Member 32–35. Oral, A ray, posterior, and basal views of cup, ×2. RGM 361 307.	57


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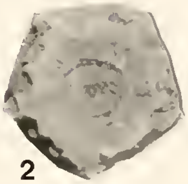
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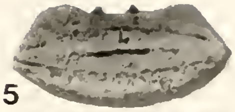
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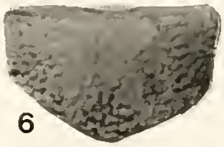
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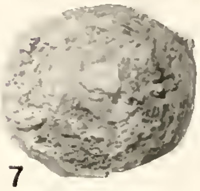
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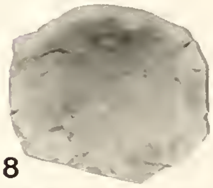
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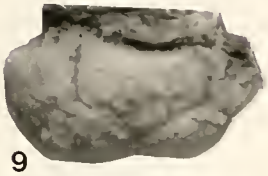
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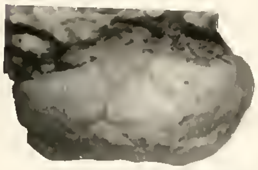
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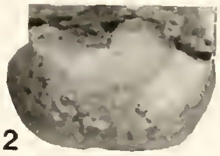
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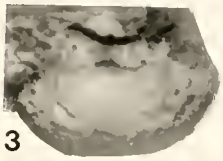
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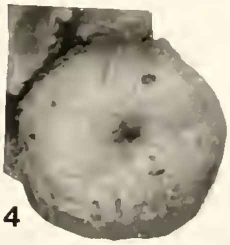
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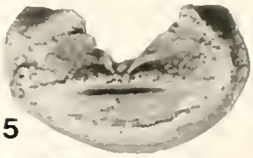
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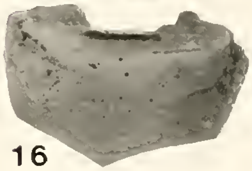
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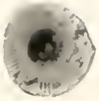
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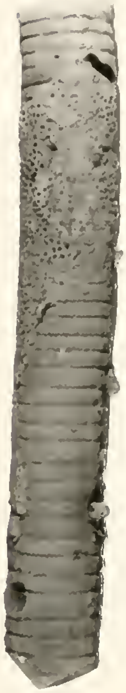
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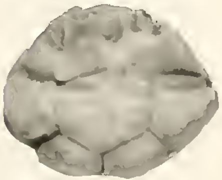
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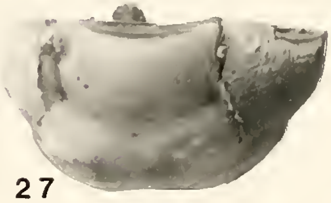
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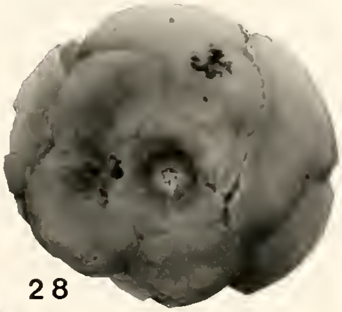
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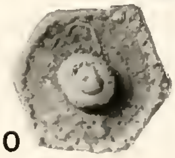
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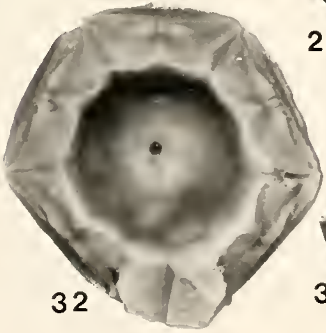
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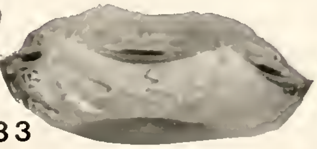
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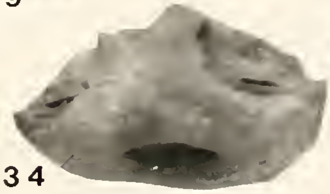
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PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate papers in two volumes each year. The series is a publication outlet for significant, longer paleontological monographs (*i.e.*, more than approximately 50 printed pages), for which high quality photographic illustrations and the large quarto format are required.

Submissions are welcome from any author, regardless of institutional or organizational affiliation. Authors must, however, be members of the Paleontological Research Institution at time of publication; annual membership is currently US$25.00. Publication costs of the *Bulletins* are heavily subsidized by the Institution, but authors are currently required to pay illustration charges at a rate of $120.00 per plate and $35.00 per text-figure.

Important references for style and format are 1) *Bulletins of American Paleontology* "Instructions for Authors" (volume 108, number 347, pages 149–153); 2) *Chicago Manual of Style* (fourteenth edition) 1993. Recent issues of the *Bulletins* provide useful guides but note changes with the "Instructions for Authors" mentioned above.

Manuscripts must be typewritten, and double-spaced *throughout* (including direct quotations, tables and references). All manuscripts should contain a table of contents, lists of text-figures and/or tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be given in the metric system, alone or in addition to their English system equivalents. The maximum dimensions for photographic plates are 178 mm × 229 mm (7 inches × 9 inches; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3½ inches) or full page (178 mm; 7 inches) width, but arrangements can be made to publish text-figures that must be larger.

Authors must provide three (3) printed copies of the text and accompanying illustrative material. Authors are *strongly* encouraged to prepare their manuscripts on word processors, as this considerably expedites publication. On initial submission, however, only printed copies of the manuscript should be sent; the disk copy should be retained so that revisions can be made after the review process. The text and line-drawings may be reproduced xerographically, but glossy prints at publication size must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

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Gil Klapper enjoying a break at Ishkarwaz, northernmost Pakistan, August, 1999. Photo courtesy of M. Cristina Perri.

PREFACE

It has been with great pleasure that we have acted as editors for this volume in honor of our dear friend and teacher, Gilbert Klapper, or as we all know him, "Gil." We thank all of those who so kindly and eagerly contributed their time and efforts to this publication. Although it has been a long time in coming, this volume emphasizes the high esteem in which we hold Gil. A few of us may dimly remember the overweight, clean-shaven, Lucky-Strike toting, meat-eating, bourbon-quaffing, irascible version of Gil in the early to mid-1960s. What a contrast to the ecologically sensitive, health conscious vegetarian and soft-spoken modern version we've all grown to love and appreciate. Although this metamorphosis may have seemed gradualistic to those who worked day-to-day with Gil, to those of us who encountered Gil less frequently, these changes were perfect examples of punctuated equilibria. We often wonder how different will Gil be/look the next time we visit with him? There are always new passions, new ideas, and new interests, all enthusiastically shared with gusto. Even so, all of us who know him recognize the many wonderful qualities that Gil has always had. All can agree that his brilliance has been constant. The cognitive pea soups we normally grope with through daily efforts, although challenging to most of us, seem no match for Gil. He inherently knows the recipe to solve the problem. One usually leaves a conversation with Gil renewed, full of curiosity, and with a feeling of direction and purpose. His unselfishness in sharing ideas and data is another of his many endearing qualities. As a mentor he is peerless. He is always available to review methods and approaches; he is always giving of his time whether over the microscope or imparting passionately what he already knows or has gleaned; he is always looking for that spark in the student he can nurture and bring forward—all the time building on the student's strengths to reach new levels of paleontological understanding. Gil set a higher standard in both his personal and professional life for his students to emulate. Most of us feel there was little we could do to match his excellence, but knew that if we could approach his passion and level of knowledge, we would consider our efforts successful.

So we dedicate this volume to Gil. It is a rather small offering for what he has given and continues to give us, but it is truly heartfelt and genuine.

James E. Barrick
H. Richard Lane

REGARDING GILBERT

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> *Excellence is not an act, but a habit.*
> —Aristotle

Like most paleontologists, Gilbert Klapper started along traditional paths of biostratigraphy and taxonomy, but it was not long before he was walking his own road, much of it unpaved. Though he looked back to where we have been and produced exemplary studies in taxonomy and biostratigraphy, it was not long before multielement taxonomy and, later, graphic correlation and shape analysis, loomed on the horizon. In these areas he became a practitioner without peer, with high originality. His performance has been astounding, but there is much more to him than scientific research.

Gilbert's wide-ranging curiosity is one of his more astonishing characteristics, but from the beginning of his university education, and doubtless before that, he had an ingrained dislike of formal lecturing, grading and examinations. During his B. S. (completed in 1956) at Stanford University, his concentration on his coursework wandered. He preferred golf to laboratories and lecture theatres. He would dearly loved to have become a disk jockey, wowing listeners with his already encyclopedic knowledge of jazz, its great performers and memorable performances. His love for jazz never waned, nor did his passion for classical music, including piano recitals and opera, but he never developed a taste for the loud, aggressive music, turbofolk, electro-pop or the incoherent nihilism that came later. Gilbert moved to the University of Kansas (Lawrence) for his M. S. (completed in 1958), worked for 18 months for Shell Oil Company in Baton Rouge, then went to the State University of Iowa (now the University of Iowa) for his Ph. D. (awarded in August 1962).

During his Ph. D. candidature, Gilbert became interested in the Upper Devonian Grassy Creek conodont fauna monographed by E. B. Branson and M. G. Mehl in 1934. Feeling something was wrong with the fauna, he marshalled the courage to travel to the University of Missouri to visit the venerable Maurice Mehl. Having arrived unannounced, Gilbert was surprised by the warm reception accorded him. When Gilbert expressed interest in the conodont fauna from the Grassy Creek shale, the genial Maurice Mehl took the wind from Gilbert's sails with the frank statement: "My boy, there is no Grassy Creek shale!" It had been based on a stratigraphic misinterpretation.

After his Ph. D., Gilbert learned much from a one-year NSF post-doctoral fellowship at the Illinois Survey and at the Geologisches Landesamt Nordrhein-Westfalen in Krefeld. This was followed by five years at the Pan American Petroleum (subsequently Amoco) Research Center in Tulsa and, finally, 30 years at the University of Iowa (1968–1998).

Brian Glenister, a colleague of Gilbert for more than 30 years at the University of Iowa, recalls that when Glenister was offered a chair at Iowa in 1967, he made acceptance conditional on creation of an additional teaching position in paleontology. Brian had specialized in conodonts for several years and, wishing to develop conodontology at Iowa, could see there were two logical candidates for the position: Gilbert and the late Willi Ziegler. Both were present at the inaugural meeting of the Pander Society in Iowa City that year, Gilbert staying at an Iowa City motel, Willi with Ann and Brian Glenister. After dinner one night at the Glenisters' and before retiring, Brian ordained that Willi and Gilbert should decide which one would take the position, and left them to it. The decision was made, but so far into the night that Gilbert, locked out of his motel, had to sleep on the Glenister couch. The decision that Gilbert should take the Iowa position and Willi develop his career back in Germany had important consequences for conodontology in particular, and for paleontology in general. Willi became, ultimately, director of the Senckenberg Museum, a highly effective member (and often chairman) of numerous German national and international scientific committees, and steadfast defender of paleontology. Both he and Gilbert were to become noteworthy for their prodigious output of pivotal and innovative publications on conodonts. It is hard to imagine them having had equivalent impact had Willi taken the Iowa position and Gilbert remained with Amoco.

At Iowa, Gilbert supervised 17 graduate students for Ph. D., and eight for M. S. degrees. He was Visiting

Professor at Oregon State University, Corvallis, in 1978, Visiting Professor at the University of Chicago in 1989, and from 1981 to 1989 was a consultant to Amoco in Tulsa and Houston, and to Amoco Canada. He has given numerous invited lectures, foremost among them being the James Hudnall Distinguished Lecturer at the University of Chicago in 1989. In April 1995, he was awarded the Pander Society Medal for his seminal contributions to studies of the Conodonta.

Gilbert focused initially on conodont taxonomy and biostratigraphy, but subsequently rose to the top with big ones: multielement taxonomy, shape analysis, and graphic correlation. He wasn't the first to toy with these ideas, but it was his insight and the sustained and elegant way in which he elaborated on these initiatives that changed the world of conodontology to completely new directions—directions which took most of us a decade or more to take on board with all their implications. Many, among them the late Willi Ziegler, were slow to accept the power of shape analysis and graphic correlation, preferring eyeballing—in Willi's case, as in Gilbert's, with an unusually perceptive eye. But Gilbert wanted to make taxonomy less subjective.

Gilbert became impressed by graphic correlation, pioneered by Alan Shaw, and in the late 1980s and 1990s gave this technique new dimensions. Fascination with shape analysis developed about the same time. Again his fervor and his unremitting concentration brought about a revolution in thinking, but, because of the drudgery involved, the techniques have been slow to gain wide acceptance.

Though he contributed elegant conodont studies on all intervals of time from Silurian to Carboniferous, with a modicum of Ordovician, he eventually focused on the Frasnian with characteristic energy, setting about improving its zonation. His work, particularly on the Montagne Noire (southern France), Canning Basin (NW Australia) and western Canada sections, aligned by graphic correlation, resulted in a scheme of 13 intervals (MN 1–13), the rubric MN being for the Montagne Noire sequences pivotal in his analysis. He insisted (and continues to insist) that graphic correlation is more precise than the zonal schemes, each named for salient taxa, elaborated over the previous 30 years, primarily by the late Willi Ziegler, Charles Sandberg, and himself.

If we leave aside the five volumes of the *Catalogue of Conodonts*—a tremendously daunting project to which he contributed a vast amount of material—and the *Treatise on Invertebrate Paleontology, Part W: Miscellanea, Supplement 2 (Conodonta)*, for which he contributed the material for all genera with Silurian or Devonian type species, there are still a surprising number of benchmark papers authored or co-authored by Gilbert. A glance at the accompanying bibliography is enough to confirm this.

A few small vignettes will exemplify Gilbert's character. For many years he lived at 804 Ronald St., Iowa City, a house teeming with books except for a Spartan lounge room: a cavernous studio dedicated to stereo equipment and an immense collection of vinyl records—his beloved "pizzas," as he calls them. He prefers "pizzas," insisting that CDs have not equalled the quality of the best LPs. Ronald Street had been the abode of two remarkable writers: Bharati Mukherjee and John Irving, both prominent in the creative writing program for which the University of Iowa has long been renowned. In fact, the garage of 804 Ronald St. was the site of an infamous, fortunately imaginary, event in Irving's *The World According to Garp*.

Gilbert is renowned for his writing style, especially for his precision, attention to detail, and absence of superfluous wordage. He has always read widely and critically: poetry, biography, essays, novels, and history. During his boyhood and youth, Gilbert benefited from a home with an intellectual atmosphere, a prime focus of which on Saturday was the Metropolitan Opera radio broadcast. From this Gilbert developed a passion for reading books, a passion which persists. Gilbert could have been a novelist, a travel writer or a poet, but insists, mistakenly, that he lacks the necessary talent. Favorite haunts of Gilbert are the Prairie Lights bookshop in Iowa City and Powell's in Chicago, where he can spend hours in quest of new and exciting authors. Great novelists and poets have been prominent among his heroes. There has been a succession of them: Paul Auster, Peter Carey, and Mark Helprin among them.

For Gilbert, attendance at a serious theater performance, reading of an excellent novel, or witnessing a brilliant production of one of the great operas, is always a moving experience. He has an uncommon ability to completely immerse himself in the lives of the participants.

Ever since he was a member of the Denver High School golf team, golf clubs have been semi-sacred items for Gilbert. In addition to various golf courses around Laurentia, he has performed at Machrihanish and Machrie in Scotland, and at Tura Beach, Mallacoota and Narooma in Australia—the last requiring that a ball be driven from cliff-top to cliff-top over a ravine with an arm of the Pacific Ocean below. He carried a golf club around northern Pakistan and Xinjiang in 1999, driving golf balls from high passes—the Lowarai, Shandur and Khunjerab passes—and across the ferocious Yarkhun River near the Pakistan-Afghanistan border. Wherever he goes, a golf club, if it can possibly be fitted in, is an essential item in his paraphernalia.

Gilbert's pursuit of excellence extends to everything. He is renowned for his superb illustrations of conodonts; he is a meticulous cook. He has been known to do a 400-mile round-trip to Chicago and back to purchase better quality garlic and olive oil than can be found in Iowa City, and for some time he was importing coffee from the island of Atiu in the Cook Islands, because of the difficulty in obtaining highest quality coffee, even by mail-order, from North American sources. Only highest quality *arabica* coffee is acceptable; *robusta* coffee is not allowed to pollute his coffee pots.

Despite hillsides infested with the prickly Mediterranean vegetation, Gilbert immensely enjoyed collaboration with Raimund Feist in sampling sequences in the Montagne Noire, and working with Phillip Playford's group in the Canning Basin. During his several visits to Australia, Gilbert was quick to adopt elements of the Australian lifestyle, such as the Akubra hat and the "G-dae!" greeting, and swiftly added a sheaf of pivotal Australian items to his arsenal of dates, sayings, and knowledge of Australian icons, outgunning mentor-colleague and expatriate Australian, Brian Glenister, with his knowledge on such matters. He has a fondness for Australian films; he includes *Breaker Morant* and *Cosi* among his favorite movies of all time. Though he enjoyed camping under the stars in the Canning Basin and relished its conodonts, he failed to be amused by its insects, especially the billions of flies with their penchant for suicide by incorporation into his sandwiches—and he a vegetarian. I recall his words, articulated with deep feeling, after his first field season in the Canning: "You didn't tell me about the flies!"

Gilbert has always had a passion for motorbikes, especially Harley-Davidsons, but there is no way he would take off around Laurentia, or around the globe, on a Harley. Though never a motorbike rider, he would surely relish the exhilaration of wind through his hair, somewhere, anywhere; but to grow old disgracefully, with black leather jacket and eagle on the back? Never!

As a man, Gilbert is especially private, unassuming and without hubris; he has made an art of listening. This tends to give his charm a hint of reserve, even a modicum of inscrutability. He has a special skill in judging character and motive, and a generally subtle, almost telepathic way of responding, in argument, in ways that take account of the weaknesses or vanity of those with whom he is exchanging opinions. His critical acumen and self-discipline are noteworthy. He despises stupidity and misuse of power. He could never abide the hauteur, the arrogance and the sarcasm of those occasional academics who should have been compassionate gurus.

Gilbert is someone who operates out of his own, intensely personal ethical code, one characterized by great compassion. Having known many colleagues, including Tamara Mashkova, who have died, or may well have died, from using bromoform and tetrabromoethane (without adequate fume-cupboards) for separating conodonts from other acid-insoluble materials, Gilbert has been a passionate campaigner against use of these highly toxic and insidious heavy liquids.

For Gilbert, science has always been above politics. Witness his generosity to colleagues from all parts of the globe, and the way he will devote hours to scrutinizing plates of photos of conodonts. I have seen him do this on railway platforms, in restaurants, in trains and buses, responding patiently, often to the same question asked repeatedly. He has a wonderfully retentive, even photographic, memory. He seems able to remember every figure on every plate he has ever seen, and even the position on the plate.

I know of no one who is more profoundly moved by the countless acts of infamy and the inhumanity that infest our globe. I recall how deeply moved he was by an exhibition of photographs—the innocence of tea workers in Rwanda just prior to the holocaust; the ship-breakers of the Chittagong shoreline in Bangladesh; the cocoa people of Brazil; the Kafkaesque textile factories of Kazakhstan; and oil-covered technicians extinguishing tornados of flame in Kuwait—by Sebastião Selgado, arguably the greatest photographer of our time, at the Art Gallery of New South Wales in 1995. In short, he has always had a soft spot for the destitute, for the countless thousands who lead haunted lives, for those confronted by frontiers for everything except dreams, for those who adapt, resist, and survive.

Gilbert can never be accused of narcissism, nor has he been one who needs the approval of his peers, yet, if we had to select the most pivotal 20 or 30 papers in conodontology, several of them would have Gilbert as an author. For him, the pursuit of perfection—the right word to convey the exact meaning, with the precise spin—has been a lifelong passion. Every task is undertaken with vigor, with minimal noise! He has no time for the sloppy, the devious, the bald assertion, the imprecise observation, or the uninformative illustration. He is a great admirer of those who can frame new questions, devise ways of answering them, and set about doing so.

He fervently admires excellence and innovation, whether it be the coruscating prose of the late Stephen Jay Gould, the "Chicago School" of paleontology, superstar athletes such as Muhammad Ali or basketball's Michael Jordan, whole galaxies of golfers, including Tiger Woods, and great jazz artists—Louis Armstrong (I can imagine Gilbert as a jazz trumpeter!), Duke Ellington, Thelonius Monk, John Coltrane, and Miles Davis, and, for a while, the new wave of Cubans, José Ferrer and the Buena Vista Social Club, to name a few—and great classical pianists—Vladimir Horowitz, Earl Wild, Jorge Bolet, Mitsuko Uchida, Sviatoslav Richter, Glen Gould and dozens more—violinists, cellists, clarinetists, and that *rara avis*, the admirable and heroic Jess Johnson, with whom he co-authored 14 papers.

Gilbert's office at the University of Iowa was notorious for its piles of papers and reprints—so enormous as to frequently cause him to work in the nearby A. K. Miller room. Visitors were discouraged from looking into his room or photographing what seemed to be a monumental clutter but, on request for a specific item, Gilbert would drive adits through the cumulates with uncanny accuracy to extract the desired items.

Gilbert taught many courses at the University of Iowa, during his later years team-teaching highly popular courses on paleontology and evolution with Ann ("Nancy") Budd. Nancy recalls that when they were team-teaching, "his favorite topics were the Cambrian explosion, the Burgess Shale, Problematica, and Lagerstätten. He particularly loved to discuss Stephen J. Gould's *Wonderful Life* with students, early experimentation, and the fact that evolution is unpredictable and that the 'tape cannot be rewound.' He backed up his teaching with numerous photos and reconstructions of the Burgess animals, and spent lots of time going over their peculiar anatomy and why it was difficult to assign these animals to higher categories." Gilbert, she says, "was a superb lecturer in introductory classes and very popular with students, punctuating his presentations with lots of stories and lots of puzzles. He also liked to discuss mass extinctions and the enigma involved in determining their cause, particularly the K/T boundary and the impact hypothesis. And then, of course, he enjoyed reviewing the evidence pro and con on punctuated equilibria. Gilbert despised grading and exams; he was at his best discussing original research papers in small group discussions, especially with honors students." For Gilbert, conversation is an art in which he orchestrates his silences with care.

For many years, Gilbert was the department's diligent member of the university's library committee; it was the perfect committee role for someone with such a passion for books and intellect. In late 1991, in one of those "demolition derbies" that seem increasingly to plague universities around the globe, Gilbert was prominent in a successful defense of the Geology Department's library from those wanting to subsume it into storage in the Main Library—to make way for more trendy initiatives.

Gilbert once participated in a marine ecology/paleoecology venture in Florida, but exposure to the Heron Island reef (southern Great Barrier Reef) and to the superb Late Cenozoic raised reefs of the Cook Islands in 1993 provided new perspectives, not only of reefs, but of their guileless inhabitants, coffee growing, and, at Oravaru Beach on Atiu, there was the opportunity to stand on the historic spot where James Cook in 1777, unaware of the magic underfoot, landed on an ancient reef superbly exhumed by intertidal activity.

How many of our colleagues, as they approach retirement, fade away with increasingly tired lectures? Some even retire into departments soon after receiving tenure! Not Gilbert! Through 1996 and 1997, almost until the day of his retirement, he was industriously revamping lectures. He found retirement in May 1998 to be especially agreeable. Inevitably, golf has figured prominently in this phase. His post-retirement peregrinations included what was an especially congenial interlude, in September 2000, with old friends in Belgium and northern Italy, including Cristina Perri and Claudia Spalletta in Bologna, and Alessandro Moretti in Padova. But he had now met Rose and had found felicity in her company. In his new domain, in Glencoe in the northern part of the Chicago agglomeration, he has a convenient linkage to Northwestern University. May he and Rose have many future pilgrimages to golf courses, *trattoria* and coffeehouses around the world!

The Gilbert Klappers are not only innovators, treading unexplored pathways, but, because of their insistence on standards, have kept the twin flags of paleontology and biostratigraphy flying vigorously. What score should we award Gilbert for his achievement? Ten out-of-10? The purists, who never award full marks, may quibble: "You've got no standards!" But let it be said, honestly: Gilbert's performance definitely warrants a 10-out-of-10, or even 11-out-of-10 as one colleague insists.

Gilbert's performance merits a standing ovation!

ACKNOWLEDGMENTS

This essay on Gilbert and his career has benefited from salient information kindly provided by Nancy Budd, Brian Glenister, Julie Golden, Roger Kaesler, and Ruth Mawson, and by photography generously made available by Cristina Perri.

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Ph. D.: H. R. Lane, J. J. Straka, J. F. Baesemann, B. Perlmutter, R. S. Nicoll, D. B. Johnson, J. E. Barrick, K. M. Chauff, T. R. McHargue, A. Dombrowski, M. C. Tynan, J. R. Groves, M. I. Pavlicek, J. E. Day, F. S. Rogers, R. A. Metzger, S. L. Benoist.

M. S.: D. B. Johnson, J. E. Barrick, D. Routh, M. C. Tynan, M. L. Woodruff, R. A. Metzger, J. A. Kralick, M. C. Carmen.

GILBERT KLAPPER'S OEUVRE

Klapper, G. J., 1958. A Late Devonian conodont fauna of the Darby Formation of the Wind River Mountains, Wyoming. M.S. thesis, University of Kansas, Lawrence, 31 pp.

Klapper, G., 1958. An Upper Devonian conodont fauna from the Darby Formation of the Wind River Mountains, Wyoming. Journal of Paleontology, vol. 32, pp. 1082–1093, pls. 141–142.

Klapper, G., and Furnish, W. M., 1962. Devonian–Mississippian Englewood Formation in Black Hills, South Dakota. Bulletin of the American Association of Petroleum Geologists, vol. 46, pp. 2071–2078.

Klapper, G., 1962. Upper Devonian and Lower Mississippian conodont zones in Montana, Wyoming and South Dakota. Ph.D. dissertation, University of Iowa.

Klapper, G., and Furnish, W. M., 1963. Conodont zonation of the early Upper Devonian in eastern Iowa. Proceedings of the Iowa Academy of Science, vol. 69, pp. 400–410.

Ziegler, W., Klapper, G., and Lindström, M., 1964. The validity of the name *Polygnathus* (Conodonta, Devonian and Lower Carboniferous). Journal of Paleontology, vol. 38, pp. 421–423.

Beckmann, H., Collinson, C., Helms, J., Huckriede, R., Klapper, G., Krebs, W., Lindström, M., Rhodes, F. H. T., Walliser, O. H., and Ziegler, W., 1965. Sind Conodonten Reste fossiler Algen (Zur Hypothese von K. Fahlbusch, 1964). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, vol. 1964 (7), pp. 385–399.

Glenister, B. F., and Klapper, G., 1966. Upper Devonian conodonts from the Canning Basin, Western Australia. Journal of Paleontology, vol. 40, pp. 777–842, pls. 85–96.

Klapper, G., 1966. Upper Devonian and Lower Mississippian conodont zones in Montana, Wyoming, and South Dakota. University of Kansas Paleontology Contributions. Paper 3, 43 pp., 6 pls.

Sandberg, C. A., and Klapper, G., 1967. Stratigraphy, age, and paleotectonic significance of the Cottonwood Canyon Member of the Madison Limestone in Wyoming and Montana. U. S. Geological Survey Bulletin, 1251, pp. B1–B70.

Klapper, G., Lindström, M., and Ziegler, W., 1967. *Polygnathus* Hinde, 1879 (Conodonta): Proposed designation of a type-species under the plenary powers. Bulletin of Zoological Nomenclature, vol. 24, pp. 239–242.

Klapper, G., and Ziegler, W., 1967. Evolutionary development of the *Icriodus latericrescens* group (Conodonta) in the Devonian of Europe and North America. Palaeontographica, Abteilung A: Palaeozoologie-Stratigraphie, vol. 127, pp. 68–82, pls. 8–11.

Klapper, G., 1968. Review: Lindström, M., Conodonts. Quarterly Reviews of Biology, vol. 42, p. 535.

Orr, R. W., and Klapper, G., 1968. Two new conodont species from Middle-Upper Devonian boundary beds of Indiana and New York. Journal of Paleontology, vol. 42, pp. 1066–1075, pls. 139–140.

Amsden, T. W., Klapper, G., and Ormiston, A. R., 1968. Lower Devonian limestone of post-Hunton age, Turkey Creek inlier, Marshall County, south-central Oklahoma. American Association of Petroleum Geologists, Bulletin, vol. 52, pp. 162–166.

Klapper, G., 1969. Lower Devonian conodont succession in central Nevada. Geological Society of America Special Paper 121, pp. 521–522.

Klapper, G., Collinson, C., Huddle, J. W., Orr, R. W., Rickard, L. V., Sandberg, C. A., Schumacher, D., Seddon, G., and Uyeno, T. T., 1969. North American Devonian conodont biostratigraphy. Geological Society of America, Abstracts with Programs, vol. 1969 (6), p. 27.

Berdan, J. M., Berry, W. B. N., Boucot, A. J., Cooper, G. A., Jackson, D. E., Johnson, J. G., Klapper, G., Lenz, A. C., Martinsson, A., Oliver, W. A., Jr., Rickard, L. V., and Thorsteinsson, R., 1969. Siluro-Devonian boundary in North America. Geological Society of America Bulletin, vol. 80, pp. 2165–2174.

Klapper, G., 1969. Lower Devonian conodont sequence, Royal Creek, Yukon Territory, and Devon Island, Canada, *with* a section on Devon Island stratigraphy by A.R. Ormiston. Journal of Paleontology, vol. 43, pp. 1–27, pls. 1–6.

Klapper, G., 1969. Lower Devonian conodont sequence, Royal creek, Yukon Territory, and Devon Island, Canada; correction. Journal of Paleontology, vol. 43, p. 855.

Klapper, G., Philip, G. M., and Jackson, J. H., 1970. Revision of the *Polygnathus varcus* group (Conodonta, Middle Devonian). Neues Jahrbuch für

Geologie und Paläontologie, Monatshefte, vol. 1970, pp. 650–667, 3 pls.

Klapper, G., Berry, W. B. N., and Boucot, A. J., 1970. Conodont correlations. *in* Correlation of the North American Silurian rocks. W. B. N. Berry and A. J. Boucot, *eds.*, Geological Society of America Special Paper 102, pp. 35–38.

Klapper, G., 1971. *Patrognathus* and *Siphonodella* (Conodonta) from the Kinderhookian (Lower Mississippian) of western Kansas and northwestern Nebraska. Kansas Geological Survey, Bulletin, vol. 202 (3), 14 pp., 2 pls.

Klapper, G., and Philip, G. M., 1971. Devonian conodont apparatuses and their vicarious skeletal elements. Lethaia, vol. 4, pp. 429–452.

Klapper, G., 1971. Sequence within the conodont genus *Polygnathus* in the New York lower Middle Devonian. Geologica et Palaeontologica, vol. 5, pp. 59–79, 3 pls.

Beinert, R. J., Klapper, G., Sandberg, C. A., and Ziegler, W., 1971. Revision of *Scaphignathus* and description of *Clydagnathus? ormistoni* n. sp. (Conodonta, Upper Devonian). Geologica et Palaeontologica, vol. 5, pp. 81–91, 2 pls.

Klapper, G., Sandberg, C. A., Collinson, C., Huddle, J. W., Orr, R. W., Rickard, L. V., Schumacher, D., Seddon, G., and Uyeno, T. T., 1971. North American Devonian conodont biostratigraphy. *in* Conodont biostratigraphy. W. C. Sweet and S. M. Bergstrom, *eds.*, Geological Society of America Memoir 127, pp. 285–316.

Amsden, T. W., and Klapper, G., 1972. Misener Sandstone (Middle-Upper Devonian), north-central Oklahoma. American Association of Petroleum Geologists Bulletin, vol. 56, pp. 2323–2334.

Klapper, G., and Philip, G. M., 1972. Familial Classification of reconstructed Devonian Conodont apparatuses. *in* Symposium on Conodont Taxonomy. Geologica et Palaeontologica, Sonderband 1, pp. 97–105, 4 pls.

Klapper, G., Lindström, M., Sweet, W., and Ziegler, W., 1973. Catalogue of conodonts. W. Ziegler, *ed.*, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, vol. 1, 504 pp., 27 pls.

Perry, D. G., Klapper, G., and Lenz, A. C., 1974. Age of the Ogilvie Formation (Devonian), northern Yukon: Based primarily on the occurrence of brachiopods and conodonts. Canadian Journal of Earth Sciences, vol. 11, pp. 1055–1097.

Klapper, G., and Murphy, M. A., 1974. Silurian–Lower Devonian conodont sequence in the Roberts Mountains Formation of central Nevada. Geological Society of America, Abstracts with Programs, vol. 1974 (6), p. 522.

Klapper, G., and Murphy, M. A., 1974. Silurian–Lower Devonian conodont sequence in the Roberts Mountains Formation of central Nevada. University of California Publications in the Geological Sciences, no. 115, 62 pp., 12 pls.

Klapper, G., 1975. Conodont zones and correlation of the Cedar Valley–State Quarry sequence; the Independence Shale problems. *in* Devonian limestone facies: Cedar Valley and State Quarry limestones in the Iowa City region. Annual Tri-State Geological Field Conference Guidebook, 39th Annual Meeting. P. H. Heckel, E. C. Kettenbrink, and G. Klapper, *eds.*, pp. 1–19. Iowa Geological Survey, Iowa City.

Klapper, G., Lindström, M., Sweet, W., and Ziegler, W., 1975. Catalogue of conodonts. W. Ziegler, *ed.* E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, vol. II, 404 pp., 25 pls.

Klapper, G., and Johnson, D. B., 1975. Sequence in conodont genus *Polygnathus* in Lower Devonian at Lone Mountain, Nevada. Geologica et Palaeontologica, vol. 9, pp. 65–83, 3 pls.

Barrick, J. E., and Klapper, G., 1976. Multielement Silurian (late Llandoverian–Wenlockian) conodonts of the Clarita Formation, Arbuckle Mountains, Oklahoma, and phylogeny of *Kockelella*. Geologica et Palaeontologica, vol. 10, pp. 59–99.

Ziegler, W., Klapper, G., and Johnson, J. G., 1976. Redefinition and subdivision of the *varcus* Zone (conodonts, Middle–?Upper Devonian) in Europe and North America. Geologica et Palaeontologica, vol. 10, pp. 109–139.

Glenister, B. F., Klapper, G., and Chauff, K. M., 1976. Conodont pearls? Science, vol. 193, pp. 571–573.

Klapper, G., 1977. Conodonts. *in* The Silurian-Devonian Boundary. A. Martinsson, *ed.* International Union of Geological Sciences, Series A, No. 5, pp. 318–319.

Klapper, G., Lindström, M., Sweet, W., and Ziegler, W., 1977. Catalogue of Conodonts. W. Ziegler, *ed.* E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, vol. III, 574 pp., 39 pls.

Klapper, G. [with contributions by D. B. Johnson], 1977. Lower and Middle Devonian conodont sequence in central Nevada. *in* Proceedings of the 1977 Annual Meeting of the Paleontological Society on Devonian of Western North America. M. A. Murphy, W. B. N. Berry, and C. A. Sandberg, *eds.*, University of California, Riverside Campus Museum Contributions, vol. 4, pp. 33–54.

Klapper, G., 1977. Lower-Middle Devonian boundary conodont sequence in the Barrandian area of Czechoslovakia. Časopis pro Mineralogii a Geologii, vol. 22, pp. 401–406. Societas Mineralogica et Geologica Bohemoslovaca, Praha.

Klapper, G., and Johnson, D. B., 1977. Lower and Middle Devonian conodont sequence in central Nevada. Geological Society of America, Abstracts with Programs, vol. 9 (7), p. 1051.

Pedder, A. E. H., and Klapper, G., 1977. Fauna and correlation of the type section of the Cranswick Formation (Devonian), Mackenzie Mountains, Yukon Territory. Geological Survey of Canada Special Paper 77-1B, pp. 227–234.

Klapper, G., and Barrick, J. E., 1978. Conodont ecology; pelagic versus benthic. Lethaia, vol. 11, pp. 15–23.

Glenister, B. F., Klapper, G., and Chauff, K., 1978. Nautiloid uroliths composed of phosphatic hydrogel. Science, vol. 199, p. 209.

Chauff, K. M., and Klapper, G., 1978. New conodont genus *Apatella* (Late Devonian), possible homeomorph *Bactrognathus* (Early Carboniferous, Osagean Series), and homeomorphy in conodonts. Geologica et Palaeontologica, vol. 12, pp. 151–164, 3 pls.

Klapper, G., Ziegler, W., and Mashkova, T. V., 1978. Conodonts and correlation of Lower–Middle Devonian boundary beds in the Barrandian area of Czechoslovakia. Geologica et Palaeontologica, vol. 12, pp. 103–116, 2 pls.

Johnson, J. G., and Klapper, G., 1978. Devonian brachiopods and conodonts from central Oregon. Journal of Paleontology, vol. 52, pp. 295–299, 1 pl.

Klapper, G., and Ziegler, W., 1979. Devonian conodont biostratigraphy. *in* The Devonian System. M. R. House, C. T. Scrutton, and M. G. Bassett, *eds.*, Special Papers in Palaeontology, vol. 23, pp. 199–224. Palaeontological Association, London.

Klapper, G., and Johnson, J. G., 1979. Review: D. E. Jackson, A. C. Lenz, and A. E. H. Pedder, Late Silurian and Early Devonian graptolite, brachiopod and coral faunas from northwestern and Arctic Canada. Geoscience Canada, vol. 6, p. 224.

Uyeno, T. T., and Klapper, G., 1980. Summary of conodont biostratigraphy of the Blue Fiord and Bird Fiord formations (Lower–Middle Devonian) at the type and adjacent areas, southwestern Ellesmere Island, Canadian Arctic Archipelago. Geological Survey of Canada, Papers, vol. 80 (1C), pp. 81–93, 3 pls.

Johnson, J. G., Klapper, G., and Trojan, W. R., 1980. Brachiopod and conodont successions in the Devonian of the northern Antelope Range, central Nevada. Geologica et Palaeontologica, vol. 14, pp. 77–115.

Johnson, J. G., Klapper, G., and Trojan, W. R., 1980. Upper range of *Stringocephalus* (Devonian Brachiopoda). Newsletters on Stratigraphy, vol. 8, pp. 232–235.

Klapper, G., and Murphy, M. A., 1980. Conodont zonal species from the *delta* and *pesavis* zones (Lower Devonian) in central Nevada. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, vol. 1980, pp. 490–504, 3 pls.

Klapper, G., and Johnson, J. G., 1980. Endemism and dispersal of Devonian conodonts. Journal of Paleontology, vol. 54, pp. 400–455, 4 pls.

Klapper, G., 1981. Systematic descriptions [All genera with Silurian and Devonian type species]. *in* Treatise on Invertebrate Paleontology. Part W: Miscellanea, Supplement 2, Conodonta. Geological Society of America, Inc., and University of Kansas, Boulder and Lawrence.

Klapper, G., Lindström, M., Sweet, W., and Ziegler, W., 1981. Catalogue of conodonts. W. Ziegler, *ed.*, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, vol. IV, 445 pp., 41 pls.

Klapper, G., Tsigler, V. [= Ziegler, W.], and Mashkova, T. V., 1981. Konodontovyye zony kak pokazateli granitsy nizhnego–srednego devona [Conodont zones as indicators of the Lower–Middle Devonian boundary]. Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya, vol. 1981 (3), pp. 91–97.

Johnson, D. B., and Klapper, G., 1981. New Early Devonian conodont species of central Nevada. Journal of Paleontology, vol. 55, pp. 1237–1250, 2 pls.

Oliver, W. A., and Klapper, G., 1981. Introduction. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.*, Part 1, Text, pp. 1–3. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Klapper, G., 1981. Review of New York Devonian conodont biostratigraphy. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.* Part 1, Text, pp. 57–65. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Oliver, W. A., and Klapper, G., 1981. Introduction. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.*, Part 2, Stop Descriptions, pp. 1–2. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Klapper, G., 1981. Bellona. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.*, Part 2, Stop Descriptions, pp. 41–42. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Kirchgasser, W. T., and Klapper, G., 1981. Taughannock Falls. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.*, Part 2, Stop Descriptions, pp. 48–50. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Klapper, G., 1981. June's Quarry, Tully. *in* Devonian Biostratigraphy of New York. W. A. Oliver, Jr. and G. Klapper, *eds.*, Part 2, Stop Descriptions, pp. 60–61. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Puchkov, V. N., Klapper, G., and Mashkova, T. V., 1982. Natural assemblages of *Palmatolepis* from the Upper Devonian of the northern Urals. Acta Palaeontologica Polonica, vol. 26, pp. 281–298 [imprint 1981].

Ziegler, W., and Klapper, G., 1982. Subcommission on Devonian Stratigraphy: Decisions since 1973 and present status. *in* On Devonian stratigraphy and palaeontology of the Ardenno-Rhenisch Mountains and related Devonian matters. W. Ziegler and R. Werner, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 55, pp. 7–12.

Ziegler, W., and Klapper, G., 1982. The *disparilis* conodont zone, the proposed level for the Middle–Upper Devonian boundary. *in* On Devonian stratigraphy and palaeontology of the Ardenno-Rhenisch Mountains and related Devonian matters. W. Ziegler and R. Werner, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 55, pp. 463–492.

Ziegler, W., and Klapper, G., 1982. Proposal of the *disparilis* conodont zone as the level for the Middle–Upper Devonian series boundary. Geological Society of America, Abstracts with programs, vol. 14 (5), p. 293.

Ziegler, W., and Klapper, G., 1982. Devonian series boundaries; Decisions of the IUGS Subcommission. Episodes, vol. 1982 (4), pp. 18–21.

Kendall, G. W., Johnson, J. G., Brown, J. O., and Klapper, G., 1983. Stratigraphy and facies across Lower Devonian–Middle Devonian boundary, central Nevada. American Association of Petroleum Geologists, Bulletin, vol. 67, pp. 2199–2207.

Bunker, B., Klapper, G., and Witzke, B., 1983. New stratigraphic interpretations of the Middle Devonian rocks of Winneshiek and Fayette counties, northeastern Iowa. Geological Society of Iowa, Field Trip Guidebook No. 39, pp. 1–38.

Klapper, G., 1983. Preliminary account of the Middle Devonian (*varcus* Zone)–Upper Devonian (Frasnian) conodont sequence in the eastern Montagne Noire. International Union of Geological Sciences Subcommission on Devonian Stratigraphy, 4 pp.

Klapper, G., and Barrick, J. E., 1983. Middle Devonian (Eifelian) conodonts from the Spillville Formation in northern Iowa and southern Minnesota. Journal of Paleontology, vol. 57, pp. 1222–1243, 6 pls.

Bunker, B. J., and Klapper, G., 1984. Conodont zones and correlation of the Cedar Valley State Quarry interval of eastern Iowa. *in* Overburden–underburden; An examination of Paleozoic and Quaternary Strata at the Conklin Quarry near Iowa City, B. J. Bunker and G. R. Hallberg, *eds.*, Field Trip Guidebook, Geological Society of Iowa, vol. 11, pp. 15–18.

Klapper, G., and Bergström, S. M., 1984. The enigmatic Middle Ordovician fossil *Archeognathus* and its relations to conodonts and vertebrates. Journal of Paleontology, vol. 58, pp. 949–976, 9 pls.

Feist, R., Kirchgasser, W. T., and Klapper, G., 1985. Proposal for a Middle–Upper Devonian boundary stratotype. *in* Devonian series boundaries; Results of World-wide Studies, W. Ziegler and R. Werner, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 75, pp. 409–410.

Feist, R., and Klapper, G., 1985. Stratigraphy and conodonts in pelagic sequences across the Middle–Upper Devonian boundary, Montagne Noire, France. Palaeontographica, Abteilung A: Palaeozoologie-Stratigraphie, vol. 188, pp. 1–18.

Klapper, G., 1985. Sequence in conodont genus *Ancyrodella* in Lower *asymmetricus* Zone (earliest Frasnian, Upper Devonian) of the Montagne Noire, France. Palaeontographica, Abteilung A: Palaeozoologie-Stratigraphie, vol. 188, pp. 19–34, 11 pls.

Witzke, B. J., Bunker, B. J., and Klapper, G., 1985. Devonian stratigraphy in the Quad Cities area, eastern Iowa–northwestern Illinois. *in* Devonian, and Pennsylvanian Stratigraphy of the Quad Cities Region, Illinois–Iowa, W. R. Hammer, R. C. Anderson, and D. A. Schroeder, *eds.*, Society of Economic Paleontologists and Mineralogists (SEPM), Great Lakes Section, 15th Annual Field Conference Guidebook, pp. 19–64.

Ziegler, W., and Klapper, G., 1985. Stages of the Devonian System. Episodes, vol. 8 (2), pp. 104–109.

Klapper, G., and Lane, H. R., 1985. Upper Devonian (Frasnian) conodonts of the *Polygnathus* biofacies, N.W.T., Canada. Journal of Paleontology, vol. 59, pp. 904–951, 11 pls.

Johnson, J. G., Klapper, G., and Sandberg, C. A., 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, vol. 96, pp. 567–587.

Johnson, J. G., Klapper, G., Murphy, M. A., and Trojan, W. R., 1986. Devonian series boundaries in central Nevada and neighboring regions, western North America. *in* Devonian Series Boundaries; Results of World-wide Studies. W. Ziegler and R. Werner, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 75, pp. 177–196 [imprint 1985]

Feist, R., Kirchgasser, W. T., and Klapper, G., 1986. Proposal for a Middle–Upper Devonian boundary stratotype. *in* Devonian Series Boundaries; Results of World-wide Studies. W. Ziegler and R. Werner, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 75, pp. 409–410 [imprint 1985]

Johnson, J. G., Klapper, G., and Sandberg, C. A., 1986. Late Devonian eustatic cycles around margin of Old Red Continent. *in* Late Devonian Events around the Old Red Continent; Field Conference in Aachen (FRG), with Excursions in the Ardenne (Belgium), the Rheinisches Schiefergebirge (FRG) and in Moravia (CSSR). M. J. M. Bless and M. Streel, *eds.*, Annales de la Société Géologique de Belgique, vol. 109, pp. 141–147.

Klapper, G., and Foster, C. T., Jr., 1986. Quantification of outlines in Frasnian (Upper Devonian) platform conodonts. Canadian Journal of Earth Sciences, vol. 23, pp. 1214–1222.

Klapper, G., 1986. Thomas Joseph Morton Schopf, 1939–1984. Memorials, Geological Society of America, vol. 16, pp. 1–5.

Klapper, G., and Foster, C. T., Jr., 1987. Outline analysis of platform conodonts. Geological Society of America, Abstracts with Programs, vol. 19 (7), p. 728.

Klapper, G., Feist, R., and House, M. R., 1987. Decision on the boundary stratotype for the Middle/Upper Devonian series boundary. Episodes, vol. 10 (2), pp. 97–101.

Klapper, G., 1988. Intent and reality in biostratigraphic zonation; a reply to Sandberg, Ziegler, and Bultynck (1988). Newsletters on Stratigraphy, vol. 19, pp. 179–183.

Klapper, G., 1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *in* Devonian of the World; Proceedings of the Second International Symposium on the Devonian System; Volume III, Paleontology, Paleoecology and Biostratigraphy. N. J. McMillan, A. F. Embry, and D. J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Memoirs, vol. 14, pp. 449–468. Canadian Society of Petroleum Geologists, Calgary [imprint 1988]

Klapper, G., and Lane, H. R., 1989. Frasnian (Upper Devonian) conodont sequence at Luscar Mountain and Mount Haultain, Alberta Rocky Mountains. *in* Devonian of the World; Proceedings of the Second International Symposium on the Devonian System; Volume III, Paleontology, Paleoecology and Biostratigraphy. N. J. McMillan, A. F. Embry, and D. J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Memoirs, vol. 14, pp. 469–478, 2 pls. Canadian Society of Petroleum Geologists, Calgary [imprint 1988]

Goodfellow, W. D., Geldsetzer, H., McLaren, D. J., Orchard, M. J., and Klapper, G., 1989. The Frasnian–Famennian extinction; current results and possible causes. *in* Devonian of the World; Proceedings of the Second International Symposium on the Devonian System; Volume III, Paleontology, Paleoecology and Biostratigraphy. N. J. McMillan, A. F. Embry, and D. J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Memoirs, vol. 14, pp. 9–21. Canadian Society of Petroleum Geologists, Calgary [imprint 1988]

Goodfellow, W. D., Geldsetzer, H., McLaren, D. J., Orchard, M. J., and Klapper, G., 1989. Geochemical and isotopic anomalies associated with the Frasnian–Famennian extinction. Historical Biology, vol. 2, pp. 51–72.

Klapper, G., 1989. The effect of graphic correlation, multielement taxonomy, and shape analysis on Upper Devonian, Frasnian conodont biostratigraphy. Geological Society of America, Abstracts with Programs, vol. 21, p. 18.

Becker, R. T., Feist, R., Flajs, G., House, M. R., and Klapper, G., 1989. Frasnian–Famennian extinction events in the Devonian at Coumiac, southern France. Compte Rendu de l'Académie des Sciences, Paris, Série II, vol. 309, pp. 259–266.

Klapper, G., 1990. [Various contributions on Devonian conodonts]. *in* The Frasnian–Famennian boundary and adjacent strata of the eastern Montagne Noire [Southern France]. R. Feist, *ed.*, Subcommission on Devonian Stratigraphy ICS/IUGS, Guidebook of the Field Meeting, 69 pp. Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier.

Klapper, G., 1990. Frasnian species of the Late Devonian conodont genus *Ancyrognathus*. Journal of Paleontology, vol. 64, pp. 998–1025.

Johnson, J. G., and Klapper, G., 1990. Lower and Middle Devonian brachiopod-dominated communities of Nevada, and their position in a biofacies-province-realm model. Journal of Paleontology, vol. 64, pp. 902–941.

Barrick, J. E., Klapper, G., and Amsden, T. W., 1990. Stop 1; Hunton Group (Late Ordovician–Early Devonian). *in* Early to Middle Paleozoic conodont biostratigraphy of the Arbuckle Mountains, southern Oklahoma, S. M. Ritter, *ed.*, Oklahoma Geological Survey, Guidebook, pp. 5–9.

Barrick, J. E., and Klapper, G., 1990. Stop 2; Henryhouse and Haragan formations (Late Silurian–Early Devonian) and Woodford Shale (Late Devonian–Early Mississippian). *in* Early to Middle Paleozoic conodont biostratigraphy of the Arbuckle Mountains, southern Oklahoma, S. M. Ritter, *ed.*, Oklahoma Geological Survey, Guidebook, pp. 11–13.

Barrick, J. E., Klapper, G., and Amsden, T. W., 1990. Late Ordovician–Early Devonian conodont succession in the Hunton Group, Arbuckle Mountains and Anadarko Basin, Oklahoma. *in* Early to Middle Paleozoic conodont biostratigraphy of the Arbuckle Mountains, southern Oklahoma. S. M. Ritter, *ed.*, Oklahoma Geological Survey, Guidebook, 55–62.

Klapper, G., and Johnson, J. G., 1990. Revisions of Middle Devonian conodont zones. Journal of Paleontology, vol. 64, pp. 934–936.

Klapper, G., Sweet, W. C., and Ziegler, W., 1991. Catalogue of conodonts. W. Ziegler, *ed.*, vol. V, 212 pp., 13 pls. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Klapper, G., and Foster, C. T., Jr., 1991. Outline analysis of Late Devonian conodonts. Geological Society of America, Abstracts with Programs, vol. 23 (5), p. 279.

Klapper, G., 1991. Accuracy of biostratigraphic zones. Palaios, vol. 6, p. 1.

Klapper, G., 1991. Multielement species-level taxonomy of *Palmatolepis* (Late Devonian, Frasnian). First Canadian Paleontology Conference and Pander Society Meeting, Program and Abstracts, p. 43.

Barrick, J. E., and Klapper, G., 1992. Late Silurian–Early Devonian conodonts from the Hunton Group (upper Henryhouse, Haragan, and Bois d'Arc formations), south-central Oklahoma. *in* Special Papers in Paleontology and Stratigraphy; a Tribute to Thomas W. Amsden. J. R. Chaplin and J. E. Barrick, *eds.*, Oklahoma Geological Survey, Bulletin, pp. 19–65, 6 pls. Oklahoma Geological Survey, Norman.

Johnson, J. G., and Klapper, G., 1992. North American Midcontinent Devonian T-R cycles. *in* Special Papers in Paleontology and Stratigraphy; a Tribute to Thomas W. Amsden. J. R. Chaplin and J. E. Barrick, *eds.*, Oklahoma Geological Survey, Bulletin, pp. 127–135. Oklahoma Geological Survey, Norman.

Kirchgasser, W. T., and Klapper, G., 1992. Graphic correlation using litho- and biostratigraphic markers in the uppermost Middle and Upper Devonian (Frasnian) of New York State. Geological Society of America, Abstracts with Programs, vol. 24, p. 32.

Klapper, G., and Kirchgasser, W. T., 1992. Zonal and graphic correlation of the New York and Australian Upper Devonian (Frasnian) conodont and ammonoid sequences. Geological Society of America, Abstracts with Programs, vol. 24, p. 26.

Klapper, G., 1992. Biostratigraphy and biogeography of Frasnian, Upper Devonian conodonts. Paleontological Society Special Publication 6, p. 166.

Ormiston, A. R., and Klapper, G., 1992. Paleoclimate controls on Upper Devonian source rock sequences and stacked extinctions. Paleontological Society Special Publication 6, p. 227.

Klapper, G., Kirchgasser, W. T., and Baesemann, J. F., 1993. Graphic correlation of the Frasnian Upper Devonian composite. Geological Society of America, Abstracts with Programs, vol. 25 (2), p. 30.

Klapper, G., and Foster, C. T., Jr., 1993. Shape analysis of the Late Devonian conodont genus *Palmatolepis*. Paleontological Society Memoir 32 (Supplement to Journal of Paleontology, vol. 67, no. 4), 35 pp.

Klapper, G., Feist, R., Becker, R. T., and House, M. R., 1994. Definition of the Frasnian/Famennian stage boundary. Episodes, vol. 16, pp. 433–441.

Klapper, G., Oliver, W. A., Jr., and Prosh, E. C., 1995. The Detroit River Group is Middle Devonian; Early Devonian age of the Detroit River Group, inferred from Arctic stromatoporoids; discussion and reply. Canadian Journal of Earth Sciences, vol. 32, pp. 1070–1077.

Klapper, G., Kirchgasser, W. T., and Baesemann, J. F., 1995. Graphic correlation of a Frasnian (Upper Devonian) composite standard. *in* Graphic correlation. K. O. Mann and H. R. Lane, *eds.*, Special Publication, SEPM (Society for Sedimentary Geology), vol. 53, pp. 177–184. SEPM, Tulsa.

Klapper, G., 1995. Preliminary analysis for Frasnian, Late Devonian, conodont biogeography. Historical Biology, vol. 10, pp. 103–117.

Johnson, J. G., Klapper, G., and Elrick, M., 1996. Devonian transgressive-regressive cycles and biostratigraphy, northern Antelope Range, Nevada; establishment of reference horizons for global cycles. Palaios, vol. 11, pp. 3–14.

Klapper, G., Kuz'min, A. V., and Ovnatanova, N. S., 1996. Upper Devonian conodonts from the Timan-Pechora region, Russia, and correlation with a Frasnian composite standard. First Australian Conodont Symposium (AUSCOS-1) and the Boucot Symposium (18–21 July 1995), Abstracts, and

Programme, p. 48. Macquarie University Centre for Ecostratigraphy and Palaeobiology, Sydney.

Klapper, G., Kuz'min, A. V., and Ovnatanova, N. S., 1996. Upper Devonian conodonts from the Timan-Pechora region, Russia, and correlation with a Frasnian composite standard. Journal of Paleontology, vol. 70, pp. 131–152.

Kelly, B. K., Manger, W. L., and Klapper, G., 1997. Conodonts from the Chattanooga Shale and the Devonian–Mississippian boundary, southern Ozark region. Geological Society of America, Abstracts with Programs, vol. 29 (6), p. 159.

Klapper, G., Murphy, M. A., and Talent, J. A., *eds.*, 1997. Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography; Studies in Honor of J. Granville ("Jess") Johnson. Geological Society of America Special Paper 321, 401 pp.

Klapper, G., 1997. Graphic correlation of Frasnian (Upper Devonian) sequences in Montagne Noire, France, and Western Canada. *in* Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography; Studies in Honor of J. Granville ("Jess") Johnson. G. Klapper, M. A. Murphy, and J. A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 113–129.

Klapper, G., 1998. Frasnian (Upper Devonian) high-resolution conodont correlations. Geological Society of America, Abstracts with Programs, vol. 30 (2), p. 28.

McLean, R. A., and Klapper, G., 1998. Biostratigraphy of Frasnian (Upper Devonian) strata in Western Canada, based on conodonts and rugose corals. Bulletin of Canadian Petroleum Geology, vol. 46, pp. 515–563.

Klapper, G., and Becker, R. T., 1998. Comparison of Frasnian (Upper Devonian) conodont zonations. *in* ECOS VII, Seventh International Conodont Symposium held in Europe. G. Bagnoli, *ed.*, Abstracts, pp. 53–54.

Klapper, G., and Becker, R. T., 1999. Comparison of Frasnian (Upper Devonian) conodont zonations. Bolletino della Società Paleontologica Italia, vol. 37, pp. 339–348.

House, M. R., Becker, R. T., Feist, R., Flajs, G., Girard, C., and Klapper, G., 2000. The Frasnian–Famennian boundary GSSP at Coumiac, southern France. Courier Forschungsinstitut Senckenberg, vol. 225, pp. 59–75.

House, M. R., Menner, V. V., Becker, R. T., Klapper, G., Ovnatanova, N. S., and Kuz'min, V., 2000. Reef episodes and sea-level change in the Frasnian of the southern Timan. Geological Society (London) Special Publication, vol. 178, pp. 147–176.

Klapper, G., 2000. Species of Spathognathodontidae and Polygnathidae (Conodonta) in the recognition of Upper Devonian stage boundaries. Courier Forschungsinstitut Senckenberg, vol. 220, pp. 153–159.

Klapper, G., 2002. [Various contributions on Devonian conodonts]. *in* The Palaeozoics of the Montagne Noire, Southern France. R. Feist, *ed.* IGCP 421, North Gondwana mid-Palaeozoic Biodynamics, and ECOS VIII, 8th European Conodont Symposium, Guidebook of Field Excursion, 85 pp. Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier.

Klapper, G., 2002. Appendix. Conodont biostratigraphic data for the Napier Range. *in* George, A. D. and Chow, N., The depositional record of the Frasnian-Famennian boundary interval in a forereef succession, Canning Basin, Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 181, pp. 371–372.

Feist, R., Klapper, G., and Lerosey-Aubril, R., 2003. Conodont based trilobite biozonation in the Late Devonian off-shore realm. Geological Society of America, Abstracts with Programs, vol. 35 (6), p. 385.

Klapper, G., Uyeno, T. T., Armstrong, D. K., and Telford, P. G., 2004. Conodonts of the Williams Island and Long Rapids formations (Upper Devonian, Frasnian–Famennian) of the Onakawana B Drillhole, Moose River Basin, northern Ontario, with a revision of lower Famennian species. Journal of Paleontology, vol. 78, pp. 371–387.

THE APPARATUS COMPOSITION AND ARCHITECTURE OF *CORDYLODUS* PANDER—CONCEPTS OF HOMOLOGY IN PRIMITIVE CONODONTS

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ABSTRACT

A clear distinction may be drawn between the perpendicular architecture of the feeding apparatus of ozarkodinid, prioniodontid and prioniodinid conodonts, in which the P elements are situated at a high angle to the M and S elements, and the parallel architecture of panderodontid and other coniform apparatuses, where two suites of coniform elements lie parallel to each other and oppose across the midline. The quest for homologies between the two architectures has been fraught with difficulty, at least in part because of the paucity of natural assemblages of coniform taxa. A diagenetically fused apparatus of *Cordylodus lindstromi* elements is here described which is made up of one rounded and two compressed element morphotypes. One of the compressed elements is bowed and asymmetrical and the other is unbowed and more symmetrical. These compressed elements are considered to be homologous with those of panderodontid apparatuses and would have lain at the caudal end of the parallel arrays, with the more symmetrical morphotypes located rostrally to the asymmetrical ones. The bowed and unbowed compressed elements of *Cordylodus* thus correspond, respectively, to the pt and pf positions of panderodontid apparatuses. In addition, the presence of symmetry transition within the rounded elements of *Cordylodus*, but not the compressed morphotypes, enables correlation of these with the S and M element locations of ozarkodinid apparatuses. By extension, the compressed elements must be homologues of the P elements. Specifically, the asymmetrical pt morphotype is homologous with the P_1 of ozarkodinids and the more symmetrical and rostral pf morphotype is homologous with the P_2 position. However, because of uncertainties over the nature of topological transformation of the rostral element array (the "rounded" or "costate" suites), it is not possible to recognize specific homologies between these elements and the M and S elements of ozarkodinids. Morphologic differentiation of P from M and S element suites thus preceded the topological transformation from parallel to perpendicular apparatus architectures.

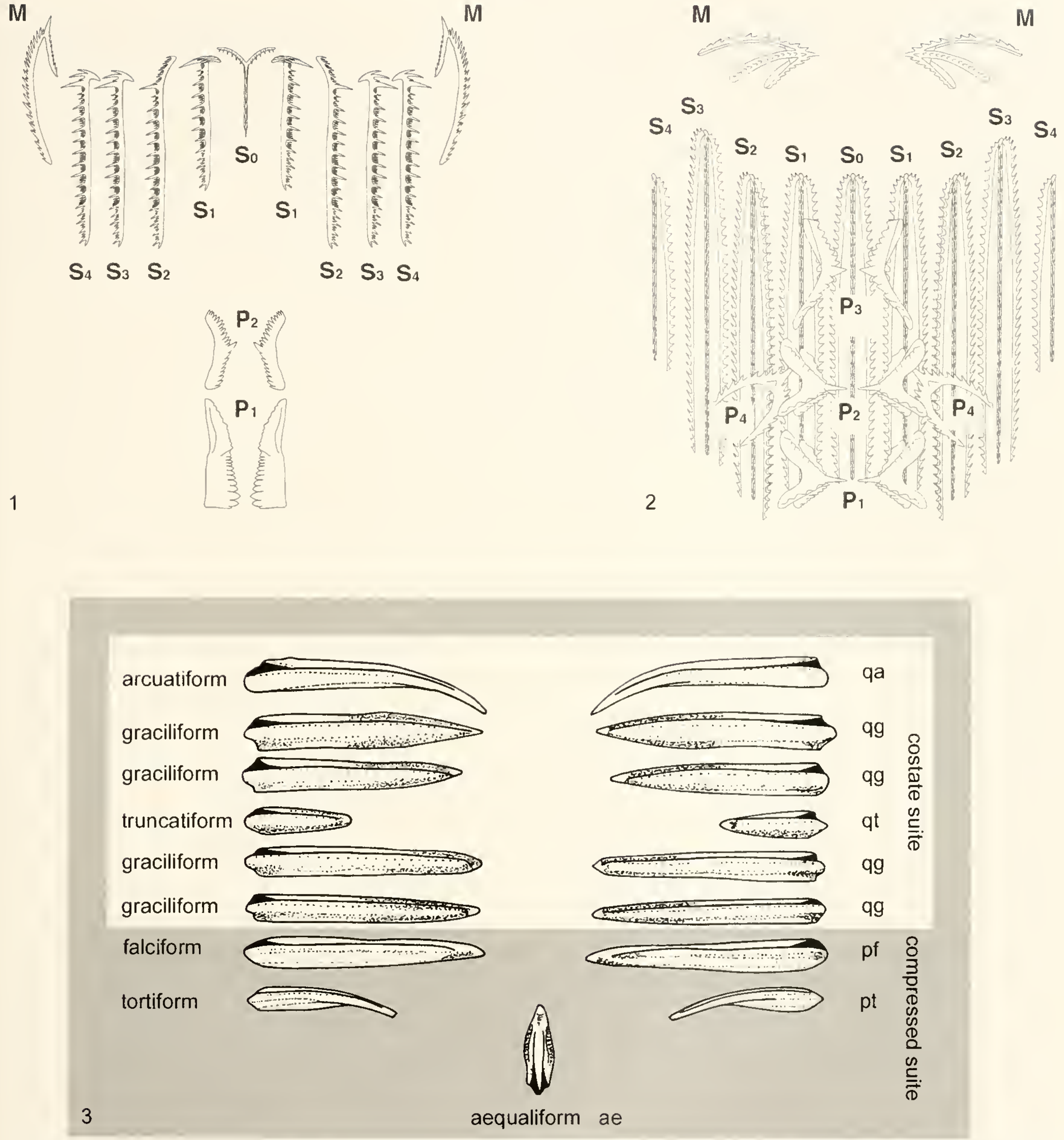
INTRODUCTION

The discovery of conodont soft tissue remains has revolutionized the scientific perception of this long-enigmatic and extinct animal group. Conodonts are now almost universally recognized as chordates and, furthermore, the available evidence indicates that they are the most primitive vertebrates to possess a mineralized skeleton (Donoghue *et al.*, 2000). Thus, the phylogeny of conodonts is no longer a subject of interest only to a specialist group of paleontologists but extends beyond, to the evolutionary and developmental biology of vertebrates. Unfortunately, conodont phylogeny is rather poorly understood in a detailed sense—and it is only through the resolution of conodont relationships that we can begin to elucidate the early stages of evolution in vertebrate skeletons. The key to recovering relationships is the identification of homology between the apparatuses of different taxa. In the absence of soft tissues, the crucial first step is to seek homology in the apparatus composition and architecture of individual taxa. Although some success has been achieved in assessing homologies between taxa with complex apparatuses (Purnell *et al.*, 2000 and references therein), it is far less certain how the apparatus composition and architecture of primitive coniform conodonts relates to that of the more derived prioniodontids, ozarkodinids and prioniodinids. As an aside, it should be noted that preliminary cladistic analysis (Sweet and Donoghue, 2001) indicates that these taxa cannot be sustained at equal, ordinal, rank—the Prioniodontida is paraphyletic with respect to Ozarkodinida + Prioniodinida. Nevertheless, these terms encapsulate useful grades of apparatus organisation and, in the interim, their use is informally maintained in this paper.

Although the multielement revolution in conodont studies began with the seminal works of Huckreide (1958), Walliser (1964), Webers (1966), and Bergström and Sweet (1966), multielement taxonomy was, and to some extent remains, slow to be taken up by workers on post-Early Paleozoic faunas. Gilbert Klapper, initially in collaboration with Graeme Philip (Klapper and Philip, 1971, 1972), was a pioneer in extending multielement taxonomy to the younger portions of the conodont record. Together with a concept of homology within the apparatus, Klapper was among the first to impress upon his peers the importance of this advance not only for systematic studies, but also for biostratigraphy. Although we remain far from a Utopian ideal in which all conodont taxa are known in a multielement sense, the early work of Klapper and others has served as a solid foundation from which later workers have been able to begin elucidating conodont diversity and disparity. For instance, conodont workers are now in a position to conclude, with a degree of certainty, that all ozarkodinids shared a common apparatus plan and architecture (Text-fig. 1.1; Nicoll and Rexroad, 1987; Purnell and Donoghue, 1998). It is also possible that this plan may be much more widely applicable among other conodont groups (Purnell and Donoghue, 1998; Purnell *et al.*, 2000). However, forays into resolving the apparatus structure of coniform conodont taxa have revealed that some possessed an apparatus of seventeen elements that were arranged within a radically different architecture (Text-fig. 1.3; Smith *et al.*, 1987; Sansom *et al.*, 1994), and the recognition of homology between the two architectural types remains far from resolution (Sansom *et al.*, 1994; Purnell and Donoghue, 1998; Purnell *et al.*, 2000). The reasons behind the failure to recognize homologies are multifarious, but include the difficulty of identifying P homologues in relatively simple coniform morphologies; the problems associated with determining the total number of individual elements within apparatuses in the absence of complete natural assemblages; and the fact that most natural assemblages represent relatively derived members of each group. A key step would be to determine the apparatus composition and architecture of less derived taxa that are more likely to be representative of the common ancestor of the two groups. The composition of these apparatuses is often well understood in terms of the number of element morphotypes but, in distinct contrast, the locational homologies of these morphotypes are poorly constrained.

As progress is made in comparing the apparatus plans and architecture of coniform conodonts with those of ozarkodinids and other derived groups, it is essential that a clear distinction be made between different degrees of inference when assessing homology within apparatuses. Homologies between conodont apparatuses can be arrived at through direct or indirect approaches, which correspond to more or less precise hypotheses of homology. The direct approach requires evidence of the relative position of each component element of an apparatus. Such evidence is sparse and relies upon the fortuitous discovery of articulated remains of conodont apparatuses on bedding plane surfaces, or cemented together by early diagenetic minerals in the form of a "fused cluster." The indirect approach extrapolates direct evidence of locational homologies to the apparatuses of taxa that are known only from collections of discrete elements. This may be achieved by comparing element morphotypes in known apparatus positions to morphotypes in discrete-element collections. However, as the phylogenetic distance between taxa grows, the likelihood is greater that dissimilar morphologies of elements will occupy homologous element positions, and extrapolations of locational homology then become more tenuous. Nevertheless, it is possible in such instances to infer homology based upon element morphotypes possessed mutually by closely related taxa for which there is no appropriate architectural template. Thus, although it will not be possible to infer locational homologies and relationships with better known taxa represented by natural assemblages, it remains possible to undertake phylogenetic analysis within these groups. Furthermore, it is possible that through the identification of common element morphotypes between taxa, connections to taxa whose locational homologies are well constrained may be made. It should be noted, however, that these are among the weakest hypotheses of homology and the most likely to be subject to radical reinterpretation upon the discovery of natural assemblages of closely related taxa.

In the past, hypotheses of locational homology be-



Text-figure 1.—**1** Apparatus architecture of ozarkodinid conodonts (after Purnell and Donoghue, 1998). **2** Apparatus architecture of balognathid prioniodontid conodonts (from Aldridge *et al.*, 1995). **3** Apparatus architecture of panderodontid conodonts (from Sansom *et al.*, 1994). Reproduced with the permission of the Palaeontological Association.

tween taxa have been conceptualized in a variety of notational schemes (*e.g.*, Klapper and Philip, 1971; Jeppsson, 1971; Sweet and Schönlaub, 1975; Barnes *et al.*, 1979; Sweet, 1981, 1988; Armstrong, 1990; Sansom *et al.*, 1994; Purnell and Donoghue, 1998; Purnell *et al.*, 2000). At the inception of the majority of these schemes, little was known regarding apparatus architecture, and the number and variety of notational schemes erected underscores the difficulty in establishing homology in the absence of locational data. This situation has been remedied in recent years through the elucidation of apparatus architecture based on data derived from natural assemblages (Aldridge *et al.*, 1987; Smith *et al.*, 1987; Purnell, 1993; Sansom *et al.*, 1994; Aldridge *et al.*, 1995; Purnell and Donoghue, 1997, 1998). This has, in turn, enabled the erection of an entirely apparatus location based scheme of element homology that directly reflects homology independently of element morphology (Purnell *et al.*, 2000).

Despite these advances, the number of taxa for which locational homologies are known directly remains small. Furthermore, the implicit assumption that the earlier conceptual schemes reflected statements of homology has broken down and the explanatory content of the associated nomenclature has been lost through overzealous use and misapplication (Purnell *et al.*, 2000).

Three approaches have been manifest with respect to the use of homology within early euconodont faunas. Some authors (*e.g.*, Nicoll, 1990, 1994; Nicoll *et al.*, 1999; Löfgren, 1997a, b, 1999) have adopted a utilitarian approach in which the P, M, S notation of Sweet and Schönlaub (1975) and Sweet (1981, 1988) is used, although in many instances homology may not be certain. Others (*e.g.*, Smith, 1990, 1991; Sansom *et al.*, 1994) have urged caution and stressed the need to be certain of locational homology before using ozarkodinid notation. This latter approach has been allied to the creation of alternative notational schemes, of which those introduced by Barnes *et al.* (1979), and modified by Armstrong (1990), Ji and Barnes (1994) and Sansom *et al.* (1994) are most applicable to coniform conodonts. A third approach has been to use adjectival descriptors for element morphotypes, which are often based on form-taxonomic names, without any attempt to identify locational homologues between genera (*e.g.*, Kennedy, 1980). All of these approaches have disadvantages. The utilitarian use of ozarkodinid notation may imply homology where none is present or the evidence is very weak; the use of alternative schemes tends to overlook homology with more derived conodonts even where the evidence seems strong (for example with Sa and M elements) and the third approach may fail to recognize homology between even closely related taxa. Clearly, it would be ideal to establish homology between at least some coniform taxa and the better-constrained architecture of ozarkodinid taxa, but this has proved to be an intractable problem given the available dataset of natural assemblages. Even where coniform architecture is well understood, as is the case with *Panderodus* (Sansom *et al.*, 1994), the element morphologies are highly derived and comparison with ozarkodinid templates (Text-fig. 1) is difficult. Architectural information from a primitive taxon, ideally one that is closely related to the latest common ancestor of the prioniodontids and coniform groups, would offer the best opportunity for comparing apparatus architecture and establishing more secure homologies.

In this contribution it is our aim to re-examine what is known regarding the apparatus composition, architecture and homologies of the Late Cambrian–Early Ordovician genus *Cordylodus*, based upon discrete-element collections and upon what little is known from natural assemblages. *Cordylodus* is a key taxon across a range of conodont research—it is an important biozonal index in the Cambrian-Ordovician boundary interval; it is one of the earliest conodonts with denticulated elements and its youngest representatives cooccur with the earliest prioniodontids (*sensu* Sweet, 1988). As part of this review we describe and figure for the first time an incomplete fused cluster of the apparatus of *Cordylodus lindstromi* Druce and Jones, 1971.

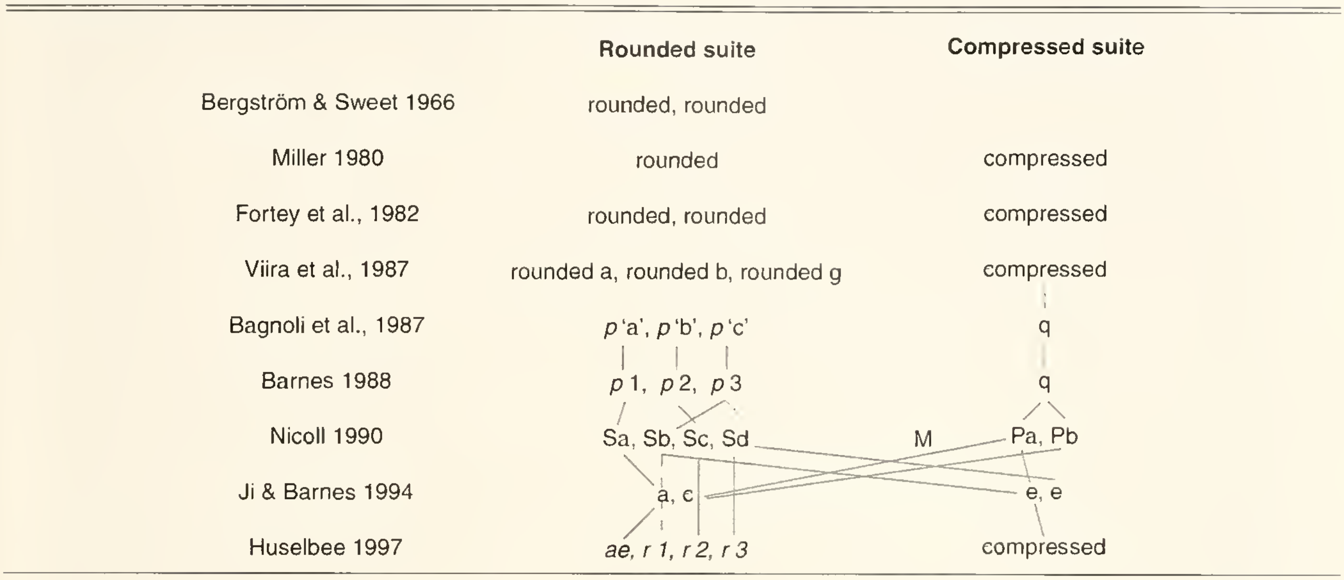
ACKNOWLEDGMENTS

Text-figures 1.1 and 1.2 are reproduced with kind permission of the Royal Society and Text-figures 1.3 and 4 with that of the Palaeontological Association. We are very grateful for the thorough reviews of Ray Ethington and Walt Sweet, which greatly improved the manuscript. Finally, we would like to dedicate this contribution to Gil Klapper, whose contributions to multielement taxonomy underpin many of the conceptual advances in conodont paleobiology over the last three decades.

EVOLVING CONCEPTS OF APPARATUS COMPOSITION IN *CORDYLODUS*

Cordylodus was one of the first conodonts to be described (Pander, 1856), and is one of three, apparently unrelated, denticulate euconodont genera that occur in the Late Cambrian and earliest Ordovician, the others being *Eodentatus* Nicoll and Shergold, 1991, and *Iapetognathus* Landing *in* Fortey *et al.*, 1982 (see Nicoll *et al.*, 1999 for review). In considering the taxonomy of *Cordylodus*, Pander (1856) adopted a form-element approach but the history of, and degree of conflict between, multielement apparatus reconstructions of the genus is perhaps more complex than for any other conodont genus (Table 1). Early apparatus reconstructions invoked a bimembrate apparatus plan that included either two "rounded" elements of different morphology (Bergström and Sweet, 1966) or one "rounded" and one "compressed" element (Mill-

Table 1.—Development of apparatus concepts within *Cordylodus* Pander, 1856, and correlations of individual morphotypes made by successive authors.



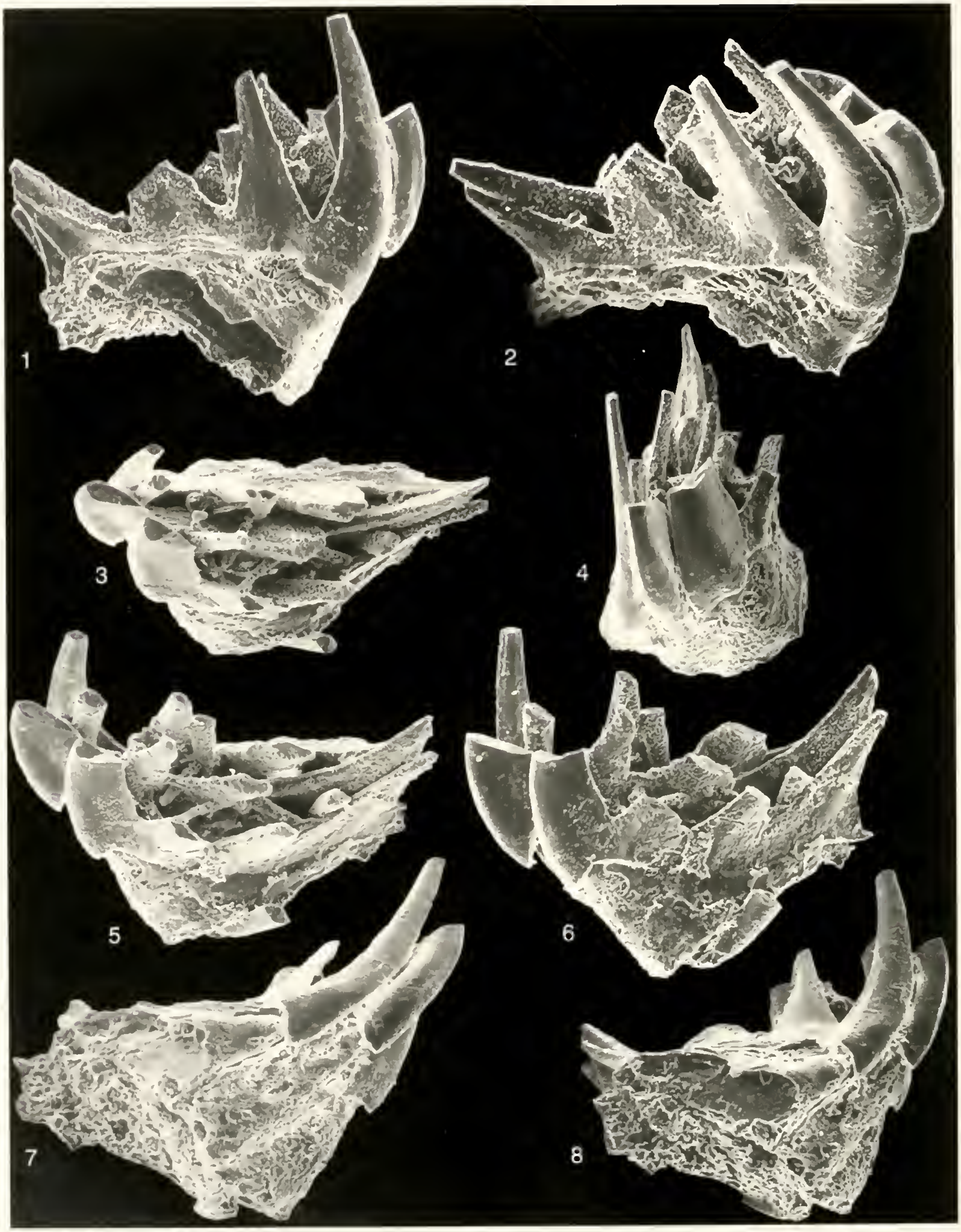
	Rounded suite		Compressed suite
Bergström & Sweet 1966	rounded, rounded		
Miller 1980	rounded		compressed
Fortey et al., 1982	rounded, rounded		compressed
Viira et al., 1987	rounded a, rounded b, rounded g		compressed
Bagnoli et al., 1987	*p*'a', *p*'b', *p*'c'		q
Barnes 1988	*p* 1, *p* 2, *p* 3		q
Nicoll 1990	Sa, Sb, Sc, Sd	M	Pa, Pb
Ji & Barnes 1994	a, c		e, e
Huselbee 1997	*ae, r 1, r 2, r 3*		compressed

er, 1980; Landing *et al.*, 1980). In both instances, the terminology employed referred to the cross-sectional profile of the cusp. A second rounded element was later recognized in *C. angulatus* Pander, 1856, suggesting that at least the younger species of the genus had a trimembrate apparatus (Fortey *et al.*, 1982). A more complex apparatus was proposed by Bagnoli *et al.* (1987), who recognized the rounded and compressed categories of earlier authors but also suggested that a symmetry transition series could be identified within the rounded category. This was composed of laterally compressed symmetrical elements, slightly asymmetrical forms with a flat inner lateral face and markedly asymmetrical types in which the inner lateral face bears a low carina and the outer face is broadly rounded. Bagnoli *et al.* recognized this apparatus structure in all but the oldest representatives of the genus, in which less morphological differentiation seemed to be present. The apparatus reconstruction of Bagnoli *et al.* (1987) was formalized by Barnes (1988), who proposed the terms *p*1, *p*2 and *p*3 for the variants in the symmetry transition series. However, Barnes preferred to express the variation in terms of both cusp curvature and posterior process orientation and morphology, rather than symmetry as Bagnoli *et al.* had done, and *C. lindstromi* was not specifically divided in this way.

A trimembrate apparatus was proposed for *Cordylodus proavus* Müller, 1959, and *C. lindstromi* by Andres (1988). This plan was extended by Ji and Barnes (1994) who identified the three basic element types—a subrounded "*a*" element, a suberect "*c*" element, and a compressed "*e*" element—but also recorded two variants for each of their *a* and *e* elements, essentially creating a quinquemembrate apparatus. The *a* elements were considered to be equivalents of the *p*1 and *p*2 of Barnes (1988), the *c* to be that of the *q*, and the *e* elements to be variants of the *p*3. This differs markedly from the scheme of Bagnoli *et al.* (1987) who considered the compressed element to be the *q*, not a *p*.

The most complex apparatus plan proposed to date for *Cordylodus* is that of Nicoll (1990, 1991, 1992). Employing the ramiform-pectiniform notation of Sweet and Schönlaub (1975), Nicoll suggested that the apparatus of *Cordylodus* was septimembrate, with Pa, Pb and Sa-Sd elements, together with an M element that was thought to be either adenticulate (*C. angulatus*, *C. caseyi* Druce and Jones, 1971, *C. proavus*) or denticulate (*C. lindstromi*). Miller and Repetski (1993) attempted to test the Nicoll model using topotype material together with comparative collections of *C. proavus* and other early *Cordylodus* species. They had only partial success; they did not recognize four separate S elements *sensu* Nicoll nor did their material contain an adenticulate M element.

Huselbee (1997) did recognize a series of four rounded elements on the basis of their symmetry, similar to the "Sa-Sd" suite of Nicoll (1990) but found no evidence for makelliform elements and only one morphotype of compressed element within her rather



Text-figure 2.—Fused cluster of *Cordylodus lindstromi* Druce and Jones, 1971 (USNM 516997) from Ibexian (Early Ordovician) strata of the Vinini Formation, Nevada, USA. Specimen recovered from USGS sample 9446-CO and deposited in the National Museum of Natural History, Washington DC, USA. **1** Lateral view of the rounded element (Element 3), ×200; the cusp of the P_2 homologue is visible behind the rounded element on the right hand side of the figure. **2** Oblique view of cluster showing the two compressed elements behind the rounded one, ×250. **3** Axial view of the cluster, ×200. The asymmetrical P_1 homologue (Element 1) is situated at the bottom of the figure, adjacent to the less bowed P_2 homologue (Element 2) which in turn abuts the rounded element (Element 3). **4** "Anterior" view of the cluster, ×230;

low-abundance faunas from NW Scotland and Greenland.

The youngest representatives of *Cordylodus*, *C. angulatus*, *C. intermedius* Furnish, 1938, *C. lindstromi*, and *C. prion* Lindström, 1955, have their last appearances in the *angulatus* Biozone (early Tremadoc). Younger species have been assigned to the genus but are based on homeomorphic elements that are present in taxa not closely related to *Cordylodus*. These include "*Cordylodus*" *horridus* Barnes and Poplawski, 1973, which is based on a denticulated Llanvirn species of *Paroistodus* (Löfgren, 1995; Albanesi and Barnes, 2000), and "*Cordylodus*" *ramosus* Hadding which is now considered to be part of the apparatus of *Spinodus spinatus* (Hadding, 1913), a Middle Ordovician genus of uncertain affinity (Dzik, 1976; Armstrong, 1997).

Clearly, there has been little concordance over the apparatus composition of, and taxonomic concepts for, *Cordylodus* despite intensive work related to selection of the Cambrian–Ordovician global boundary stratotype and point. Although there is mounting consensus from Bagnoli *et al.* (1987) through Nicoll (1990) to Huselbee (1997) for the presence of a suite of rounded elements defined by differences in symmetry, there is little agreement on the number of compressed elements (including makelliform elements) within the apparatus. Natural assemblages have the capacity to provide tests for these competing apparatus models.

NATURAL ASSEMBLAGES OF *CORDYLODUS*

Only two natural assemblages of *Cordylodus* have been recorded to date, both of which are fused clusters. Andres (1988, pl. 13, figs. 1, 2) figured a cluster assigned to *C. proavus* Müller elements that incorporates at least three elements. However, it is not possible to interpret the element morphologies present from the plate alone and recourse to the original material will be necessary for detailed reappraisal. Preliminary notes on another cluster of elements referred to *Cordylodus* were made by Repetski (1980) and Repetski and Szaniawski (1981), but the specimen has never before been figured or described in detail. The fused cluster includes three complete elements and three element fragments assigned to *C. lindstromi* Druce and Jones (Text-figs. 2, 3). It was recovered through acid digestion of U.S. Geological Survey sample 9446-CO from the Vinini Formation, Elko County, Nevada, U. S. A. (SE¼, sec. 19, T 35 N, R 53 E). The associated fauna includes *Cordylodus angulatus* Pander, 1856, *Cordylodus intermedius* Furnish, 1938, *Iapetognathus sprakersi* (Landing *in* Landing *et al.*, 1996) and *Variabiloconus bassleri* (Furnish, 1938), indicating an *angulatus* or early *manitouensis* Biozone age (Skullrockian, early Ibexian, earliest Ordovician; Ross *et al.*, 1997). The protoconodont *Phakelodus tenuis* (Müller, 1959) is also present, both as isolated elements and clusters, together with the phosphatized embryos of bilaterian metazoans.

DESCRIPTION OF *CORDYLODUS LINDSTROMI* CLUSTER

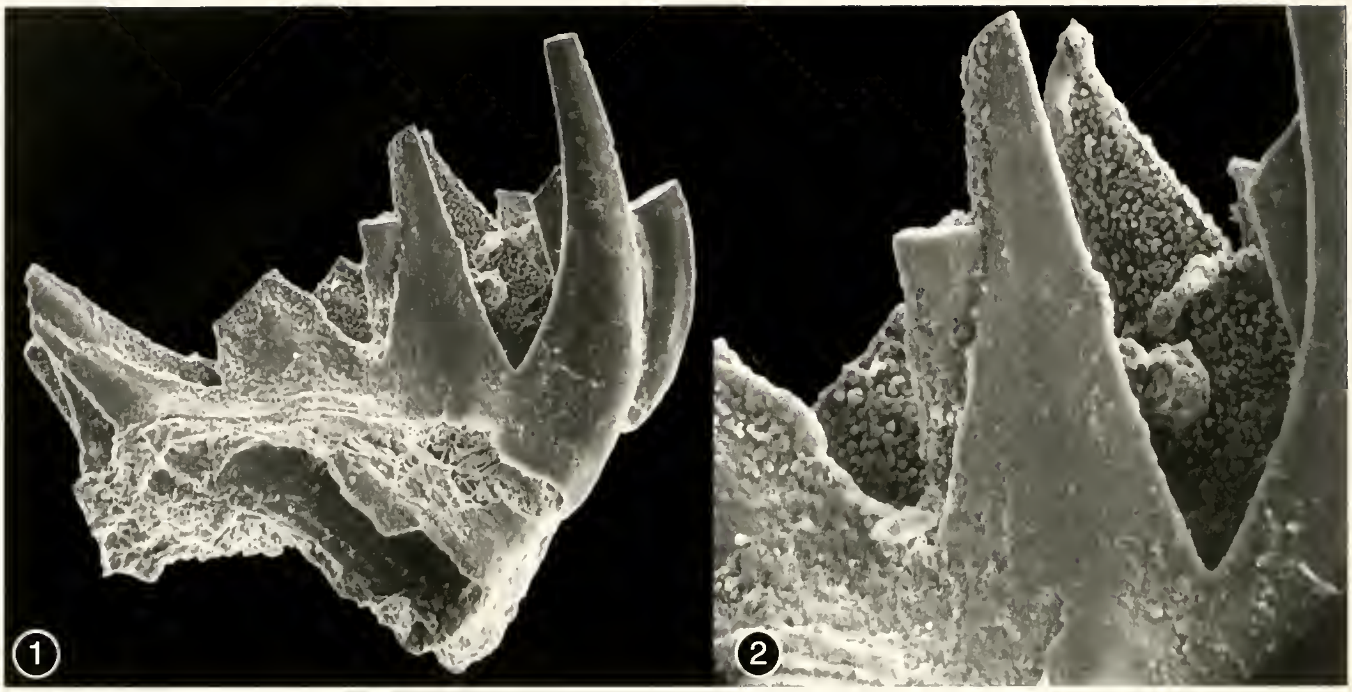
The cluster (Text-fig. 2) comprises three complete elements, together with cusp and denticle fragments of at least two others—the latter fragments oppose the more complete elements with the long axes of the cusps and denticles parallel to each other. The complete elements are fused by their lateral faces and there is no evidence of *post mortem* disruption. Element 1 (Text-fig. 2.3–2.6) has compressed cusp which is proclined-erect in the preserved portion. Faint carina at base of outer face. Outer face broadly convex toward posterior margin, but more tightly convex at anterior margin. Inner face flat; cusp therefore asymmetrical in cross-section and twisted inwards relative to posterior process. Element strongly bowed. In lateral aspect, basal margin has marked 100° inflection. Three denticles. First and second denticles are asymmetrically triangular in lateral profile with steeper posterior margin. Third denticle is more slender and reclined than more anterior denticles. First denticle has convex outer face and flat inner face. Denticles two and three are more symmetrical and biconvex in cross-section.

Element 2 (Text-fig. 2.3–2.6) is sandwiched between the other two elements and, in consequence, the morphology is partly obscured. Cusp as broad as Element 1 and strongly compressed; erect to proclined in preserved portion. Outer and inner faces broadly convex resulting in more symmetrical cross-section than Element 1; element gently bowed. Basal margin has similar inflection to Element 1 when viewed in lateral profile. Three denticles. First denticle is complete, narrow and short. Second denticle is more triangular with steeper posterior margin than anterior margin. Third denticle more reclined than other two.

Element 3 (Text-figs. 2, 3) is the most complete element. Cusp narrower and markedly less compressed

←

P_1 homologue on the right. **5, 6** Oblique axial and oblique "anterior" views, ×200; the P_1 homologue is the nearest element. **7, 8** Each element has a distinct basal body, which remains separate until the basal part of the cluster where they become fused into a single mass; ×225, ×200. It is unclear whether this is a primary feature relating to the apparatus or a consequence of the early diagenesis that produced the cluster.



Text-figure 3.—Opposed cusp and denticle tips in the fused cluster of *Cordylodus lindstromi* Druce and Jones, 1971 (USNM 516997). **1** Lateral view of the rounded element (Element 3 showing the fused cusp and first denticle of the opposing element, ×225. **2** Close-up of the cusps and denticles showing the precise alignment, ×500. The similarity in cusp and denticle cross-sections can be seen in Text-figure 2.3.

than Elements 1 and 2; slightly bowed to inner. Inflection in basal margin beneath posterior margin of cusp. Three denticles. First denticle is narrow and triangular, with posterior margin markedly steeper than anterior. Junction of cusp with first denticle lower than that between first and second denticles. Second denticle more broadly triangular in lateral profile than either of other denticles. Denticles symmetrically biconvex in cross-section. Third denticle more reclined than first two.

All elements have a basal body, which in Element 3 has a hollow, conical interior surface. Incremental growth lines are apparent on the inner surface of the basal body (Text-figs. 2.8, 3.1) The basal bodies of each element remain distinct for almost their entire lengths but are fused into a single mass at the base; it is not certain whether this is a primary or diagenetic feature.

An opposed and inverted cusp fragment is attached to the cusp of Element 3 and is of similar morphology; an inverted denticle, which may belong to the same element, is attached to the first denticle of Element 3 (Text-fig. 3). An additional inverted denticle is attached to the flank of Element 1, and a third inverted denticle is attached between Elements 1 and 2 at the anterior end of the third denticles of these two elements. The opposing cusp and denticle fragments are parallel to their counterparts.

Microspheres, of phosphatic composition and probable bacterial origin, coat many of the element surfaces (Text-fig. 3.2) and were presumably involved in the early *post mortem* mineralization that resulted in element fusion.

COMPARISON WITH MULTIELEMENT RECONSTRUCTIONS OF *CORDYLODUS*

Elements 1 and 2 are compressed elements. The only apparatus reconstructions of *Cordylodus* to have included two morphotypes of compressed element are those of Nicoll (1990) and Ji and Barnes (1994). Element 1 resembles the Pa element of Nicoll (1990) in that the cusp is twisted inwards relative to the posterior process. In turn, Element 2 conforms to the description of Nicoll's Pb element type in being more symmetrical in cross-section and in being untwisted relative to the posterior margin. As in Nicoll's material, the cusps of the compressed elements are keeled on their anterior and posterior margins, and the basal cavity extends along the posterior process. Ji and Barnes (1994) also documented variations in the compressed elements and recognized two types based on differences in cusp curvature, basal cavity shape and symmetry. In particular, one compressed element morphotype was considered to be more compressed than the other (Ji and Barnes, 1994, p. 31) and, on this basis, the less compressed morphotype may correlate with the Element 1. It is not, however, possible on the basis of their figures to correlate directly with the elements in the cluster.

Element 3 is a "rounded" element and is probably equivalent to Nicoll's (1990) Sb element. The first denticle is deflected outwards relative to the cusp and second denticle; the cusp is biconvex in cross-section and the anterior margin is rounded in its lower part. It corresponds to one of the two categories of "*a*" morphotype recognized by Ji and Barnes (1994).

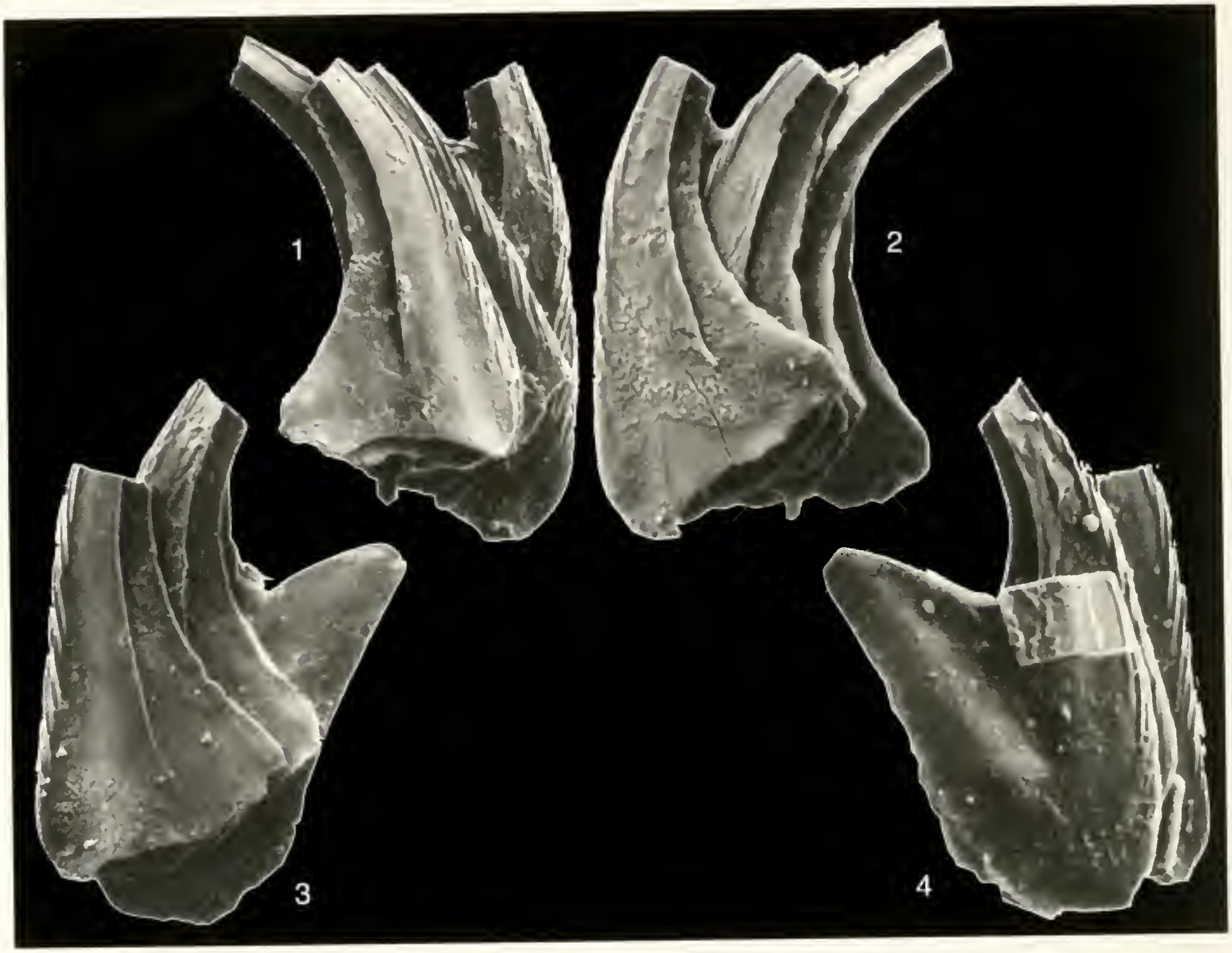
The two compressed elements within the half apparatus of *Cordylodus lindstromi* are closely comparable to the pf and pt elements of the compressed suite in *Panderodus* described by Sansom *et al.* (1994). Furthermore, the posteriormost pt pair in *Panderodus* is markedly asymmetrical and the elements have twisted cusps similar to that of Element 1.

COMPARATIVE APPARATUS ARCHITECTURE OF *CORDYLODUS*

The construction of apparatus architecture models depends to a large degree on the availability of bedding plane assemblages and fused clusters, which can provide three-dimensional data on element disposition once the effects of collapse generated by decay are removed (see Briggs and Williams, 1981; Aldridge *et al.*, 1987; Purnell and Donoghue, 1999 for reviews of the technique). The vast majority of natural assemblages described to date are of prioniodontid, prioniodinid and ozarkodinid taxa, with a relatively very small number of coniform taxa represented. Partly because of the relative abundance of natural assemblages and partly because of the presence of associated soft tissues in the Granton *Lagerstätte*, ozarkodinids have tended to be used as the *Bauplan* for complex conodonts (Aldridge *et al.*, 1987; Purnell and Donoghue, 1998). Ozarkodinid apparatuses contain two pairs of P elements located at the caudal end of the apparatus, with the P_2 pair rostral to the P_1 elements (Text-fig. 1.1). The ramiform S elements are oriented with their long caudal ("posterior") processes parallel to the long axis of the trunk. M elements flank the battery of S elements but lie, at rest, in an oblique rostrolateral orientation. The long axes of the S and M elements lie at a high angle to those of the P elements, producing an approximately "perpendicular" architecture.

Prioniodontid conodonts are less derived than ozarkodinids and a smaller number are represented by natural assemblages. *Promissum* has the best-constrained architecture (Text-fig. 1.2), and it has been suggested that its architecture could be typical of the Prioniodontida as a whole (Aldridge *et al.*, 1995). Four pairs of P elements lie in pairs along the midline, but were located between, and dorsal to, the sinistral and dextral suites of S elements, not caudal to them (Aldridge *et al.*, 1995). The M elements occupy a rostro-lateral position similar to those in ozarkodinids. However, the element morphology of *Promissum*, whilst potentially typical of the Balognathidae, is not typical of the Prioniodontida as a whole and the small number of available natural assemblages from other prioniodontid taxa suggests that a simpler architecture was characteristic of the group. Clusters and associated isolated collections of *Oepikodus* (Smith, 1991), *Paracordylodus* (Stouge and Bagnoli, 1988, pl. 8, figs. 17a, b; Tolmacheva and Purnell, 2002) and *Phragmodus* (Repetski *et al.*, 1998; Barrett, 2000) suggest that the possession of four pairs of P elements was not general for prioniodontids, and that the more common architecture for the group may have been more similar to that of ozarkodinids than to *Promissum*.

The only well-constrained architectural model for a coniform taxon is that of *Panderodus* (Text-fig. 1.3). A large number of fused clusters and a bedding plane assemblage with associated soft tissue from the Waukesha *Lagerstätte* of Wisconsin, U. S. A., have been used to produce a detailed model for the apparatus of *Panderodus* (Smith *et al.*, 1987; Sansom *et al.*, 1994). Eight pairs of elements oppose across the midline of the apparatus, and Smith *et al.* (1987, p. 100) concluded that they must have been arranged in life as parallel and opposed arrays, with either the rostral elements more closely spaced or with all of the elements located on an arched support. This arrangement contrasts markedly with the geometry of S elements in prioniodontids, prioniodinids and ozarkodinids, which are parallel to the midline. Some morphological differentiation is evident in the elements of *Panderodus;* Sansom *et al.* (1994) recognized two principal locational domains—a rostral costate suite and a caudal compressed suite—and all of these elements are parallel to each other, contrasting with the perpendicular architecture of the ozarkodinids. A third domain occupied by a single symmetrical element lies on the midline. It is immediately tempting to consider the compressed suite as the homologues of the P locations in ozarkodinid apparatuses. However, *Panderodus* lacks a clearly defined "symmetry transition series" of morphologically intergrading elements, making unequivocal identification of S homologues difficult. In consequence, it remains a possibility that the two pairs of compressed elements may be homologues not of P elements but of other members of the apparatus. Sansom *et al.* (1994) therefore argued for a conservative approach until supporting evidence was forthcoming. Parenthetically, the concept of symmetry transition has been principally used to differentiate suites of elements rather than to imply locational homology. Neverthe-



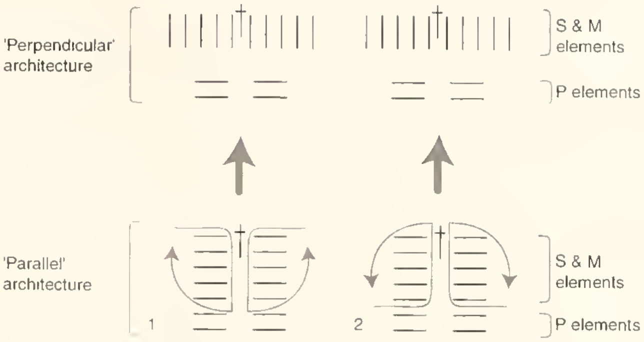
Text-figure 4.—*Besselodus arcticus* Aldridge, 1982, from the Cincinnatian (Late Ordovician) Aleqatsiaq Fjord Formation of Washington Land, western North Greenland (MGUH 15071) showing a single cluster that split into two during original preparation. **1, 2** Lateral views of sub-cluster "a" (×330). **3, 4** Lateral views of sub-cluster "b" (×330). The original plane of fusion between the two sub-clusters lay between the lateral faces of the uppermost elements in Text-figures 4.1 and 4.3. The full array comprises six laterally costate, bilaterally symmetrical non-geniculate elements and one geniculate element, which is located at the end of the array. Reproduced with the permission of the Palaeontological Association.

less, some authors have used this concept to infer location directly, despite the fact that all available evidence indicates the contrary—symmetry transition cannot be used as a tool in predicting the sequence of S elements within the ramiform array (Aldridge *et al.*, 1987; Purnell and Donoghue, 1998). It is clear, however, that morphologically intergrading elements do frequently comprise the suite of S elements and, thus, this character provides a predictive tool in distinguishing S from M or P elements from elements in other positions (although this tool appears to be inapplicable to prioniodinids; Purnell and von Bitter, 1996).

The availability of a well-constrained architectural model for at least one coniform taxon, albeit a rather derived form, enables the appraisal of less well-preserved and/or less plentiful cluster material of other taxa. A cluster of *Besselodus* elements (Text-fig. 4) figured by Aldridge (1982) is a single half apparatus with little morphological differentiation. It includes six laterally costate, bilaterally symmetrical elements fused by their lateral faces and a single geniculate element at one end of the array. In the absence of elements from the opposing half of the apparatus this cluster could be incorporated into either a panderodontid or an ozarkodinid architectural model and there is also no direct control over rostro-caudal polarity in the array. However, Sansom *et al.* (1994) concluded that the architecture of *Besselodus* conformed to the panderodontid model on the basis of correlations between elements present in isolated collections and would thus be expected to have a parallel architecture. Critical evidence for the conformity of a given apparatus to either the panderodontid or the ramiform-pectiniform model thus lies in the geometry of the respective halves of the apparatus. In the panderodontid architectural model, elements are arranged along the rostral-caudal axis and are opposed cusp tip to cusp tip, a geometry referred to as parallel-reversed by Landing (1976, p. 1078).

Although far from complete, the fused cluster of *Cordylodus lindstromi* elements may be used to provide some constraints on the apparatus architecture of the genus. Firstly, given the presence of a distinct suite of morphologically intergrading "symmetry transition" elements in the apparatus of *Cordylodus*, we can discriminate a suite of homologues to the S elements of ozarkodinids. This leaves a suite of compressed elements that represent either P or M elements. Given that the compressed elements occur paired in the cluster, it is likely that they represent a pair of P homologues. The occurrence of P homologues aligned in parallel and in juxtaposition to an S homologue indicates that *Cordylodus* possessed overall apparatus geometry that was more similar to panderodontids than to ozarkodinids. Finally, the presence of two compressed elements adjacent to each other, with the more asymmetrical morphotype at the end of the array, is consistent with them being locational homologues of the compressed domain in the apparatus architecture of *Panderodus*. Therefore, it follows that the compressed suite in *Panderodus* is homologous with the P positions in ozarkodinids and their kin. More specifically, we can identify the asymmetrical compressed elements of *Panderodus* and *Cordylodus* apparatuses as P_1 homologues (*sensu* Purnell *et al.*, 2000), and the more rostral symmetrical elements are P_2 homologues.

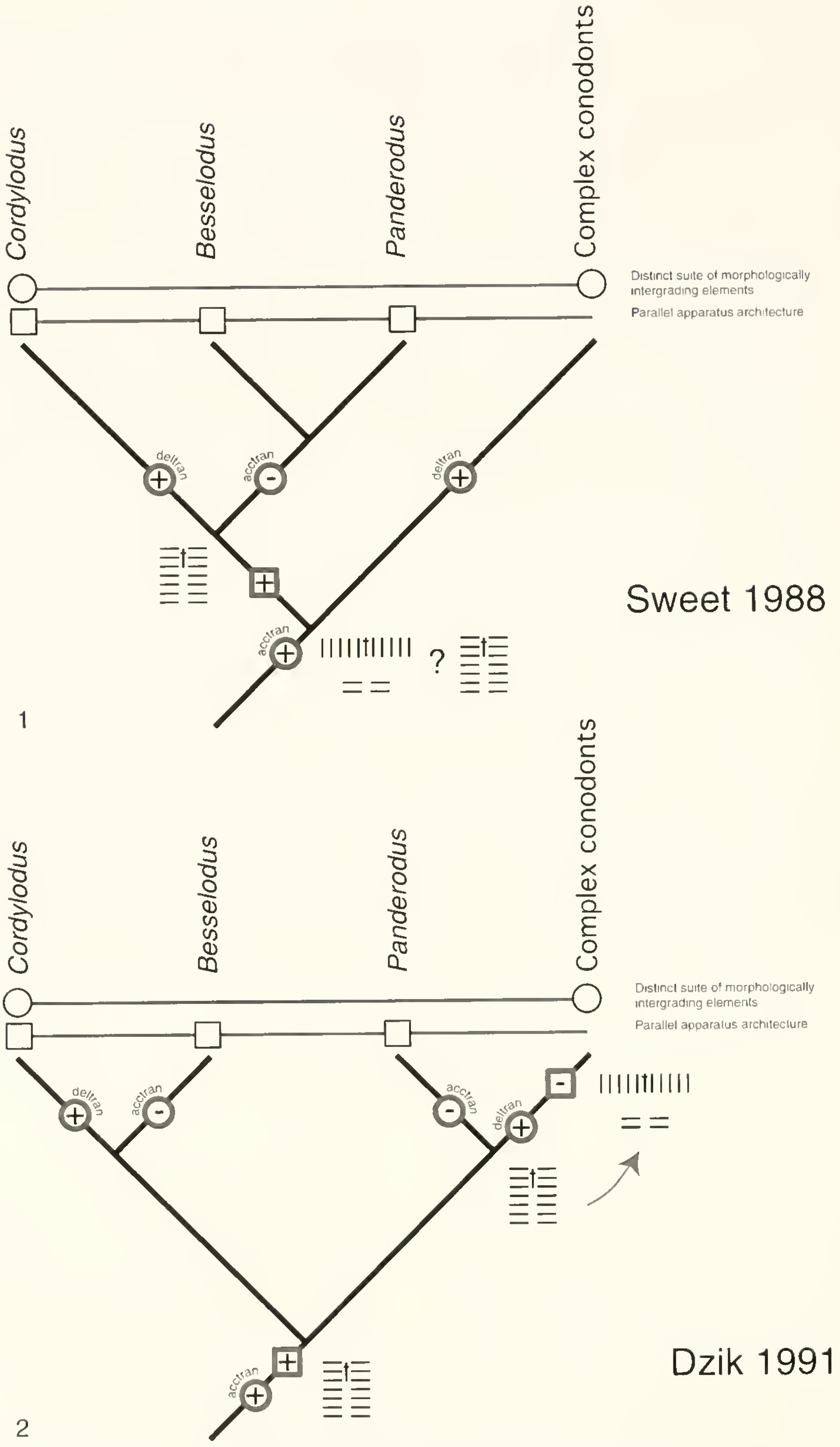
It is tempting to extend from these homologies and identify specific S_{0-4} and M locational homologues among the apparatuses of *Cordylodus* and *Panderodus*. However, because of the architectural differences between the "parallel" apparatuses of *Cordylodus* and *Panderodus*, and the "perpendicular" apparatuses of prioniodontids and their kin, this is not possible because we have no knowledge of the transformational relationship between the S and M *versus* P locations in these two fundamentally different architectural types. For instance, the element position immediately adjacent to the putative P_2 of *Cordylodus* and *Panderodus* could represent either the S_1 or S_4 depending upon the direction in which the left and right halves of the S array have rotated relative to each other (Text-fig. 5). The possibility must also be entertained, however, that the element position immediately adjacent to the P_2 in parallel apparatuses represents the M location, or even another P location. In addition, Dzik (1991) has suggested that the axial (and therefore unpaired) S_0 location of prioniodontids may be homologous to paired abaxial S_0 locations in apparatuses with parallel architecture. There is simply insufficient evidence to reconcile these competing hypotheses.



Text-figure 5.—Alternative patterns of transformation from the parallel architecture of *Cordylodus*, *Panderodus* and *Besselodus*, to the perpendicular apparatus architecture typical of prioniodontids, prioniodinids and ozarkodinids. The differing methods of transforming the parallel architecture are illustrated in the left and right halves of the figure. Given these alternatives, it is not possible to identify specific M and S element homologues in parallel and perpendicular apparatuses, although it is possible to recognize P_1 and P_2 homologues and the overall homology of the M and S array of perpendicular apparatus architecture with the anterior suite of elements ("costate" or "rounded") in parallel architectures.

One direction in which progress can be made is in attempting to resolve the primitive apparatus architecture of the earliest euconodonts and its relationship to locational homologies. To do this, parallel and perpendicular architectures must be considered with respect to one or more phylogenetic trees. In the absence of a generally accepted hypothesis of relationships for conodonts, we have adopted and compared the rival schemes of Sweet (1988) and Dzik (1991) and mapped onto these trees the architectural characteristics of those taxa for which data are available. The differing implications for architectural evolution of the conodont apparatus under these schemes can be seen in Text-figure 6. Under the hypothesis of relationships proposed by Sweet (1988), it is not possible to resolve unequivocally whether parallel or perpendicular architectures are representative of the latest common ancestor of the taxa concerned; both hypotheses are equally likely. However, under the scheme of relationships proposed by Dzik (1991), it is possible to resolve unequivocally that the latest common ancestor of all four taxa possessed a parallel, rather than perpendicular apparatus architecture.

The functional implications of architectural trans-



Text-figure 6.—Inferences of the relative phylogenetic timing of apparatus architectural transformation in taxa for which data are available, based upon the hypotheses of relationships proposed by (1) Sweet (1988) and (2) Dzik (1991). Given that it is not possible to unequivocally infer the relative timing of transformation and/or the primitive apparatus architecture of all the conodonts considered, we have presented the alternative implications of early (ACCTRAN) and late (DELTRAN) transformation. Whilst it is not possible to reconcile primacy between parallel and perpendicular architectures under the scheme proposed by Sweet (1988), following Dzik (1991) it is possible to infer unequivocally that parallel architecture is primitive with respect to perpendicular architecture.

formation of the apparatus, from parallel to perpendicular, are unclear. However, it is clear that morphological and, by implication, functional differentiation of P from M and S elements preceded the transformation from parallel to perpendicular architectures. Indeed, since morphological differentiation of the apparatus is common to all of the taxa considered, it is possible to conclude that their latest common ancestor possessed an apparatus composed of morphologically distinct element suites.

FUTURE DEVELOPMENTS

Further resolution of locational homology in primitive conodonts will require better quality data in the form of complete natural assemblages. More specifically, these data are required for taxa that can provide insight into the transformational pattern/s through which apparatus architecture was remodelled from the plesiomorphic parallel arrangement to the perpendicular architecture that is characteristic of all prioniodontids currently known from natural assemblages. Nevertheless, the further resolution and refinement of locational homologies and architectures among parallel apparatus-bearing taxa will help to provide a much clearer understanding of plesiomorphic euconodont characteristics.

CONCLUSIONS

1) Elements 1 and 2 are "compressed" elements. Element 1 has an asymmetrical cusp cross-section and is bowed. Element 2 is symmetrical in cross-section and only gently bowed. The presence of two morphotypes of compressed element in the cluster affirms the apparatus reconstructions of Nicoll (1990) and Ji and Barnes (1994), the only apparatus reconstructions of *Cordylodus* that have incorporated two morphotypes of compressed elements.
2) The compressed element suite of the *Panderodus* apparatus (*sensu* Sansom *et al.*, 1994) may, with some confidence, be considered as a homologue of the compressed elements in *Cordylodus*. The rounded and compressed elements lay parallel to each other in the apparatus and, together with the closely aligned opposing cusp and denticle tips of the rounded elements, this indicates that *Cordylodus lindstromi* had a parallel panderodontid architecture rather than a perpendicular ozarkodinid type.
3) Consideration of the available natural assemblage material allows a hypothesis to be advanced that elements in the compressed suite of *Cordylodus* (and *Panderodus*) may be considered as reasonable candidates for locational homologues of ozarkodinid P_1 and P_2 elements.
4) Although it is possible to differentiate between homologues of P and S/M elements, it is not possible to identify specific S_1–S_4 and M homologues.
5) The morphological differentiation of elements into P, M and S homologues preceded the topological transformation of the apparatus that produced the characteristic ramiform-pectiniform apparatus architecture of ozarkodinids, prioniodontids and prioniodinids.

REFERENCES CITED

Albanesi, G.L., and Barnes, C.R.
2000. Subspeciation within a punctuated equilibrium evolutionary event: phylogenetic history of the Lower–Middle Ordovician *Paroistodus originalis–P. horridus* complex (Conodonta). Journal of Paleontology, vol. 74, pp. 492–502.

Aldridge, R.J.
1982. A fused cluster of coniform conodont elements from the Late Ordovician of Washington Land, Western North Greenland. Palaeontology, vol. 25, pp. 425–430.

Aldridge, R.J., Purnell, M.A., Gabbott, S.E., and Theron, J.N.
1995. The apparatus architecture and function of *Promissum pulchrum* Kovács-Endrödy (Conodonta, Upper Ordovician), and the prioniodontid plan. Philosophical Transactions of the Royal Society of London, Series B, vol. 347, pp. 275–291.

Aldridge, R.J., Smith, M.P., Norby, R.D., and Briggs, D.E.G.
1987. The architecture and function of Carboniferous polygnathacean conodont apparatuses. *in* Palaeobiology of conodonts. R.J. Aldridge, *ed.*, Ellis Horwood, Chichester, pp. 63–76.

Andres, D.
1988. Strukturen, apparate und phylogenie primitiver conodonten. Palaeontographica, Abt. A, vol. 200, pp. 105–152.

Armstrong, H.A.
1990. Conodonts from the Upper Ordovician–Lower Silurian carbonate platform of North Greenland. Gronlands Geologiske Undersogelse Bulletin, vol. 159, pp. 1–151.
1997. Conodonts from the Ordovician Shinnel Formation, Southern Uplands, Scotland. Palaeontology, vol. 40, pp. 763–797.

Bagnoli, G., Barnes, C.R., and Stevens, R.K.
1987. Lower Ordovician (Tremadocian) conodonts from Broom Point and Green Point, Western Newfoundland. Bollettino della Società Paleontologica Italiana, vol. 25, pp. 145–158.

Barnes, C.R.
1988. The proposed Cambrian–Ordovician global boundary stratotype and point (GSSP) in Western Newfoundland, Canada. Geological Magazine, vol. 125, pp. 381–414.

Barnes, C.R., Kennedy, D.J., McCracken, A.D., Nowlan, G.S., and Tarrant, G.A.
1979. The structure and evolution of Ordovician conodont apparatuses. Lethaia, vol. 12, pp. 125–151.

Barnes, C.R., and Poplawski, M.L.S.

1973. Lower and Middle Ordovician conodonts from the Mystic Formation, Quebec, Canada. Journal of Paleontology, vol. 47, pp. 760–790.

Barrett, S.F.

2000. The function, histology and classification of selected prioniodontid conodonts. Unpublished Ph.D. thesis, University of Leicester. 196 pp.

Bergström, S.M., and Sweet, W.C.

1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. Bulletins of American Paleontology, vol. 50, pp. 271–441.

Briggs, D.E.G., and Williams, S.H.

1981. The restoration of flattened fossils. Lethaia, vol. 16, pp. 1–14.

Donoghue, P.C.J., Forey, P.L., and Aldridge, R.J.

2000. Conodont affinity and chordate phylogeny. Biological Reviews, vol. 75, pp. 191–251.

Druce, E.C., and Jones, P.J.

1971. Cambro-Ordovician conodonts from the Burke River structural belt, Queensland. BMR Bulletin, vol. 110, pp. 1–159.

Dzik, J.

1976. Remarks on the evolution of Ordovician conodonts. Acta Palaeontologica Polonica, vol. 21, pp. 395–455.

1991. Evolution of the oral apparatuses in the conodont chordates. Acta Palaeontologica Polonica, vol. 36, pp. 265–323.

Fortey, R.A., Landing, E., and Skevington, D.

1982. Cambrian–Ordovician boundary sections in the Cow Head Group, western Newfoundland. *in* Cambrian–Ordovician boundary: sections, fossil distribution and correlation. M.G. Bassett and W.T. Dean, *eds.*, National Museum of Wales, Cardiff, pp. 95–129.

Furnish, W.M.

1938. Conodonts from the Prairie du Chien (Lower Ordovician) beds of the Upper Mississippian Valley. Journal of Paleontology, vol. 12, pp. 318–340.

Hadding, A.

1913. Undre Dicellograptusskiffern i Skane jamte nagre darmet ekivalenta bildninger. Lunds Univ. Arsk. n. f. Avd., vol. 9, pp. 1–90.

Huckreide, R.

1958. Die Conodonten der Mediterranean Trias und ihr stratigraphischer Wert. Paläontologische Zeitschrift, vol. 32, pp. 141–175.

Huselbee, M.Y.

1997. Late Cambrian to earliest Ordovician (Ibexian) conodont evolution and biogeography of Greenland and northwest Scotland. Unpublished Ph.D. thesis, University of Birmingham, 296 pp.

Jeppsson, L.

1971. Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. Lethaia, vol. 4, pp. 101–123.

Ji, Z., and Barnes, C.R.

1994. Lower Ordovician conodonts of the St. George Group, Port-au-Port Peninsula, western Newfoundland. Palaeontographica Canadiana, vol. 11, pp. 1–149.

Kennedy, D.J.

1980. A restudy of conodonts described by Branson and Mehl, 1933, from the Jefferson City Formation, Lower Ordovician, Missouri. Geologica et Palaeontologica, vol. 14, pp. 45–76.

Klapper, G., and Philip, G.M.

1971. Devonian conodont apparatuses and their vicarious skeletal elements. Lethaia, vol. 4, pp. 429–452.

1972. Familial classification of reconstructed Devonian conodont apparatuses. Geologica et Palaeontologica, Sonderband 1, pp. 97–114.

Landing, E.

1976. "*Prooneotodus*" *tenuis* (Müller, 1959) apparatuses from the Taconic Allochthon, Eastern New York: construction, taphonomy and the protoconodont "supertooth" model. Journal of Paleontology, vol. 51, pp. 1072–1084.

Landing, E., Ludvigsen, R., and von Bitter, P.H.

1980. Upper Cambrian to Lower Ordovician conodont biostratigraphy and biofacies, Rabbitkettle Formation, District of Mackenzie. Life Sciences Contribution, Royal Ontario Museum, vol. 126, pp. 1–42.

Landing, E., Westrop, S.R., and Knox, L.A.

1996. Conodonts, stratigraphy, and relative sea-level changes of the Tribes Hill Formation (Lower Ordovician, east-central New York). Journal of Paleontology, vol. 70, pp. 656–680.

Lindström, M.

1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. Geologiska Föreningens i Stockholm Förhandlingar, vol. 76, pp. 517–604.

Löfgren, A.

1995. The probable origin of the Ordovician conodont "*Cordylodus*" *horridus*. Geobios, vol. 28, pp. 371–377.

1997a. Conodont faunas from the upper Tremadoc at Brattefors, south-central Sweden, and reconstruction of the *Paltodus* apparatus. Geologiska Föreningens i Stockholm Förhandlingar, vol. 119, pp. 257–266.

1997b. Reinterpretation of the Lower Ordovician conodont apparatus *Paraoistodus*. Palaeontology, vol. 40, pp. 913–929.

1999. A septimembrate apparatus model for the Ordovician conodont genus *Cornuodus* Fåhraeus, 1966. Bollettino della Società Paleontologica Italiana, vol. 37, pp. 175–186.

Miller, J.F.

1980. Taxonomic revisions of some Upper Cambrian and Lower Ordovician conodonts with comments on their evolution. University of Kansas Paleontological Contributions, vol. 99, pp. 1–44.

Miller, J.F., and Repetski, J.E.

1993. Taxonomy, morphology, and biostratigraphic position of topotype material of *Cordylodus proavus* from the Upper Signal Mountain Limestone, Arbuckle Mountains, Oklahoma. Geological Society of America Abstracts with Programs, vol. 25, pp. 68.

Müller, K.J.

1959. Kambrische conodonten. Zeitschrift der Deutsche Geologische Gesellschaft, vol. 3, pp. 523–540.

Nicoll, R.S.

1990. The genus *Cordylodus* and a latest Cambrian–earliest Ordovician conodont biostratigraphy. BMR Journal of Australian Geology and Geophysics, vol. 11, pp. 529–558.

1991. Differentiation of Late Cambrian–early Ordovician species of *Cordylodus* (Conodonta) with biapical basal cavities. BMR Journal of Australian Geology and Geophysics, vol. 12, pp. 223–244.

1992. Evolution of the conodont genus *Cordylodus* and the Cambrian-Ordovician boundary. *in* Global Perspectives on Ordovician Geology. B.D. Webby and J.R. Laurie, *eds*, Balkema, Rotterdam, pp. 105–113.

1994. Seximembrate apparatus structure of the Late Cambrian coniform conodont *Teridontus nakamurai* from the Chatsworth Limestone, Georgina Basin, Queensland. AGSO Journal of Australian Geology and Geophysics, vol. 15, pp. 367–379.

Nicoll, R.S., Miller, J.F., Nowlan, G.S., Repetski, J.E., and Ethington, R.L.

1999. *Iapetonudus* (n. gen.) and *Iapetognathus* Landing, unusual earliest Ordovician multielement conodont taxa and their utility for biostratigraphy. Brigham Young University Geology Studies, vol. 44, pp. 27–101.

Nicoll, R.S., and Rexroad, C.B.

1987. Re-examination of Silurian conodont clusters from Northern Indiana. *in* Palaeobiology of conodonts. R.J. Aldridge, *ed.*, Ellis Horwood, Chichester, pp. 49–61.

Nicoll, R.S., and Shergold, J.H.

1991. Revised Late Cambrian (pre-Payntonian–Datsonian) conodont biostratigraphy at Black Mountain, Georgina Basin, western Queensland, Australia. BMR Journal of Australian Geology and Geophysics, vol. 12, pp. 93–118.

Pander, C.H.

1856. Monographie der fossilen Fische des Silurischen Systems der russisch-baltischen Gouvernements. Akademie der Wissenschaften, St. Petersburg, 91 pp.

Purnell, M.A.

1993. The *Kladognathus* apparatus (Conodonta, Carboniferous): homologies with ozarkodinids and the prioniodinid Bauplan. Journal of Paleontology, vol. 67, pp. 875–882.

Purnell, M.A., and Donoghue, P.C.J.

1997. Skeletal architecture and functional morphology of ozarkodinid conodonts. Philosophical Transactions of the Royal Society of London, Series B, vol. 352, pp. 1545–1564.

1998. Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts. Palaeontology, vol. 41, pp. 57–102.

1999. Flattened fossils, physical modelling and the restoration of collapsed skeleton. *in* Functional morphology of the invertebrate skeleton. E. Savazzi, *ed.*, John Wiley & Sons Ltd., Chichester, pp. 91–99.

Purnell, M.A., Donoghue, P.C.J., and Aldridge, R.J.

2000. Orientation and anatomical notation in conodonts. Journal of Paleontology, vol. 74, pp. 113–122.

Purnell, M.A., and von Bitter, P.H.

1996. Bedding-plane assemblages of *Idioprioniodus*, element locations, and the Bauplan of prioniodinid conodonts. *in* Sixth European conodont symposium (ECOS VI), abstracts. J. Dzik, *ed.*, Instytut Paleobiologii PAN, Warsaw, pp. 48.

Repetski, J.E.

1980. Early Ordovician fused conodont clusters from the western United States. *in* Second European conodont symposium (ECOS II), Guidebook, Abstracts. H.P. Schönlaub, *ed.*, Abhandlungen der Geologischen Bundesanstalt, vol. 35, pp. 207–209.

Repetski, J.E., Purnell, M.A., and Barrett, S.F.

1998. The apparatus architecture of *Phragmodus*. *in* Seventh International Conodont Symposium held in Europe, Abstracts. G. Bagnoli, *ed.*, Bologna–Modena, pp. 91–92.

Repetski, J.E., and Szaniawski, H.

1981. Paleobiologic interpretation of Cambrian and earliest Ordovician conodont natural assemblages. U.S. Geological Survey Open-File Report, vol. 81–743, pp. 169–172.

Ross, R.J., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E., and Repetski, J.E.

1997. The Ibexian, lowermost Series in the North American Ordovician. *in* Early Paleozoic biochronology of the Great Basin, western United States. M.E. Taylor, *ed.*, U. S. Geological Survey Professional Paper 1579, pp. 1–50.

Sansom, I.J., Armstrong, H.A., and Smith, M.P.

1994. The apparatus architecture of *Panderodus* and its implications for coniform conodont classification. Palaeontology, vol. 37, pp. 781–799.

Smith, M.P.

1990. The Conodonta—palaeobiology and evolutionary history of a major Palaeozoic chordate group. Geological Magazine, vol. 127, pp. 365–369.

1991. Early Ordovician conodonts of East and North Greenland. Meddelelser om Gronland, Geoscience, vol. 26, pp. 1–81.

Smith, M.P., Briggs, D.E.G., and Aldridge, R.J.

1987. A conodont animal from the lower Silurian of Wisconsin, U.S.A., and the apparatus architecture of panderodontid conodonts. *in* Palaeobiology of conodonts. R.J. Aldridge, *ed.*, Ellis Horwood, Chichester, pp. 91–104.

Stouge, S., and Bagnoli, G.

1988. Early Ordovician conodonts from Cow Head Peninsula, western Newfoundland. Palaeontographica Italica, vol. 75, pp. 89–178.

Sweet, W.C.

1981. Macromorphology of elements and apparatuses. *in* Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 2, Conodonta. R.A. Robison, *ed.*, Geological Society of America and the University of Kansas Press, Lawrence, pp. W5–W20.

1988. The Conodonta: morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum. Clarendon Press, Oxford, 212 pp.

Sweet, W.C., and Donoghue, P.C.J.

2001. Conodonts: past, present and future. Journal of Paleontology, vol. 75, pp. 1174–1184.

Sweet, W.C., and Schönlaub, H.P.

1975. Conodonts of the genus *Oulodus* Branson and Mehl, 1933. Geologica et Palaeontologica, vol. 9, pp. 41–59.

Tolmacheva, T.Y., and Purnell, M.A.

2002. Apparatus composition, growth, and survivorship of the Lower Ordovician conodont *Paracordylodus gracilis* Lindström, 1955. Palaeontology, vol. 45, pp. 209–228.

Viira, V., Sergeyeva, S., and Popov, L.

1987. Earliest representatives of the genus *Cordylodus* (Conodonta) from Cambro-Ordovician boundary beds of north Estonia and Leningrad region. Proceedings of the Academy of Sciences of the Estonian SSR, Geology, vol. 36, pp. 145–153.

Walliser, O.H.

1964. Conodonten des Silurs. Abhandlungen hessisches Landesamt für Bodenforschung, Wiesbaden, vol. 41, pp. 1–106.

Webers, G.F.

1966. The Middle and Upper Ordovician conodont faunas of Minnesota. Minnesota Geological Survey, Special Publication Series, vol. SP-4, pp. 1–123.

A CONODONT-BASED STANDARD REFERENCE SECTION IN CENTRAL NEVADA FOR THE LOWER MIDDLE ORDOVICIAN WHITEROCKIAN SERIES

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ABSTRACT

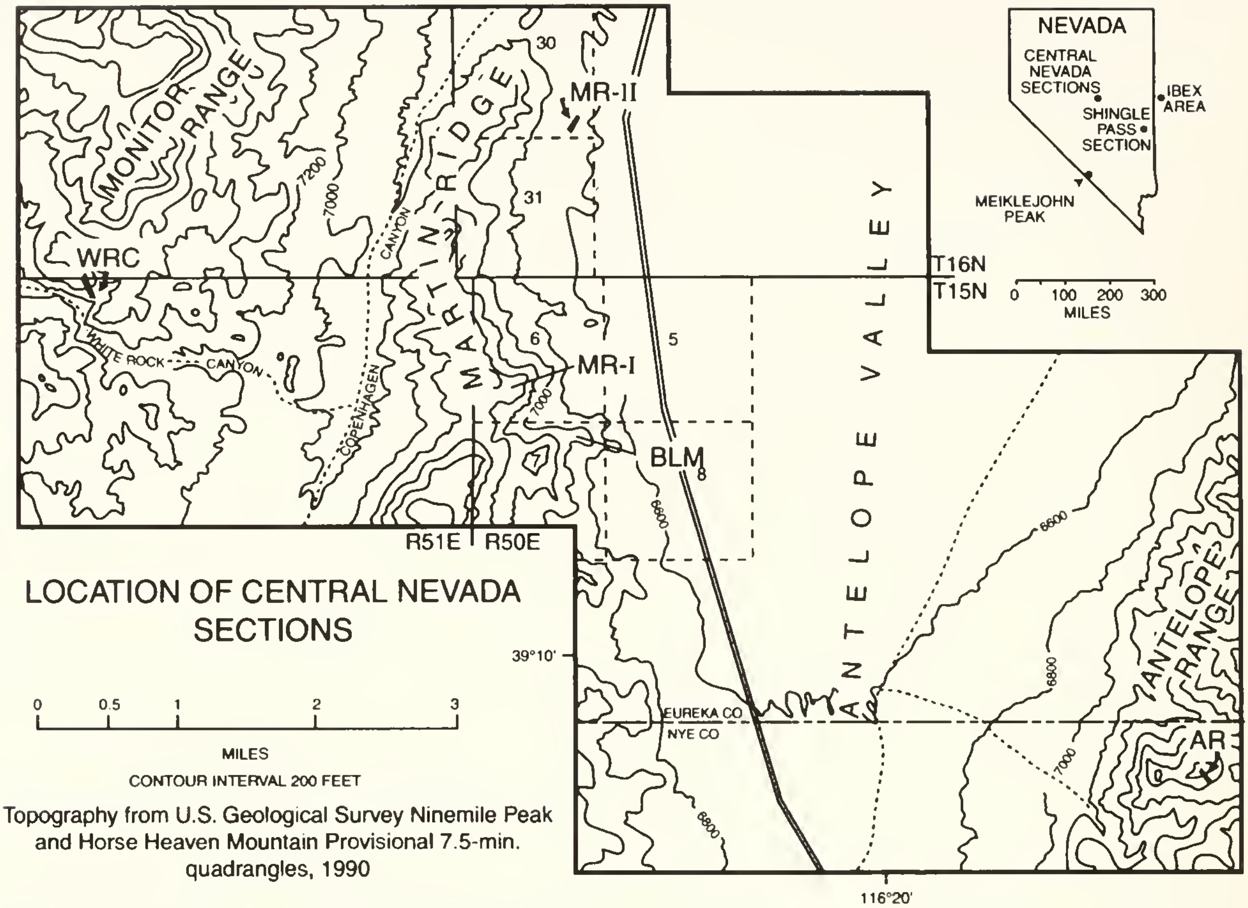
Ranges of conodonts in stratigraphic sections at five localities in the Monitor and Antelope ranges of central Nevada are used graphically to assemble a standard reference section for the lower Middle Ordovician Whiterockian Series. The base of the series is officially 0.3 m above the base of the Antelope Valley Limestone in the stratotype in Whiterock Canyon (Monitor Range). The top is the level at which *Baltoniodus gerdae* makes a brief appearance in an exposure of the Copenhagen Formation on the flanks of Hill 8308 in the western Antelope Range. Graphic compilation of the sections considered in this report also indicates that a level correlative with the base of the Whiterockian Series in the stratotype section is 66 m above the base of the Antelope Valley Limestone in its *de facto* type section on Martin Ridge in the eastern part of the Monitor Range. Ranges, diversity, and the composition of the conodont faunas differ markedly in lithofacies adjacent to the basal boundary of the series; hence we are unable to identify a single conodont species, in a credible developmental sequence, to serve as biological marker of that boundary.

INTRODUCTION

The Whiterockian Series has been recognized since 1982 as the lower of the two series that compose the North American Middle Ordovician. In the scheme proposed by Ross *et al.* (1982) the Whiterockian follows the Lower Ordovician Ibexian Series and precedes the upper Middle Ordovician Mohawkian Series. The Upper Ordovician is the Cincinnatian Series.

Conodonts of the Ibexian Series are well known (Ethington and Clark, 1982; Ross *et al.*, 1997), and their distribution has been thoroughly documented in the Ibex District of western Utah, which includes the standard section of that series. In addition, Sweet and Tolbert (1997) have described a section near Shingle Pass in the southern Egan Range, Nevada, that is not only a useful template for the composite Ibexian standard but also serves as the Ibexian reference section in a network of Ordovician sections compiled graphically by Sweet (1979; 1984; 1995a, 1995b). In the latter two publications, Sweet describes the progressive development of a composite standard that includes rocks assignable to the upper Whiterockian, the Mohawkian, and the Cincinnatian Series. That composite is based on conodont range-data from more than 80 sections in central and eastern North America.

Although the identity and ranges of conodonts in different parts of the Whiterockian Series are now fairly well known (*e.g.*, Ethington and Schumacher, 1969; Bradshaw, 1969; Harris *et al.*, 1979; Stouge, 1984; Bauer, 1987; Ross and Ethington, 1991), no reference section that spans the entire series has been established in the central Nevada type area. Such a section is essential to linking the Ibexian and the upper Whiterockian-Mohawkian-Cincinnatian standards and thus completing the graphic framework for the North American Ordovician recently summarized by Sweet



Text-figure 1.—Location of central Nevada sections considered in this report. WRC = Whiterock Canyon section; BLM = BLM Fence section; MR-I = Martin Ridge South section; MR-II = Martin Ridge North section; AR = Hill 8308 section, Antelope Range. Inset outline map of Nevada also shows approximate location of the Meiklejohn Peak, Ibex Area, and Shingle Pass sections with which central Nevada sections are correlated in this report.

(1995a, 1995b). It is thus the purpose of this report to describe graphic assembly of a continuous, conodont-based Whiterockian reference standard using information derived from five stratigraphic sections in central Nevada, and to show how this composite section might be used to link previously described reference sections for the Ibexian, Mohawkian, and Cincinnatian Series.

ACKNOWLEDGMENTS

Carrie Wilson and Karen Tyler, Department of Geological Sciences, The Ohio State University, prepared the line drawings that accompany this report. We have also relied heavily on an excellent, unpublished Bachelors Thesis prepared by Alice W. Spencer in 1984 while she was an undergraduate advisee of Reuben J. Ross, Jr., at the Colorado School of Mines, Golden, Colorado. We also thank Stanley J. Finney and Reuben J. Ross, Jr. for thorough reviews, which have helped improve our report.

THE SECTIONS

For reasons of structure, access, and facies, we have not identified a single section that spans the entire Whiterockian Series in its type area. Hence, the reference section we describe is a composite, assembled primarily from information at five sites in the Monitor and Antelope ranges of central Nevada (Text-fig. 1) but including important data from the Meiklejohn Peak section of southern Nevada abstracted from reports by Ross and Ethington (1992) and Harris *et al.* (1979).

WHITEROCK CANYON SECTION (WRC)

The Whiterock Canyon section, in the Monitor Range, is located and described in recent publications by Ross and Ethington (1991, 1992), whose reports also include diagrams that chart the ranges in the section of conodonts and other fossils. The WRC section includes the upper 43 m of the Ibexian Ninemile Formation and the lower 120 m of the superjacent Antelope Valley Limestone. A spike, implanted 0.3 m above the base of the Antelope Valley Limestone formally marks the base of the Whiterockian Series. In August 1998, Ethington and Sweet (with the assistance of R. Ripperdan and J. Cooper) collected additional samples from the uppermost Ninemile and the lower few meters of the Antelope Valley. We include in this report information on the conodonts isolated from these samples by Ethington.

BLM FENCE SECTION (BLM)

This long section is in the NE¼ sec. 7, T 15 N, R 50 E (Horse Heaven and Ninemile Canyon, Nevada, 7.5-min. quadrangles). The section, is on the east side of Martin Ridge, in the Monitor Range, and roughly parallels an east-west fence established by the Bureau of Land Management. The base of the section is accessible by vehicle on a track along the fence that joins the county road at the foot of Martin Ridge about one mile southeast of the section we here describe as MR-1. The BLM section includes 407 m of Antelope Valley Limestone succeeded by an unmeasured, unsampled and poorly exposed succession of largely clastic rocks representing the Copenhagen Formation. The Antelope Valley was sampled at 5- to 6-m intervals on July 30, 1966 by Ethington and Dietmar Schumacher and revisited by the same persons in June 1968. The Copenhagen Formation was not sampled. Conodonts derived from the 47 samples processed are identified here for the first time.

MARTIN RIDGE SOUTH SECTION (MR-1)

This readily accessible section on the east side of Martin Ridge, is the *de facto* type section of the Antelope Valley Limestone. It is situated in the center of the SW¼ of section 6, T 15 N, R 50 E (Horse Heaven Mountain, Nevada, 1:62,500 quadrangle). On the long east-trending ridge up which this section was measured, 342 m of the Antelope Valley Limestone are exposed. The basal contact of the formation is not exposed at this locality, but sandy beds poorly exposed in a swale beyond the topmost carbonate beds of the Antelope Valley suggested to Harris *et al.* (1979) that the section includes the upper contact, with the Copenhagen Formation. Our studies indicate, on the other hand, that some 71 m of the upper Antelope Valley have probably been cut out along a fault.

In August 1975, Anita Harris and Reuben J. Ross, Jr., measured the MR-I section and collected 49 large carbonate samples from it at 5- to 6-m intervals. Some of the conodonts Harris recovered from acid residues of these samples were illustrated in a 1979 report by Harris *et al.*, and they were also made available to Sweet (1995b), who used their ranges in a preliminary graphic attempt to link his Ibexian and Mohawkian composite standards.

MARTIN RIDGE NORTH SECTION (MR-II)

The short Martin Ridge North section is 3.2 km north of the MR-1 section, in the SE¼ of section 30, T 16 N, R 50 E (Horse Heaven Mountain, Nevada, 1: 62,500 quadrangle). In the section at this locality, near the north end of Martin Ridge (Monitor Range), the uppermost beds of the Antelope Valley Limestone are succeeded directly by sandy strata of the Copenhagen Formation. The section, which is a little more than 16 m thick, was closely sampled in 1975 by Anita G. Harris, and a diagrammatic view of it is given in figure 17 of the 1979 report by Harris *et al.* Conodonts recovered from this short section represent a very different fauna from that in the uppermost Antelope Valley Limestone at the MR-1 locality, and this led Harris *et al.* (1979) to speculate that the upper Antelope Valley in MR-1 had either been cut out along an unrecognized fault, or that "differences in environmental conditions during deposition resulted in two distinct but coeval conodont biofacies." Our studies indicate that the first of these explanations is almost certainly the correct one.

HILL 8308 SECTION (AR)

The Hill 8308 section, which includes the upper 50 m of the Antelope Valley Limestone, a complete Copenhagen Formation, and the lowermost beds of the Eureka Quartzite, is situated on the flanks of hill 8308 in the SW¼ of section 24, T 15 N, R 50 E (Horse Heaven Mountain, Nevada, 1:62,500 quadrangle). The section was measured and sampled for conodonts in 1975, 1978, and 1982 by Anita G. Harris, Alice W. Spencer, and Reuben J. Ross, Jr., assisted in 1982 by J. Webber and R. T. Lierman. A diagrammatic view of the section is given in figure 3 of Harris *et al.* (1979) and conodonts recovered from the Copenhagen Formation are the subjects of an excellent, unpublished 1984 Bachelor's Thesis by Alice W. Spencer.

THE CONODONTS

In compiling a standard reference section for the Whiterockian Series we have had available to us information on the measured ranges of 134 species-level conodont taxa. However, only the 88 species listed in Table 1 are known from two or more sections and are thus usable in graphic correlation. A majority of the 88 species listed in Table 1 are well-known taxa that have been described and illustrated in recent reports and require no emendation or modification. A few, however, are of especial importance in correlating Whiterockian sections or in characterizing Whiterock-

Table 1.—Whiterockian Conodont species.*

Index No.		Index No.	
2	*Amorphognathus tvaerensis*	72	*P. panderi*
3	*Ansella jemtlandica*	73	*Parapanderodus asymmetricus*
4	*A. nevadensis*	74	*P. emarginatus*
5	*A. robusta*	75	*P. striatus*
8	*Baltoniodus gerdae*	76	*Paraprioniodus* n. sp.
9	*B. variabilis*	77	*P. costatus*
11	*Belodina compressa*	79	*Paroistodus originalis*
12	*B. monitorensis*	80	*P. parallelus*
16	*Cahabagnathus friendsvillensis*	81	*Periodon aculeatus*
17	*C. sweeti*	82	*P. flabellum*
18	*Chosonodina rigbyi*	83	*P. gladysi*
21	*Colaptoconus quadraplicatus*	84	*P. grandis*
22	*Cornuodus longibasis*	86	*Phragmodus flexuosus*
24	*Dapsilodus mutatus*	87	*P. inflexus*
25	*D. variabilis*	88	*P. undatus*
28	*Dischidagnathus primus*	89	*Plectodina aculeata*
29	*Drepanodus arcuatus*	90	*P. tenuis*
31	*Drepanoistodus angulensis*	91	*Polyplacognathus ramosus*
32	*D. forceps*	92	*Prattognathus rutriformis*
33	*D. suberectus*	94	*Protopanderodus elongatus*
35	*Eoplacognathus elongatus*	95	*P. gradatus*
36	*E. foliaceus-reclinatus*	96	*P. leonardii*
37	*Erraticodon balticus*	97	*P. rectus*
40	*Fahraeusodus marathonensis*	98	*P. robustus*
42	*Histiodella altifrons*	99	*P. varicostatus*
43	*H. holodentata*	100	*Protoprioniodus aranda*
44	*H. minutiserrata*	101	*P. nyintii*
45	*H. serrata*	102	*P. papilosus*
46	*H. sinuosa*	105	*Pteracontiodus alatus*
50	*Juanognathus jaanussoni*	107	*P. cryptodens*
51	*J. variabilis*	108	*P. gracilis*
52	*Jumudontus gananda*	110	*Pygodus anserinus*
54	"*Loxodus*" *curvatus*	111	*P. serrus*
55	*Microzarkodina flabellum*	112	*Reutterodus andinus* of E. & C.
56	*Multioistodus subdentatus*	115	*Scalpellodus latus* of Cooper
57	*Neomultioistodus compressus*	117	*Scandodus* sp. *aff. S. flexuosus*
58	*Oelandodus costatus*	119	"*Scandodus*" *sinuosus*
59	*Oepikodus communis*	121	*Scolopodus rex*
60	*O. evae*	122	*Spinodus* sp. *aff. S. spinatus*
61	*Oistodus lanceolatus*	124	*Staufferella falcata*
62	*O. multicorrugatus*	127	*Thrincodus palaris*
64	*O.* n. sp.	130	*Tripodus combsi*
67	*Paltodus jemtlandicus*	132	*Walliserodus ethingtoni*
69	*P. sweeti*	134	*Yaoxianognathus abruptus*
71	*Panderodus gracilis*		

* Gaps in index-no. sequence indicate that the list includes only species used in correlation.

ian faunas. We illustrate these species on Plate 1 and append the following notes about them.

Ansella

Species of *Ansella* are represented by *A. nevadensis* and *A. robusta* in the upper part of the standard reference section assembled herein, and by *A. jemtlandica* (Pl. 1, figs. 4–7) in the lower. *A. jemtlandica* is also known from the lower part of the Antelope Valley Limestone in the Meiklejohn Peak section (MJP) and in early Whiterockian strata in the northern Ranger Mountains of southern Nevada (Ross and Ethington, 1992).

Baltoniodus gerdae

Baltoniodus gerdae (Bergström) (Pl. 1, figs. 20, 21). Since 1982, the first occurrence of this species has been used to mark the base of the upper Middle Ordovician Mohawkian Series, and thus the top of the subjacent Whiterockian Series (Ross *et al.*, 1982). In central Nevada, representatives of *B. gerdae* have been collected from the AR section and they have also been reported from high in the Antelope Valley Limestone in the Meiklejohn Peak section of southern Nevada (Harris *et al.*, 1979). Both occurrences are of great importance in effecting the correlations described in this report.

Histiodella

Species of *Histiodella* characterize early Whiterockian conodont faunas in the Nevada, Utah, and Oklahoma sections considered in this report and we illustrate elements typical of several species in Plate 1. *Histiodella altifrons* (Pl. 1, figs. 23, 24), the earliest Whiterockian species, has smooth-edged albid, carminate and alate elements that are subtriangular in lateral view. The carminate elements of *H. minutiserrata* have minutely serrated margins; those of *H. sinuosa* (Pl. 1, fig. 22) have crenulate posterior margins; and comparable elements of *H. serrata* (Pl. 1, fig. 32) display a distinct cusp, a conspicuously denticulated posterior process, and a steeply sloping, denticulated anterior process. *H. holodentata*, adequately diagnosed and illustrated by Ethington and Clark (1982, pl. 4, figs. 1, 3, 4, 16), is the youngest *Histiodella* species recognized thus far in central Nevada.

The morphologic progression from *Histiodella altifrons* through *H. minutiserrata* to *H. sinuosa*, *H. serrata*, and *H. holodentata* suggests evolutionary development and the sequence is repeated in every section for which we currently have information. However, McHargue (1982) demonstrated from study of huge collections of *Histiodella* from the Joins Formation of south-central Oklahoma that carminate elements with the characters we have used to identify species of the genus appear gradually in populations so that there is considerable stratigraphic overlap between elements with the characters of one species and those with characters of its successor. Thus, for example, elements typical of *H. minutiserrata* appear first in Joins collections dominated by smooth-margined forms like the ones we have recognized as *H. altifrons*. In like manner, anteriorly denticulated elements like those of *H. sinuosa* appear early in the range of Joins collections dominated by the minutely serrated elements we identify as *H. minutiserrata*. Because most of our samples from Nevada and Utah contain only a few *Histiodella* elements, the composition of the populations from which they were drawn cannot be determined. Thus, although *Histiodella* was a distinctive component of early Whiterockian conodont faunas, we have found it difficult to use the ranges of its species very effectively in graphic correlation.

Neomultioistodus compressus

The semi-hyaline elements of *Neomultioistodus compressus* (Pl. 1, figs. 14–19) dominate collections from the Joins and Oil Creek formations of south-central Oklahoma. They also occur in samples from lower Whiterockian strata in western Utah and eastern Nevada, but are not numerous in those samples or in the few from central Nevada that yield them. We illustrate an array of typical specimens from the base of the Antelope Valley Limestone in the WRC section primarily as examples of a Whiterockian fauna that is present in central Nevada but only weakly represented there.

Oistodus n. sp.

Several samples from the BLM, Martin Ridge South (MR-I) and Whiterock Canyon sections yield large elements (Pl. 1, fig. 31) reminiscent of those of *Oistodus multicorrugatus*, but with a tall, posteriorly-inclined denticle atop the short posterior process. The species represented by these elements is useful in graphic correlation, but we defer formal diagnosis to a systematic treatment of Whiterockian conodonts now in preparation.

Paraprioniodus n. sp.

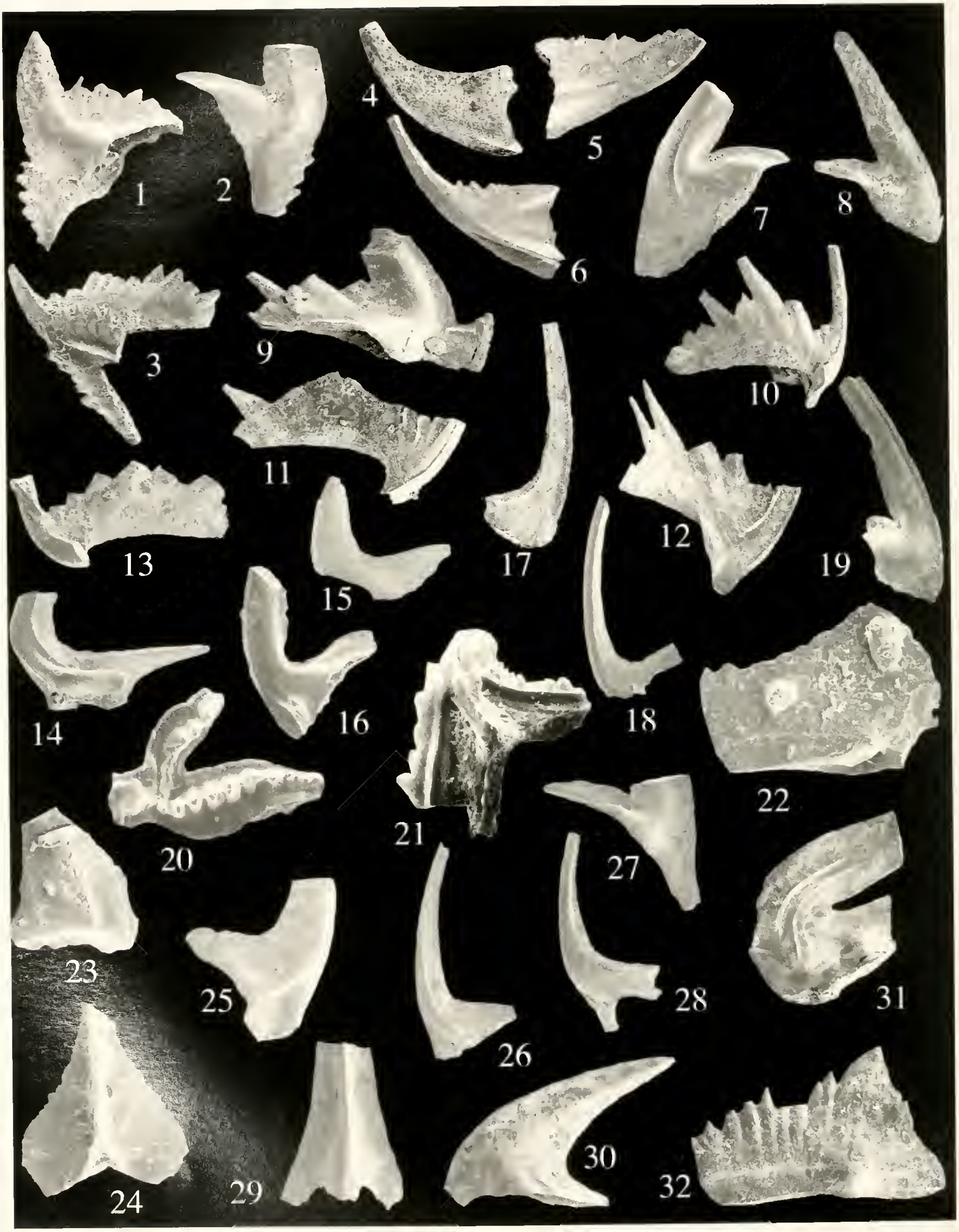
In their report on Ibexian conodonts, Ethington and Clark (1982) identified this species as *Paraprioniodus costatus* (Mound) and provided excellent illustrations of components of its multielement apparatus. Studies of large collections from the Joins and Oil Creek formations of south-central Oklahoma suggest that *P. costatus* had a geniculate coniform element in the M position, rather than the dolabrate form Ethington and Clark illustrated. Joins and Oil Creek faunas are currently under study by Jeffrey A. Bauer, of Shawnee State University, who will name, diagnose and illustrate this new species, so we list it here in open nomenclature.

Periodon gladysi

Periodon gladysi Albanesi, 1998 (Pl. 1, figs. 1–3), based on specimens from the San Juan Formation of the Argentine Precordillera, has not previously been reported from North America. It is represented in two of the sections (BLM, WRC) considered in this report and is important in correlating those sections. We illustrate three specimens from WRC and compare them on Plate 1 with elements of *Periodon flabellum* (Pl. 1, figs. 8–13) which is known from the BLM, MR-I, and WRC sections in central Nevada, the Meiklejohn Peak (MJP) section in southern Nevada, and from Ordovician strata in the Argentine Precordillera regarded by Albanesi (1998) as of mid- to late Arenigian age.

Tripodus combsi (Plate 1, figs. 25–30)

From elements in lower Whiterockian strata in western Utah, Ethington and Clark (1982) assembled a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multielement species for which they used the name *Tripodus laevis* Bradshaw. In 1984, Stouge recognized a species whose apparatus is identical to that of Ethington and Clark's *T. laevis*, but also includes elements like those Bradshaw (1969) named *Acodus combsi*. We now agree with Stouge's reconstruction and his choice of "*combsi*" as trivial name; however, because the apparatus includes the type form-species of Bradshaw's *Tripodus*, we follow the conservative procedure of assigning the species to *Tripodus*, rather than *Acodus*, whose apparatus anatomy is still unkown.

ASSEMBLY OF WHITEROCKIAN STANDARD

Using the data on stratigraphic ranges of conodonts summarized in Appendix A and the graphic-correlation procedures described by Shaw (1964), we have assembled a standard reference section for the Whi-

←

PLATE 1

Figures are digital images of conodont elements from Whiterockian strata in central Nevada. Numbers prefixed by OSU refer to catalog of the Orton Museum of Geology, The Ohio State University, Columbus, Ohio. Numbers prefixed by USNM refer to catalog of the U. S. National Museum, Washington, DC.

- 1–3. *Periodon gladysi* Albanesi, 1998
  - 1. Pa element, lateral view, ×90. 10 m above base of Antelope Valley Limestone, Whiterock Canyon section. OSU 51151.
  - 2. M element, lateral view, ×102. 10 m above base of Antelope Valley Limestone, Whiterock Canyon section. OSU 51152.
  - 3. Sa element, lateral view, ×99. 10 m above base of Antelope Valley Limestone, Whiterock Canyon section. OSU 51153.
- 4–7. *Ansella jemtlandica* (Löfgren, 1978)
  - 4. Sb element, lateral view, ×55. 4.5 m above base Antelope Valley Limestone, Whiterock Canyon section. OSU 51154.
  - 5. Sc element, lateral view, ×55. 4.5 m above base Antelope Valley Limestone, Whiterock Canyon section. OSU 51155.
  - 6. Sa element, lateral view, ×55. 4.5 m above base Antelope Valley Limestone, Whiterock Canyon section. OSU 51156.
  - 7. M element, lateral view, ×55. 4.5 m above base Antelope Valley Limestone, Whiterock Canyon section. OSU 51157.
- 8–13. *Periodon flabellum* (Lindström, 1955)
  - 8. M element, lateral view, ×60. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51158.
  - 9. Pa element, lateral view, ×55. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51159.
  - 10. Sd element, lateral view, ×65. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51160.
  - 11. Sb element, lateral view, ×65. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51161.
  - 12. Sc element, lateral view, ×65. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51162.
  - 13. Sa element, lateral view, ×70. Basal 0.15 m Antelope Valley Limestone, Whiterock Canyon section. OSU 51163.
- 14–19. *Neomultioistodus compressus* (Harris and Harris, 1965)
  - 14. Sa element, lateral view, ×75. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51164.
  - 15. Sc element, lateral view, ×60. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51165.
  - 16. Pa element, lateral view ×75. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51166.
  - 17. Pb? element, lateral view, ×60. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51167.
  - 18. Sb element, lateral view, ×75. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51168.
  - 19. M element, lateral view, ×50. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51169.
- 20, 21. *Baltoniodus gerdae* (Bergström, 1971)
  - 20. "Amorphognathiform" P element, view of upper surface, ×33. 126 m above base of Hill 8308 section, Antelope Range. USNM 258551. [specimen also illustrated as fig. 15, pl. 5, in Harris *et al.*, 1979]
  - 21. "Prioniodontiform" P element, lateral view, ×44. 126 M above base of Hill 8308 section, Antelope Range. USNM 258550. [specimen also illustrated as fig. 14, pl. 5, in Harris *et al.*, 1979].
- 22. *Histiodella sinuosa* (Graves and Ellison, 1941)
  - 22. P element, lateral view, ×105. 16.8 m above base of Antelope Valley Limestone, Whiterock Canyon section. OSU 51170.
- 23, 24. *Histiodella altifrons* Harris, 1962
  - 23. P element, lateral view, ×140. 41.5 m above base Ninemile Formation, Whiterock Canyon section. OSU 51171.
  - 24. Sa element, posterior view, ×140. 41.5 m above base Ninemile Formation, Whiterock Canyon section. OSU 51172.
- 25–30. *Tripodus combsi* (Bradshaw, 1969)
  - 25. Sc element, lateral view, ×61. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51173.
  - 26. Sbb element, lateral view, ×60. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51174.
  - 27. M element, lateral view, ×60. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51175.
  - 28. Sba element, lateral view, ×61. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51176.
  - 29. Sa element, posterior view, ×70. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51177.
  - 30. P element, lateral view, ×62. Basal ledge of Antelope Valley Limestone, Whiterock Canyon section. OSU 51178.
- 31. *Oistodus* n. sp.
  - 31. Lateral view, ×45. 14.5 m above base of Antelope Valley Limestone, Whiterock Canyon section. OSU 51179.
- 32. *Histiodella serrata* Harris, 1962
  - 32. P element, lateral view, ×120. 54 m above base Antelope Valley Limestone, Whiterock Canyon section. OSU 51180.

terockian Series in central Nevada, the type area. Our procedures are summarized as follows:

Preliminary Steps

The BLM section includes the greatest thickness of Antelope Valley Limestone in any of the five sections for which we have information. Further, the BLM section continues upward to the Copenhagen Formation without any obvious break. Consequently, we chose this section as the base, or reference section, for compilation of a standard.

Like the BLM section, section MR-II, at the north end of Martin Ridge includes the upper few meters of the Antelope Valley, the Antelope Valley/Copenhagen contact, and the lower few meters of the Copenhagen. Section MR-II is too short to be integrated graphically, but it provides important information on stratigraphically significant conodonts in the boundary interval. Hence, on the assumption that the Antelope Valley/Copenhagen contact is at the same level (407 m) in both BLM and MR-II, we added range information from MR-II to BLM and used the combined section as the base for further graphic correlations. Ranges of conodonts in the combined section are listed in the column of Appendix A headed BLM+MRII.

The graph of Text-figure 2A compares ranges of conodont species common to the AR section and the combined BLM+MII section. Although the plotted array is rather diffuse, a line of correlation (LOC) with a slope of 1.0 and an X-axis intercept of 357 bisects a much narrower array that includes the upper range limits of species 31 (*Drepanoistodus angulensis*) and 76 (*Paraprioniodus* n. sp.), the first and last occurrences of species 36 (*Eoplacognathus foliaceus–reclinatus*), and the Antelope Valley/Copenhagen contact (plotted as an "x"). Thus, in the column of Appendix A headed AR+357, we have added 357 m to ranges in the AR column, and, in the column headed CS-1 we have combined BLM+MII and AR ranges.

A final step in this preliminary phase of assembly involved graphic comparison of section MR-I with CS-1. This comparison is depicted in Text-figure 2B. Although there was probably little appreciable difference in rock-accumulation rate between MR-I and nearby BLM, the slope coefficient (0.93) of the LOC in Text-figure 2B suggests that rock accumulated slightly more rapidly at MR-I than at BLM. We suspect, however, that the slight difference in accumulation rate suggested by the lower coefficient is more probably attributable to differences in section-measurement procedures and placement of samples. In any event, we used the LOC given in Text-figure 2B to determine BLM-equivalent ranges for species identified in MR-I and used these in compiling a composite section that utilizes range information from the three Monitor Range sections and the one in the northern Antelope Range. That composite section is indicated in Appendix A in the column headed WRCS-1.

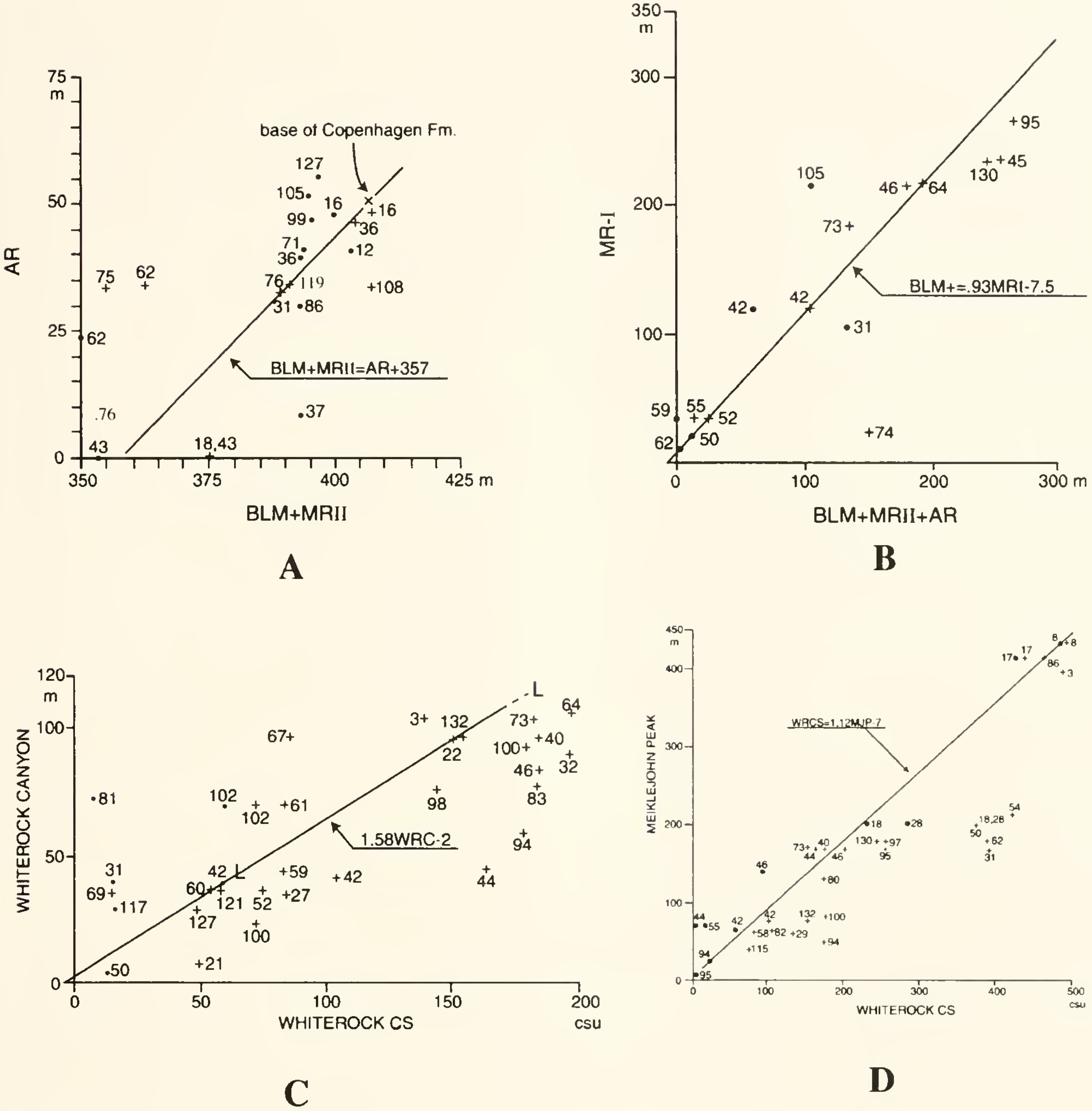
Logically, addition of the Whiterock Canyon section (WRC) would have been the next step in assembly of a Whiterockian standard section, for that section includes the "spike" that officially marks the base of the series (Ross and Ethington, 1991). However, Appendix A indicates that there are substantial differences in the ranges of critical species in the two sections and these differences would influence graphic correlation. For example, in WRC, *Histiodella altifrons* and *Tripodus combsi* make their debut at the same level (40 m), whereas in WRCS-1 the first occurrence of *T. combsi* precedes that of *H. altifrons* by 60 m. Also, *H. altifrons* has a very short range (10 m) in WRC, but is represented through 45 m of strata in WRCS-1. Additionally, Ninemile Formation samples below the 40 m level in WRC yield many conodonts of Ibexian stamp that are largely unrepresented in the lower part of WRCS-1.

Integration of Meiklejohn Peak Section

Because of the problems with the Whiterock Canyon section (WRC) just mentioned, our next step was integration of the section at Meiklejohn Peak, Nevada (MJP), which was established by Ross and Ethington (1991, 1992) as a reference section for the basal part of the Whiterockian Series. In composing the graph of Text-figure 2D, we combined range data for conodonts from the *Orthidiella* Zone (or Zone L) given by Ross and Ethington (1992) with data from the upper part of the Antelope Valley Limestone given in text-fig. 13 of Harris *et al.* (1979). This information was then plotted (on the Y axis) against ranges (on the X axis) of the same conodont species in WRCS-1. The LOC of Text-figure 2D lacks control in its mid-portion, but is otherwise a credible indication of the relation between Whiterockian strata in these two parts of Nevada. Using the LOC equation, WRCS = 1.12 MJP − 7, we then added information from the Meiklejohn Peak section to the Whiterock CS. The now more inclusive WRCS-2 is in Appendix A.

Compilation of Whiterock Canyon Section

With data from Meiklejohn Peak included in WRCS-2, we then plotted range data from the section in Whiterock Canyon (WRC) that includes the basal stratotype of the Whiterockian Series (Ross and Ethington, 1991). This plot, shown in Text-figure 2C, results in an array that is quite diffuse and might be interpreted in several ways. The LOC shown in Text-figure 2C is drawn at the interface between segments



Text-figure 2.—A, Graphic correlation of Hill 8308 (AR) section with combined BLM and MRII sections. B, Graphic correlation of Martin Ridge South (MR-I) section with composite section BLM+MRII+AR. C, Graphic correlation of Whiterock Canyon section with a Whiterock CS, which is a composite of information from BLM, MRI, MRII, AR, and MJP. D, Graphic correlation of Meiklejohn Peak (MJP) section with the Whiterock CS, a composite of information from BLM, MRI, MRII, and AR. In all graphs, dots represent common range bases; crosses mark common range tops. In A, "x" marks base of Copenhagen Formation; in C, "Ls" mark base and top of brachiopod Zone L projected from MJP section. Numbers near dots and crosses are keyed to species numbers in Table 1.

of the graph that include (on the right) a majority of the upper range limits and (on the left) all but one of the plotted first occurrences. In fitting this line we were also influenced by projection from the Meiklejohn Peak section of the lower and upper limits of the *Orthidiella* Zone, which has been equated with Zone L of Ross (1951). These limits are shown in Text-figure 2C as "L's". Because the spike implanted at 43 m in the WRC section officially marks the base of the Whiterockian Series (and the *Orthidiella* Zone), we are now able to project that level into the Whiterockian Composite section (WRCS-3). It is thus 66 csu above the base of that section, or 66 m above the base of the exposed Antelope Valley Limestone in the BLM section on the east side of Martin Ridge.

REGIONAL CORRELATIONS

Over the years, conclusions derived from biostratigraphic studies at other localities in western North America have crystallized into concepts of "basal Whiterockian" that have been widely applied and accepted (*e.g.*, Ross *et al.*, 1997; Sweet and Tolbert, 1997; Fortey and Droser, 1996). Thus, our next step in establishing a Whiterockian standard was to compare the Whiterock CS (WRCS-3) graphically with well-established sections in other parts of the country known, or reputed to include strata of Whiterockian age. For this purpose we considered sections in the Ibex District of western Utah (Hintze, 1952; Ross *et al.*, 1997); the Shingle Pass section in the southern Egan Range of eastern Nevada (Sweet and Tolbert, 1997); a West Spring Creek-Simpson section on the southern flank of the Arbuckle Mountains in south-central Oklahoma; and the Mohawkian-Cincinnatian Composite Standard Section (MC-CS) assembled by Sweet (1995a, 1995b) from sections at more than 80 localities in Midcontinent and eastern United States and including supposed equivalents of the upper Whiterockian (=Chazyan) in its lower part.

Correlation with Midcontinent Composite Standard

In the graph of Text-figure 3A, we compare ranges of conodont species in WRCS-3 with ranges of upper Whiterockian species in the MC-CS. This procedure is identical to the one employed by Sweet (1995b), but, with the better-controlled range data of the present study, yields a LOC described by a slightly different equation. Using MC-CS = 0.658 WRCS + 559, the equation of the LOC drawn in Text-figure 3A, ranges summarized in WRCS-3 were translated into MC-CS values, with the results listed in the column of Appendix B headed *.658 + 559 and a new composite section was assembled from the lowest and highest range values in the two sets. Those values are listed in Appendix B in the column headed MC-CS-1.

Correlation with Arbuckle Mountains Section

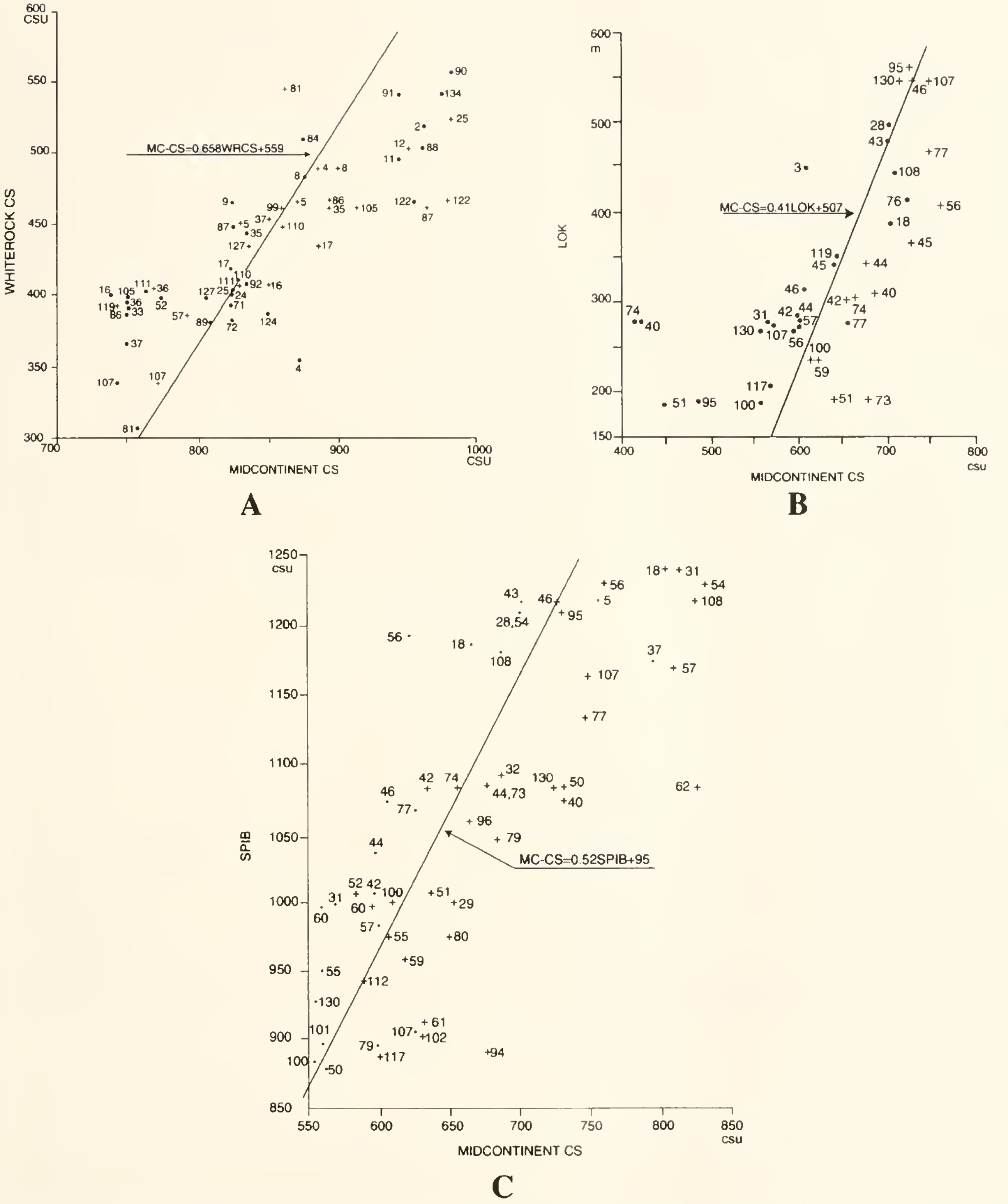
Following creation of a composite section stated in terms of MC-CS, we then compared ranges of conodont species assembled in that section graphically with those in a 557-m section (LOK) on the south flank of the Arbuckle Mountains in south-central Oklahoma that includes the upper part of the West Spring Creek Formation and the Joins and Oil Creek formations. The graph of Text-figure 3B displays results of the comparison of LOK with a MC-CS now augmented by data from Whiterockian sections in central Nevada. The LOC of this graph was fitted to an array of range-limits that are well controlled in both MC-CS and LOK. LOK values were then converted to MC-CS values by use of the equation, MC-CS = 0.41LOK + 507 and a new composite was composed by selecting the lowest and highest range values for each species from the two data sets. That composite is listed in the column of Appendix B headed MC-CS-2.

Correlation with Shingle Pass-Ibex Area Composite Section

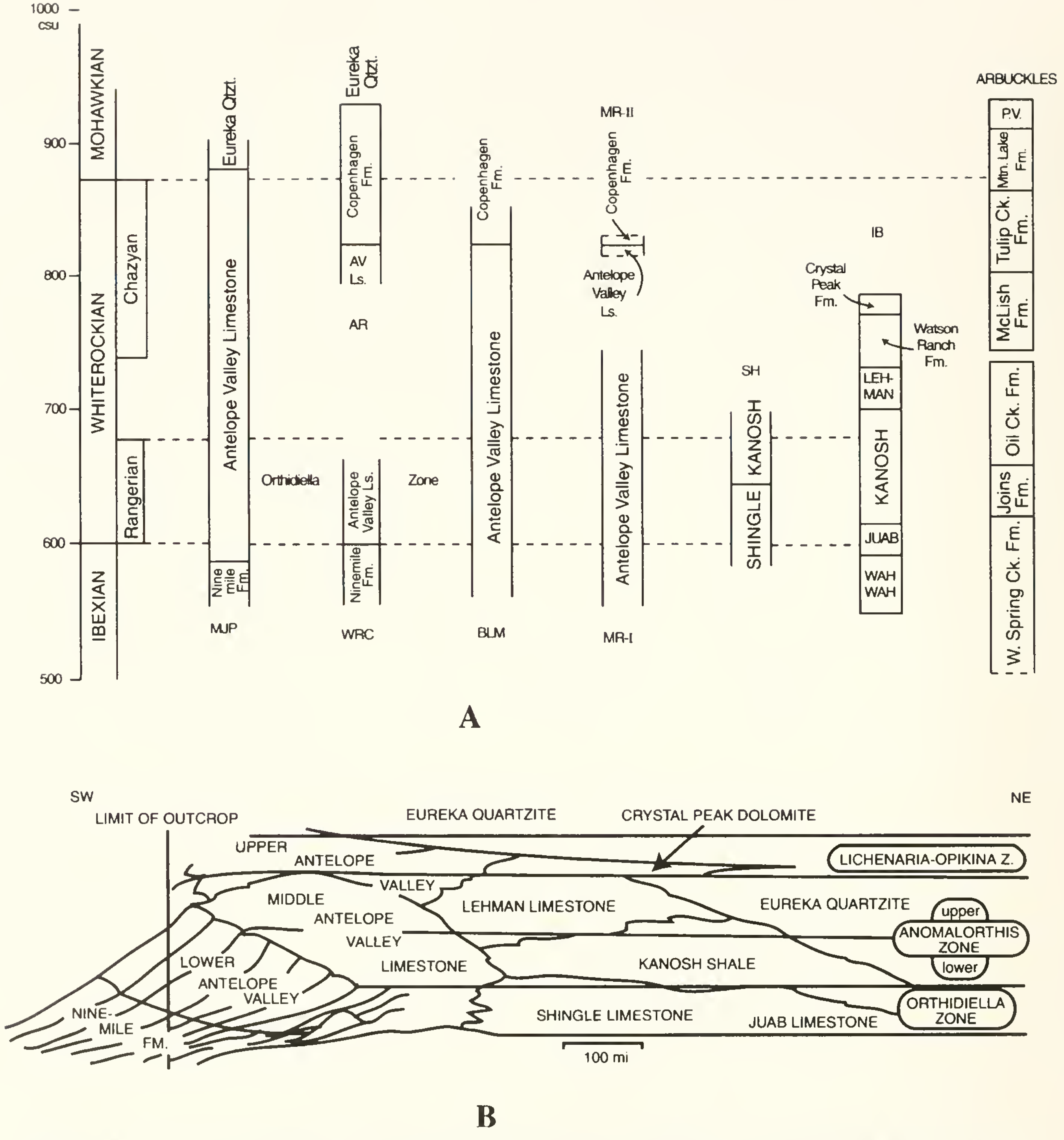
Finally, in Text-figure 3C we compare MC-CS-2 graphically with data from a regional composite section (SPIB) that combines range information from sections at Shingle Pass, in eastern Nevada, and the Ibex District of western Utah. This regional composite, given in detail in Appendix 3 of Sweet and Tolbert (1997), is primarily of Ibexian conodont species, but also includes information on the ranges of Whiterockian species in its upper part. The well-controlled LOC of Text-figure 3C is described by the equation, MC-CS = 0.52 SPIB + 95, and we used this equation to convert SPIB range values into MC-CS-equivalent ones. MC-CS and converted SPIB values were then combined, as previously, into a new MC-CS-3, which now summarizes range data from central and eastern Nevada, western Utah, south-central Oklahoma and the lower part of a Midcontinent composite section. Ranges in this augmented MC-CS are stated in terms of the Midcontinent Composite Standard Section, which now includes information from the base to the top of the Ordovician System in the United States.

CONCLUSIONS

In Text-fig. 4, the results of our conodont-based correlation of Whiterockian sections in Nevada, Utah, and Oklahoma (Text-fig. 4A) are compared with a diagrammatic representation of the facies components of the Whiterockian shelf published by Ross *et al.* (1989) (Text-fig. 4B). In most respects the results of the two studies agree, but they differ in at least two obvious aspects. First, the upper limit of the *Orthidiella* brachiopod Zone, controlled in Text-figure 4A by the sections at Meiklejohn Peak and Whiterock Canyon, projects into the conodont-based framework at a level well above the middle of the Kanosh Shale, at Ibex, and thus to about the mid-point of the supposedly superjacent *Anomalorthis* brachiopod Zone shown in Text-figure 4B. Unfortunately, scaled ranges of the brachiopod species that define the *Anomalorthis* Zone are not available for sections in our graphically compiled network, so we cannot evaluate this disparity in



Text-figure 3.—Graphic correlation of A, Midcontinent CS and Whiterock CS; B, Arbuckle Mountains (LOK) section, and C, Shingle Pass-Ibex Area composite section with a Midcontinent Composite Section that includes values projected from the Whiterock Composite section. In all three graphs, dots mark common range bases and crosses mark common range tops. Numbers near dots and crosses are keyed to species numbers in Table 1.



Text-figure 4.—A. Diagrammatic assembly of the sections correlated graphically in this report. Vertical scale is that of the Midcontinent Composite Standard Section (Sweet, 1995b). MJP = Meiklejohn Peak section; AR = Hill 8308 section in Antelope Range; WRC = Whiterock Canyon section; BLM = BLM Fence section; MR-II = Martin Ridge North section; MR-I = Martin Ridge South section; SH = Shingle Pass section, southern Egan Range, Nevada; IB = Ibex area composite section, western Utah; Arbuckles = section along Interstate Highway 35 on south flank of Arbuckle Mountains, Carter County, Oklahoma. B. Diagrammatic cross-section of the Whiterockian carbonate shelf reconstructed by Ross *et al.*, 1989.

results. It may be noted, however, that *Anomalorthis* occurs within the *Orthidiella* Zone at a number of places, so both lateral and vertical intergradation of the two biostratigraphic zones is probable.

Second, Ross *et al.* (1997) drew the Ibexian-Whiterockian boundary in the Ibex District of western Utah at the level 8.5 m below the top of the Wah Wah Limestone in Hintze's (1952) section J at which brachiopods of Zone L (the *Paralenorthis–Orthidiella* Zone) first appear. Ethington (in Ross *et al.*, 1997), however, drew the same boundary 2.8 m lower in the Wah Wah, at the level of first appearance of the conodont *Tripodus combsi* (then *Tripodus laevis*). Sweet and Tolbert (1997) followed the same procedure in defining the base of the Whiterockian Series in the Shingle Pass section. In the central Nevada sections considered in this report, however, *T. combsi* appears for the first time at least 66 m below the projected level of the basal stratotype of the Whiterockian Series, and this certainly limits its usefulness in defining the Whiterockian base regionally. Furthermore, the base of the *Orthidiella* Zone, controlled in our conodont-based framework by the Meiklejohn Peak and Whiterock Canyon sections, projects to a level well above the base of the Juab Limestone in the Ibexian standard section. Because control on the ranges of conodonts is tighter than on ranges of brachiopods critical to defining the limits of Zone L in the Ibex District, we suspect that slight revision in placement of the Ibexian-Whiterockian boundary there may be in order.

Finally, we cannot point to a single conodont species in a credible developmental sequence that will be useful regionally in defining the base of the Whiterockian Series, and we suspect that this is also the case with the brachiopod and trilobite species that have been used thus far so effectively in Whiterockian biostratigraphy in the western United States. However, in the graphic procedure we have used in assembling a standard section for the Whiterockian Series, it is not necessary to rely on such icons. That is, even though the stratotypical base of the Whiterockian has been established in the Whiterock Canyon section at the level of first occurrence there of the brachiopod *Orthidiella*, that same level may be identified with confidence in sections that lack *Orthidiella* if those sections can be correlated through graphic comparison of the ranges of the conodont or other species they have in common.

REFERENCES CITED

Albanesi, G.L.

1998. Taxonomia de conodontes de las secuencias Ordovicicas del Cerro Potrerillo, Precordillera Central de San Juan, R. Argentina. Actas de la Academia Nacional de Ciencias (Córdoba, Argentina), vol. 12, pp. 101–252.

Bauer, J.A.

1987. Conodonts and conodont biostratigraphy of the McLish and Tulip Creek Formations (Middle Ordovician) of south-central Oklahoma. Oklahoma Geological Survey Bulletin 141, 58 pp.

Bradshaw, L.E.

1969. Conodonts from the Fort Peña Formation (Middle Ordovician), Marathon Basin, Texas. Journal of Paleontology, vol. 43, pp. 1137–1168.

Ethington, R.L., and Clark, D.L.

1982. Lower and Middle Ordovician conodonts from the Ibex area, western Millard County, Utah. Brigham Young University, Geology Studies, vol. 28, pt. 2, pp. 1–155 [imprint 1981].

Ethington, R.L., and Schumacher, D.

1969. Conodonts of the Copenhagen Formation (Middle Ordovician) in central Nevada. Journal of Paleontology, vol. 43, pp. 440–484.

Fortey, R.A., and Droser, M.L.

1996. Trilobites at the base of the Middle Ordovician, western United States. Journal of Paleontology, vol. 70, pp. 73–99.

Harris, A.G., Bergström, S.M., Ethington, R.L., and Ross, R.J., Jr.

1979. Aspects of Middle and Upper Ordovician conodont biostratigraphy of carbonate facies in Nevada and southeast California and comparison with some Appalachian successions. Brigham Young University, Geology Studies, 26, pp. 7–33.

Hintze, L.F.

1952. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey, Bulletin 48, 249 pp.

McHargue, T.R.

1982. Ontogeny, phylogeny, and apparatus reconstruction of the conodont genus *Histiodella*, Joins Fm., Arbuckle Mountains, Oklahoma. Journal of Paleontology, vol. 56, pp. 1410–1433.

Ross, R.J., Jr.

1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. Peabody Museum Natural History, Bulletin 6, 161 pp.

Ross, R.J., Jr., Adler, F.J., Amsden, T.W., Bergström, S.M., Carter, C., Churkin, J., Jr., Cressman, E.A., Derby, J.R., Dutro, J.T., Jr., Ethington, R.L., Finney, S.C., Fisher, D.W., Fisher, J.H., Harris, A.G., Hintze, L.F., Ketner, K.B., Kolata, D.L., Landing, E., Neuman, R.B., Sweet, W.C., Pojeta, J., Jr., Potter, A.W., Rader, E.K., Repetski, J.E., Shaver, R.H., Thompson, T.L., and Webers, G.F.

1982. The Ordovician System in the United States of America: Correlation chart and explanatory notes. International Union Geological Sciences, Publication 12, 73 pp.

Ross, R.J., Jr., and Ethington, R.L.

1991. Stratotype of Ordovician Whiterock Series, with an appendix on graptolite correlation of the topmost Ibexian by C. E. Mitchell. Palaios, vol. 6, pp. 156–173.

1992. North American Whiterock Series suited for global correlation. *in* Global Perspectives on Ordovician Geology. B.D. Webby and J.R. Laurie, *eds.* A.A. Balkema, Rotterdam, Netherlands, pp. 135–152.

Ross, R.J., Jr., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E., and Repetski, J.E.

1997. The Ibexian, lowermost series in the North American Ordovician, with a section on Echinoderm Biostratigraphy by James Sprinkle and Thomas E. Guensburg. United States Geological Survey Professional Paper 1579-A, 49 pp.

Ross, R.J., Jr., James, N.P., Hintze, L.F., and Poole, F.G.

1989. Architecture and evolution of a Whitrockian (early Middle Ordovician) carbonate platform, Basin Ranges of western U. S. A. *in* Controls on carbonate platform and basin development. P.D. Crevello, J.L. Wilson, J.F. Sarg, and J.F. Read, *eds.*, Society of Economic Paleontologists and Mineralogists, Special Publication 44, pp. 167–185.

Shaw, A.B.

1964. Time in Stratigraphy. McGraw-Hill, New York, 365 pp.

Stouge, S.S.

1984. Conodonts of the Middle Ordovician Table Head Formation, western Newfoundland. Fossils and Strata, no. 16, 145 pp.

Sweet, W.C.

1979. Late Ordovician conodonts and biostratigraphy of the western Midcontinent Province. Brigham Young University Geology Studies, vol. 26, pt. 3, pp. 45–86.

1984. Graphic correlation of upper Middle and Upper Ordovician rocks, North American Midcontinent Province, U. S. A. *in* Aspects of the Ordovician System. D.L. Bruton, *ed.*, Palaeontological Contributions from the University of Oslo, No. 295, pp. 23–35.

1995a. A conodont-based composite standard for the North American Ordovician: Progress report. *in* Ordovician Odyssey: Short papers for the Seventh International Symposium on the Ordovician System. J.D. Cooper, M.L. Droser, and S.C. Finney, *eds.*, Pacific Coast Section Society for Sedimentary Geology (SEPM), Fullerton, CA, pp. 15–20.

1995b. Graphic assembly of a conodont-based composite standard for the Ordovician System of North America. *in* Graphic Correlation. K.O. Mann and H.R. Lane, *eds.*, SEPM Society for Sedimentary Geology, Special Publication 53, pp. 139–150.

Sweet, W.C., and Tolbert, C.M.

1997. An Ibexian (Lower Ordovician) reference section in the southern Egan Range, Nevada, for a conodont-based chronostratigraphy. United States Geological Survey Professional Paper 1579-B, pp. 53–84.

Appendix A.—Stratigraphic ranges of conodont species ("#" corresponds to "Index No." in Table 1) in meters, by section. MJP = Meiklejohn Peak section; BLM = BLM section; MRII = Martin Ridge North section; AR = Hill 8308 section; MRI = Martin Ridge South section; WRC = Whiterock Canyon section.

#	BLM	MRII	BLM-+MRII	AR	AR+357	CS-1	MRI	*.93-7.5	WRCS-1	MJP	*1.12-7	WRCS-2	WRC	*1.58-2	WRCS-3
2				161–186	518–543	518–543			518–543			518–543			518–543
3										70–130	71–139	71–139	40–104	61–162	61–162
4	354–405		354–405	90–130	447–487	354–487			303–487	214–400	233–441	233–487			233–487
5		0–16	393–409	15–94	372–451	372–451	334	303	303–451			303–451			303–451
8				125–130	482–487	482–487			482–487	437	482	482–487			482–487
9				107	464	464			464			464			464
11				138–186	495–543	495–543			495–543			495–543			495–543
12		10–16	403–409	41–145	398–502	398–502			398–502			398–502			398–502
16		7–14	400–407	47	404	400–407			400–407			400–407			400–407
17				61–77	418–434	418–434			418–434	426	470	418–470			418–470
18	354–375		354–375	0	357	354–375	274–334	247–303	247–375	201	218	218–375			218–375
21										20–50	15–49	15–49	8	11	11–49
22										135–140	144–150	144–150	0–90	(–2)–140	(–2)–150
24				43–161	400–518	400–518			400–518			400–518			400–518
25		10–14	403–407	138–166	495–523	403–523			403–523			403–523			403–523
28	375		375			375	334	303	303–375	201	218	218–375			218–375
29							0–163	(–8)–144	(–8)–144	5–60	(–1)–60	(–8)–144	0–76	(–2)–118	(–8)–144
31	136–391		136–391	0–33	357–390	136–391	104–334	89–303	89–391	20–170	15–183	15–391	40–101	61–158	15–158
32	0–196		0–196			0–196			0–196	20–50	15–49	0–196	0–90	(–2)–140	(–2)–196
33	332–405	4–16	332–409	34–109	391–566	332–566			332–566			332–566			332–566
35				86–104	443–461	443–461			443–461			443–461			443–461
36		0–11	393–404	39–46	396–403	393–404			393–404			393–404			393–404
37		0–14	393–407	8–97	365–454	365–454			365–454			365–454			365–454
40	18–178		18–178			18–178	32–214	22–192	18–192	40–170	38–183	18–192	0–79	(–2)–151	(–2)–192
42	60–105		60–105			60–105	121	105	60–105	65–75	66–77	60–105	40–43	61–66	60–105
43	354–375		354–375	0	357	354–375				201–214	218–233	218–375			218–375
44							137–195	120–174	354–375	70–170	71–183	71–183	40–46	61–71	61–183
45	251		251			251	163–284	144–257	120–174			144–257	82–101	128–158	128–257
46	92–215		92–215			92–215	121–221	105–198	144–257	140–170	150–183	92–215	47–84	72–131	72–215
50	12–261		12–261			12–261	21–264	120–238	92–215	65–75	66–77	12–261	0–39	(–2)–60	(–2)–261
51									12–261				0–76	(–2)–118	(–2)–118
52	0–22		0–22			0–22	0–32	(–8)–22	(–8)–22	30–40	27–38	(–8)–38			(–8)–38
54				15–63	372–420	372–420			372–420	201–214	218–233	218–420			218–420
55	0–12		0–12			0–12	32	22	0–22	55–70	55–71	0–71			0–71
56							339	308	308			308			308
57	309–346		309–346	29	386	309–386	130–334	113–303	113–386			113–386	40–104	61–162	61–386
58													26–36	39–55	39–55
59							0–104	(–8)–89	(–8)–89	40–65	38–66	(–8)–89	0–43	(–2)–66	(–8)–89
60										5–55	(–1)–55	(–1)–55	0–36	(–2)–55	(–2)–55
61	0–60		0–60			0–60	0–104	(–8)–89	(–8)–89			(–8)–89	0–70	(–2)–109	(–8)–109
							151	133	133			133			133
62	0–362		0–362	24–33	381–390	0–390	11–292	3–264	0–390	170–180	183–195	0–390			0–390
64	105–196		105–196			105–196	214	198	105–198			105–196	5–106	6–165	6–196
67										70–80	71–83	71–83	40–97	61–151	61–151

Appendix A—Continued.

#	BLM	MRII	BLM-+MRII	AR	AR+357	CS-1	MRI	*.93-7.5	WRCS-1	MJP	*1.12-7	WRCS-2	WRC	*1.58-2	WRCS-3
69										5–20	(−1)–15	(−1)–15	0–39	(−2)–60	(−2) 60
71		0–16	393–409	40–209	397–566	393–566			393–566			393–566			393–566
72				26–47	393–404	383–404			383–404			383–404			383–404
73	0–136		0–136			0–136	21–186	12–165	0–165	70–170	71–183	0–183	40–104	61–162	0–183
74	12–150		12–150			12–150	21	12	12–150			12–150			12–150
75	0–354		0–354	0–33	257–390	0–390	11–334	3–303	0–390			0–390	0–97	(−2)–151	(−2)–390
76	354–391		354–391	8–33	365–390	354–391	274	247	247–391			247–391			247–391
77							318	288	288			288			288
79							104–214	89–192	89–192			89–192	40–101	61–158	61–192
80							137–214	120–192	120–192	70–130	71–139	71–139	0–15	(−2)–22	(−2)–139
81	6–72	0–14	6–407	30–183	387–540	6–540			6–540	70–170	71–183	6–540	71–104	110–162	6–540
82	0		0			0	0–130	(−8)–113	(−8)–113	5–65	(−1)–66	(−8)–113	0–79	(−2)–123	(−8)–123
83	92–178		92–178			92–178			92–178			92–178	40–76	61–118	61–178
84				153–209	510–566	510–566			510–566			510–566			510–566
86	405	0–13	393–405	29–109	386–466	386–466			386–466	237–419	258–462	258–466			258–466
87				90–104	447–461	447–461			447–461			447–461			447–461
88				145–209	502–566	502–566			502–566			502–566			502–566
89				24–92	381–449	381–449			381–449			381–449			381–449
90				200	557	557			557			557			557
91				183–192	540–549	540–549			540–549			540–549			540–549
92		14–16	407–409			407–409			407–409			407–409			407–409
94	22–178		22–178			22–178			22–178	25–50	21–49	21–178	0–60	(−2)–93	(−2)–178
95	0–251		0–251			0–251	21–236	12–212	0–251	5–170	(−1)–183	(−1)–251	0–104	(−2)–162	(−2)–251
96										5–20	(−1)–15	(−1)–15	0–104	(−2)–162	(−2)–162
97	0–251		0–251			0–251			0–251	170–180	183–195	0–251			0–251
98										70–135	71–144	71–144	40–76	61–118	61–144
99		2	395	42–104	399–461	395–461			395–461			395–461			395–451
100	0–12		0–12			0–12	0–32	(−8)–22	(−8)–22	60–70	60–71	(−8)–71	22–29	33–44	(−8)–71
	112–178		112–187			112–178			112–178	70–80	71–83	71–178	43–94	66–147	66–178
101	0–12		0–12			0–12			0–12			0–12			0–12
102										60–70	60–71	60–71	70	109	60–109
105		2–14	395–407	51–114	408–461	395–461			395–461			395–461			395–461
	332–391		332–391			332–391			332–391			332–391			332–391
107							274–321	247–291	247–291			247–291			247–291
108	332–375	0–14	332–407	0–33	357–390	332–407			332–407			332–407			332–407
110		16	409	90	447	409–447			409–447			409–447			409–447
111		9–14	402–407			402–407			402–407			402–407			402–407
112													8–29	11–44	11–44
115	0–79		0–79			0–79			0–79	30–40	27–38	0–79			0–79
117										20–50	15–49	15–49	29		15–49
119	215–391		215–391	0–33	357–390	215–391	144–334	126–303	126–391			126–391		44	126–394
121										5–60	(−1)–60	(−1)–60	0–39	(−2)–60	(−2)–60
122				109	466	466			466			466			466
124				29–131	386–488	386–488			386–488			386–488			386–488
127		4–14	397–407	61–77	418–434	397–434			397–434			397–434			397–434
130	0–242		0–242			0–242	0–236	(−8)–212	(−8)–242	65–180	66–195	(−8)–242	40–101	61–158	(−8)–242
132							121–186	105–165	105–165	5–75	(−1)–77	(−1)–165	40–97	61–151	(−1)–165
134				183–200	540–557	540–557			540–557			540–557			540–557

Appendix B.—Stratigraphic ranges of conodont species ("#" corresponds to "Index No." in Table 1) in meters, by section. MC-CS = Midcontinent CS; WR-CS = Whiterock CS; LOK = Arbuckles section; SPIB = Shingle Pass-Ibex CS. *See text for discussion of adjustments.

#	MC-CS	WRCS-3	*.658+559	MC-CS-1	LOK	*0.41+507	MC-CS-2	SPIB	*.52+95	MC-CS-3
2	960–1025	518–543	900–916	900–1025			900–1025			900–1025
3	750–806	61–162	606–666	606–806	447–554	690–734	606–806			606–806
4	871–883	233–487	712–879	712–883			712–883			712–883
5	544–830	303–451	758–856	544–856			544–856	1219–1322	729–782	544–856
8	876–899	482–487	876–879	876–899			876–899			876–899
9	824–871	464	864	824–871			824–871			824–871
11	942–1015	495–543	885–916	885–1015			885–1015			885–1015
12	773–933	398–502	821–889	773–933			773–933			773–933
16	737–849	400–407	822–827	737–849			737–849			737–849
17	822–885	418–470	834–868	822–885			822–885			822–885
18		218–375	702–806	702–806	385–532	665–725	665–806	1186–1240	712–740	665–806
21		11–49	567–591	567–591			567–591			567–591
22		(–2)–150	558–658	558–658			558–658	318–870	260–547	260–658
24	823–1140	400–518	822–900	822–1140			822–1140			822–1140
25	823–979	403–523	824–903	823–979			823–979			823–979
28		218–375	702–806	702–806	493–532	709–725	702–806	1209–1223	724–731	702–806
29		(–8)–144	554–654	554–654	0–13	507–512	507–654	420–999	313–614	313–654
31		15–158	569–663	569–663	272–559	619–736	569–736	999–1240	614–740	569–740
32		(–2)–196	558–688	558–688			558–688	381–1092	293–663	293–688
33	750-1276	332–566	777–931	750–1276			750–1276			750–1276
35	834–893	443–461	850–862	834–893			834–893			834–893
36	750–768	393–404	818–825	750–825			750–825			750–825
37	750–850	365–454	799–858	750–858			750–858	1172–1332	704–788	704–858
40		(–2)–192	558–685	558–685	275–557	620–735	558–735	611–1072	413–652	413–735
42		60–105	598–628	598–628	275–298	620–629	598–629	1006–1082	618–658	598–658
43		218–375	702–806	702–806	477–557	703–735	702–806	1216–1240	727–740	702–806
44		61–183	599–679	599–679	280–342	621–647	599–679	1036–1082	634–658	599–679
45		128–257	643–728	643–728	344–364	648–656	643–728			643–728
46		72–215	606–700	606–700	313–544	635–730	606–730	1072–1216	652–727	606–730
50		(–2)–261	558–731	558–731			558–731	879–1082	552–658	552–731
51		(–2)–118	558–637	558–637	188	584	558–637	660–1006	438–618	438–637
52		(–8)–38	554–584	554–584			554–584	753–1006	487–618	487–618
54		218–420	702–835	702–835			702–835	1209–1229	724–734	702–835
55		0–71	559–606	559–606			559–606	950–974	589–601	559–606
56		308	762	762	268–404	617–673	617–762	1193–1230	715–735	617–762
57		61–386	599–813	599–813	272–557	619–735	599–813	984–1168	607–702	599–813
58		39–55	585–595	585–595			585–595			585–595
59		(–8)–89	554–618	554–618	0–231	507–602	507–618	660–959	438–593	438–618
60		(–2)–55	558–595	558–595			558–595	995	612	558–612
61		(–8)–109	554–631	554–631			554–631	830–911	527–569	527–631
		133	647	647			647			647
62		0–390	559–816	559–816	0–557	507–735	507–816	853–1082	539–658	507–816
64		6–196	563–688	563–688			563–688			563–688
67		61–151	599–658	599–658			599–658			599–658
69		(–2)–60	558–598	558–598			558–598			558–598
71	822–1263	393–566	818–931	818–1263			818–1263			818–1263
72	822–1261	383–404	811–825	811–1261			811–1261			811–1261
73		0–183	559–679	559–679	6–188	509–584	509–679	739–1082	479–658	479–679
74		12–150	567–658	567–658	279–298	621–629	567–658	600–1082	407–658	407–658
75		(–2)–390	558–816	558–816	0–554	507–734	507–816	353–1223	279–731	279–816
76		247–391	722–816	722–816	410–557	675–735	675–816			675–816
77		288	749	749	275–462	620–696	620–749	1067–1132	650–684	620–749
79		61–192	599–685	599–685			599–685	896–1044	561–638	561–685
80		(–2)–139	558–650	558–650			558–650	391–974	298–601	298–650
81	757–859	6–540	563–914	563–914			563–914			563–914
82		(–8)–123	554–640	554–640			554–640			554–640
83		61–178	599–676	599–676			599–676			599–676
84	874–1134	510–566	895–931	874–1134			874–1134			874–1134
86	749–892	258–466	729–866	729–892			729–892	1302–1332	772–788	729–892
87	824–962	447–461	853–862	824–962			824–962			824–962

Appendix B—Continued.

#	MC-CS	WRCS-3	*.658+559	MC-CS-1	LOK	*0.41+507	MC-CS-2	SPIB	*.52+95	MC-CS-3
88	960–1259	502–566	889–931	889–1259			889–1259			889–1259
89	807–1009	381–449	810–854	807–1009			807–1009			807–1009
90	980–1268	557	926	926–1268			926–1268			926–1268
91	942–1024	540–549	914–920	914–1024			914–1024			914–1024
92	834	407–409	827–828	827–834			827–834			827–834
94		(–2)–178	558–676	558–676			558–676	794–891	508–558	508–676
95		(–2)–251	558–724	558–724	188–557	584–735	558–735	739–1210	479–724	479–735
96		(–2)–162	558–666	558–666			558–666	640–1059	428–646	428–666
97		0–251	559–724	559–724			559–724			559–724
98		61–144	599–654	599–654			599–654			599–654
99	750–859	395–451	819–862	750–862			750–862			750–862
100		(–8)–71	554–606	554–606	188–231	584–602	554–606	884–999	554–614	554–614
		66–178	602–676	602–676			602–676			602–676
101		0–12	559–567	559–567			559–567	896–1006	561–618	559–618
102		60–109	598–631	596–631			596–631	903	565	565–631
105	750–913	395–461	819–862	750–913			750–913			750–913
107		247–291	722–750	722–750	272–547	619–731	619–750	905–1161	566–699	566–750
108		332–407	777–827	777–827	441–554	688–734	688–827	1181–1216	709–727	688–827
110	828–859	409–447	828–853	828–859			828–859			828–859
111	762–828	402–407	824–827	762–828			762–828			762–828
112		11–44	566–588	566–588			566–588	758–944	489–586	489–588
115		0–79	559–611	559–611			559–611			559–611
117		15–49	569–591	569–591	206	591	569–591	240–888	220–557	220–591
119		126–394	642–816	642–816	349–557	650–735	642–816			642–816
121		(–2)–60	558–598	558–598			558–598	318–691	260–454	260–598
122	952–976	466	866	866–976			866–976			866–976
124	849–1152	386–488	813–880	813–1152			813–1152			813–1152
127	805–885	397–434	820–845	805–885			805–885			805–885
130		(–8)–242	554–718	554–718	268–544	617–730	554–730	928–1082	578–658	554–730
132		(–1)–165	558–668	558–668			558–668	548–800	380–511	380–668
134	972–1114	540–557	914–926	914–1114			914–1114			914–1114

ORDOVICIAN CONODONTS AND STRATIGRAPHY OF THE ST. PETER SANDSTONE AND GLENWOOD SHALE, CENTRAL UNITED STATES

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ABSTRACT

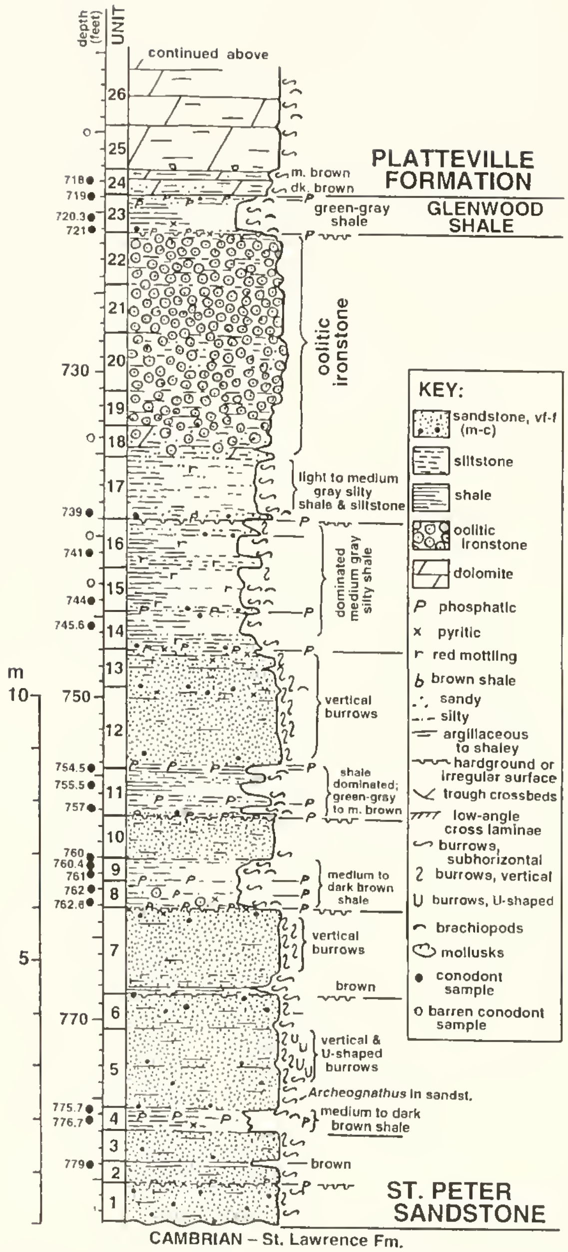
The age of the St. Peter Sandstone in the central and northern Midcontinent has long been considered equivocal because of the general absence of biostratigraphically useful fossils. Conodonts recovered from the St. Peter Sandstone in Iowa, Minnesota, Nebraska, and Kansas for this study help place some age constraints on this renowned formation in its northern and western extent. Faunas from the lower St. Peter include *Phragmodus flexuosus*, *Cahabagnathus* sp., and *Leptochirognathus* sp., and a late Whiterockian (Chazyan) correlation is indicated. Juvenile or immature elements of *P. flexuosus* from these collections show morphologies trending toward *P. cognitus* and *P. inflexus*, and paedomorphic derivation of these latter species is proposed. Diverse assemblages of hyaline forms also occur in the St. Peter strata (*Erismodus* spp., *Erraticodon* sp., *Curtognathus* sp., *Coleodus* sp., *Archeognathus* sp., *Stereoconus* sp., others) along with various albid elements (*Plectodina* sp., *Eoplacognathus* sp., others). The overlying Glenwood Shale contains abundant conodonts dominated by *Phragmodus cognitus*, *Erismodus* sp., and *Chirognathus duodactylus*, and the fauna is interpreted as an early Mohawkian (Blackriveran) association. Certain thin shale units in the St. Peter–Glenwood succession represent condensed intervals, in part reflected by their exceptionally high conodont abundances. Some organic-rich phosphatic shale units in the lower St. Peter of western Iowa have produced equivalent yields of tens of thousands of conodonts per kilogram, and many Glenwood Shale samples yield thousands of conodonts per kilogram. Previous depositional models have proposed that the St. Peter is primarily a succession of littoral and nearshore facies forming a broadly diachronous transgressive sheet sand. However, broad-scale diachroneity cannot be demonstrated with available biostratigraphic control. The recognition of condensed marine shale units, phosphorites, ironstones, and pyritic hardgrounds in the western facies tract of the St. Peter Sandstone has necessitated a re-evaluation of previous regional models of St. Peter deposition. The St. Peter is interpreted to be a composite stratigraphic interval deposited during a succession of transgressive-regressive sedimentary cycles. Transgressive episodes in some cycles were marked by offshore sediment condensation or starvation within a stratified seaway.

INTRODUCTION

Discovery of St. Peter Conodonts

The St. Peter Sandstone is a widespread sandstone-dominated Ordovician stratigraphic unit recognized across much of the central United States. Because the St. Peter is bounded below by a major cratonic unconformity of unknown duration (Sauk-Tippecanoe unconformity of Sloss, 1963) and because it failed to produce any biostratigraphically useful fossils after many decades of study, its age was long considered equivocal. In the 1970s indigenous conodonts were found in the type area of the St. Peter (Olsen, 1976). Clark and Miller (1971) and Grether and Clark (1980) recovered conodonts from the basal Readstown Member of the St. Peter in Wisconsin, but all of these were reworked from underlying units. Indigenous conodonts were described and illustrated from the St. Peter Sandstone of Indiana by Rexroad *et al.* (1982). Witzke's routine logging of a core from northwest Iowa (Loc. CQ, see Appendix) in 1978 revealed the presence of rich and abundant conodont faunas during hand-lens examination of an interbedded shale unit (unit 8, Text-fig. 1) within the St. Peter succession. Subsequent processing of the shales produced large conodont collections of potential biostratigraphic significance. W. M. Furnish and Gilbert Klapper generously provided additional conodont collections from a core of St. Peter Sandstone at St. Paul, Minnesota (Loc. SP) that they acquired from Bruce Olsen and Fred Sawin of the University of Minnesota.

Witzke (1980, 1992) provided some preliminary statements about the St. Peter conodont faunas from the St. Paul and Camp Quest cores, and Klapper (*in*



Text-figure 1.—Graphic lithologic section of St. Peter–Glenwood succession from Camp Quest core, Locality CQ, northwest Iowa (see Appendix). Conodont sample numbers correspond to collections tabulated in Table 1.

Klapper and Bergström, 1984, p. 968) also examined these collections as part of the seminal study of *Archeognathus*. Although accomplished at a painstakingly slow rate, additional conodont collections were assembled from the St. Peter Sandstone and overlying Glenwood Shale at additional localities in Iowa, Nebraska, and Kansas, and these, together with the Camp Quest and St. Paul samples, form the basis of this report. To date, over 16,000 conodont elements have been recovered from the St. Peter–Glenwood interval in four states (Tables 1 and 2; Appendix).

Study Area

Core and outcrop sections of the St. Peter–Glenwood interval were examined at scattered locations across a broad area of the central United States in portions of Iowa, Minnesota, Kansas, Missouri, Nebraska, and Kansas (Text-fig. 2). Some of these sections were sampled and processed for conodonts with varying degrees of success (solid black circles on Text-fig. 2; see also Text-fig. 3). Outcrop sections in these states are limited to the greater Mississippi Valley area of northeast Iowa, southeast Minnesota, and eastern Missouri, as well as the margins of the Ozark Dome. The greatest geographic extent of the St. Peter Sandstone in these states occurs in the subsurface, stretching between the Ozark Dome to the south and the broad Transcontinental Arch to the north. Much of the Transcontinental Arch was emergent during St. Peter–Glenwood deposition, and shorelines apparently bordered the margins of this feature (Witzke, 1980). Later erosional episodes beveled the St. Peter edge around the Transcontinental Arch, Ozark Dome, and Wisconsin Dome obscuring the original depositional limits of the formation. However, a structural sag (Nebraska Sag, Text-fig. 2) marks the location where Ordovician seas breached the Transcontintal Arch at times, and a poorly-known stratigraphic linkage between the Winnipeg Formation of the Williston Basin and equivalent units in the central United States is preserved in that area. The St. Peter Sandstone also extends across areas of Arkansas, Wisconsin, Illinois, Indiana, and Michigan, but these states are not included in this report.

Conodont Processing and Recovery

Sampling from the St. Peter and Glenwood formations was limited entirely to shale and mudstone lithologies (primarily 5 cm diameter NX core splits), and conodonts were recovered from many of these samples. No attempt was made to sample the dominant sandstone lithologies of the St. Peter, although conodonts occur within at least some of the sandstone units as well. Hand lens examination of one sandstone at Locality CQ (unit 5, Text-fig. 1) revealed denticles of *Archeognathus*, and Rexroad *et al.* (1982) and Shaw (1990) recovered conodonts from sandstones in Indiana and Illinois. The shale and mudstone samples used for this study were relatively small, varying between 50 and 800 grams (most averaging about 200 gm). Green and gray shales were initially soaked in Stoddard's solvent, then decanted and soaked in water for partial to complete disaggredation. Organic-rich brown shales proved much more difficult to disaggregate, but

Table 1.—St. Peter, Glenwood, and Platteville conodonts, Camp Quest core, Iowa.

CQ sample (depth, ft)	779	776.7	775.7	762.8	762	761	70.4	760	757	755.5	754.5	745.6	744	741	739	721	720.3	719	718	706.4
cono/kg	18	1103	66,587	22,400	1559	464	395	275	1267	12	50	25	37	7	33	4586	3696	30	8	92
Phragmodus flexuosus—Pa		6	280	231	95	4	2		5						1?					
Pb		6	569	196	92	2		1	9											
M		5	480	416	158	12	4	2	2											
S (all types)		22	3140	1333	337	34	13	3	9											
Phragmodus cognitus—Pa																138	62		1	1
Pb																115	52			1
M																148	52			2
S (all types)																552	186	3	1	9
Phragmodus spp. (fragments)		(25)	(1246)	(372)	(208)	(15)	(4)	(1)	(6)							(273)	(104)	(6)		(4)
Phragmodus? sp.			3	1																
Phramodus cf. *inflexus*																	1			
Plectodina spp.			34	25	3											7	9			1
?*Bryantodina* sp.									4											
Bryantodina typicalis																17	40			
indet. rhipidognathid? sp.																39	6			
indet. balognathid? sp.																2				
Cahabagnathus sp.		2	7		1															
Eoplacognathus sp.		1	3	2?					1?											
Polyplacognathus ramosus																				3
indet. gen. sp. A		4																		
indet. gen. sp. B					1															
Erismodus spp. (all types)	2	66	72	213	184	4	13	2	117	1		1	5	1	14	210	25	3		
Erism. spp. (fragments)		(10)	(45)	(163)	(77)	(2)	(1)		(102)							(90)	(2)	(1)		
Erraticodon sp.		42	25	47	24				65						3?					
Errat. sp. (fragments)		(20)	(19)	(36)	(2)				(20)											
Curtognathus sp.		2	59	94	1				13											
Chirognathus duodactylus																91	5	1		
cf. *Chirognathus* sp.			1						3											
Coleodus spp.		4		15	3										1					
Archeognathus sp.		2	2		7					1										
cf. *Archeognathus* sp.		2		3	4				2?		1		2			7	1			
Stereoconus sp.															1					
Drepanoistodus suberectus		14	216		1								2			3	55			6
?drepanoistodontid sp.			34																	
Oistodus? *venustus*																1	5			
Oneotodus? *ovatus*												1	2		1	7				
Staufferella sp.		1																		
misc. indet. elements		1	69	53	17	2										7				
indet. fragments		(4)	(577)	(635)	72)	(3)	(3)								(4)	(139)	(53)			
scolecodonts		8	351	49	1		2		10				1			40	247	9		
inarticulate brachiopods			x	x		x	x	x	x	x			x			x	x			
other invertebrates						x							x				x			

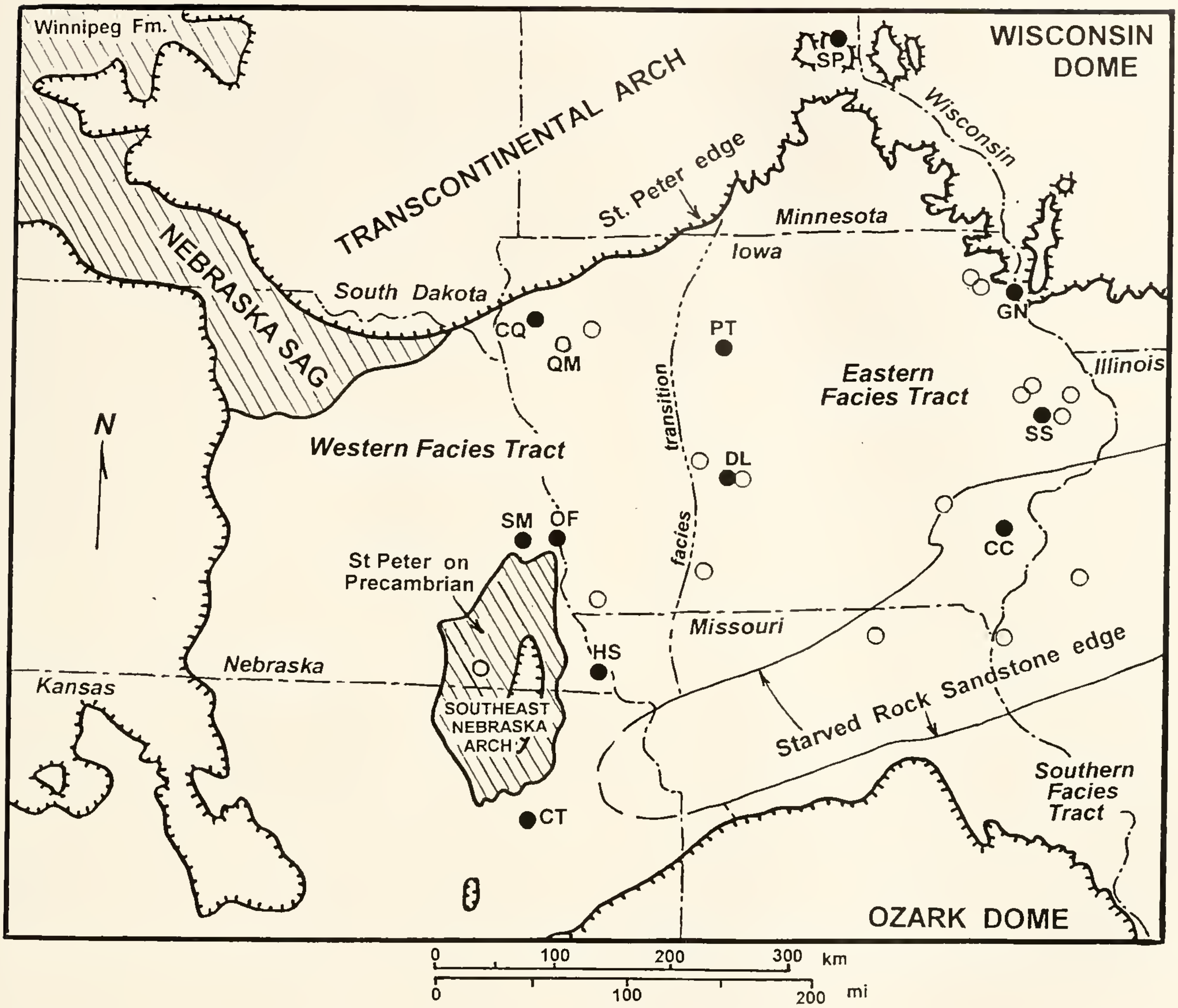
Table 2.—St. Peter-Glenwood conodont occurrences, Iowa, Nebraska, Kansas, Minnesota.

Sample	SP-L	SP-U	O-1977	S-1162	S-1161	S-1159	S-1158	H-3579	C-3387	C-3386	GN	D-1748	J-1021	SS753
Phragmodus cf. *ambiguus*—P			2						9	17				
M			2						29	23				
S (all types)			1						38	59				
Phragmodus cognitus—Pa				2								4	135	224
Pb				1									137	101
M				2								5	162	133
S (all types)				2								15	278	342
Phragmodus cf. *inflexus*—PA					2	2	3				140			
Pb					2		3				142			
M					4	3	12				263			
S (all types)					6	2	41				237			
Phragm. spp. (fragments)	(2)						(5)	(2)	(6)	(30)	(153)	(16)	(107)	(457)
Plectodina sp.			2		3	5	5				226	3	9	23
Bryantodina typicalis											14		19	40
?*Bryantodina* sp.			5	1	1		2							
cf. *Appalachignathus* sp.		1												
indet. gen. sp. C			2											
Cahabagnathus sp.									4					
Eoplacognathus sp.										3				
Erismodus spp. (all types)	35	17	113		1	1	6	10	65	55	285	17	144	97
Erismodus spp. (fragments)	(7)	(3)	(19)					(9)	(25)	(32)	(61)		(59)	(11)
Erraticodon sp.			6					1?	4	9				
Erraticodon sp. (fragments)										(3)				
Curtognathus sp.		1									15			
Chirognathus duodactylus											1	11	31	16
cf. *Chirognathus* sp.										2				
cf. *Leptochirognathus* sp.	1	1												
Coleodus spp.	1		6											
Archeognathus sp.	1	3									9			
cf. *Archeognathus* sp.	3	2	9						10					
indet. multioistodontid? sp.			4						3?					
Stereoconus sp.	2	1												
cf. *Mixoconus* sp.	19	14	3											
Drepanoistodus suberectus			1	14	21	8	23		3		154	2	41	5
indet. coniform spp.	2			2			6						1	
Panderodus sp.				1	18	3	33				22			
Oneotodus ? *ovatus*	2		5							6	8	1		10
Staufferella sp.									1		3		1	
?*Pseudooneotodus* sp.											2		1	
misc. indet. elements						1				3	1	1	4	4
indet. fragments	(1)	(3)	(4)	(10)	(24)	(11)	(48)		(23)	(33)	(59)	(4)	(90)	(115)
scolecodonts									22		73	12	52	12
inarticulate brachiopods			x						x		x	x	x	x
other invertebrates			x						x		x			
astraspid plates			121						x					

repeated baths in common household bleach (for periods of months to years) slowly oxidized the organic cements resulting in progressive breakdown. The disaggregated shale residues were screened, dried, and manually picked. Yields were highly variable, although some individual samples yielded hundreds to thousands of elements. The most productive samples were some of the organic-rich brown shales which gave normalized yields commonly in excess of 1000 conodonts per kilogram. Two exceptionally productive samples from the lower St. Peter (CQ-775.7, 762.8) gave normalized yields of 66,500 and 22,400 conodonts per kilogram, respectively (if broken elements are counted, yields to 91,000 conodonts/kg are recognized). Most of Glenwood green-gray shale samples were highly productive yielding equivalents of 1100 to 5000 conodonts per kilogram.

ACKNOWLEDGMENTS

We are particularly grateful to Gilbert Klapper for his assistance and support during many phases of this project. His encouragement following the discovery of



Text-figure 2.—Study area and locality map. Hachured lines mark erosional edge of St. Peter Sandstone in the central United States and lower Winnipeg Formation in South Dakota (edge modified from Bunker *et al.*, 1988). Starved Rock Sandstone edge after Nunn (1986). State borders (broken lines) and major structural features are shown. Solid black circles show locations of St. Peter–Glenwood conodont samples; two-letter labels designate localities (see Appendix; all are subsurface core samples except Locality GN). Open circles show locations of additional St. Peter cores. St. Peter unconformably overlies Cambrian-Lower Ordovician strata across most of area. Area where St. Peter or Winnipeg overlies Precambrian crystalline basement denoted by diagonal ruling.

St. Peter conodonts in western Iowa led to continuing investigation. He willingly provided St. Peter conodont collections from Minnesota that are incorporated in this study. His help in identifying certain taxa, especially the enigmatic *Archeognathus*, is clearly valued.

Numerous individuals contributed to the goals of this report, providing materials, information, assistance, and critical discussion along the way. We acknowledge helpful input from Bill Furnish, Steve Schutter, Ray Anderson, Bill Bunker, Greg Ludvigson, Bob McKay, John Pope, Tony Runkel, Anita Harris, and Stig Bergström. The cooperation and assistance of Marv Carlson and Lynn Watney enabled subsurface core materials to be sampled at the Nebraska and Kansas Geological Surveys, respectively. We gratefully acknowledge the helpful review comments of Stephen Leslie, Ray Ethington, and Jim Barrick.

STRATIGRAPHY OF THE ST. PETER–GLENWOOD SUCCESSION

Historic Development of Stratigraphic Nomenclature

The St. Peter Sandstone was originally named for sandstone exposures near the mouth of the St. Peter's

River (now known as the Minnesota River) at St. Paul, Minnesota (Owen, 1847, pp. 169–170), and the type locality was designated in that area in the bluff face below Fort Snelling (Stauffer. 1934; Stauffer and Thiel, 1941). The St. Peter Sandstone has been applied as a stratigraphic label for an Ordovician sandstone-dominated formation across a vast area of the North American continental interior, and it surely constitutes one of the most geographically widespread stratigraphic units recognized on the continent. Across most of its extent, the St. Peter is bounded below by the Sauk-Tippecanoe cratonic unconformity (Sloss, 1963), and it is capped by various Ordovician shale, sandstone, and/or carbonate units. The St. Peter Sandstone is overlain at its type locality and across most of the study area by a relatively thin shale interval known as the Glenwood Shale. The Glenwood type locality was defined in northeast Iowa (Glenwood Township, Winneshiek County), where it is subdivided locally into a lower arenaceous shale and an upper non-sandy shale (Calvin, 1906, p. 75). It is a green-gray noncalcareous shale only 1 to 2 m in thickness across most of its extent.

Templeton and Willman (1963) united the St. Peter and Glenwood formations of the Upper Mississippi Valley within the Ancell Group together with carbonate-dominated facies of the Dutchtown and Joachim formations to the south (southern Illinois, Missouri, Indiana). In general, the Dutchtown and Joachim formations have been considered lateral lithofacies equivalents of the St. Peter and Glenwood formations to the north. Templeton and Willman (1963) further subdivided the St. Peter and Glenwood into a series of members. The main body of widespread St. Peter sheet sand was termed the Tonti Member. The Starved Rock Sandstone was originally included as a member of the St. Peter (ibid.), but its lateral interfingering with and superposition above characteristic green-gray Glenwood shales in southeastern Iowa and northern Missouri has prompted its inclusion within the Glenwood Formation in those areas (Nunn, 1986; Agnew, 1955, p. 1733). The Starved Rock Sandstone is an elongate east-west-trending sandstone body (Text-fig. 2) that generally serves to separate Glenwood shales to the north from the Joachim Formation to the south.

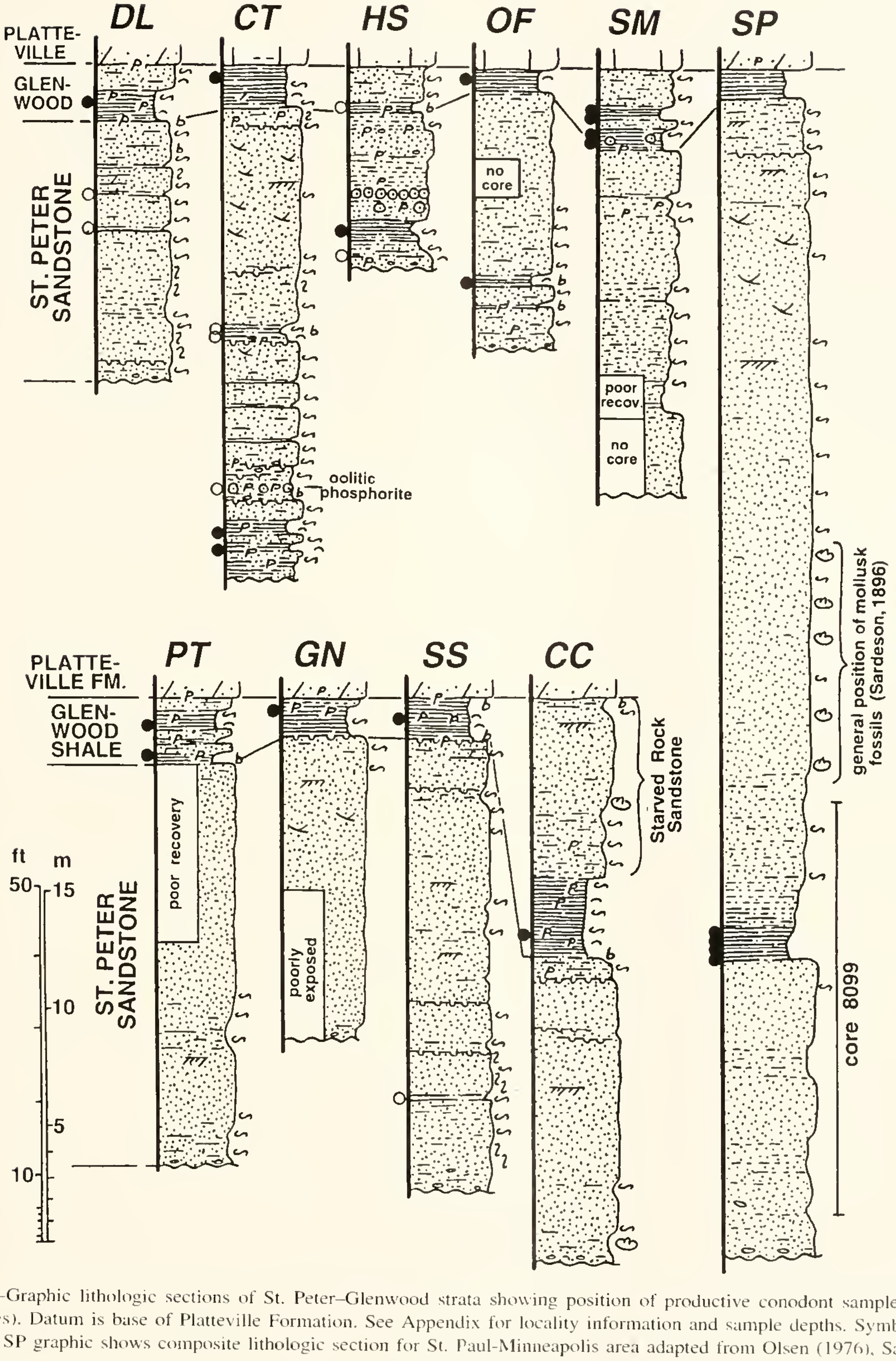
Lithofacies of the Ancell Group

Eastern Facies Tract

A general eastern facies tract (Text-fig. 2) of the St. Peter–Glenwood interval is recognized that extends from the eastern portion of the study area in central Iowa and the Upper Mississippi Valley area (eastern Iowa, Minnesota) eastward across Wisconsin and northern Illinois into Michigan and northeastern Indiana. The St. Peter Sandstone is by exceptionally pure quartzarenite lithologies across this region. A reworked coarse-grained residual unit in the basal St. Peter is commonly recognized (variously termed the Readstown or Kress Member), and thick karst- and valley-filling successions (up to 150 m thick) in the lower St. Peter locally infill a complex erosional surface developed on underlying strata (primarily the Lower Ordovician Prairie du Chien Group). Other than such valley-filling successions, the St. Peter displays regional thickness patterns that likely reflect variations in depositional accommodation and sediment supply. The St. Peter commonly ranges between 15 and 25 m in thickness (locally to 125 m) across eastern Iowa, and it generally thickens northward into the Twin City Basin of Minnesota (45–50 m thick in the type area). Thicknesses vary across Wisconsin and northern Illinois (commonly 25–60 m; locally to 200 m), and the St. Peter dramatically thickens eastward into the Michigan Basin (100–350 m).

The Tonti Member is characterized by fine to medium-grained sandstones (minor coarse horizons) containing limited amounts of argillaceous material over most of this area. Sedimentary structures are often difficult to resolve in the sandstones, but burrowing and cross-stratification are present, and nonmarine aeolian facies are identified in southern Wisconsin (Dott *et al.*, 1986). Although dominated by clean quartzarenite, argillaceous sandstone and silty shale units occur within the main body of the St. Peter, and burrowed slightly argillaceous sandstones are present across much of the area. A silty shale to argillaceous siltstone unit occurs 10 to 20 m above the base of the St. Peter type area of Minnesota (Thiel, 1935; Stauffer and Thiel, 1941; Olsen, 1976), and conodonts have been recovered from this unit (Text-fig. 3, Loc. SP). Thin siltstones and shales (generally green-gray) as well as sandy dolomite beds are present locally within the Tonti Member of Illinois (Lamar, 1928), Wisconsin (Mai and Dott, 1985), and eastern Iowa. Irregular surfaces and hardgrounds, some impregnated with pyrite and apatite crusts, exist at several positions within the Tonti interval of eastern Iowa and Minnesota (*e.g.*, Text-fig. 3, Locs. SS, CC; Thiel, 1935, p. 606). Eastward into the Michigan Basin the St. Peter includes complex lithofacies characterized by stacked sequences of quartzose and quartzo-feldspathic sandstone, dolomite, and thin shale with minor anhydrite (Barnes *et al.*, 1992; Nadon *et al.*, 2000).

A relatively thin (1–3 m) interval of green-gray Glenwood Shale overlies the St. Peter in Iowa and Minnesota. This feldspathic shale includes concentrations of skeletal and nonskeletal apatite (Schutter.



Text-figure 3.—Graphic lithologic sections of St. Peter–Glenwood strata showing position of productive conodont samples used for this study (solid circles). Datum is base of Platteville Formation. See Appendix for locality information and sample depths. Symbols as in Text-figure 1. Locality SP graphic shows composite lithologic section for St. Paul-Minneapolis area adapted from Olsen (1976), Sardeson (1896), and Thiel (1935).

1996), and argillaceous sandstones or siltstones may be present. Eastward into Wisconsin the Glenwood is represented by a thin interval variably displayed as a phosphatic green shale or an argillaceous bioturbated phosphatic sandstone (Fraser, 1976; Choi and Simo, 1998). The Glenwood across northern Illinois forms a thicker facies complex (to 45 m), including silty argillaceous sandstone, dolomite, and green-gray phosphatic shale. The Glenwood in the Michigan Basin (to 80 m) is characterized by complex facies of sandstone, dolomite, and shale (Nadon *et al.*, 2000). Shaley strata locally included in the upper Glenwood may be lateral facies equivalents of the lower Platteville Formation (Fraser, 1976; Sloan, 1972; Mossler, 1985).

The eastern facies tract of the Glenwood Formation interfaces along its southern margin in Illinois and southeastern Iowa with the Starved Rock Sandstone (the "Re-Peter" of Agnew, 1955), an elongate body of marine sandstone. This fine- to coarse-grained, partly argillaceous sandstone reaches thicknesses up to 70 m, and it intercalates with sandstones and shales of the Glenwood along its northern margin (Templeton and Willman, 1963; Nunn, 1986). The Glenwood Shale includes facies of brown organic-rich shale near the margins of the Starved Rock complex in southern Iowa and northward into portions of central and eastern Iowa.

Southern Facies Tract

Although outside the study area of this report, facies relationships within the Ancell Group south of the Starved Rock Sandstone body are described here because these strata have yielded biostratigraphically significant conodont faunas that are comparable to St. Peter–Glenwood faunas to the north (*e.g.*, Branson and Mehl, 1933b; Youngquist and Cullison, 1946; Andrews, 1967; Rexroad *et al.*, 1982; Klapper and Bergström, 1984; Ethington *et al.*, 1986). Southward across eastern Missouri (Thompson, 1991), southern Illinois (Templeton and Willman, 1963), and Indiana (Droste *et al.*, 1982), the Ancell Group (reaching thicknesses to 210 m) becomes dominated by carbonate facies of the Dutchtown and Joachim formations. The St. Peter Sandstone occupies the basal Ancell Group in this area, but the sandstone is replaced progressively southward by carbonate facies of the Dutchtown Formation. The St. Peter is fine- to medium-grained quartz sandstone with minor interbeds of argillaceous sandstone, green-gray silty shale, and dolomite (Dapples, 1955; Thompson, 1991; Droste *et al.*, 1982). By contrast, the Dutchtown is dominated by dark argillaceous dolomite and limestone facies, sandy in part, with interbeds of green-gray and brown organic-rich shale.

The upper Ancell Group is formed by the carbonate-dominated Joachim Formation, which merges with the southern margin of the Starved Rock Sandstone body. The dolomite and limestone lithologies are variably argillaceous, silty, sandy, or stromatolitic, and interbeds of anhydrite and green-gray and brown to black organic shales occur in some intervals (Thompson, 1991; Droste *et al.*, 1982; Kolata and Noger, 1991). Regional lithofacies relationships north and south of the Starved Rock Sandstone suggest general stratigraphic equivalence of the Glenwood and Joachim formations. From its vertical and lateral stratigraphic relations, the Dutchtown Formation is likely a facies equivalent of some part of the St. Peter Sandstone in the northern facies tract.

Western Facies Tract

St. Peter and Glenwood strata across western Iowa, eastern Nebraska, northwestern Missouri, and northeastern Kansas form a distinctive but poorly known western facies tract of the Ancell Group (Text-fig. 2). This facies tract, which is restricted to the subsurface, was the primary focus of this study and the source of most of our St. Peter conodonts. It is distinguished by its higher argillaceous and phosphatic content and by occurrences of interbedded organic shale and oolitic ironstone. The western facies tract of the Ancell Group merges with the eastern facies tract across central Iowa, and lithostratigraphic equivalency is clearly apparent. The Ancell Group in the western facies tract is similar in thickness to that seen in eastern Iowa, generally ranging between 15 and 30 m (locally thinner around the Southeast Nebraska Arch, 9–22 m; see Text-fig. 2).

The western facies tract of St. Peter Sandstone is dominated by fine- to medium-grained sandstone similar to that seen in other regions, but in contrast with the eastern facies tract, it contains higher proportions of argillaceous sandstone and interbedded shale. Unlike the eastern facies, the western St. Peter includes medium to dark brown, locally black, organic-rich shale units, commonly with phosphatic clasts and pyrite cements (*e.g.*, Locs. CQ, CT, OF). Oolitic phosphorite, oolitic ironstone (goethite/hematite), or oolitic pyrite occur as scattered grains to discrete beds and are associated locally with organic shales. The organic shales commonly overlie pyrite- and apatite-impregnated sandstone hardgrounds, and coarse quartz grains are associated with some of these surfaces. Scattered burrows (including *Chondrites*) and silt to sand laminae are seen in the brown shale units. Gray and green-gray silty shale units, phosphatic to glauconitic in part, and siltstones also occur in the western St. Peter facies.

The St. Peter sandstones commonly are burrowed. Horizontal burrows occur above the interbedded shales, but vertical (*Skolithos*) and U-shaped burrow forms occur in the upper parts of some sandstone units (*e.g.*, units 5, 7, 12–13, Text-fig. 1). Planar and cross stratification is present in some sandstones. Occurrences of oolitic ironstone are restricted to the western facies of the Ancell Group. Ironstone units (dominantly goethite ooids) occur at several different stratigraphic positions within the St. Peter Sandstone succession, locally reaching thicknesses up to 2 to 4 m. Oolitic ironstones are present at localities in Kansas, eastern Nebraska, and western Iowa, and they are most abundant in the area of the Southeast Nebraska Arch (Leatherock, 1945; Witzke, 1980; Berendsen and Doveton, 1997).

The Glenwood Shale can be recognized in the western facies tract, although equivalent strata in Nebraska and northeast Kansas commonly are included within an expanded upper St. Peter Sandstone. These strata generally resemble the Glenwood Shale of the eastern facies tract and are dominated by relatively thin intervals of green-gray shale, phosphatic in part, or argillaceous sandstone. However, minor brown organic-rich shale and oolitic ironstone units also occur.

The western facies tract of the Ancell Group is replaced southward into southern Kansas and Oklahoma by strata included within a portion of the Simpson Group. Informal lithostratigraphic subdivisions are applied to this interval in southern Kansas, where the succession of sandstone, in part highly phosphatic to pyritic, green sandy shale, and dolomite (Doveton *et al.*, 1990), resembles the St. Peter-Platteville interval to the north. Although exact lithostratigraphic relationships are not known with certainty, most workers have correlated the St. Peter of northeast Kansas and the western facies tract with a portion of the McLish-Tulip Creek succession in Oklahoma (*e.g.*, Dapples, 1955; Suhm, 1997; Sweet, 1992).

FOSSILS OF THE ST. PETER–GLENWOOD INTERVAL

Excluding bioturbation and the conodont microfauna of the Glenwood, strata of the Ancell Group commonly have been characterized as unfossiliferous across most of their extent. Nevertheless, a number of fossils have been identified within the eastern and western facies tracts during the course of this study, and previous workers have recognized fossils within St. Peter–Glenwood strata. Sardeson (1896) collected and described a mollusk-dominated marine invertebrate fauna from the middle part of the St. Peter Sandstone in Minnesota that includes a variety of bivalve and gastropod taxa as well as nautiloids, monoplacophorans, bryozoans, inarticulate brachiopods, and orthid brachiopods (also see listing by Sloan, 1987). All carbonate shell material is dissolved, and Sardeson's St. Peter macrofauna is preserved primarily as sandstone molds. Bivalve molds have also been recognized in the lower St. Peter of southeastern Iowa (Loc. CC, Text-fig. 3). Residues from the St. Peter Sandstone in the western facies tract have produced, in addition to the conodonts, scattered to abundant scolecodonts and phosphatic inarticulate brachiopod shell material (see Tables 1, 2). Whole inarticulate shells have been identified in some of the cores. Small phosphatized gastropod steinkerns, indeterminate phosphatic tubes, and ostracodes were also recovered from the St. Peter shales.

Phosphatic tubercles and dermal plates from two St. Peter samples (Table 2) resemble vertebrate material known from other Ordovician localities (Elliot *et al.*, 1991). The most abundant sample (O-1977) yielded common nodose and tuberculated plates similar to those of astraspid heterostracans (Denison, 1967). Probable heterostracan material is also known from the Glenwood Shale of the Upper Mississippi Valley area (Schutter, 1996), and "fragmental plates of fossil fish" have been found in phosphatic sandstones of the Simpson Group in Kansas (Doveton *et al.*, 1990, p. 11).

The Glenwood Shale in both the eastern and western facies tracts has yielded a poorly preserved invertebrate fauna. Bivalve molds and phosphatic steinkerns of gastropods are known (Schutter, 1996). Inarticulate brachiopod shell material and scolecodonts are common in some conodont residues. Various dolomitized, phosphatized, or pyritized skeletal grains indicate an open-marine benthic fauna in the formation, including sponge spicules, echinoderm ossicles, bryozoans, articulate brachiopods (orthids, strophomenids, rhynchonellids), graptolites, conularids, ostracodes, and trilobite fragments (Stauffer, 1935; Schutter, 1996; this study). Bivalve molds occur in the Starved Rock Sandstone of Iowa (Loc. CC, Text-fig. 3). Invertebrate carbonate shells are dissolved or replaced in most St. Peter–Glenwood facies, suggesting that calcium carbonate was unstable in the respective depositional and/or diagenetic environments.

DEPOSITIONAL AND PALEOECOLOGIC INTERPRETATIONS

Previous Studies

Most previous interpretions have concluded that the St. Peter Sandstone is primarily a shallow-water marine shelf sand, although aeolian facies are recognized in areas of southern Wisconsin (Dott *et al.*, 1986). Various workers have stressed nearshore, littoral, shoreface, peritidal, and/or aeolian sedimentary processes and environments to explain the transportation and accumulation of the mature quartz sands that typify the St. Peter. The main body of the St. Peter (Tonti Member) commonly has been interpreted as a "transgressive sheet sand" (Fraser, 1976), and Dapples (1955, p. 466) envisioned "an unbroken series of individual shorelines integrated along the transgressing sea [to produce] a blanket or sheet-type sandstone." In a similar manner, some have suggested that the St. Peter is a "composite" sandstone formed by stacked successions of small-scale transgressive and regressive shallow-shelf and shoreface deposits (Thiel, 1935; Sloss, 1963; Mazzullo and Ehrlich, 1983), and that such oscillations resulted in "spasmodic seaward dispersal of sand superimposed upon a background of continual transgression" (Dott *et al.*, 1986, p. 365). Mazzullo and Ehrlich (1983, p. 117) recognized cyclic successions marked by variations in grain shape attributed to aeolian and littoral sediment influx, and they suggested extremely slow rates of overall sediment accumulation for the St. Peter.

Deposition of the Glenwood Shale has generally been attributed to renewed marine transgression marked by the accumulation of mud and sand in a variety of nearshore to offshore settings (Fraser, 1976; Choi and Simo, 1998). Peritidal carbonate facies are recognized in the Glenwood succession in its eastern extent, but the Glenwood is entirely characterized by marine facies in its western extent. Schutter (1996) interpreted the Glenwood Shale of Iowa and Minnesota to be a condensed section reflected, in part, by high concentrations of conodonts and nonskeletal phosphate. Lateral stratigraphic equivalency of the Glenwood in that area (1–3 m thick) with the dramatically thicker Starved Rock Sandstone (to 70 m) to the south underscores the relative condensation of the Glenwood Shale. The Starved Rock body has been interpreted as an offshore "marine bar complex" (Nunn, 1986) or a "lowstand shoreline complex" (Schutter, 1996, p. 62).

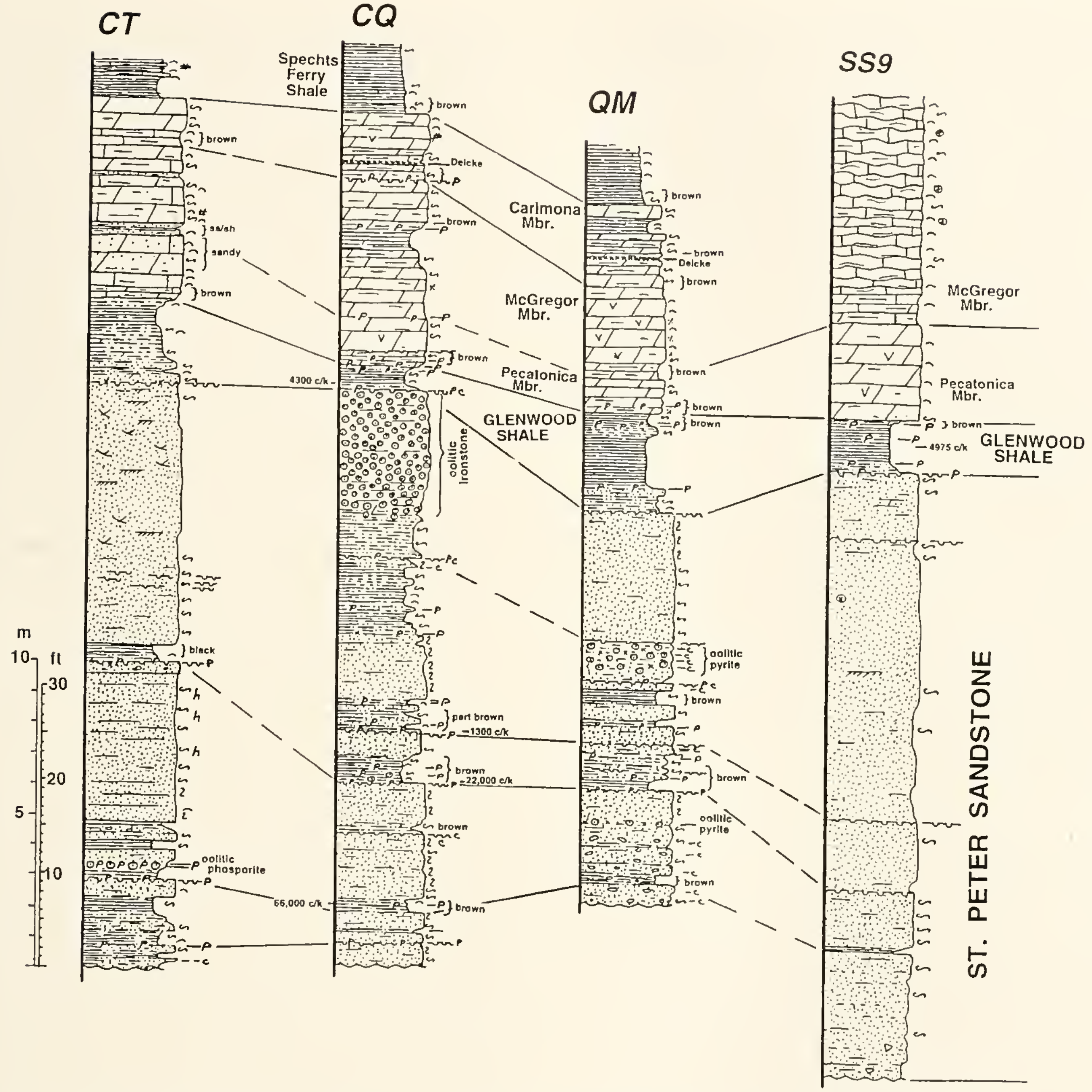
ANCELL GROUP PALEOECOLOGIC AND DEPOSITIONAL INTERPRETATIONS FOR STUDY AREA

The recognition that the St. Peter Sandstone includes conodont-rich organic and phosphatic brown to black shale units, phosphorites, and ironstones in the western facies tract necessitates a re-evaluation of previously proposed depositional interpretations. In particular, the extremely high abundances of conodonts in some of the brown shales (up to 66,000 conodonts per kilogram) strongly suggest that these shales represent condensed marine intervals. Watney *et al.* (1997, pp. 267–8) identified "laterally extensive organic-rich, pyritic" shale units in the St. Peter Sandstone of northeast Kansas that they "interpreted to be condensed sections" deposited in "deeper, anoxic-marine, sediment starved" environments.

The paucity of benthic fauna and the preservation of abundant organic matter and pyrite in these condensed shale units suggests that inhospitable dysoxic to anoxic benthic environments were present at least episodically during St. Peter deposition. Relatively high conodont diversity (>10 species) in these shale units is evidence that some portion of the water column was capable of supporting a marine fauna. While it is possible that some Ordovician conodont taxa had a nektobenthic life habit (Barnes and Fåhræus, 1975), their occurrence in dysoxic-anoxic benthic facies seems more consistent with a pelagic mode of life for most of the St. Peter conodont taxa. It is likely that a stratified water column, marked by an oxygenated surface layer and a dysoxic to anoxic bottom layer, characterized areas of the Midcontinent shelf during portions of St. Peter deposition (a quasi-estuarine epicontinental circulation system described by Witzke, 1987).

Oolitic ironstones, phosphorites, and phosphatic lags in the St. Peter succession also are interpreted to mark episodes of sediment condensation or starvation. Some sedimentologists consider ironstone and phosphorite occurrences to be products of condensed sedimentation during periods of reduced sediment influx associated with marine transgression (*e.g.*, Brett *et al.*, 1998; Van Houten, 2000; Witzke and Bunker, 1996). Starved transgressive surfaces punctuate the sandstone succession, represented in places by pyrite- and apatite-impregnated hardgrounds. Pyrite encrustations and ooidal pyrite further indicate that dysoxic to anoxic conditions were present at least episodically during St. Peter deposition.

The St. Peter–Glenwood interval in the western facies tract is characterized by a stacked succession of depositional cycles. Depending on their duration and geographic extent, such cycles may represent parasequence- or sequence-scale depositional packages. Each cycle is marked by a condensed shale unit at its base, which commonly overlies a pyritic hardground surface. The most densely sampled condensed shale interval (Loc. CQ; Text-fig. 1, units 8–9) shows a progressive upward decrease in relative condensation reflected by declining conodont abundances (from 22,400 conodonts/kg at the base to 275 conodonts/kg at the top; see Table 1). Scattered ironstone ooids occur in some of the condensed shales (*e.g.*, CQ 762). The condensed shale unit grades upward into a thicker sandstone interval in the upper part of each cycle. Many sandstone units display an upward increase in bioturbation and vertical burrowing, indicating as an upward-shallowing succession with increasing oxygenation. Recurring cyclic patterns of condensed shale



Text-figure 4.—Proposed stratigraphic correlations of St. Peter through Platteville succession in four core sections, northeast Kansas to eastern Iowa (localities given in Appendix and shown on Text-fig. 2). Relationships dashed where uncertain. Platteville Formation comprises the Pecatonica and McGregor members (thinned and condensed in western Iowa). Carimona Member and Spechts Ferry Shale are included in the lower Decorah Formation; position of the widespread Deicke K-bentonite is shown. Symbols as in Text-figure 1. Additional symbols: V (vuggy), c (coarse sand), h (horizontal laminae), c/k (conodonts per kilogram), ⊗ (echinderm debris), # (bryozoans).

and sandstone deposition are displayed in the CQ core (Text-fig. 1; units 3–4, 4–6, 7, 8–10, 11–13). Similar and possibly correlative cyclic units are present throughout the western facies tract (Text-figs. 3, 4).

Although information is insufficient to demonstrate unequivocal stratigraphic relationships, some of the condensed shale units in the western facies tract probably correlate to pyritic hardground surfaces within the sandstone-dominated succession of eastern Iowa (hypothetical correlations shown on Text-fig. 4). We believe such surfaces mark widespread sediment starvation across the eastern shelf corresponding to episodes of regional transgression and eustatic deepening. Similarly, the deepening-shallowing sandstone cycles recognized in the St. Peter of Minnesota (Mazzullo and Ehrlich, 1983) may correlate with shale-sandstone cycles of the western facies tract.

Condensed brown shale units with high conodont abundances have not been recognized within the upper St. Peter interval in the western facies tract, and changing patterns of regional sedimentation are proposed, marked by higher rates of sediment accumulation, overall shallower depositional conditions, and less pronounced cyclicity. The upper St. Peter is variably dominated by silty shale or massive sandstone, cross-stratified in part. Although less well developed than in the lower St. Peter, episodes of sediment condensation are indicated by phosphate-enriched horizons and oolitic ironstones in the upper St. Peter. A significant regional transgression is interpreted for the deposition of the overlying Glenwood Shale, which we consider to be a widespread condensed interval, characterized by high conodont abundances and phosphatic enrichment across a broad region. Organic brown shale facies are associated locally with the Glenwood interval, suggesting bottom dysoxia or anoxia in areas of the transgressing sea. Following Glenwood transgression, which onlapped siliciclastic source areas, regional deposition of subtidal carbonate facies (Platteville Formation) ensued. Compared to eastern and southern facies tracts, the Platteville Formation significantly thins to the west (Text-fig. 4) where it is interpreted to be, in part, a condensed interval.

Depositional Summary

The recognition of condensed sedimentary units in the St. Peter Sandstone of the western facies tract obviates conventional interpretations of the formation as simply a composite product of littoral and nearshore sedimentation forming a broadly diachronous transgressive sheet sand. St. Peter depositional models must also accommodate organic-rich marine shale, ironstone, and phosphatic-pyritic deposition within the succession. Sediment accumulation became highly attenuated at times across areas of the cratonic shelf, probably during transgressive sea-level events. Organic, phosphatic, and pyritic deposition is interpreted to have occurred during such deepening episodes within a stratified dysoxic or anoxic water mass under general quasi-estuarine circulation (Witzke, 1987). The general absence of carbonate material in the Ancell Group across vast areas of the central Midcontinent suggests episodic calcite undersaturation within the stratified water mass (Witzke, 2001). High proportions of juvenile or immature conodont elements are characteristic of some of the condensed shales. Witzke (2001) proposed that fluctuations and sporadic overturn of the pycnocline may have triggered bioevents within the seaway, resulting in high juvenile and adult mortality of the pelagic conodont faunas.

The St. Peter sandstone units of the western facies tract (and likely the eastern tract as well) probably accumulated as the seaway shallowed and sandy sediments were transported across the shelf. Regional shallowing broke down seaway stratification, enabling oxygenated benthic environments to become widespread. Multiple transgressions and regressions of the St. Peter seaway resulted in a complex stack of depositional cycles in the eastern and western facies tracts, as proposed by previous workers. The extreme sediment condensation proposed for the organic conodont-rich shales of the western facies tract suggests that deposition of the St. Peter Sandstone was a geologically slow process in the cratonic sea. This interpretation echoes the earlier suggestions of Mazzullo and Ehrlich (1983, p. 117) that St. Peter sands accumulated at extremely slow rates. Interpretations of the western facies tract have necessitated a re-evaluation of regional models of St. Peter deposition to incorporate ideas of episodic sediment condensation and starvation.

BIOSTRATIGRAPHIC INTERPRETATIONS OF THE ST. PETER CONODONTS

Previous Correlations and Age Interpretations of the St. Peter Sandstone

Because the St. Peter Sandstone overlies a major cratonic megasequence boundary (the Sauk-Tippecanoe boundary of Sloss, 1963) across most of its extent and because of the general absence of biostratigraphically useful faunas from the sandstone lithologies, the age of the formation has been difficult to resolve. Rich conodont faunas recovered from the overlying Glenwood Shale in the Upper Mississippi Valley area indicated a Mohawkian age for that unit (Stauffer, 1935, p. 131), thereby constraining the age at the top of the St. Peter Sandstone. Various authors have proposed correlations and age relationships of the St. Peter Sandstone based primarily on extrapolated regional lithostratigraphic inferences. Sardeson (1896, p. 83) was the first to propose a specific correlation: "The Saint Peter thus remains to be correlated with the Chazy, [but] this correlation cannot be said to be undoubtedly established." Many subsequent workers followed suit in considering the St. Peter to be primarily of Chazyan age (*e.g.*, Stauffer and Thiel, 1941; Dapples, 1955; Agnew, 1955). Dapples (1955) and Suhm (1997) proposed correlation of the St. Peter Sandstone with the McLish and Tulip Creek formations of Oklahoma of presumed "late Chazy" age. However, other stratigraphers suggested that the St. Peter was primarily of Blackriveran age (*e.g.*, Templeton and

Willman, 1963; Thompson, 1991). Sweet and Bergström (1976) considered the St. Peter–Glenwood interval in the Iowa-Minnesota area to be primarily of Blackriveran age (uppermost Chazyan locally at base), but the St. Peter of Missouri-Arkansas was shown to be an older unit of Chazyan age.

A graphic correlation of conodont faunas from the Upper Mississippi Valley Ordovician succession proposed by Sweet (1984, 1987) extrapolates a line of correlation which projects the St. Peter Sandstone within the *Belodina compressa* and possibly the uppermost *Plectodina aculeata* chronozones (i.e., middle to late Blackriveran) on his constructed Composite Standard Section. Sweet (1987) considered the overlying Glenwood Shale at St. Paul and in northeast Iowa to lie within the *Phragmodus undatus* chronozone (of latest Blackriveran to earliest "Trentonian" age). Straight-line graphic extrapolations require relatively constant rates of sediment accumulation for the duration of the section under consideration, and the possibility of condensed sedimentation for portions of the St. Peter–Glenwood interval could modify such correlations. However, Sweet (1987, p. 168) suggested that the Glenwood Shale "may have accumulated rather rapidly relative to those that represent the same interval of time in the standard reference section in Kentucky."

Previous Correlations of St. Peter Conodont Faunas

Clark and Miller (1971) and Grether and Clark (1980) recovered conodonts from the basal St. Peter, Readstown Member, but these are all reworked forms derived from underlying strata of the Lower Ordovician Prairie du Chien Group. The first non-reworked conodonts reported from the St. Peter Sandstone were recovered in Minnesota (Loc. SP) and western Iowa (Loc. CQ), and Witzke (1980, p. 5) listed form and multielement taxa (including *Phragmodus flexuosus*) from these localities suggestive of a "late Chazyan" correlation. Witzke (1992) subsequently expanded the listing of St. Peter conodonts from these localities as well as localities in Nebraska and Kansas, and reported occurrences of *P. flexuosus, Cahabagnathus, Eoplacognathus, Erraticodon* cf. *balticus, ?Leptochirognathus*, and other forms. He suggested similarities with upper Simpson and Dutchtown faunas and proposed a "late Chazyan–early Blackriveran" age for the conodont faunas of the St. Peter Sandstone. Witzke's suggested correlations were disputed by subsequent workers. Ethington *et al.* (1986, p. 10) wrote: "Witzke [1980] interpreted the St. Peter conodonts to be indicative of Chazyan age, although the genera he listed were not characteristic of Chazyan faunas elsewhere." Barnes *et al.* (1996, p. 48) further indicated that "some of the faunal elements identified by Witzke (1992) appear to be late Paleozoic contaminants." In both cases, the taxa in question were not identified.

Rexroad *et al.* (1982) recovered elements of of seven species of conodonts from the St. Peter Sandstone in southwestern Indiana. They correlated this fauna with the Dutchtown Formation of Chazyan age. Shaw (1990) later recovered conodonts from the St. Peter Sandstone (basal Tonti Member) of northern Illinois (LaSalle Co.), including *Coleodus* sp., *Lunidens vitreus*, and *Scapulidens primus*. The latter two species were previously known only from the Dutchtown Formation of Indiana (see Ethington *et al.*, 1986), and a "late Whiterockian [Chazyan] or early Mohawkian age" was tentatively proposed for the St. Peter (Shaw, 1990).

Sweet (1992) reported a succession of Ordovician conodont faunas from the subsurface of Kansas, although only informal lithostratigraphic labels were used to describe the stratigraphic succession. "Subsurface Unit A" yielded a conodont fauna that included *Phragmodus ambiguus* (= *P. flexuosus* morphotype B), *Cahabagnathus friendsvillensis, Erraticodon* cf. *balticus*, and others. He correlated "Subsurface Unit A" with the Mclish Formation of Oklahoma and indicated a late Whiterockian (Chazyan) age. The Kansas Geological Survey assigned this stratigraphic interval at one of Sweet's subsurface localities (Loc. CT of this report) to the St. Peter Sandstone (see Watney *et al.*, 1997). However, Sweet (1992, p. 187) considered this interval to be considerably older than any portion of the St. Peter Sandstone of southeast Minnesota.

Additional conodont collections have been noted from the subsurface St. Peter Sandstone of the Michigan Basin, where the formation reaches considerably greater thicknesses than elsewhere in the Midcontionent (up to 350 m; Barnes *et al.*, 1992; Nadon *et al.*, 2000). Bergström *et al.* (1994) identified "*Archeognathus* and *Multioistodus* faunas" as well as occurrences of *Leptochirognathus* and *Paraprioniodus* from the St. Peter of the Michigan Basin; they recognized a "diversity of Mohawkian assemblages in the [overlying] Glenwood Fm." Barnes *et al.* (1996) reported occurrences of *Archeognathus* spp., *Multioistodus* spp., *Coleodus* spp., and *Erismodus* spp. from the upper St. Peter in Michigan, and they noted *Phragmodus flexuosus* (morphotype A) from the Glenwood. They indicated a "medial to late Whiterockian age" for the Michigan St. Peter which they regarded as "older than the bulk of the St. Peter of the Upper Mississippi Valley" where the formation "appears to be, in part, Mohawkian in age" (Barnes *et al.*, 1996, p. 49).

BIOSTRATIGRAPHIC RELATIONS OF ST. PETER–GLENWOOD CONODONT FAUNAS

The collections of conodonts from the St. Peter and Glenwood recovered for this study include forms of potential biostratigraphic significance. The abundance of *Phragmodus flexuosus* from the lower and middle St. Peter in the CQ core is important, as this species was considered to be restricted to the Chazyan (upper Whiterockian) by Klapper and others (1981, p. 256) and Sweet and Bergström (1976). The North American Composite Standard Section later constructed by Sweet (1984) extended the range upward from the Chazyan into the basal Mohawkian (lower Blackriveran), overlapping with the lower range of *P. inflexus* in its upper part (see also Leslie and Bergström, 1995; Bauer, 1994). Occurrences of *P.* cf. *ambiguus* in the St. Peter of Nebraska and Kansas is consistent with a similar age range, as *P. ambiguus* is known only from Chazyan and basal Blackriveran strata (Bauer, 1994; highest occurrences overlap slightly with the lowest *Eoplacognathus elongatus* in the lower Bromide Fm.).

Occurrences of *Cahabagnathus* in the St. Peter of Iowa and Kansas are of particular importance, even though the small to fragmentary aspect of our specimens does not permit a clear species-level classification. *Cahabagnathus* is primarily a Chazyan genus (Sweet, 1984), but a late form (*C. carnesi*) apparently extends into the lowermost Blackriveran (Bergström and Carnes, 1976; Bergström, 1983). The presence of a continuous denticle row on the stelliplanate element joining anterior and posterior processes on the St. Peter specimens precludes assignment of these forms to late species of *Cahabagnathus* that show a denticle gap between the processes (*i.e.*, *C. sweeti*, *C. carnesi*). This indicates a pre-*C. sweeti* Zone age and supports correlation within some portion of the *C. friendsvillensis* Zone (see zonal subdivisions of Sweet, 1984). The St. Peter specimens most closely resemble *C. directus* (from the McLish) and *C. friendsvillensis*. Sweet (1992) previously reported *C. friendsvillensis* from the same Kansas core (Loc. CT) used in this report. The occurrences of *Cahabagnathus* in the lower St. Peter obviate a Blackriveran age and are most consistent with an early to middle Chazyan (*C. friendsvillensis* Zone) correlation (or a late Llanvirnian age in the British Series: see Bergström, 1983; Webby, 1998). Fragmentary elements of *Eoplacognathus* from the St. Peter of Iowa and Kansas are not identifiable at the species level, but the preserved material is similar to *E. foliaceus* and *E. reclinatus* (see Systematic discussion). If this evaluation is correct, these forms likely pre-date *E. elongatus* and would support a Chazyan correlation.

Leptochirognathus is restricted to the upper Whiterockian (Sweet, 1984), supporting a Chazyan age for the shale interval within the St. Peter Sandstone at St. Paul, Minnesota (Loc. SP). *Erraticodon* sp. is a locally common conodont in the St. Peter, and the genus is not known to occur above the Whiterockian. However, the species represented in the St. Peter is more derived than other described *Erraticodon* species (reduction or loss of lateral or posterior processes), and any biostratigraphic significance remains to be demonstrated. Occurrences of diverse assemblages of other hyaline conodont taxa in the St. Peter collections are generally consistent with a Chazyan and/or Blackriveran age, but the biostratigraphic ranges of many of these taxa remain uncertain. The lower St. Peter has yielded an *Erismodus* species resembling *E. arbucklensis* (a species not known to range above the Chazyan; Bauer, 1987, 1994). Indeterminate Genus and species B from the St. Peter of Iowa may represent a late surviving form within the serrate *Histiodella* clade, possibly supporting a Whiterockian age. However, the phylogenetic identity of this taxon remains unclear, and any biostratigraphic inferences are tentative. Although serrate *Histiodella* are most characteristic of mid-Whiterockian associations (Sweet, 1984), serrate forms are noted to locally overlap with the range of *P. flexuosus* (Harris *et al.*, 1979; Moskalenko, 1973). An upward range extension of such forms into the Chazyan is postulated consistent with the composited range of serrate *Histiodella* (*H. serrata*) reported by Sweet (1995).

The preponderance of biostratigraphic evidence indicates a Chazyan age for the lower to middle St. Peter succession even in the paleogeographically most shoreward areas of St. Peter deposition bordering the Transcontinental Arch (*e.g.*, Locs. CQ, SP). Broadscale regional diachroneity of the lower St. Peter cannot be demonstrated with the available biostratigraphic control. In general, the lower St. Peter faunas share similarities with associations reported from the Dutchtown Formation of Missouri (Klapper and Bergström, 1984, p. 954; Youngquist and Cullison, 1946) and McLish Formation of Oklahoma (Bauer, 1987). However, the upper part of the St. Peter Sandstone has produced sparse conodont collections of limited biostratigraphic significance, and the correlation of this interval remains uncertain. The stratigraphic position of these strata above Chazyan faunas and below the Glenwood Shale (interpreted to be of Blackriveran age) suggests a late Chazyan or early Blackriveran age for the upper St. Peter.

The conodont faunas of the overlying Glenwood Shale were initially interpreted by Stauffer (1935, p. 131) to be of Mohawkian age. Sweet (1984, 1987) constructed a graphic correlation that incorporated

Glenwood Shale conodont collections from southeast Minnesota (data of Webers, 1966) and northeast Iowa. The positions of the Glenwood faunas were plotted against his Composite Standard Section (CSS) resulting in a graphic correlation of the Glenwood Shale with a relatively short interval on the CSS. Sweet's (1984, 1987) correlations proposed that the Glenwood Shale in the Upper Mississippi Valley is primarily of post-Blackriveran age corresponding to the lower part of the *Phragmodus undatus* Zone (and locally into the highest part of the *Belodina compressa* Zone). The overlying Platteville Formation was included as a post-Blackriveran unit within the *P. undatus* Zone. Sweet (1987, p. 168) discussed plotting anomalies for northeast Iowa between the K-bentonites (higher in the succession) and the "line of correlation" defined by the first- and last-occurrence positions of certain conodont taxa. If the Glenwood is a condensed section as proposed by Schutter (1996), a straight-line graphic extrapolation through the St. Peter–Glenwood may significantly underestimate the duration of that interval. The presence of the Deicke K-bentonite higher in the succession firmly constrains an upper age limit of the St. Peter and Glenwood faunas of Iowa and Minnesota (Kolata *et al.*, 1986).

The well-known invertebrate faunas of the overlying Platteville Formation (sub-Carimona Member) in the Upper Mississippi Valley have been interpreted consistently to be of Blackriveran age (*e.g.*, Cooper, 1956; Kolata, 1975; DeMott *et al.*, 1987). If these correlations are correct, the underlying Glenwood Shale must also be no younger than Blackriveran. However, a Blackriveran age for the Glenwood-Platteville interval is at odds with the correlations of Sweet (1984, 1987). It is unclear if the modified base of the Mohawkian noted for Sweet's (1995) CSS changes the earlier Glenwood-Platteville correlations, as the composite ranges for some Glenwood-Platteville taxa (*Polyplacognathus ramosus*, *Phragmodus inflexus*) have been modified from that given in earlier versions. The ranges of certain Glenwood-Platteville taxa given for Sweet's (1984, 1987) CSS indicate first appearances at or above the highest Blackriveran (including *Phragmodus cognitus*, *Polyplacognathus ramosus*, *Scyphiodus primus*, *Chirognathus duodactylus*, *Bryantodina typicalis*). However, some of these taxa are known to co-occur with Blackriveran and Chazyan faunas elsewhere, and significant range modifications are suggested. *Scyphiodus* and *P. ramosus* co-occur with *Appalachignathus delicatulus* and other Blackriveran taxa in the Mackenzie Mountains (Tipnis *et al.*, 1979, p. 58), *Scyphiodus primus* co-occurs with *Phragmodus flexuosus* and *Cahabagnathus friendsvillensis* in Chazyan strata of Kansas (Sweet, 1982, p. 1045), and *Chirognathus duodactylus* co-occurs with *Cahabagnathus sweeti* in Oklahoma (Bauer, 1994). We recommend that the Glenwood and Platteville conodont faunas of the Upper Mississippi Valley be recorrelated to accommodate Blackriveran ranges in the Ordovician CSS. Further study is needed to resolve the apparent discrepencies between the Blackriveran age indicated by the Platteville invertebrate fauna and the Glenwood-Platteville correlations of Sweet (1984, 1987).

Our present interpretation is that the Glenwood Shale in Iowa, Minnesota, and Nebraska is a relatively condensed unit of Blackriveran age. *Polyplacognathus ramosus* and *Belodina compressa* were identified from the Glenwood Shale by Stauffer (1935), Webers (1966), and Sweet (1987). These species were not recognized in any of the Glenwood collections used for this study nor in the Washington Avenue (Minneapolis) Glenwood collections of Webers (1966) and Stauffer (1935), but they are common in overlying Platteville strata. Strata included in the upper Glenwood Shale in parts of Minnesota are considered to be lateral lithofacies equivalents of lower Platteville strata elsewhere (Sloan, 1972; Mossler, 1985). Therefore, it is likely that some of the Minnesota Glenwood conodont collections may include samples that post-date the Glenwood Shale succession in sections across most of Iowa and the Twin Cities area of Minnesota. Further study of the lithostratigraphic relations of Glenwood strata in Minnesota is needed, but two separate lithostratigraphic units may be inadvertently lumped together under this label (*i.e.*, a lower "true Glenwood" and an upper shale unit correlative with the lower Platteville).

SYSTEMATIC PALEONTOLOGY

Introduction

A full systematic paleontologic treatment of the St. Peter–Glenwood conodont faunas is not presented in this report for several reasons. First, the conodont collections are dominated by a few well-known taxa whose classification, diagnoses, descriptions, synonymies, and occurrences are well established in the literature (*e.g.*, *Phragmodus flexuosus*, *P. cognitus*, *Drepanoistodus erectus*). Second, many of the rarer taxa are represented in the collections by fragmentary or problematic materials that are not well suited for formal systematic treatment. Additional specimens and further study are deemed necessary to resolve the species-level (and in some cases genus-level) taxonomic placement of these taxa. Finally, certain taxa, some abundantly represented in the collections, display a broad range of morphologic variation that has proven difficult to constrain in a clear systematic manner without additional study. Further study may clarify the species-level taxonomy of forms left in indeterminate status (open nomenclature) for this report, especially elements assigned to the genera *Erismodus*, *Erraticodon*, and *Curtognathus*.

All conodont collections are permanently reposited in the Paleontology Repository, Department of Geoscience, University of Iowa (Iowa City, Iowa). Illustrated specimens and selected reference materials are assigned catalog numbers (SUI prefix). Terminology and element locational notation largely follow Sweet (1981, 1988).

Order **PROTOPANDERODONTIDA** Sweet, 1988

Family **PROTOPANDERODONTIDAE** Lindström, 1970

Genus **ONEOTODUS** Lindström, 1955

Oneotodus? ovatus (Stauffer, 1935)

Plate 4, figure 5

Discussion.—Distictive small coniform elements with albid cusps and an expanded flat sub-circular hyaline base are assigned to *Oneotodus? ovatus*. This species is scattered in samples from the St. Peter Sandstone (Locs. CQ, SP, OF, CT) and Glenwood Shale (Locs. CQ, GN, DL, SS; see also Stauffer, 1935; Webers, 1966). Bauer (1987, p. 23) questioned the generic assignment of this species, as the flat base does not conform with the diagnosis of *Oneotodus* given by Ethington and Brand (1981).

Genus **PSEUDOONEOTODUS** Drygant, 1974

Pseudooneotodus species

Discussion.—A few specimens from the Glenwood Shale of Iowa (GN, J-1021) are squat conical forms with a pointed apical denticle (centrally to posteriorly located), thin walls, an oval basal outline, and a broadly excavated base. These specimens (SUI 99484, 99485) are assigned to an indeterminate species of *Pseudooneotodus* (similar to *P.* cf. *beckmanni* of Leslie, 2000). Squat conical elements from other Ordovician units include *Lepodus minutus* Branson and Mehl, 1933a, *L.* sp. Webers, 1966, and *Ambalodus mitratus* Moskalenko, 1973 (= *P. mitratus*, see Leslie, 2000), but these forms all differ from the Iowa specimens in possessing lobate to triangular basal outlines.

Genus **STAUFFERELLA** Sweet, Thompson, and Satterfield, 1975

Staufferella cf. **S. falcata** (Stauffer, 1935)

Plate 4, figure 10

Discussion.—A few fragmentary symmetrical (Sa) elements from the Glenwood Shale of Iowa are assigned to *Staufferella* sp. cf. *S. falcata* (type *S. falcata* from the Glenwood Shale of Minnesota, Stauffer, 1935). Symmetrical specimens from the St. Peter Sandstone (C-3387, CQ-776.7) possess lateral costae that are slightly narrower and not basally alate as in *S. falcata*. It is unclear if a posterior groove or keel is present, as the posterior faces are broken on these specimens. An unassigned species of *Staufferella* from the McLish and Tulip Creek formations of Oklahoma (Bauer, 1987) is more narrowly tapered at the tip.

Family **DREPANOISTODONTIDAE** Fåhraeus and Nowlan, 1978

Genus **DREPANOISTODUS** Lindström, 1971

Drepanoistodus suberectus (Branson and Mehl, 1933b)

Plate 4, figures 1, 2, 6, 7

Discussion.—Coniform elements assigned to *Drepanoistodus suberectus* are scattered to common in samples from the St. Peter and Glenwood formations in the study area. The skeletal apparatus of this well-known and widespread Ordovician species includes several types of coniform elements (Bergström and Sweet, 1966; Sweet, 1988; Bauer, 1987), and the St. Peter–Glenwood specimens are largely indistinguishable from previously published descriptions of the species. However, a few specimens of geniculate coniform elements (*e.g.*, Pl. 4, fig. 2) from the lowermost sample in the CQ core (CQ-776.7) display a smaller cusp angle than generally seen for *D. suberectus*, and these bear some resemblance to *D. angulensis* (see description by Bauer, 1987, p. 16).

Indeterminate ?drepanoistodontid species

Discussion.—A collection of small hyaline non-geniculate coniform elements with recurved cusps from the lower St. Peter Sandstone (CQ-775.7) resemble *Drepanoistodus* in general mophology. However, these forms possess deep flaring subcircular basal cavities of notably larger proportions than seen in typical *Drepanoistodus*. In addition, the basal cavity extends upward from one-third to over one-half the length of the cusp. These forms likely represent a previously undescribed taxon, possibly a drepanoistodontid.

Order **PANDERODONTIDA** Sweet, 1988

Family **PANDERODONTIDAE** Lindström, 1970

Genus **PANDERODUS** Ethington, 1959

Panderodus species

Plate 4, figure 4

Discussion.—Recurved coniform elements bearing a longitudinal furrow from the Glenwood Shale of eastern Iowa (Loc. GN) and equivalent strata in eastern Nebraska (Loc. SM) are identified as *Panderodus* sp.

Order **PRIONIODONTIDA** Dzik, 1976

Family **OISTODONTIDAE?** Lindström, 1970

Genus **OISTODUS** Pander, 1856

Oistodus? venustus Stauffer, 1935

Discussion.—Rare squat geniculate coniform elements from the Glenwood Shale in the CQ core (SUI 99486) are identical to the form species *Oistodus venustus* described from the Glenwood Shale of Minnesota by Stauffer (1935) and Webers (1966). The generic assignment is queried following Bauer (1994, p. 363). This form species may be associated with the apparatus of one or more species of *Dapsilodus* (ibid.) or some other taxon (Bergström and Sweet, 1966), but no *Dapsilodus* or other species association has been recognized in the Iowa samples.

Indeterminate Genus and species B

Plate 1, figure 2; Text-figure 5

Discussion.—A single broken denticulated blade from the lower St. Peter Sandstone of western Iowa (CQ-762) does not resemble any other conodont recovered from the formation. The specimen is albid (hyaline base) and bears eight subequal erect to slightly reclined denticles that are fused for half or more of their length. The blade is thin and possesses a narrow basal trough that runs the length of the specimen. The denticles and upper part of the blade are marked by numerous fine microstriations (Text-fig. 5). The overall morphologic details of this specimen most closely resemble those described for some species included in the genus *Histiodella* (see McHargue, 1982), including the thin blade-shaped form, the narrow basal trough, and the finely striated aspect of the upper margins. Although differences are noted in the denticulation and basal margin, the St. Peter specimen shares many morphologic features in common with the anterior process of the "bladelike element" of *H. holodentata* Ethington and Clark, 1981, and the late-stage "denticulate morphotype" of *Histiodella* (McHargue, 1982). The broken aspect of the single St. Peter specimen and the relatively late stratigraphic occurrence of this form make assignment to *Histiodella* ill advised at present, and it is left in indeterminate status for this report. For the most part, *Histiodella* is not known to co-occur with *Phragmodus flexuosus* in most stratigraphic sections. However, serrate *Histiodella* are noted by Harris *et al.* (1979, p. 13, figs. 4, 17) to overlap with the range of *P. flexuosus* in the upper Antelope Valley Limestone in the Monitor Range of Nevada. Moskalenko (1973) also reported the co-occurrence of *P. flexuosus* and an undescribed species of *Histiodella* in Siberia. A single specimen of a serrate *Histiodella* (*H.* n. sp. 2, Harris *et al.*, 1979) was noted from the lower McLish Formation of Oklahoma, although Bauer (1987, p. 9) considered the conodonts from that interval to be reworked. Sweet (1995) revised the composited range of *Histiodella* to extend well into the Chazyan (overlapping with the ranges of *P. flexuosus* and *Cahabagnathus friendsvillensis*). It is proposed that the St. Peter specimen may represent a late surviving member within the serrate *Histiodella* clade.

Family **BALOGNATHIDAE?** Hass, 1959

Indeterminate balognathid? species

Discussion.—A small indeterminate pastinate element from the Glenwood Shale (CQ-721) displays a Y-shaped finely denticulated upper margin All processes are thin (same width as the denticles). The slightly curved lateral process is subequal in length to the anterior process. The central cusp is small, roughly equal in size to the adjoining denticles. This element does not resemble any described Ordovician taxon, but its pastinate morphology may suggest inclusion within the Balognathidae or Polyplacognathidae.

Family **POLYPLACOGNATHIDAE** Bergström, 1981

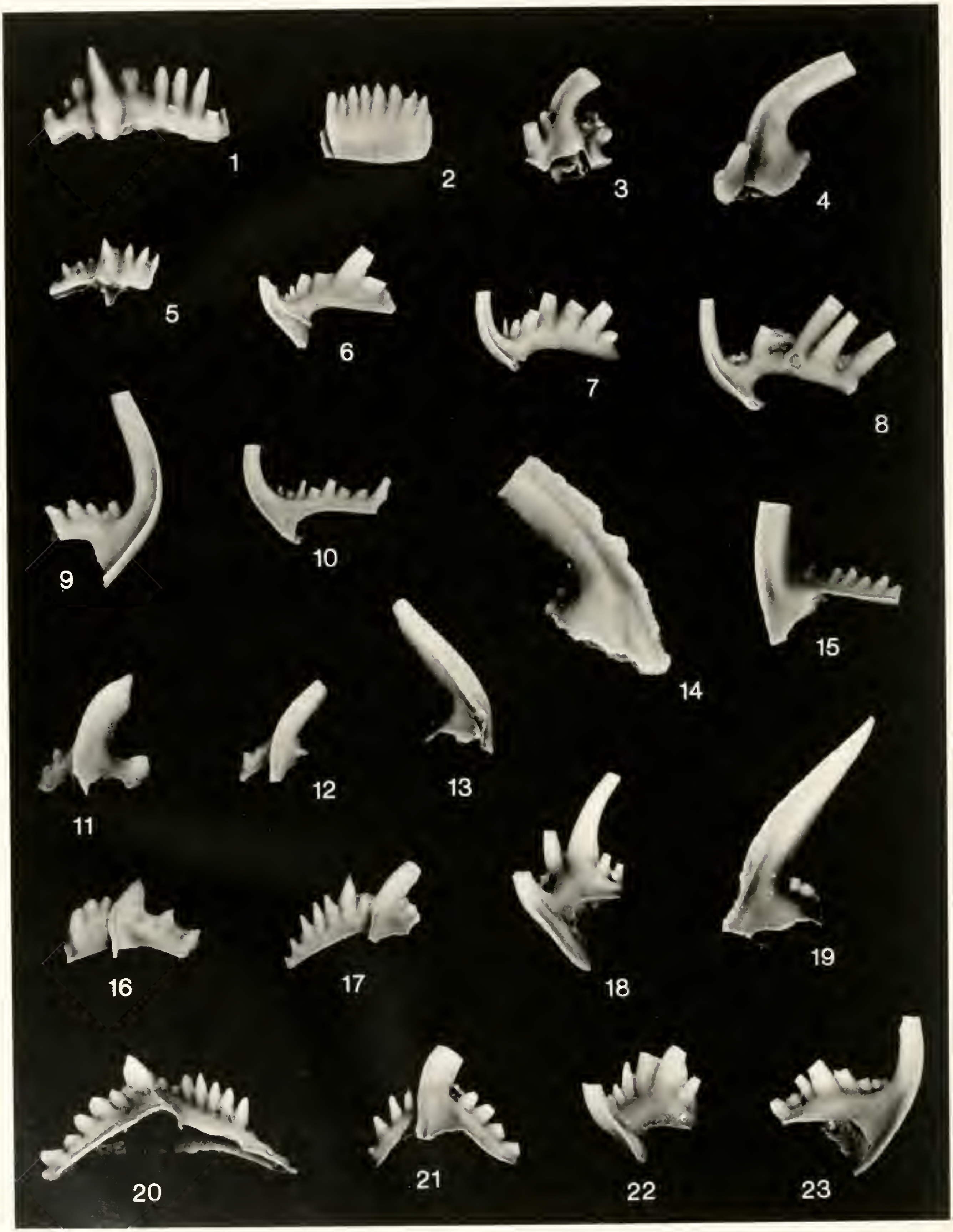
Genus **CAHABAGNATHUS** Bergström, 1983

Cahabagnathus species

Plate 2, figures 1, 2, 7

Discussion.—Small collections of partial to fragmentary elements from the lower St. Peter Sandstone of western Iowa (CQ-776.7, 775.7, 762) and northeastern Kansas (C-3387) include distinctive forms assigned to *Cahabagnathus*, although the species assignment is unclear. The most complete Iowa specimen is a small, presumably juvenile, pastiniplanate element with the anterior process missing (Pl. 2, fig. 1); the broad rounded posterior process resembles that seen in *C. directus* Bauer, 1987 (a species named from the McLish Formation of Oklahoma). It also bears some resemblance to *C.* n. sp. B of Leslie and Lehnert (1999) from the Joachim Dolomite of Arkansas. Additional Iowa specimens include broken stelliplanate elements with straight rows of denticles; these specimens most closely resemble *C. directus* and *C. friendsvillensis* (Bergström, 1971).

Specimens from Kansas include fragmentary stelliplanate and pastiniplanate elements displaying ridges and nodes (Pl. 2, figs. 2, 7). The posterior process of the pastiniplanate elements is broadly rounded; the denticle row is not in a straight line; a continuous denticle row joins anterior and posterior processes (no gap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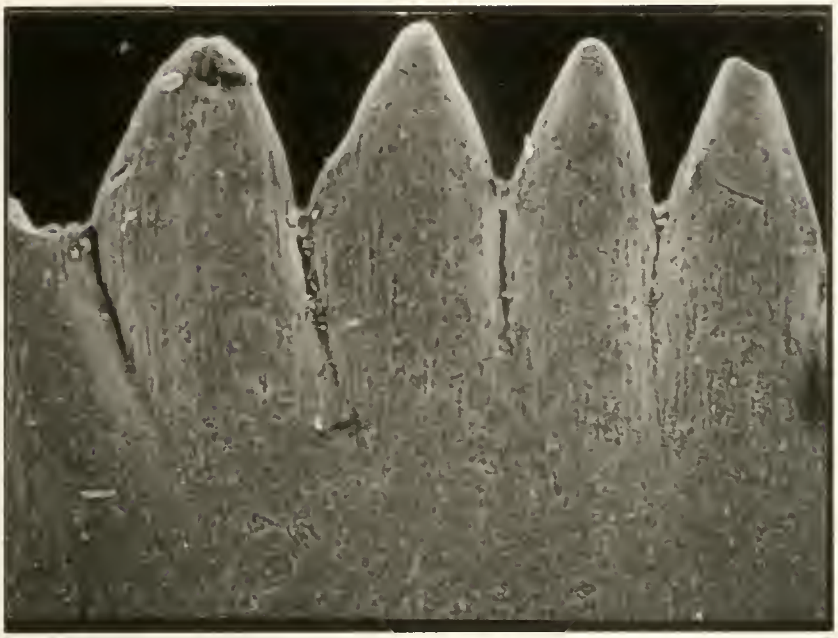


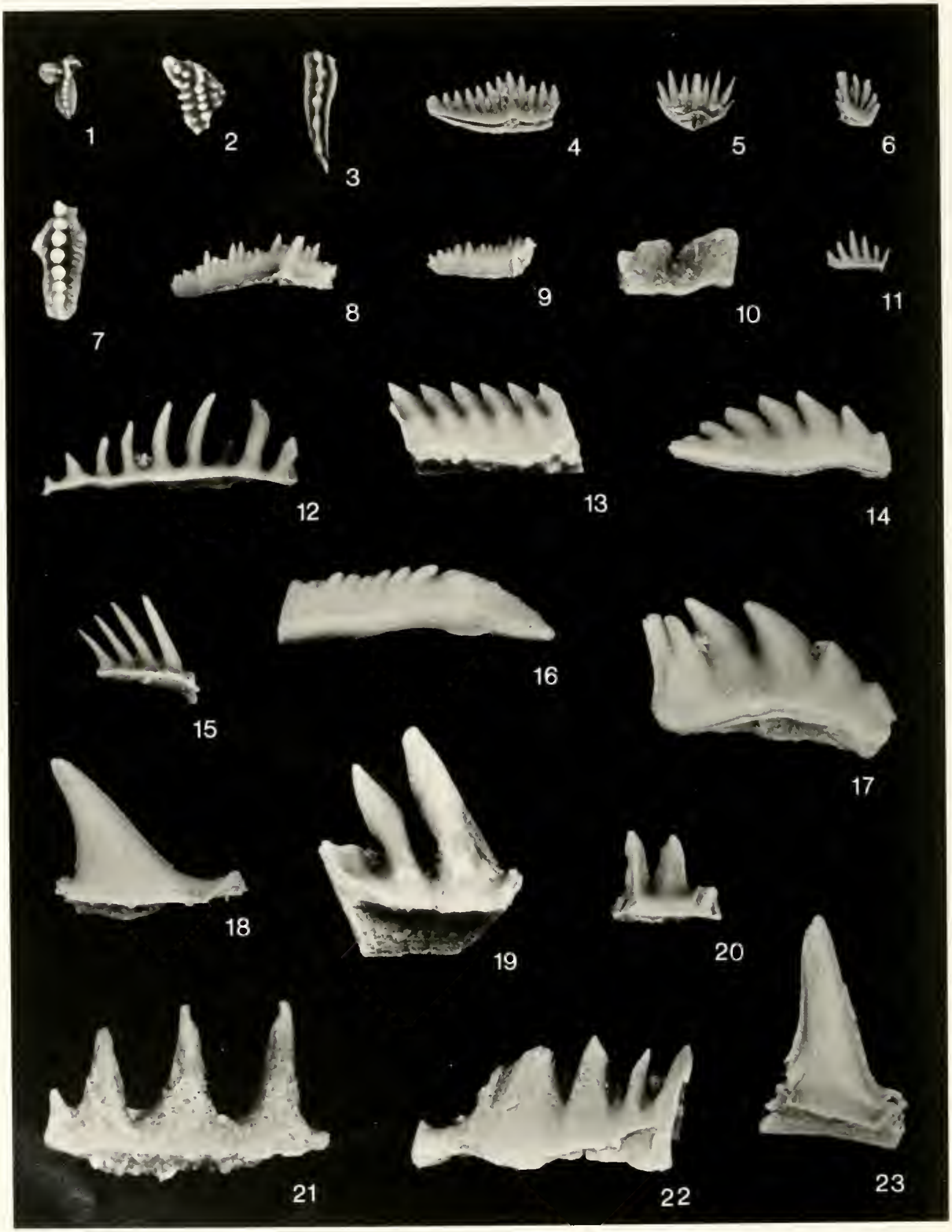
Text-figure 5.—Indeterminate Genus and species B; SEM photomicrograph of denticles showing microstriations (SUI 95016). ×350 (310 μm field of view).

←

PLATE 1

All figures (photographs) ×40. Specimens lightly coated with ammonium chloride sublimate.

- 1, 5. Indeterminate Genus and species A
    - 1. Pastinate P element; SUI 95014, CQ-776.7.
    - 5. Stellate P element; SUI 95015, CQ-776.7.
- 2. Indeterminate Genus and species B
    - 2. fragmentary blade-like element; SUI 95016, CQ-762.
- 3, 4. *Plectodina* sp.
    - 3. Sb element; SUI 95017, SM (S-1158).
    - 4. Sb element; SUI 95018, SM (S-1159).
- 6–17. *Phragmodus flexuosus* Moskalenko, 1973
    - 6. Sb element; SUI 95019, CQ-762.
    - 7. Sa element; SUI 95020, CQ-762.
    - 8. Sa element; SUI 95021, CQ-762.
    - 9. Sc element; SUI 95022, CQ-762.
    - 10. Sc element; SUI 95023, CQ-762.
    - 11. Pb element; SUI 95024, CQ-762.
    - 12. Pb element; SUI 95025, CQ-762.
    - 13. Pb element; cusp; SUI 95026, CQ-62
    - 14. M element; cusp; SUI 95027, OF (O-1977).
    - 15. M element; SUI 95028, CQ-762.
    - 16. Pa element; SUI 95029, CQ-762.
    - 17. Pa element; SUI 95030, CQ-762.
- 18–23. *Phragmodus cognitus* Stauffer, 1935
    - 18. Sa element; SUI 95031, CQ-720.3.
    - 19. Pb fragment; SUI 95032, CQ-720.3.
    - 20. Pa, aberrant specimen with incipient dichognathiform process; SUI 95033, CQ-720.3.
    - 21. Pb element; SUI 95034, CQ-720.3.
    - 22. Sb element; SUI 95035, CQ-720.3.
    - 23. Sc element; SUI 95036, CQ-720.3.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as in *C. sweeti*). These specimens most closely resemble *C. directus* and *C. friendsvillensis*. Sweet (1992) reported the occurrence of *C. friendsvillensis* from the same Kansas core (Loc. CT) in a stratigraphic interval he termed "Subsurface Unit A"; this interval is assigned to the St. Peter Sandstone following the stratigraphic classification of this core section by the Kansas Geological Survey (Watney *et al.*, 1997).

Genus **EOPLACAGNATHUS** Hamar, 1966

Eoplacognathus species

Plate 2, figure 3

Discussion.—Rare elements from the lower St. Peter Sandstone of western Iowa (CQ-776.7, 775.7) and northeastern Kansas (C-3386) are assigned to *Eoplacognathus*, although species assignment is precluded by the fragmentary nature of the specimens. Most specimens are broken anterior processes that are slightly curved and distally-pointed; the pointed and curved aspect of these specimens is most similar to that of *E. foliaceus* (see Bergström, 1971) and *E.* sp. (of Bauer, 1987). Some of these are not readily distinguishable from the anterolateral process of stelliplante elements of *Cahabagnathus* (see illustrated specimen). However, additional Iowa specimens (CQ-775.7) preserve the central region of the pastiniplanate elements and show an enlarged denticle (or cusp) at the junction of the three processes; this character has been observed only in *E. reclinatus* (see Bergström, 1971), a European species. Elements informally classified as "*E. foliaceus–E. reclinatus* transition" from Nevada (Harris *et al.*, 1979) and the morphologically similar *E.* sp. from the McLish Formation (Bauer, 1987) differ from the St. Peter specimens in possessing a sinuous row of denticles on the anterior process of the pastiniplanate elements. Although differing from these Nevada and Oklahoma specimens, the lower St. Peter occurrences may also show transitional aspects between *E. foli-*

←

PLATE 2

All figures (photographs) ×40. Specimens lightly coated with ammonium chloride sublimate.

- 1, 2, 7. *Cahabagnathus* sp.
  - 1. juvenile pastiniplanate element; SUI 95037, CQ-776.7.
  - 2. fragmentary pastiniplanate element; SUI 95038, CT (C-3387).
  - 7. broken process of stelliplanate element; SUI 95039, CT (C-3387).
- 3. *Eoplacognathus* sp.
  - 3. broken process; SUI 95040, CT (C-3386).
- 4, 5. *Chirognathus duodactylus* Branson and Mehl, 1933a
  - 4. Sa element ("*C. multidens*"); SUI 95041, CQ-721.
  - 5. Sb? element; SUI 95042, CQ-721.
- 6, 11. cf. *Chirognathus* sp.
  - 6. indeterminate element; SUI 95043, CT (C-3386).
  - 11. indeterminate element; SUI 95044, CT (C-3386).
- 8, 9. Indeterminate Genus and species C
  - 8. Pa element; SUI 95045, O-1977.
  - 9. elongate broken process; SUI 95046, O-1977.
- 10. cf. *Leptochirognathus* sp.
  - 10. fragmentary element with compressed denticles; SUI 95047, SP-L (12–13.5).
- 12. cf. *Coleodus* sp.
  - 12. indeterminate bar-like element; SUI 95048, CQ-776.7.
- 13, 14, 16, 17. *Coleodus* sp.
  - 13. broken blade; SUI 95049, CQ-776.7.
  - 14. complete element; SUI 95050, CQ-762.
  - 16. nearly complete element; SUI 95051, OF (O-1977).
  - 17. nearly complete element; SUI 95052, OF (O-1977).
- 15. *Erraticodon* sp.
  - 15. broken process with reclined denticles (for comparison with *Coleodus* and *Archeognathus*); SUI 95053, CQ-762.
- 18, 21, 23. *Archeognathus* sp.
  - 18. isolated denticle; SUI 95054, CQ-762.
  - 21. conjoined denticles; SUI 95055, SP-U (25.5–27).
  - 23. isolated denticle; SUI 95056, CQ-762.
- 19, 20, 22. cf. *Archeognathus* sp.
  - 19. conjoined denticles, basal groove displayed; SUI 95057, CQ-762.
  - 20. conjoined denticles; SUI 95058, CT (C-3387).
  - 22. partial crown; SUI 95059, CQ-762.

aceus and *E. reclinatus* in possessing an enlarged denticle (like *E. reclinatus*) but with a slightly curved anterior process (like *E. foliaceus*). Fragmentary pastiniplanate elements from higher in the St. Peter (CQ-762.8, 757) are tentatively included with *E.* sp.

Family **MULTIOISTODONTIDAE** Harris, 1964

Genus **LEPTOCHIROGNATHUS** Branson and Mehl, 1943

cf. **Leptochirognathus** species

Plate 2, figure 10

Discussion.—Two fragmentary specimens from the lower St. Peter shale unit at St. Paul, Minnesota (Loc. SP), are tentatively identified as an indeterminate species of cf. *Leptochirognathus.* The illustrated specimen is hyaline and preserves two large laterally compressed denticles with relatively sharp upper margins, features characteristic of the genus. The denticles are relatively short with rounded margins, and a shallow basal trough extends the length of the specimen. The specimen bears some resemblance to the graciliform element of *L. quadratus* ("*L. gracilis*") described by Branson and Mehl (1943, p. 377), which includes a "short, stout, somewhat rounded" first denticle, and a long trough-like basal cavity. However, most described elements of *Leptochirognathus* are characterized by compressed elongate pointed denticles, aspects not seen on the St. Peter specimen (although rounded to blunted denticles are illustrated for an element of *L.* n. sp. from Nevada by Harris *et al.*, 1979, pl. 1, fig. 18, and described for the anterior denticle of the quadratiform element of *L*?. sp. 1 from the Tyner Fm., Oklahoma, Bauer, 1989). The second St. Peter specimen preserves one relatively stout compressed pointed denticle, but its fragmentary nature makes inclusion here tenuous.

Indeterminate multioistodontid? species

Discussion.—Four indeterminate hyaline elements from the lower St. Peter of Nebraska (O-1977) are included here. Two bipennate elements with a long recurved cusp (posterior process 4 denticles, shortened anterior process 1 to 2 denticles) resemble the "cyrtoniodiform" elements of *Paraprioniodus costatus* illustrated by Rexroad *et al.* (1982, fig. 7) from the Everton Dolomite. Two pastinate "prioniodiform" elements display shorter cusps flanked by posterior and anterior processes with one to two denticles, a short lateral process with a single denticle, and a broad basal cavity. Gross morphologic similarities with *Paraprioniodus* suggest tentative relationships with the Multioistodontidae. A few fragmentary elements from the lower St. Peter of Kansas (C-3387) have compressed costate cusps similar to some multioistodontid taxa (*e.g.*, *Neomultioistodus*).

Family **PLECTODINIDAE** Sweet, 1988

Genus **PLECTODINA** Stauffer, 1935

Plectodina species

Plate 1, figures 3, 4

Discussion.—Various specimens from the St. Peter Sandstone and Glenwood Shale of Iowa and Nebraska are assigned to *Plectodina*, but, for the most part, these small and generally fragmentary elements are not easily identified to species level. These elements are left in open nomenclature, although morphologic differences in the length and denticulation of the posterior process of the Sc elements between the St. Peter samples and Glenwood samples suggest that more than one species is probably represented. It is possible that some small Pa and Pb elements of *Plectodina* have been inadvertently included with *Phragmodus* in Tables 1 and 2, but the distinctive S elements of *Plectodina* are more easily distinguished, especially the digyrate Sb elements. *Plectodina* is a rare taxon throughout the St. Peter Sandstone, but it is locally common in the some Glenwood Shale samples (*e.g.*, Loc. GN). Most, if not all, specimens of *Plectodina* from the Glenwood Shale are probably assignable to *Plectodina aculeata* (Stauffer, 1930). M elements from one St. Peter sample (CQ-775.7) resemble *Plectodina* sp. illustrated by Bauer (1987) from the McLish Formation of Oklahoma.

Family **CYRTONIODONTIDAE** Hass, 1959

Genus **BRYANTODINA** Stauffer, 1935

Bryantodina typicalis Stauffer, 1935

Discussion.—Distinctive thin blade-like multidenticulate pectiniform and ramiform elements of *Bryantodina typicalis* occur in some Glenwood Shale samples (GN, CQ720.3, J-1021, SS-753). This well-known species was first described from the Glenwood Shale of Minnesota (Stauffer, 1935; see also Webers, 1966).

?Bryantodina species

Discussion.—A few fragmentary thin blade-like multidenticulate carminate pectiniform and ramiform elements were recovered from two St. Peter samples (CQ-757, O-1977). The denticulation and thin blade-like aspect of these specimens bear resemblance to *Bryantodina typicalis* from the Glenwood Shale. However, their fragmentary nature precludes clear taxonomic assignment, and they are provisionally labeled as? *Bryantodina* sp. The best preserved Pa element (SUI 99487) has 9 erect partially fused denticles on the posterior process and 3 denticles on the anterior process. Ramiform fragments also show erect partially fused small denticles. Bryantodiniform elements recovered from Glenwood Shale equivalents in eastern Nebraska (S-1158, 1161, 1162) are fragmentary, and these specimens are tentatively labeled as *?Bryantodina* sp., although they likely represent fragments of *B. typicalis*. Specimens provisionally labeled as "*Bryantodina*" sp. were reported from the McLish Formation of Oklahoma by Bauer (1987).

Genus **PHRAGMODUS** Branson and Mehl, 1933b

Phragmodus flexuosus Moskalenko, 1973
Plate 1, figures 6–17

Discussion.—Elements of *Phragmodus flexuosus* are the dominant conodonts of the lower to middle St. Peter Sandstone in western Iowa (Loc. CQ, see Table 1). Mature conodont elements in the St. Peter collections agree in most salient details with the descriptions given for the apparatus of *P. flexuosus* in Klapper *et al.* (1981) and Bauer (1987; *P. flexuosus* morphotype A). Moskalenko (1972, 1973) apparently included additional elements within her apparatus reconstruction that are not recognized in the St. Peter collections. P elements are differentiated (Pa, Pb) in the St. Peter collections, thereby precluding assignment to *P. ambiguus* Bauer, 1994. Mature Pa and Pb elements are dichognathiform in all samples. However, immature Pa elements (one-fifth to one-half the length of the largest specimens) are variably dichognathiform to ozarkodiniform in a few samples. Small immature elements of *Phragmodus* are abundant in samples CQ-775.7 and CQ-762.8, and, although the mature Pa elements of *P. flexuosus* are indistinguishable in the two samples, the immature specimens differ between the two samples. The lower sample (CQ-775.7) contains small Pa elements dominated by dichognathiform morphologies, but a few specimens lack the dichognathiform process (*i.e.*, are ozarkodiniform). By contrast, all small immature Pa elements in the higher sample (CQ-762.8) are ozarkodiniform with no trace of a dichognathiform process or "wrinkle." In this respect, these small immature Pa elements are largely indistinguishable from those of the Midcontinent endemic species *P. cognitus* Stauffer, 1935. However, because no larger mature specimens of *P. cognitus* are recognized in the St. Peter samples, and because the small ozarkodiniform Pa elements grade into the larger dichognathiform Pa elements of *P. flexuosus* (sample CQ-775.7), it seems likely that the small ozarkodiniform Pa elements represent a juvenile ontogenetic stage present within some populations of *P. flexuosus*. This interpretation may explain the subsequent phylogenetic origin of *P. cognitus* via paedomorphosis from certain Midcontinent North American stocks of *P. flexuosus*.

M elements of *P. flexuosus* within the St. Peter samples are generally dolabrate, unlike the exclusively geniculate coniform (oistodontiform) M elements of *P. polystrophos* Watson, 1988 (= *P. harrisi* of Bauer, 1989). Most St. Peter specimens display four denticles on the posterior process, but some specimens, both mature and immature, variably display from one to five denticles. Immature small M elements are common in samples CQ-775.7 and CQ-762.8, and interesting variations are noted. The lower sample (CQ-775.7) includes common geniculate coniform elements (adentidulate posterior process), but some specimens show one to three denticles on the posterior process. By contrast, the upper sample (CQ-762.8) contains immature small M elements dominated by dolabrate morphologies with three to four denticles on the posterior process, but some show reduced denticles (1 to 2) and a few appear to be geniculate coniform. Variation of M-element morphology was discussed by Bauer (1989, p. 103), and he proposed that the apparatus of *P. flexuosus* likely "possessed both types of M elements" (dolabrate and coniform). Likewise, Moskalenko (1972, 1973) included both dolabrate and geniculate coniform elements within her apparatus reconstruction of *P. flexuosus*.

Sc elements in all samples are cordylodontiform and display a relatively straight posterior process with faintly sinuous denticles. Mature Sa and Sb elements are similar in general morphology (phragmodontiform) and are distinguished from the Sc elements by the presence of small lateral processes (seen as narrow ridges or costae) marginal to the cusp and a broadly arched and sinuous posterior process. Unlike the Sc elements, which bear relatively uniformly sized small denticles on the posterior process, the posterior processes of the Sa and Sb elements display one or more (generally two or three) large denticles similar in size to the cusp. Large numbers of immature Sa and Sb elements (one-fifth to one-half the size of the larger specimens) are contained in samples CQ-775.7 and CQ-762.8, and significant variations are seen between these samples. The lower sample (CQ-775.7) contains small Sa and Sb elements similar in general morphology to that of the co-occurring larger specimens, each displaying a broadly arched posterior process with one or two large denticles (subequal in size to the cusp). However, the small specimens are notably less sinuous than the larger mature specimens. Mature Sa and Sb elements in the higher sample (CQ-762.8) are indistinguishable from those in the lower sample. However, immature small specimens in this sample are markedly different in two aspects: 1) the posterior process is arched anteriorly, but the process is straight posteriorly (and non-sinuous to slightly sinuous); and 2) the posterior process consistently shows only a single large denticle (at the inflection where the anterior arch straightens posteriorly). These morphologies are not generally characteristic of *P. flexuosus* but more closely resemble that seen in *P. inflexus* Stauffer, 1935 and *P. undatus* Branson and Mehl, 1933b (see Leslie and Bergström, 1995). It could be argued that these small specimens should actually be assigned to *P. inflexus*, but this assignment is rejected for two reasons: 1) no larger specimens of *P. inflexus* occur within any of the St. Peter samples; and 2) the co-occurring small Sc elements (same sizes as the small Sa and Sb elements) are cordylodontiform (dolabrate), unlike the phragmodontiform Sc elements of *P. inflexus* (see Leslie and Bergström, 1995). If these small Sa and Sb elements (CQ-762.8) belong within the sample of *P. flexuosus*, it seems reasonable to suggest that significant morphologic changes in the phragmodontiform elements first appeared during juvenile ontogenic development in certain (St. Peter?) populations of *P. flexuosus*. It is proposed that these juvenile morphologies later became incorporated in the mature morphology of the descendent species (*P. inflexus*) by paedomorphosis (paralleling changes in the Pa elements discussed above).

If this proposition has any validity, the taxonomic differentiation of *P. flexuosus* and *P. inflexus* may prove difficult for small (juvenile) elements. The following quote from Klapper *et al.* (1981, p. 261, underlines added) is of note: "The skeletal apparatus of *Phragmodus inflexus* Stauffer is closely similar to that of its predecessor, *P. flexuosus* Moskalenko, but differs in being composed of typically *much smaller elements* that are laterally compressed and commonly fragile rather than large and robust." However, such size distinctions, particularly when co-occurring with larger elements of *Phragmodus*, may conceivably reflect ontogenetic growth stages of a single species in some cases. An abundance of small specimens in certain samples may alternatively reflect two different things: 1) the specimens represent a species that is characteristically small, or 2) the sample is skewed toward juvenile specimens, possibly due to high juvenile mortality in particular depositional settings. When both small and large elements are present in the same sample, ontogenetic variation should be considered. Bauer (1994) reported that the ranges of *P. flexuosus* and *P. inflexus* overlap in the Bromide Formation of Oklahoma. If the small Sa and Sb elements from the St. Peter samples discussed above are assigned to *P. inflexus*, a similar overlap could also be interpreted. Nevertheless, an ontogenetic explanation of morphologic variation within a single species (*P. flexuosus*) is considered a more likely explanation for the St. Peter samples. The species-level taxonomic assignment of small, presumably juvenile, elements of *Phragmodus* may inadvertently omit consideration of those distinguishing characters that appear in later stages of ontogenetic development. This is of special concern if paedomorphic evolution characterizes any portion of the *Phragmodus* lineage. It is recommended that species of *Phragmodus* should ideally be defined by characters present in the largest elements of any collection, as such elements likely were derived from fully mature individuals.

Phragmodus cognitus Stauffer, 1935
Plate 1, figures 18–23

Discussion.—Elements of *Phragmodus cognitus* dominate certain collections from the Glenwood Shale of Iowa (*e.g.*, CQ-721, J-1021, SS-753), and the species also occurs in equivalent strata of the uppermost St. Peter Sandstone or Glenwood Shale in eastern Nebraska (S-1162) and southeastern Minnesota (Stauffer, 1935). *Phragmodus cognitus* is apparently endemic to the continental interior of North America, and it is best known from the Upper Mississippi Valley area where it ranges as high as the Decorah Shale (Leslie, 2000). It is primarily distinguished from other species of *Phragmodus* by the presence of an ozarkodiniform Pa element (Leslie and Bergström, 1995; Klapper *et al.*, 1981), unlike the dichognathiform P elements seen in other species of the genus. The Pb element of *P. cognitus*, however, is dichognathiform. Collections containing relatively large elements of *Phragmodus* from CQ-720.3, CQ-721, and SS-753 agree in most salient details with the diagnosis of *P. cognitus* given by Klapper *et al.* (1981, p. 251). Most Pa elements are ozarkodiniform, but a few of the largest specimens are aberrant in showing an incipient dichognathiform anterior process and an expanded basal cavity (Pl. 1, fig. 20). The occurrence of a dichognathiform-like process on the largest (presumably gerontic) specimens may indicate convergence towards the Pa structure of *P. inflexus* or *P. flexuosus* late in the ontogeny of some populations of *P. cognitus*. Klapper *et al.* (1981, p. 251) noted "riblike expansions of outer side [of Pa element] vertically beneath cusp" for *P. cognitus* that are reminiscent of a greatly reduced dichognathiform process. They indicated that the S elements of *P. cognitus* display a "straight bladelike" process posterior of the arched anterior region, but noted that some specimens apparently belonging to this species show "slightly twisted" denticles. Similar twisting is seen in some specimens from CQ-720.3, CQ-721, and SS-

753, and a few fragmentary posterior processes are slightly sinuous (less so than seen in *P. flexuosus*).

Phragmodus cf. **P. ambiguus** Bauer, 1994

Discussion.—Collections from the lower St. Peter Sandstone of eastern Nebraska (O-1977) and northeast Kansas (C-3387, 3386) include scattered to common elements of a species of *Phragmodus* similar in most respects to *P. flexuosus* discussed above. However, unlike the collections of *P. flexuosus* from the lower St. Peter of western Iowa, only one type of P element was noted in the Nebraska and Kansas samples. The P elements from these collections (SUI 99488, SUI 99489) are not particularly well preserved or abundant, but the angle formed by the processes is relatively constant in all specimens (similar to that seen in the Pb elements of *P. flexuosus*). Where preserved, the posterior process bears 3 denticles. No broad-angled forms resembling the Pa elements of *P. flexuosus* were noted in these collections. Bauer (1987, p. 25) originally described forms from the McLish of Oklahoma that lacked differentiated P elements as "*P. flexuosus* morphotype B," and he subsequently named this taxon *P. ambiguus* Bauer, 1994. The Kansas and Nebraska forms are tentatively allied with this species. Alternatively, the absence of differentiated Pa elements could be a preservational artifact related to the small collection sizes. The associated M (dolabrate) and S elements are largely indistinguishable from *P. flexuosus* s.s. *P. ambiguus* is known from McLish and lower Bromide formations in Oklahoma and the Chazy Group of New York (Bauer, 1994). Sweet (1992) also reported *P. flexuosus* morphotype B (= *P. ambiguus*) from the St. Peter at Locality CT and elsewhere in the Kansas subsurface.

Phragmodus cf. **P. inflexus** Stauffer, 1935

Discussion.—Phragmodus inflexus is primarily distinguished from *P. cognitus* by its dichognathiform Pa element, which may display a denticulate (single denticle) anterior process (Leslie and Bergström, 1995; Klapper *et al.*, 1981). Some specimens of *Phragmodus* from the Glenwood Shale of eastern Iowa (GN) and eastern Nebraska (S-1158, S-1159, S-1161) are not included within *P. cognitus* because the Pa elements are dichognathiform, although the anterior process is adenticulate and is not as prominently developed as in typical *P. inflexus*. The associated *Phragmodus* elements (Pb, M, S) from these collections are largely indistinguishable from those of *P. cognitus*. Because of the presence of dichognathiform Pa elements, *Phragmodus* elements from these collections are provisionally labeled *P.* sp. cf. *P. inflexus*. A single Pa element from CQ-720.3 displays a denticulate anterior process and is assigned to *P.* sp. cf. *P. inflexus*, although this specimen occurs within collections otherwise dominated by *P. cognitus*. A denticulate anterior process on one or both of the P elements is given as a diagnostic character of *P. inflexus* by Klapper *et al.* (1981, p. 262), but they acknowledged that "anteriorly adenticulate dichognathiform elements that are otherwise closely similar to anteriorly denticulated specimens occur in many collections of *P. inflexus*." As such, it seems probable that the denticulation of the dichognathiform process displays variation within the species.

The type specimens of both *P. cognitus* and *P. inflexus* come from the same locality and stratum in the Glenwood Shale of southeastern Minnesota (Stauffer, 1935), and, if both species are valid taxa, they are apparently contemporaneous and sympatric in the North American Midcontinent. Both species succeed *P. flexuosus* stratigraphically, and immature elements of *Phragmodus* occur in the underlying St. Peter Sandstone that resemble both *P. cognitus* and *P. inflexus*. The apparent difficulty in differenting *P. inflexus* and *P. cognitus* in some Iowa Glenwood collections, and the co-occurrence of these two species in Minnesota, raises issues about their taxonomic status. Geographic and paleo-environmental variations may need to be considered in a regional stratigraphic evaluation of this *Phragmodus* plexus. Although speculative, the possibility that *P. inflexus* and *P. cognitus* may be geographic or ecophenotypic variants of a single species is raised here.

Phragmodus? species

Discussion.—Rare fragmentary elements (SUI 99490, SUI 99491) from the lower St. Peter Sandstone (CQ-775.7, CQ 762.8) resemble forms from the Bromide, McLish, and Tulip Creek formations of Oklahoma that Bauer (1994) classified as *Phragmodus? arcus* Webers, 1966. These St. Peter specimens include S elements with erect laterally compressed denticles. Dichognathiform P elements tentatively associated with this taxon possess denticulate processes and a compressed cusp. These forms differ from ?*P. arcus* discussed by Bauer (1994) in the apparent absence of lateral costae on the S-element cusps, and the P elements are dichognathiform and lack the sharp angle between posterior and anterior processes. *Phragmodus arcus* was first described by Webers (1966) for certain distinctive phragmodiform S elements from the Platteville Formation of Minnesota.

Indeterminate Genus and species C

Plate 2, figures 8, 9

Discussion.—Two indeterminate conodont elements with multi-denticulated elongate thin processes were recovered from the lower St. Peter Sandstone in the Offutt Air Force Base core, Nebraska (O-1977). The most complete specimen is carminate, with one long process (anterior?) bearing 15 erect partially-fused denticles and the shorter broken process (posterior?) preserving 6 denticles. A small shallow basal cavity is seen below the cusp. A second specimen is tentatively associated with this form, and displays a broken elongate process bearing 13 denticles. The numerous small denticles seen on these specimens invite comparison with other highly denticulated Ordovician taxa, especially *Bryantodina* and *Appalachignathus*. However, the St. Peter forms are more highly denticulate than any known species of *Bryantodina*, and, in addition, *Bryantodina* characteristically displays a proportionately larger cusp and a basal groove than the St. Peter specimens. P elements of *Appalachignathus* are more highly denticulate than the St. Peter specimens and also display a basal groove, and any relationships seem unlikely. Genus and species C probably represents a new taxon, possibly allied with *Bryantodina*.

Family **RHIPIDOGNATHIDAE?** Lindström, 1970

Genus **APPALACHIGNATHUS** Bergstrom, Carnes, Ethington, Votaw, and Wigley, 1974

cf. **Appalachignathus** species

Discussion.—A single broken Pb (?) element (SUI 99492) from the St. Peter Sandstone at St. Paul, Minnesota, preserves 12 semi-erect partially fused denticles, and a basal groove extends the length of the specimen. The multidenticulate aspect as well as the basal groove suggest similarities with *Appalachignathus*, a rare but widespread conodont genus from Chazyan and Blackriveran strata of North America (Bergström *et al.*, 1974). The fragmentary nature of the specimen, however, precludes clear assignment. An additional fragment from the Glenwood Shale (CQ-721) also resembles *Appalachignathus*, but assignment is even more tenuous. Bergström *et al.* (1974) noted the possible presence of the genus in the Glenwood Shale of Minnesota.

Indeterminate rhipidognathid? species

Discussion.—Small elements from the Glenwood Shale of Iowa (CQ-720.3, 721) share some aspects with the Rhipidognathidae. Two types of symmetrical alate elements both display posterior processes reduced to a sharp ridge. One type has lateral processes bearing a single denticle, whereas the other form has five denticles on each lateral process (the latter grossly resembles Sa elements of *Rhipidognathus* and *Appalachignathus*). Associated angulate elements are slightly arched with a prominent cusp and reduced processes with three or four small denticles; these grossly resemble the M elements of *Rhipidognathus* illustrated by Sweet (1988, p. 76). These types of conodont elements have not been previously reported from the Glenwood Shale, and they likely represent an undescribed taxon, possibly a rhipidognthid.

Order **PRIONIODINIDA** Sweet, 1988

Family **CHIROGNATHIDAE** Branson and Mehl, 1944

Genus **CHIROGNATHUS** Branson and Mehl, 1933a

Chirognathus duodactylus Branson and Mehl, 1933a

Plate 2, figures 4, 5

Discussion.—Elements of *Chirognathus duodactylus* are common in many samples from the Glenwood Shale of Minnesota (Stauffer, 1935; Webers, 1966) and Iowa (this study). The apparatus-based species *C. duodactylus* was clarified by Sweet (1982), who synonymized a plethora of form species originally named from the Glenwood and Harding formations (Stauffer, 1935; Branson and Mehl, 1933a). The distinctive symmetrical Sa element (form species "*C. multidens*") is an elongate element in the Iowa Glenwood collections bearing 6 to 8 denticles on each process (*e.g.*, Pl. 2, fig. 4; see also Stauffer, 1935, pl. 9, fig. 40, for Minnesota Glenwood example). However, additional illustrated Sa elements from the Harding, Winnipeg, and Glenwood formations (Branson and Mehl, 1933a, pl. 2, fig. 43 type "*C. multidens*"; Sweet, 1955, pl. 27, fig. 1; Sweet, 1982, pl. 1, fig. 16; Webers, 1966, pl. 5, fig. 2) are less elongate, bearing 6 or fewer denticles per process. Such variations were incorporated within the multi-element species *C. duodactylus* by Sweet (1982), as followed here.

cf. **Chirognathus** species

Plate 2, figures 6, 11

Discussion.—A few small hyaline elements from the St. Peter Sandstone are questionably compared to *Chirognathus*. Specimens from northeast Kansas (C-3386; Pl. 2, figs. 6, 11) and western Iowa (CQ-775.7) resemble *Chirognathus* in size, basal development, and denticulation, but these may alternatively represent juvenile *Erismodus*. Three small specimens from the Iowa St. Peter (CQ-757) are more clearly identifiable as *Chirognathus*, including an Sc element and two Sa elements bearing four to five denticles per process. These latter specimens resemble *C. duodactylus*, although they are not presently assigned to this species because of the limited collection. Although Sweet (1984) considered *C. duodactylus* to be an exclusively

Mohawkian conodont, a longer range is indicated for the genus consistent with the St. Peter occurrences. Klapper *et al.* (1991, p. 46) noted the co-occurrence of *Chirognathus* and *Phragmodus flexuosus* in the "Simpson Group" of south-central Kansas, which they considered the oldest known specimens of the genus. Sweet (1992) subsequently reported *C. duodactylus* immediately above *P. flexuosus* in the Kansas subsurface. Bauer (1994) listed the co-occurrence of *C. duodactylus* and *P. ambiguus* in the lower Bromide Formation of Oklahoma. Tipnis *et al.* (1979) noted *Chirognathus* sp. within the range of *P. flexuosus* in the Mackenzie Mountains.

Genus **CURTOGNATHUS** Branson and Mehl, 1933b

Curtognathus species

Discussion.—Small dominantly hyaline elements assigned to an indeterminate species of *Curtognathus* are noted in only a few samples (Tables 1, 2), but they are moderately common in two lower St. Peter samples (CQ-775.7, 762.8; collections SUI 99493, SUI 99494). Following the recommendation of Leslie (2000, p. 1133) these forms are left in open nomenclature: "Until the apparatus of the genus is established, there is little point in trying to define apparatus-based species" of *Curtognathus*. The St. Peter elements show a broad range of morphological intergradation that closely resembles that illustrated for "?*Curtognathus typus*" from the Dutchtown Formation of eastern Indiana by Ethington *et al.* (1986). Curtognathiform, trucherognathiform, and cardiodelliform elements are recognized, but polycaulodiform elements were not recovered. Although dominantly hyaline, some specimens preserve traces of white matter in the denticle tips.

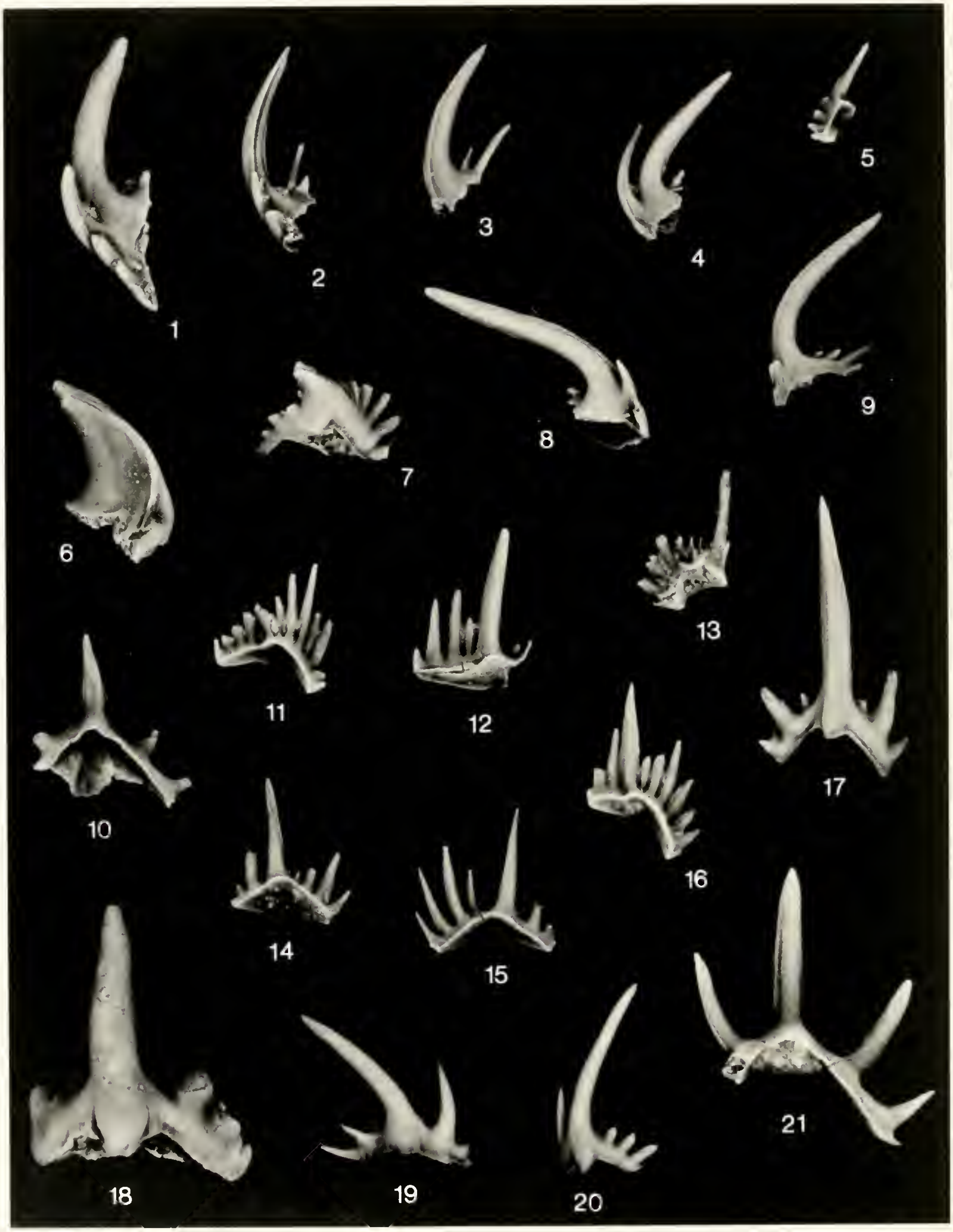
Genus **ERISMODUS** Branson and Mehl, 1933a

Erismodus species

Plate 3, figures 1–3, 7, 9, 10, 12–15, 17–21; Plate 4, figure 11

Discussion.—Hyaline elements included in unassigned species of *Erismodus* are among the most abundant conodonts found in the St. Peter Sandstone and Glenwood Shale, and a bewildering array of forms are present. Following the advice of Leslie (2000, p. 1135), until a full revision of *Erismodus* and its contained species is completed, it is advisable to leave most forms in open nomenclature, as "assigning elements of the plexus a formal specific name is not deemed appropriate." As observed by Andrews (1967, p. 890) in the Joachim Dolomite of Missouri, many elements of *Erismodus* show a "high degree of intraspecific variability" and some collections display a "complete gradation" in morphology between many previously-defined form species. Elements of *Erismodus* occur in almost all productive samples used in this study, and *Erismodus* is the dominant conodont in some St. Peter samples (CQ-757, O-1977, H-3579, SP-L). Many hundreds of specimens were recovered, and a representative selection is illustrated on Plate 3. Sweet (1982) diagnosed *Erismodus* with a septimembrate apparatus, and he synonymized many form taxa originally described from the Glenwood Shale (Stauffer, 1935; Webers, 1966) within the multi-element species *E. quadridactylus* (Stauffer, 1935). Most specimens recovered from the Glenwood Shale during this study are probably assignable to *E. quadridactylus*. However, many specimens from the St. Peter Sandstone collections do not conform to the diagnosis of *E. quadridactylus*, and additional species are probably represented. In addition to *E. quadridactylus*, several additional multi-element species of *Erismodus* have been proposed from Ordovician strata of the North America, including *E. arbucklensis*, *E. typus*, and *E. radicans* (see discussions in Bauer, 1987, 1994; Leslie, 2000). Some St. Peter specimens resemble elements of these species, but additional forms also seem to be present.

Several generalized morphologic categories are recognized in the St. Peter *Erismodus* collections: 1) large robust forms with relatively thick rounded denticles and cusps, Sa-Sb elements show a prominent downward-projecting process ("boss") beneath the cusp (Pl. 3, figs. 1, 18); 2) gracile forms with slender elongate pointed denticles and cusps, generally circular in section (Pl. 3, figs. 2, 3, 15, 20); 3) gracile forms with variably costate laterally compressed denticles and cusps (Pl. 3, figs. 12, 14); 4) forms with widely spaced denticles and broadly expanded basal cavities, some with an aboral "boss" (Pl. 3, figs. 10, 21); and 5) relatively squat forms with short closely-spaced denticles and shortened cusps (Pl. 3, fig. 7). Although a full analysis of the St. Peter collections has not been undertaken, some of these categories share morphologic similarities with previously recognized species, including *E. typus* (category 1), *E. radicans*, *E. asymmetricus*, and *E. symmetricus* (category 2), and *E. arbucklensis* and *E. quadridactylus* (category 3). Collections from the lower St. Peter include common *Erismodus* elements (Pl. 3, figs. 12, 14, 19) that more closely resemble *E. arbucklensis*, a species originally described by Bauer (1987) from the McLish Formation of Oklahoma, than *E. quadridactylus*. Additional elements with widely spaced denticles and broadly expanded basal cavities (category 4) cannot be clearly associated with any presently-defined multi-element species, but these share some similarities with the form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species *E. expansus* (Branson and Mehl, 1933b; see also Andrews, 1967). The relatively squat elements (category 5) do not clearly resemble any named form species, suggesting that an unnamed taxon likely occurs in the St. Peter faunas. Additional robust forms (*e.g.*, Pl. 4, fig. 11) are tentatively included with *Erismodus.*

Genus **ERATICODON** Dzik, 1978

Erraticodon species
Plate 2, figure 15; Plate 3, figures 4–6, 8, 11, 16;
Plate 4, figures 12–24

Discussion.—Hyaline elements characterized by long slender pointed denticles and that differ in morphologic details from those included in *Erismodus* are here assigned to an unnamed species of *Erraticodon.* Elements of *Erraticodon* sp. are scattered to common in collections from the lower to middle St. Peter Sandstone (CQ, O-1977, CT), and a few specimens from the upper St. Peter (CQ-739) are tentatively included as *E.* sp. However, *Erraticodon* is absent in all Glenwood Shale collections. Post-Lower Ordovician occurrences of *Erraticodon* include *E. balticus* Dzik from Europe, Australia, and Arkansas (Dzik, 1978; Watson, 1988; Leslie *et al.*, 2000), ?*E. balticus* from Newfoundland (Stouge, 1984), *E.* sp. cf. *E. balticus* from Oklahoma and Kansas (Bauer, 1987; Sweet, 1992), *E.* aff. *E. balticus* from Utah and Alabama (Ethington and Clark, 1981; Shaw *et al.*, 1990), and *E.* sp. from Nevada (Harris *et al.*, 1979). *E.* sp. from the St. Peter does not clearly conform to any of these illustrated forms. Pending a complete re-evaluation of the genus, the St. Peter specimens likely comprise a new species. *Erraticodon* apparently possesses a septimembrate apparatus (Watson, 1988). In general, the St. Peter *Erraticodon* sp. differs from these other occurrences in showing reduction or loss of the third (lateral or posterior) processes on the Pa, Sba, Sbb, and Sa elements and a general expansion of the basal cavity. In addition, the interpreted M element of the St. Peter species does not appear to be dolabrate as in the other occurrences. Such contrasting morphologies, as well as the general morphologic plasticity of elements displayed in the collections, have made homologies of the St. Peter elements difficult to constrain. Nevertheless, an attempt has been made to follow the elemental notation of Bauer (1987). It is possible that some of the non-homologous elements here included in the apparatus may belong to other unnamed or unrecognized taxa.

The interpreted Pa element of the St. Peter species (Pl. 3, fig. 4; Pl. 4, figs. 12, 13, 15, 16) resembles that of *Erraticodon* cf. *E. balticus* from the McLish Formation (Bauer, 1987), but most specimens lack the very short, adenticulate lateral process of that form. However, one specimen (from CQ-775.7) does display

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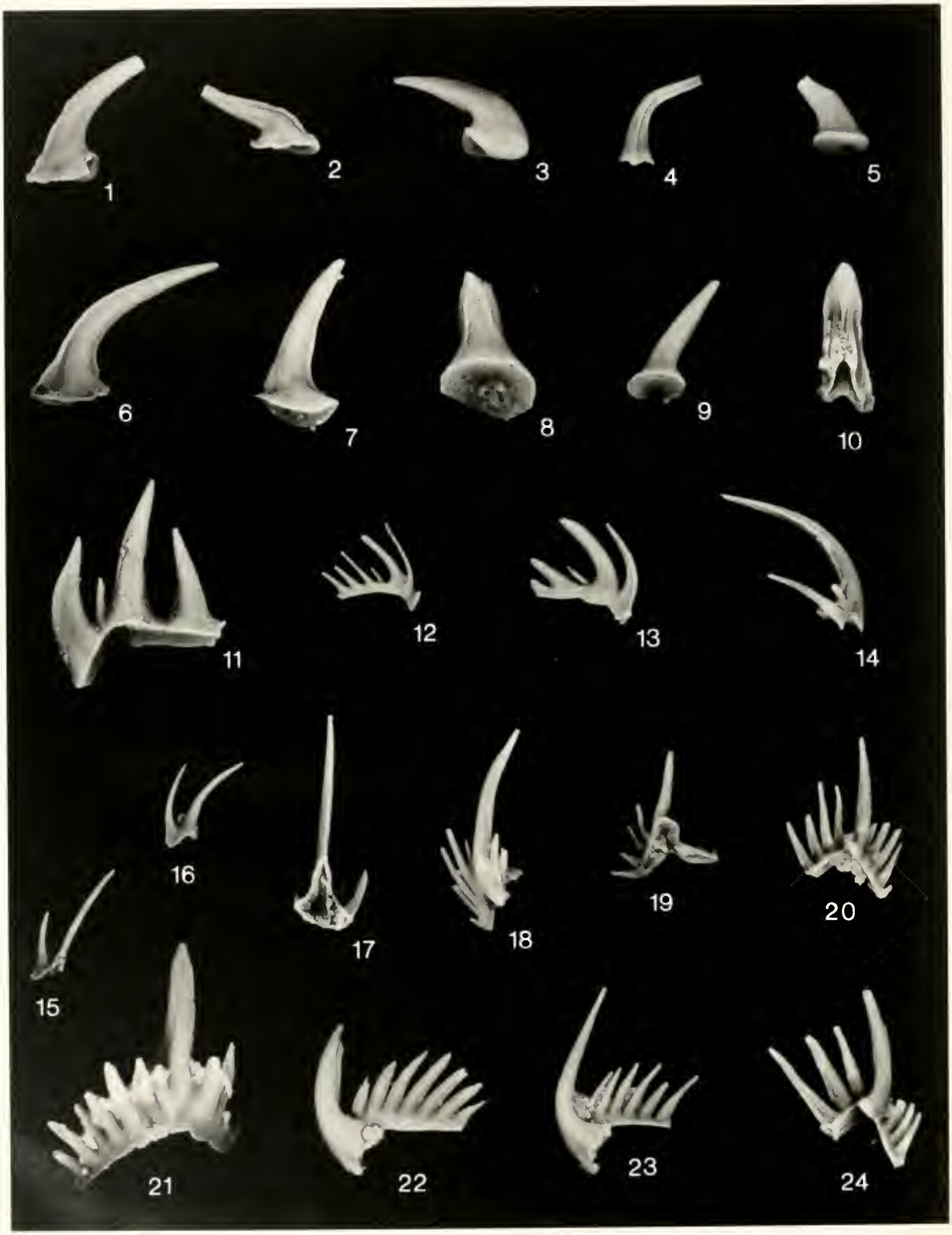
Plate 3

All figures (photographs) ×40. Specimens lightly coated with ammonium chloride sublimate.

1–3, 7, 9, 10, 12–15, 17–21. *Erismodus* spp.
- 1. Sc element; SUI 95060, OF (O-1977).
- 2. Sc element; SUI 95061, CQ-776.7.
- 3. Sc element; SUI 95062, CQ-762.
- 7. indeterminate robust element; SUI 95063, OF (O-1977).
- 9. Sc element; SUI 95064, CQ-762.
- 10. robust Sa element; SUI 95065, CQ-776.7.
- 12. Sb? element; SUI 95066, CT (C-3387).
- 13. Pb? element; SUI 95067, SP-L (9–10.5).
- 14. Sba element; SUI 95068, CQ-762.
- 15. Sba element; SUI 95069, CQ-762.
- 17. Sa element; SUI 95070, CQ-776.7.
- 18. Sa element; SUI 95071, CT (C-3387).
- 19. Sbb element; SUI 95072, CQ-762.
- 20. Sbb element; SUI 95073, CQ-762.
- 21. Sa element; SUI 95074, CQ-776.7.

4–6, 8, 11, 16. *Erraticodon* sp.
- 4. Pa element (broken); SUI 95075, CQ-762.
- 5. M? element; SUI 95076, CQ-776.7.
- 6. cusp, Sba? element; SUI 95077, CT (C-3387).
- 8. Sc element; SUI 95078, CQ-762.
- 11. Pb element; SUI 95079, CQ-776.7.
- 16. Pb element; SUI 95080, CQ-776.7.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a short adenticulate lateral process. The posterior process is long with four to seven slender reclined denticles. The short anterior process bears one to two denticles, and the proximal denticle is costate and subequal in size to the cusp. The Pa element bears a superfical resemblance to the Sc elements of *Erismodus*, but the large anterior denticle and the long posterior process serve to distinguish them.

Pb elements are tentatively included with the St. Peter species (Pl. 3, figs. 11, 16), but these forms also resemble Pb elements of *Erismodus* and may alternatively belong there. Unlike the Pb element of *Erraticodon* sp. cf. *E. balticus* from the McLish Formation (Bauer, 1987), the St. Peter form shows a more broadly developed basal cavity. The element is arched, with one elongate process (6–9 denticles decreasing in size distally) and one shorter process (2–4 denticles). The cusp is slender and round to compressed in cross-section.

The M elements included within the genus *Erraticodon* have been described to be dolabrate ("neoprioniodiform") in most previous investigations. With the possible exception of one small fragmentary indeterminate specimen, however, no dolabrate elements are associated with the St. Peter *E.* sp. Instead, a co-occurring distinctive bipennate or digyrate element (Pl. 4, fig. 19; Pl. 3, fig. 5) is tentatively interpreted to represent the M element of the St. Peter species. This element bears a superficial resemblance to the M element of *E. quadridactylus* illustrated by Bauer (1994), but it possesses an enlarged basal cavity. The basal cavity shows a large lateral bulge beneath the cusp. Of six specimens recovered, only one preserves a small posterior (?) process that bears four tiny denticles, but on the other specimens this process is greatly reduced or broken.

The Sa element is alate (Pl. 4, fig. 17) and displays a distinctive knife-like cusp with a sharp posterior margin. The cusp is offset posteriorly with respect to the two lateral processes, and its sharp-edged margin expands basally to form a short pointed adenticulate posterior process. The basal cavity is relatively deep

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PLATE 4

All photographs ×40. Specimens lightly coated with ammonium chloride sublimate.

1, 2, 6, 7. *Drepanoistodus suberectus* (Branson and Mehl, 1933b)
    1. homocurvatiform element; SUI 95081, SM (S-1162).
    2. geniculate coniform element (aff. *D. angulensis*); SUI 95082, CQ-776.7.
    6. homocurvatiform element; SUI 95083, CQ-776.7.
    7. suberectiform element; SUI 95084, SM (S-1162).
3. *Stereoconus* sp.
    3. coniform element; SUI 95085, CQ-739.
4. *Panderodus* sp.
    4. coniform element; SUI 95086, SM (S-1162).
5. *Oneotodus*? *ovatus* (Stauffer, 1935)
    5. coniform element; SUI 95087, SP-L (10.5–12).
8, 9. *Mixoconus* sp.
    8. sub-erect coniform element; SUI 95088, SP-U (27–28.5).
    9. reclined coniform element; SUI 95089, SP-L (9–10.5).
10. *Staufferella* sp. cf. *S. falcata* (Stauffer, 1935)
    10. symmetrical element, broken base; SUI 95090, CQ-776.7.
11. *Erismodus* sp.
    11. robust Pa? element; SUI 95091, CQ-762.8.
12–24. *Erraticodon* sp.
    12. Pa element; SUI 95092, CQ-762.
    13. Pa element; SUI 95093, CQ-762.
    14. Sc element; SUI 95094, CQ-776.7.
    15. broken Pa? element with cusp and anterior denticle; SUI 95095, CT (C-3386).
    16. broken Pa element with cusp and anterior denticle; SUI 95096, CT (C-3386).
    17. Sa element; SUI 95097, CT (C-3387).
    18. Sbb? element; SUI 95098, CQ-776.7.
    19. M? element; SUI 95099, CQ-776.7.
    20. Sba? element; SUI 95100, CQ-776.7.
    21. Sba? element; SUI 95101, OF (O-1977).
    22. Sc? element; SUI 95102, CQ-776.7.
    23. Sc? element; SUI 95103, CQ-776.7.
    24. Sba? element; SUI 95104, CQ-776.7.

and roughly triangular in outline. This Sa element differs from other species of *Erraticodon* in lacking denticulation of the posterior process. The sharp-edged knife-like cusp is distinctive even in broken specimens, and a number of such broken specimens are identified in the St. Peter collections. The lateral processes are short and possess two to three denticles.

Two types of Sb elements (Sba, Sbb) are recognized in the St. Peter species. The Sba element (Pl. 4, figs. 20, 21, 24) differs from the homologous element of *E.* cf. *balticus* from the McLish Formation (Bauer, 1987) in showing a greatly reduced posterior process. In some specimens the posterior process is reduced to a short adenticulate point or node similar to that seen in the Sa element. However, some specimens from the lowest samples of the CQ core (CQ-776.7) display one to two small denticles fused to the lower part of the cusp. The presence of these posterior denticles clearly allies the St. Peter form with *Erraticodon* (and not *Erismodus*), and in this respect resembles the reduced posterior process of the illustrated "plectospathodiform" element of *E. balticus* and *E.* aff. *E. balticus* with one or two denticles (see Dzik, 1978; Watson, 1988; Ethington and Clark, 1981). The cusp is laterally compressed and offset posteriorly with respect to the adjoining lateral processes. The cusp is costate and displays a sharp-edged posterior margin (Pl. 3, fig. 6) similar to that of the Sa element. The lateral processes angle downward from the cusp and are of subequal length but show asymmetric denticulation. One process generally has larger and longer cusps than the other (Pl. 4, fig. 24). Most specimens bear four denticles on each process, but the number of denticles varies from three to seven in the St. Peter collections.

The interpreted Sbb element (Pl. 4, fig. 18) of the St. Peter species is digyrate, and displays a long pointed costate cusp. The lateral processes are highly asymmetric, and the longer one is bent outward about 130° from the axial plane of the cusp. The larger lateral process bears five slender denticles that decrease in size laterally. The smaller lateral process is greatly reduced and includes two small denticles attached directly to the lower portion of the cusp. The posterior process is reduced to a pointed nub at the base of the cusp similar to that of the Sa, Sba elements.

The interpreted Sc elements (Pl. 4, figs. 22, 23) of *Erraticodon.* sp. from the St. Peter Sandstone are distinctive bipennate forms generally with a long curved cusp and a prominent posterior process bearing six to eight elongate denticles. The cusp is roughly circular in cross-section, and in one specimen the cusp is reduced to a squat rounded knob. The preservation in many specimens of small relict denticles or nodes fused along one side of the lower cusp belies the presence of a greatly reduced anterior (or lateral) process. Variably one or two relict denticles or nodes are present, completely fused their entire length onto the cusp. Except for the preservation of these relict denticles, the element would appear dolabrate. A few specimens show discrete and more elongate anterior denticles along the cusp margin (Pl. 4, fig. 14; Pl. 3, fig. 8).

Order **UNKNOWN**

Family **COLEODONTIDAE** Branson and Mehl, 1944

Genus **ARCHEOGNATHUS** Cullison, 1938

Archeognathus species

Plate 2, figures 18, 21, 23

Discussion.—Fragmentary elements from the St. Peter Sandstone (CQ-776.7, 775.7, 762, 755.5; SP-L, SP-U, C-3386) characterized by relatively large, robust suberect to slightly reclined fibrous denticles with a basal groove are assigned to *Archeognathus* sp. These are likely conspecific with *A. primus* Cullison, 1938, from the Dutchtown Formation of Missouri (described in detail by Klapper and Bergström, 1984), but the absence of complete specimens that preserve the characteristic basal structure precludes a species-level assignment. The denticles of *Archeognathus* are generally discrete but are interconnected along the basal groove by thin laminae (ibid.). This fragile basal interconnection is displayed on the St. Peter specimens, both broken and multi-denticled specimens (see bases of Pl. 2, figs. 18, 21). Klapper (in Klapper and Bergström, 1984, p. 968) had previously examined specimens from the CQ core in western Iowa and suggested that specimens Witzke (1980, p. 5) had labeled as *Neocoleodus* (from CQ-762, 721) may represent *Archeognathus.*

cf. **Archeognathus** species

Plate 2, figures 19, 20, 22

Discussion.—Most specimens of *Archeognathus primus* display a series of discrete unfused denticles interconnected by thin basal laminae (Klapper and Bergström, 1984). Specimens from the St. Peter Sandstone and Glenwood Shale that display partially fused denticles along an expanded basal bar are tentatively designated as cf. *Archeognathus* sp. (see Tables 1, 2). These specimens display denticles of similar size and structure to those included in *A.* sp. and possess a basal groove similar to that seen in *Coleodus.* The partially fused denticles of these forms bear resemblance to portions of the crown of one specimen of *A. primus* described by Klapper and Bergström (1984, p. 956), which includes a segment with four denticles "fused to midheight." That specimen clearly demonstrates that *Archeognathus* can variably display multi-denticulate segments with partially fused denticles, lending credence to the inclusion of similar St. Peter and Glenwood specimens within the genus.

Genus **COLEODUS** Branson and Mehl, 1933a

Coleodus species

Plate 2, figures 13, 14, 16, 17

Discussion.—Collections from the St. Peter Sandstone of western Iowa (CQ-7765.7, 762.8, 762, 739), Minnesota (SP-L), and Nebraska (O-1977) contain scattered distinctive blade-like multi-denticulated hyaline elements with a basal trough. These specimens are included within the genus *Coleodus,* but species resolution is hampered by wide morphological variations within the collections as well as the lack of a modern systematic evaluation of previously described species. A number of form species of *Coleodus* have been described from North America and Siberia based largely on denticulation and profile, but intraspecific variability within these forms remains largely unstudied and an apparatus-based reconstruction has not been proposed. However, Ethington *et al.* (1986, pp. 13–15) raised the possibility that a variety of forms (including the form species *C. simplex* and *C. delicatus*) may be "parts of an apparatus" of a single species. Their proposal seems reasonable, and it is possible that many of the forms and form species of *Coleodus* should be included within a single multi-element species. They further recognized two distinct types of elements associated with another species (*C.*? sp. C), suggesting that *Coleodus* and related forms contained multi-element apparatuses. Klapper and Bergström (1984, p. 974) "considered the possibility that [*Coleodus* and *Archeognathus*] were elements of the same apparatus," but this idea "requires additional evidence."

Elements included in *Coleodus* from the St. Peter Sandstone display morphologic variations categorized as follows: 1) long straight-bladed forms for most of length, relatively uniform denticulation, denticles fused except at tips, denticles uniformly reclined, relatively deep basal trough (Pl. 2, fig. 13); 2) long slightly curved or arched multi-denticled forms, uniform height for most of length (diminishes posteriorly), small denticles mostly fused except at tips (may be completely fused in anterior or posterior regions), denticles reclined at similar angle, basal trough shallow and narrow (Pl. 2, fig. 16); 3) short slightly arched forms with few denticles (6–9), height and width varies with length (tapers posteriorly), denticles of nonuniform size, fused except at tips, denticles variably reclined (angle decreases posteriorly, *i.e.*, less erect), broad shallow basal trough (Pl. 2, fig. 14); 4) similar to category 3 except denticles increase in size and become more erect posteriorly, denticles variably fused and discrete (Pl. 2, fig. 17); 5) relatively straight forms with discrete unfused sub-vertical denticles, prominent basal trough; 6) relatively straight forms with completely fused denticles (denticles may be indistinguishable), upper margin forms ridge or blade, prominent basal trough; and 7) relatively straight forms, narrow bar at base bearing large sub-erect to curved discrete denticles, shallow basal trough (Pl. 2, fig. 12). It remains speculative whether these morphologic variations represent more than one species of *Coleodus,* or whether these forms can all be accommodated within a single multi-element species concept. If the latter option is followed, most of these forms should probably be referred to *C. simplex* Branson and Mehl.

Some of the morphologic categories of *Coleodus* recognized in the St. Peter collections resemble forms described from other localities, but the species-level classification of these previously-described forms remains confusing. *Coleodus simplex,* the type species of the genus, was originally described by Branson and Mehl (1933a) from the Harding Sandstone of Colorado, and their cotypes have broadly arched blades bearing a completely fused fine vertical denticulation. However, Branson and Mehl (1933a, pl. 1, figs. 23) also included straight-bladed forms bearing slightly reclined denticles (unfused at tips) within *C. simplex* (these forms resemble St. Peter category 1). Similar morphologies were also assigned to *C. simplex* from the Dutchtown Formation of Missouri (Youngquist and Cullison, 1946, pl. 90, fig. 16), the St. Peter Sandstone of Indiana (Rexroad *et al.*, 1982, pl. 2, fig. 12), and a queried reference from the Dutchtown Formation of Indiana (Ethington *et al.*, 1986, pl. 2, fig. 26). Additional material referred to *C. simplex* includes slightly arched forms with nonuniform reclined denticles (unfused at tips) from the Tyner of Oklahoma (Bauer, 1989, fig. 4.5), straight forms with large unfused discrete nonuniform reclined denticles from the St. Peter Sandstone of Indiana (Rexroad *et al.*, 1982, pl. 2, fig. 11), and arched forms with completely fused vertical denticles from Siberia (Moskalenko, 1970, pl. IX, fig. 8). As a form-species concept, it is clear that *C. simplex* has been used by various authors to encompass a broad range of morphologic variation.

Branson and Mehl (1933b) described additional form species of *Coleodus* from the Joachim Formation of Missouri, *C. delicatus* and *C.*? *levis. Coleodus delicatus* has a broadly arched profile with strongly reclined to curved fused denticles (inclination decreases posteriorly, *i.e.*, less erect). Similar forms have been assigned to *Coleodus delicatus* from the Harding, Winnipeg, and Dutchtown formations (Sweet, 1955, 1982; Ethington *et al.*, 1986). *C. pectiniformis* was proposed as a new species from the Dutchtown Formation by Youngquist and Cullison (1946) for a form similar to *C. delicatus* but with a more arched blade and slightly less fused denticles; synonymy with *C. delicatus* seems likely. Similar forms from the Rockcliffe Formation of Ontario were assigned to *C. pectiniformis* by Copeland *et al.* (1989), who also included a specimen with largely unfused discrete curved denticles within the species. Forms included within *Coleodus* show significant variation in the fusion of the denticles along the blade: 1) completely fused with indistinguishable denticulation (as for *C.? levis*), 2) completely fused denticles but individual denticles outlined by shallow furrows (like type *C. simplex*), 3) mostly fused denticles but with distal margins free (*e.g.*, *C. delicatus* and many referred *C. simplex*), 4) partially fused denticles dominate but blade bears some unfused discrete denticles (*e.g.*, *C.?* sp. C Ethington *et al.*, 1986), and 5) unfused discrete denticles along most or all of blade (*e.g.*, Rexroad *et al.*, 1982, pl. 2, fig. 11; *C. confinus* Moskalenko, 1970). This spectrum of denticular fusion is also displayed in the St. Peter collections used for this study.

A form with largely discrete denticles "much like *Coleodus*" from the Harding Sandstone was designated a new genus and species by Branson and Mehl (1933a, p. 24), *Neocoleodus spicatus*. The status of this taxon remains uncertain, but the holotype is not congeneric with *Archeognathus* (Klapper and Bergström, 1984, p. 968). As originally noted by Branson and Mehl (1933a), *N. spicatus* (holotype) shares similarities with *Coleodus* and conceivably may be synonymous. In particular, some forms included within categories 4 and 5 above (*e.g.*, Rexroad *et al.*, 1982, pl. 2, fig. 11; this study Pl. 2, fig. 17) display denticulation similar to that seen in *N. spicatus*. Other forms assigned to various species of *Neocoleodus* (*e.g.*, Youngquist and Cullison, 1946; Moskalenko, 1970) are more likely referable to *Archeognathus* (Klapper and Bergström, 1984, p. 968). An additional form from the St. Peter Sandstone of western Iowa (Pl. 2, fig. 12) bears discrete denticles above a thin bar. The specimen displays a shallow basal trough and is tentatively labeled as cf. *Coleodus* sp., but it may alternatively be allied with *Archeognathus* or represent a new taxon. The denticles are smaller and more gracile than those described for *Archeognathus* (Klapper and Bergström, 1984).

Genus **MIXOCONUS** Sweet, 1955

cf. **Mixoconus** species

Plate 4, figures 8, 9

Discussion.—Erect to reclined or slightly recurved coniform elements that bear longitudinal grooves and carinae are the second most abundant type of conodont elements recognized from the lower St. Peter shale unit at St. Paul, Minnesota (Loc. SP). The bases are unexcavated or show a very shallow excavation. The elements all flare outward to the basal margin forming one of two basal outlines. One type displays a circular or nearly circular basal outline (Pl. 4, figs. 8, 9); some specimens are slightly lobate on the anterior surface. The other type shows an ovoid basal outline that is slightly lobate in anterior and posterior directions. The grooved and carinated character of the cusp and the slightly lobate aspect of the basal area are features shared with *Mixoconus*, and the St. Peter specimens are provisionally allied with that genus. However, the type and only described species of *Mixoconus*, *M. primus* Sweet, 1955, is decidedly more lobate than the St. Peter forms (especially anteriorly) and displays more prominent rounded carinae. The St. Peter forms also share similarities with certain coniform Siberian species included within *Stereoconus* (especially *S. circulus*, *S. turaensis*, *S. bicostatus*) by Moskalenko (1970). The generic assignment of these Siberian forms is questionable, however, as the circular to ovoid basal areas and the circular to broadly ovoid cross section of the carinated cusps differ significantly from the type description of *Stereoconus* from the Harding Sandstone (Branson and Mehl, 1933a). Pending further study, the St. Peter and Siberian forms should probably be included within one or more new taxa.

Genus **STEREOCONUS** Branson and Mehl, 1933a

Stereoconus species

Plate 4, figure 3

Discussion.—A few specimens of fibrous laterally-compressed recurved coniform elements from the St. Peter Sandstone of western Iowa (CQ-739) and Minnesota (SP-L, SP-U) are considered to belong to an unassigned species of *Stereoconus*. The surfaces are smooth, and the base displays a shallow basal depression with rounded to slightly bulbous basal margins. The St. Peter specimens bear resemblance to the form species *S. robustus* Branson and Mehl, 1933a.

Order and Family **UNKNOWN**

Indeterminate Genus and species A

Plate 1, figures 1, 5

Discussion.—Four pectiniform elements from the lower St. Peter Sandstone (CQ-776.7) are not assigned to any named taxon pending further comparative study. All specimens show one or two prominent adenticulate lateral processes extending downward and outward from the cusp, and all possess a basal groove under the full length of the element. The elements are albid, with white matter most abundant in the denticles and cusps. The largest and most complete specimen (Pl. 1, fig. 1) is a pastinate P element with a slightly bulbous lateral process. The cusp is proclined with a short anterior process (3 short denticles) and a more elongate posterior process (4 large suberect denticles, 3 small distal denticles); the distal region of the posterior process is bent inward forming a hook-like curve. A second nearly complete specimen (Pl. 1, fig. 5) is similar, but it is pastinate with two short adenticulate lateral processes. The anteror process possesses four small denticles, and the broken posterior process retains three large sub-erect denticles. Although these elements display many distinctive features, they are not clearly assignable to any known genus. The short adenticulate lateral processes bear a superficial resemblance to the so-called "anticusps" of some forms of *Erismodus* (*e.g.*, "*E. typus*," "*E. dutchtownensis*"; see Youngquist and Cullison, 1946; Andrews, 1967), but the "anticusps" of *Erismodus* are the anterior and posterior processes (cusp of Genus & species A angled in different plane). In addition, *Erismodus* is a hyaline form, whereas Genus and species A is albid.

REFERENCES CITED

Agnew, A.F.

1955. Facies of Middle and Upper Ordovician rocks of Iowa. American Association of Petroleum Geologists Bulletin, vol. 39, pp. 1703–1752.

Andrews, H.E.

1967. Middle Ordovician conodonts from the Joachim Dolomite of eastern Missouri. Journal of Paleontology, vol. 41, pp. 881–901.

Barnes, C.R., and Fåhræus, L.E.

1975. Provinces, communities, and the proposed nektobenthic habit of Ordovician conodontophorids. Lethaia, vol. 8, pp. 133–149.

Barnes, D.A., Harrison, W.B., III, and Shaw, T.H.

1996. Lower-Middle Ordovician lithofacies and interregional correlation, Michigan basin, U.S.A. *in* Paleozoic sequence stratigraphy, views from the North American craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America, Special Paper 306, pp. 35–54.

Barnes, D.A., Lundgren, C.E., and Longman, M.W.

1992. Sedimentology and diagenesis of the St. Peter Sandstone, central Michigan Basin, United States. American Association of Petroleum Geologists Bulletin, vol. 76, pp. 1507–1532.

Bauer, J.A.

1987. Conodonts and conodont biostratigraphy of the McLish and Tulip Creek formations (Middle Ordovician) of south-central Oklahoma. Oklahoma Geological Survey, Bulletin 141, 58 pp.

1989. Conodont biostratigraphy and paleoecology of Middle Ordovician rocks of eastern Oklahoma. Journal of Paleontology, vol. 63, pp. 92–107.

1994. Conodonts from the Bromide Formation (Middle Ordovician), south-central Oklahoma. Journal of Paleontology, vol. 68, pp. 358–376.

Berendsen, P., and Doveton, J.H.

1997. Middle Ordovician ironstones in Kansas: subsurface markers of paleoshorelines for the Midcontinent. *in* Simpson and Viola groups in the southern Midcontinent. K.S. Johnson, *ed.*, Oklahoma Geological Survey, Circular 99, pp. 164–171.

Bergström, S.M.

1971. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America. *in* Symposium on conodont biostratigraphy. W.C. Sweet and S.M. Bergström, *eds.*, Geological Society of America, Memoir 127, pp. 83–161.

1981. Familty Polyplacognathidae. *in* Treatise on invertebrate paleontology. R.C. Moore, *ed.*, Part W, Supplement 2 (Conodonta), by D.L. Clark *et al.*, Geological Society of America and University of Kansas Press, pp. W129–W131.

1983. Biogeography, evolutionary relationships, and biostratigraphic significance of Ordovician platform conodonts. Fossils and Strata, no. 15, pp. 35–58.

Bergström, S.M., and Carnes, J.B.

1976. Conodont biostratigraphy and paleoecology of the Holston Formation (Middle Ordovician) and associated strata in eastern Tennessee. *in* Conodont paleoecology. C.R. Barnes, *ed.*, Geological Association of Canada, Special Paper No. 15, pp. 27–57.

Bergström, S.M., Carnes, J.B., Ethington, R.L., Votaw, R.B., and Wigley, P.B.

1974. *Appalachignathus*, a new multielement conodont genus from the Middle Ordovician of North America. Journal of Paleontology, vol., 48, pp. 227–235.

Bergström, S.M., Miller, M.A., Wood, G.D., Barker, G.D., Lane, H.R., Thompson, S., and Benson, H.

1994. Lower (Ibexian) and Middle (Whiterockian and Mohawkian) Ordovician palynomorphs and conodonts from the Michigan Basin: Exploration aspects of biostratigraphy, thermal maturity, and paleoenvironmental analyses. American Association of Stratigraphic Palynologists, Program and Abstracts, 27th Annual Meeting, p. 3.

Bergström, S.M., and Sweet, W.C.

1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky, and its lateral equivalents in Ohio and Indiana. Bulletins of American Paleontology, vol. 50, pp. 271–441.

Branson, E.B., and Mehl, M.G.

1933a. Conodont studies no. 1: Conodonts from Harding sandstone of Colorado; from the Bainbridge (Silurian) of Missouri; from the Jefferson City (Lower Ordovician) of Missouri. Missouri University Studies, vol. 8, no. 1, pp. 1–72.

1933b. Conodont studies no. 2: Conodonts from the Joachim (Middle Ordovician) of Missouri; from the Plattin (Middle

Ordovician) of Missouri; from the Maquoketa-Thebes (Upper Ordovician) of Missouri; a study of Hinde's types of conodonts preserved in the British Museum. Missouri University Studies, vol. 8, no. 2, pp. 77–167.

1943. Ordovician conodont faunas from Oklahoma. Journal of Paleontology, vol. 17, pp. 374–387.

1944. Conodonts. *in* Index Fossils of North America. H.W. Shimer and R.R. Shrock, *eds.*, Wiley, New York, pp. 235–246.

Brett, C.E., Baarli, B.G., Chowns, T., Cotter, E., Driese, S., Goodman, W., and Johnson, M.E.

1998. Early Silurian condensed intervals, ironstones, and sequence stratigraphy in the Appalachian foreland basin. *in* Silurian cycles: linkages of dynamic stratigraphy with atmospheric, oceanic, and tectonic changes: James Hall centennial volume. E. Landing and M.E. Johnson, *eds.*, New York State Museum Bulletin 491, pp. 89–143.

Bunker, B.J., Witzke, B.J., Watney, L.W., and Ludvigson, G.A.

1988. Phanerozoic history of the central midcontinent, United States. *in* Sedimentary cover—North American craton. L.L. Sloss, *ed.*, Geological Society of America. The Geology of North America, vol. D-2, pp. 243–260, pl. 4.

Calvin, S.

1906. Geology of Winneshiek County. Iowa Geological Survey, Annual Report, vol. 16, pp. 39–146.

Choi, Y.S., and Simo, J.A.

1998. Ramp facies and sequence stratigraphic models in an epeiric sea: the Upper Ordovician mixed carbonate-siliciclastic Glenwood and Platteville formations, Wisconsin, USA. *in* Carbonate ramps. V.P. Wright and T.P. Burchette, *eds.*, Geological Society of London, Special Publication, vol. 149, pp. 437–456.

Clark, D.L., and Miller, J.F.

1971. St. Peter Sandstone. *in* Conodonts and biostratigraphy of the Wisconsin Paleozoic. D.L. Clark, *ed.*, University of Wisconsin, Geological and Natural History Survey, Information Circular 19, p. 14.

Cooper, G.A.

1956. Chazyan and related brachiopods. Smithsonian Miscellaneous Collections, vol. 127, 1245 pp., 127 pls.

Copeland, M.J., Parkins, W.G., and Nowlan, G.S.

1989. A Lower Middle Ordovician microfauna from Ottawa, Ontario. Geological Survey of Canada, Bulletin 396, pp. 1–19.

Cullison, J.S.

1938. Dutchtown fauna of southeastern Missouri. Journal of Paleontology, vol. 12, pp. 219–228.

Dapples, E.C.

1955. General lithofacies relationship of St. Peter Sandstone and Simpson Group. American Association of Petroleum Geologists Bulletin, vol. 39, pp. 444–467.

DeMott, L.L.

1987. Platteville and Decorah trilobites from Illinois and Wisconsin (edited by R.E. Sloan, F.C. Shaw, and R.P. Tripp). *in* Middle and Late Ordovician lithostratigraphy and biostratigraphy of the Upper Mississippi Valley. R.E. Sloan, *ed.*, Minnesota Geological Survey, Report of Investigations 35, pp. 63–98.

Denison, R.H.

1967. Ordovician vertebrates from the western United States. Field Museum of Natural History, Fieldiana Geology, vol. 16, no. 6, pp. 131–192.

Dott, R.H., Jr., Byers, C.W., Fielder, G.W., Stenzel, S.R., and Winfree, K.E.

1986. Aeolian to marine transition in Cambro-Ordovician cratonic sheet sandstones of the northern Mississippi valley, U.S.A. Sedimentology, vol. 33, pp. 345–367.

Doveton, J.H., Charpentier, R.R., and Metzger, E.P.

1990. Lithofacies analysis of the Simpson Group in south-central Kansas. Kansas Geological Survey, Petrophysical Series 5, 34 pp.

Droste, J.B., Abdulkareem, T.F., and Patton, J.B.

1982. Stratigraphy of the Ancell and Black River Groups (Ordovician) in Indiana. Indiana Department of Natural Resources, Geological Survey, Occasional Paper 36, 15 pp.

Drygant, D.M.

1974. Prostye Konodonty Silura i nizov Devona Volyno-Podolya. Paleontol. Sb. L'vov Univ., vol. 10, pp. 64–70, 2 pls. [Simple conodonts of the Silurian and lowermost Devonian of Volyn-Podolia.]

Dzik, J.

1976. Remarks on the evolution of Ordovician conodonts. Acta Palaeontologica Polonica, vol. 21, pp. 395–455.

1978. Conodont biostratigraphy and paleogeographical relations of the Ordovician Mójcza Limestone (Holy Cross Mts, Poland). Acta Palaeontologica Polonica, vol. 23, pp. 51–72.

Elliot, D.K., Blieck, A.R.M., and Gagnier, P.Y.

1991. Ordovician vertebrates. *in* Advances in Ordovician geology. C.R. Barnes and S.H. Williams, *eds.*, Geological Survey of Canada, Paper 90-9, pp. 93–106.

Ethington, R.L.

1959. Conodonts of the Ordovician Galena formation. Journal of Paleontology, vol. 33, pp. 257–292.

Ethington, R.L., and Brand, U.

1981. *Oneotodus simplex* (Furnish) and the genus *Oneotodus* (Conodonta). Journal of Paleontology, vol. 55, pp. 239–247.

Ethington, R.L., and Clark, D.L.

1981. Lower and Middle Ordovician conodonts from the Ibex area, western Millard County, Utah. Brigham Young University Geology Studies, vol. 28, part 2, 160 pp.

Ethington, R.L., Droste, J.B., and Rexroad, C.B.

1986. Conodonts from subsurface Champlainian (Ordovician) rocks of eastern Indiana. Indiana Department of Natural Resources, Geological Survey, Special Report 37, 31 pp.

Fåhraeus, L.E., and Nowlan, G.S.

1978. Franconian (Late Cambrian) to early Champlainian (Middle Ordovician) conodonts from the Cow Head Group, western Newfoundland. Journal of Paleontology, vol. 52, pp. 444–471.

Fraser, G.S.

1976. Sedimentology of a Middle Ordovician quartz arenite-carbonate transition in the Upper Mississippi Valley. Geological Society of America Bulletin, vol. 86, pp. 833–845.

Grether, W.J., and Clark, D.L.

1980. Conodonts and stratigraphic relationships of the Readstown Member of the St. Peter Sandstone in Wisconsin. Geoscience Wisconsin, vol. 4, pp. 1–24.

Hamar, György

1966. The Middle Ordovician of the Oslo region, Norway. 22. Preliminary report on conodonts from the Oslo-Asker and Ringerrike districts. Nor. Geol. Tidsskr., vol. 46, pp. 27–83.

Harris, A.G., Bergström, S.M., Ethington, R.L., and Ross, R.J., Jr.

1979. Aspects of Middle and Upper Ordovician conodont biostratigraphy of carbonate facies in Nevada and southeast

California and comparison with some Appalachian successions. *in* Conodont biostratigraphy of the Great Basin and Rocky Mountains. C.A. Sandberg and D.L. Clark, *eds.*, Brigham Young University Geology Studies, vol. 26, part 3, pp. 7–43.

Harris, R.W.

1964. Subgenera of the conodont genus *Multioistodus* in Simpson-Burgen (Ordovician Arbuckle) conodonts from Oklahoma. Oklahoma Geology Notes, no. 24, pp. 108–118.

Hass, W.H.

1959. Conodonts from the Chappel Limestone of Texas. U.S. Geological Survey, Professional Paper 294J, pp. 365–400.

Klapper, G., and Bergström, S.M.

1984. The enigmatic Middle Ordovician fossil *Archeognathus* and its relations to conodonts and vertebrates. Journal of Paleontology, vol. 58, pp. 949–976.

Klapper, G., Lindström, M., Sweet, W.C., and Ziegler, W.

1981. Catalogue of Conodonts, volume IV. W. Ziegler, *ed.* E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 317 pp.

1991. Catalogue of Conodonts, volume V.W. Ziegler, *ed.* E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 212 pp.

Kolata, D.R.

1975. Middle Ordovician echinoderms from northern Illinois and southern Wisconsin. Paleontological Society, Memoir 7, 74 pp.

Kolata, D.R., Frost, J.K., and Huff, W.D.

1986. K-bentonites of the Ordovician Decorah Subgroup, Upper Mississippi Valley: correlation by chemical fingerprinting. Illinois State Geological Survey, Circular 537, 30 pp.

Kolata, D.R., and Noger, M.C.

1991. Tippecanoe I subsequence, Middle and Upper Ordovician Series. *in* Interior cratonic basins. M.W. Leighton, D.R. Kolata, D.F. Oltz, and J.J. Eidel, *eds.*, American Association of Petroleum Geologists, Memoir 51, pp. 89–99.

Lamar, J.E.

1928. Geology and economic resources of the St. Peter Sandstone of Illinois. Illinois State Geological Survey, Bulletin 53, 175 pp.

Leatherock, C.

1945. The correlation of rocks of Simpson age in north-central Kansas with the St. Peter Sandstone and associated rocks in northwestern Missouri. Kansas Geological Survey, Bulletin 60, pp. 1–16.

Leslie, S.A.

2000. Mohawkian (Upper Ordovician) conodonts of eastern North America and Baltoscandia. Journal of Paleontology, vol. 74, pp. 1122–1147.

Leslie, S.A., and Bergström, S.M.

1995. Element morphology and taxonomic relationships of the Ordovician conodonts *Phragmodus primus* Branson and Mehl, 1933, the type species of *Phragmodus* Branson and Mehl, 1933, and *Phragmodus undatus* Branson and Mehl, 1933. Journal of Paleontology, vol. 69, pp. 967–974.

Leslie, S.A., Clegg-Scala, C., and Beland, P.E.

2000. Event stratigraphy and conodont biostratigraphy of the Joachim Dolomite of northern Arkansas. Geological Society of America, Abstracts with Programs, v. 32, no. 3, p. A-33.

Leslie, S.A., and Lehnert, O.

1999. New insight into the phylogeny and paleogeography of *Cahabagnathus* (Conodonta). 8th International Symposium on the Ordovician System. Acta Universitatis Carolinae, Geologica, v. 43, no. 1–2, pp. 443–446.

Lindström, M.

1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. Geol. Foeren. Stockholm Foerh., vol. 76, h. 4 (1954), no. 21, pp. 517–603.

1970. A suprageneric taxonomy of the conodonts. Lethaia, vol. 3, pp. 427–445.

1971. Lower Ordovician conodonts of Europe. *in* Symposium on conodont biostratigraphy. W.C. Sweet and S.M. Bergstrom, *eds.*, Geological Society of America Memoir 127, pp. 21–61.

Mai, H., and Dott, R.H., Jr.

1985. A subsurface study of the St. Peter Sandstone in southern and eastern Wisconsin. University of Wisconsin, Geological and Natural History Survey, Information Circular 47, 26 pp.

Mazzullo, J.M., and Ehrlich, R.

1983. Grain-shape variation in the St. Peter Sandstone: a record of eolian and fluvial sedimentation of an Early Paleozoic cratonic sheet sand. Journal of Sedimentary Petrology, vol. 53, pp. 105–119.

McHargue, T.R.

1982. Ontogeny, phylogeny, and apparatus reconstruction of the conodont genus *Histiodella*, Joins Formation, Arbuckle Mountains, Oklahoma. Journal of Paleontology, vol. 56, pp. 1410–1433.

Moskalenko, T.A.

1970. Konodonty krivolutskogo yarusa (sredniy ordovik) Sibirskoy Platformy. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki, vol. 61, 116 pp.

1972. Ordovician conodonts of the Siberian Platform and their bearing on multielement taxonomy. Geologica et Palaeontologica, vol. 1, pp. 47–55.

1973. Konodonty srednego i verzhnego ordovika Sibirskoy Platformy. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki, vol. 137, 143 pp.

Mossler, J.H.

1985. Sedimentology of the Middle Ordovician Platteville Formation, southeastern Minnesota. Minnesota Geological Survey, Report of Investigations 33, 27 pp.

Nadon, G.C., Simo, J.A., Dott, R.H., Jr., and Byers, C.W.

2000. High-resolution sequence stratigraphic analysis of the St. Peter Sandstone and Glenwood Formation (Middle Ordovician), Michigan Basin, U.S.A. American Association of Petroleum Geologists Bulletin, vol. 84, pp. 975–996.

Nunn, J.R.

1986. The petrology and paleogeography of the Starved Rock Sandstone in southeastern Iowa, western Illinois, and northeastern Missouri. Unpublished MS thesis, University of Iowa, Iowa City, 144 pp.

Olsen, B.M.

1976. Stratigraphic occurrence of argillaceous beds in the St. Peter Sandstone, Twin Cities Basin. Unpublished MS thesis, University of Minnesota, Minneapolis, 89 pp.

Owen, D.D.

1847. Preliminary report of the geological survey of Wisconsin and Iowa. U.S. General Land Office Report. U.S. 30th Congress, 1st Session, pp. 160–173.

Pander, C.H.

1856. Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements. Akademie der Wissenschaften, St. Petersburg, 91 pp.

Rexroad, C.B., Droste, J.B., and Ethington, R.L.

1982. Conodonts from the Everton Dolomite and the St. Peter Sandstone (Lower Middle Ordovician) in a core from southwestern Indiana. Indiana Department of Natural Resources, Geological Survey, Occasional Paper 39, 13 pp.

Sardeson, F.W.

1896. The Saint Peter Sandstone. Bulletin Minnesota Academy of Science, vol. 4, pp. 64–87.

Schutter, S.R.

1996. The Glenwood Shale as an example of a Middle Ordovician condensed section. *in* Paleozoic sequence stratigraphy, views from the North American craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America, Special Paper 306, pp. 55–65.

Shaw, T.H.

1990. A conodont fauna from the base of the St. Peter Sandstone (Ordovician), north-central Illinois. Geological Society of America, Abstracts with Programs, vol. 22, no. 5, p. 44.

Shaw, T.H., Roberson, K.E., and Harris, A.G.

1990. Lithostratigraphy and conodont biostratigraphy across the Lower-Middle Ordovician disconformity (early to middle Whiterockian) at Pratt Ferry, Alabama. U.S. Geological Survey, Bulletin 1895, pp. C1–C13.

Sloan, R.E.

1972. Notes on the Platteville Formation, southeastern Minnesota. *in* Field Trip guidebook for Paleozoic and Mesozoic rocks of southeastern Minnesota. Minnesota Geological Survey, Guidebook Series 4, pp. 43–53.

1987. The St. Peter Sandstone of southeastern Minnesota: fauna. *in* Middle and Late Ordovician lithostratigraphy and biostratigraphy of the Upper Mississippi Valley. R.E. Sloan, *ed.*, Minnesota Geological Survey, Report of Investigations 35, pp. 50–51.

Sloss, L.L.

1963. Sequences in the cratonic interior of North America. Geological Society of America Bulletin, vol. 74, pp. 93–114.

Stauffer, C.R.

1930. Conodonts from Decorah Shale. Journal of Paleontology, vol. 4, pp. 121–128.

1934. Type Paleozoic sections in the Minnesota Valley. Journal of Geology, vol. 42, pp. 337–357.

1935. Conodonts of the Glenwood beds. Geological Society of America Bulletin, vol. 46, pp. 125–168.

Stauffer, C.R., and Thiel, G.A.

1941. The Paleozoic and related rocks of southeastern Minnesota. Minnesota Geological Survey, Bulletin 29, 261 pp.

Stouge, S.S.

1984. Conodonts of the Middle Ordovician Table Head Formation, western Newfoundland. Fossils and Strata, no. 16, 145 pp.

Suhm, R.W.

1997. Simpson stratigraphy of the southern Midcontinent. *in* Simpson and Viola groups in the southern Midcontinent. K.S. Johnson, *ed.*, Oklahoma Geological Survey, Circular 99, pp. 3–38.

Sweet, W.C.

1955. Conodonts from the Harding Formation (Middle Ordovician) of Colorado: Journal of Paleontology, vol. 29, pp. 226–262.

1981. Glossary of morphological and structural terms for conodont elements and apparatuses. *in* Treatise on invertebrate paleontology. R.C. Moore, *ed.*, Part W, Supplement 2 (Conodonta), by D.L. Clark *et al.*, Geological Society of America and University of Kansas Press, pp. W60–W67.

1982. Conodonts from the Winnipeg Formation (Middle Ordovician) of the northern Black Hills, South Dakota. Journal of Paleontology, vol. 56, pp. 1029–1049.

1984. Graphic correlation of upper Middle and Upper Ordovician rocks, North American Midcontinent Province, U.S.A. *in* Aspects of the Ordovician System. D.L. Bruton, *ed.*, Palaeontological Contributions from the University of Oslo, no. 295, Universitetsforlaget, pp. 23–25.

1987. Distribution and significance of conodonts in Middle and Upper Ordovician strata of the Upper Mississippi Valley region. *in* Middle and Late Ordovician lithostratigraphy and biostratigraphy of the Upper Mississippi Valley. R.E. Sloan, *ed.*, Minnesota Geological Survey, Report of Investigations 35, pp. 167–172.

1988. The Conodonta: morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum. Clarendon Press, Oxford, 212 pp.

1992. Middle and Late Ordovician conodonts from southwestern Kansas and their biostratigraphic significance. *in* Special papers in paleontology and stratigraphy: a tribute to Thomas W. Amsden. J.R. Chaplin and J.E. Barrick, *eds.*, Oklahoma Geological Survey, Bulletin 145, pp. 181–191.

1995. Graphic assembly of a conodont-based composite standard for the Ordovician System of North America. *in* Graphic correlation. K.O. Mann and H.R. Lane, *eds.*, SEPM Society for Sedimentary Geology, Special Publication No. 53, pp. 139–150.

Sweet, W.C., and Bergström, S.M.

1976. Conodont biostratigraphy of the Middle and Upper Ordovician of the United States Midcontinent. *in* The Ordovician System. M.G. Bassett, *ed.*, Proceedings Palaeontological Association Symposium, University of Wales Press and National Museum of Wales, Cardiff, pp. 121–151.

Sweet, W.C., Thompson, T.L., and Satterfield, I.R.

1975. Conodont stratigraphy of the Cape Limestone (Maysvillian) of eastern Missouri. Missouri Department of Natural Resources, Division of Research and Technical Information, Geological Survey, Report on Investigations 57, pt. 1, pp. 1–60.

Templeton, J.S., and Willman, H.B.

1963. Champlainian Series (Middle Ordovician) in Illinois. Illinois State Geological Survey, Bulletin 89, 260 pp.

Thiel, G.A.

1935. Sedimentary and petrographic analysis of the St Peter Sandstone. Geological Society of America Bulletin, vol. 46, pp. 559–614.

Thompson, T.L.

1991. Paleozoic succession in Missouri, part 2, Ordovician System. Missouri Department of Natural Resources, Division of Geology and Land Survey, Report of Investigations no. 70, 282 pp.

Tipnis, R.S., Chatterton, B.D.E., and Ludvigsen, R.

1979. Ordovician conodont biostratigraphy of the southern District of Mackenzie, Canada. *in* Western and Arctic Canadian biostratigraphy. C.R. Stelck and B.D.E. Chatterton, *eds.*, Geological Association of Canada, Special Paper 18, pp. 39–91.

Van Houten, F.B.

2000. Ooidal ironstones and phosphorites—a comparison from a stratigrapher's view. *in* Marine authigenesis: from global to microbial. C.R. Glenn, L. Prévôt-Lucas, and J. Lucas, *eds.*, SEPM Society for Sedimentary Geology, Special Publication no. 66, pp. 127–132.

Walney, W.L., Stephens, B., and Newell, K.D.

1997. Shallowing-upward events and their implications for internal correlations and depositional environment of the St. Peter Sandstone in the Forest City Basin, northeastern Kansas. *in* Simpson and Viola groups in the southern Midcontinent. K.S. Johnson, *ed.*, Oklahoma Geological Survey, Circular 99, pp. 267–275.

Watson, S.T.

1988. Ordovician conodonts from the Canning Basin (W. Australia). Palaeontographica Abt. A, vol. 203, pp. 91–147.

Webby, B.D.

1998. Steps toward a global standard for Ordovician stratigraphy. Newletters on Stratigraphy, vol. 36, pp. 1–33.

Webers, G.F.

1966. The Middle and Upper Ordovician conodont faunas of Minnesota. Minnesota Geological Survey, Special Publication Series, no. 4, 123 pp.

Witzke, B.J.

1980. Middle and Upper Ordovician paleogeography of the region bordering the Transcontinental Arch. *in* Paleozoic paleogeography of the west-central United States. T.D. Fouch and E.R. Magathan, *eds.*, Society of Economic Paleontologists and Mineralogists, Rocky Mountain Section, pp. 1–18.

1987. Models for circulation patterns in epicontinental seas applied to Paleozoic facies of North American craton. Paleoceanography, vol. 2, pp. 229–248.

1992. Conodonts of the St. Peter Sandstone and Chazyan-Blackriveran correlations in the Iowa area. Geological Society of America, Abstracts with Programs, vol. 24, no. 4, p. 72.

2001. Condensed sedimentation and conodont bioevents in the St. Peter Sandstone (Ordovician), central Midcontinent. Geological Society of America, Abstracts with Programs, vol. 33, no. 4, p. 7.

Witzke, B.J., and Bunker, B.J.

1996. Relative sea-level changes during Middle Ordovician through Mississippian deposition in the Iowa area, North American craton. *in* Paleozoic sequence stratigraphy, views from the North American craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America, Special Paper 306, pp. 307–330.

Youngquist, W., and Cullison, J.S.

1946. The conodont fauna of the Ordovician Dutchtown Formation of Missouri. Journal of Paleontology, vol. 20, pp. 579–590.

Appendix.—Locality Register, St. Peter–Glenwood conodont collections.

Loc. CQ. Camp Quest core D-21, Lemars; NW SW NW SW sec. 2, T92N, R45W, Plymouth Co., Iowa (stored at Iowa DNR-Geological Survey). See Table 1 and Text-figure 1 for sample depths.

Loc. QM. Quimby core, NW NW NE sec. 34, T90N, R41W, Cherokee Co., Iowa (stored at Iowa DNR-Geological Survey). Basal St. Peter sampled by T. H. Shaw.

Loc. PT. Peterson No. 1 core, Vincent, Northern Natural Gas; NE NE NE NW sec. 10, T 90 N, R 27 W, Webster Co., Iowa (stored at Iowa DNR-Geological Survey). Sample depth 1209 ft, Glenwood Shale.

Loc. DL. Hummell No. 1 core, Adel, Northern Natural Gas, NE NW NW sec. 18, T 79 N, R 28 W, Dallas Co., Iowa (stored at Iowa DNR-Geological Survey). Sample depth 1747–1749 ft (D-1748), Glenwood Shale.

Loc. SS. SS-9 core, Millbrook Farms, Cominco; NW NE NE sec. 29, T 84 N, R 1 E, Jackson Co., Iowa (stored at Iowa DNR-Geological Survey). Sample depth 753 ft (SS-753), Glenwood Shale.

Loc. CC. Cairo-Columbus Junction gas storage structure, A. Jordan No. 1 core; SW NW NW SW sec. 32, T 75 N, R 4 W, Louisa Co., Iowa (stored at Iowa DNR-Geological Survey). Sample depth 1021 ft (J-1021), Glenwood Shale.

Loc. GN. Guttenberg North, Great River Road X-56 roadcut; NE SW NW sec. 32, T 93 N, R 2 W, Clayton Co., Iowa. Productive sample 1.2 ft below top of Glenwood Shale.

Loc. SP. St. Paul, core 8099, Minnesota Geological Survey; NE NW NE sec. 6, T 28 N, R 22 W, Ramsey Co., Minnesota. Samples collected by Olsen (1976) from shale unit about 45 ft above base of St. Peter Sandstone; SP-L includes lower samples (labeled 0 to 13.5″); SP-U includes upper samples (labeled 19.5–38.5″).

Loc. SM. Smith No. 1, Northern Natural Gas; SW SE SW sec. 23, T 13 N, R 11 E, Sarpy Co., Nebraska (stored at Univ. Nebraska, Conservation and Survey Division). Sample depths 1158.3, 1159, 1161, 1161.8 ft (S-1158, S-1159, S-1161, S-1162), Glenwood Shale or upper St. Peter.

Loc. OF. Offutt Air Force Base core, U.S. Army Corps of Engineers; SE SE NW sec. 11, T 13 N, R 13 E, Sarpy Co., Nebraska (stored at Univ. Nebraska, Conservation and Survey Division). Sample depths 1949 ft (O-1949), Glenwood Shale; 1977 ft (O-1977), St. Peter Sandstone.

Loc. HS. Hustead No. A-1 core; SE NE SE sec. 2, T 2 N, R 16 E, Richardson Co., Nebraska (stored at Univ. Nebraska, Conservation and Survy Division). Sample depth 3579 ft (H-3579), St. Peter Sandstone; barren samples 3562, 3562.7, 3583.2 ft.

Loc. CT. Carter No. 2-A Davis core; sec. 33, T 13 S, R 10 E, Wabaunsee Co., Kansas (stored at Kansas Geological Survey). Sample depths 3323 ft (C-3323), "Glenwood"; St. Peter samples 3358.2 ft (barren), 3358.7 ft (barren), 3381–3381.8 ft (barren); 3386 ft (C-3386), 3387 ft (C-3387). See also "Unit A" fauna reported by Sweet (1992).

CONODONT BIOSTRATIGRAPHY OF THE SCOTCH GROVE AND LAPORTE CITY FORMATIONS (LATE LLANDOVERY–EARLY WENLOCK; SILURIAN) IN EASTERN IOWA

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ABSTRACT

Conodont faunas from the Scotch Grove–LaPorte City formations allow correlation to an interval in the Silurian standard conodont zonation ranging from the *eopennatus* Zone to within the *Ozarkodina sagitta rhenana* Superzone (Llandovery to lower Wenlock). The relationship between units in this study is complicated by both the presence of lateral facies relationships and diagenetic controls on the carbonate rocks in the study area. There does not appear to be a lithologic control on sparse conodont faunas.

ACKNOWLEDGMENTS

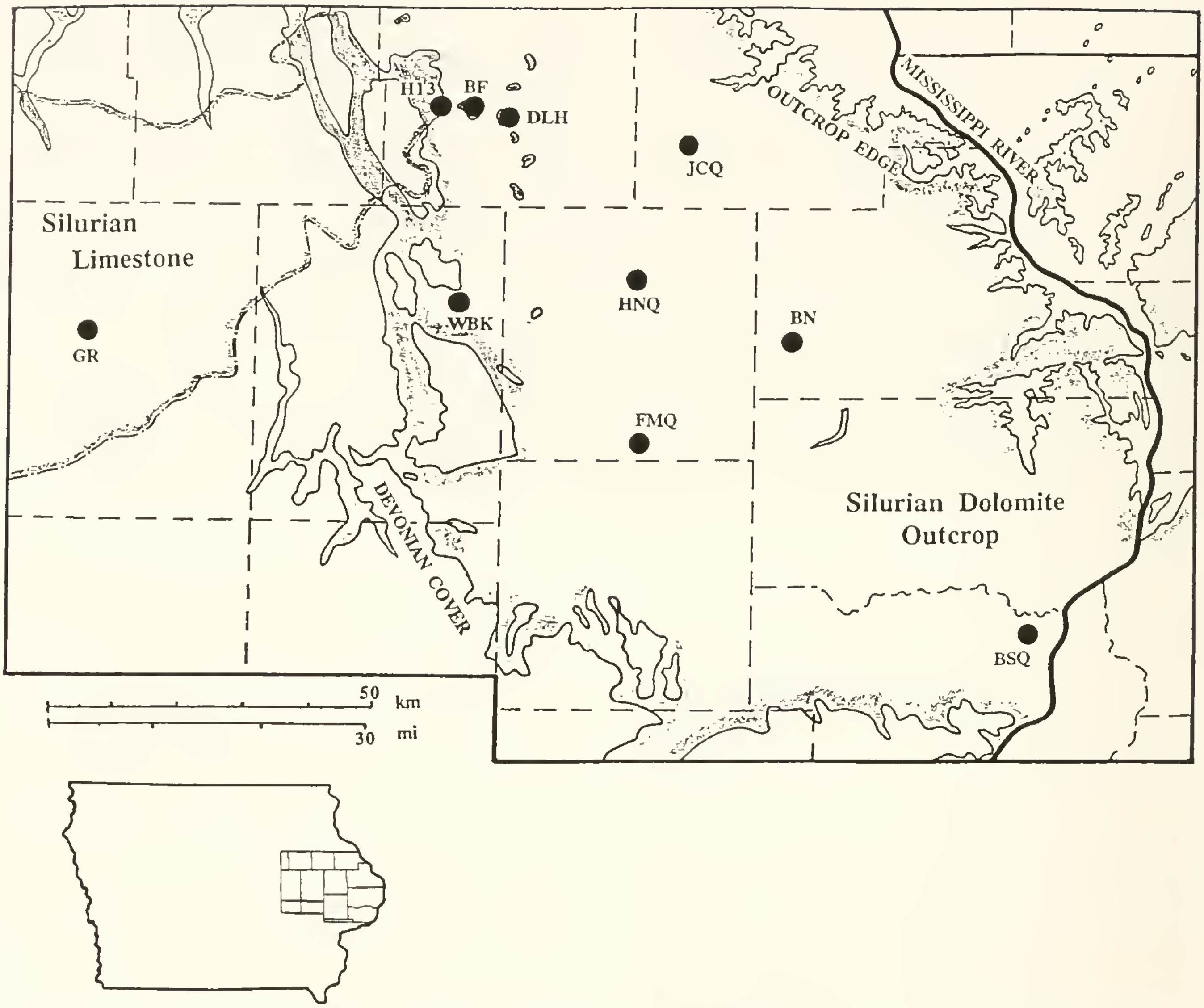
The author would like to thank Gilbert Klapper for his support and guidance in all aspects of paleontologic research including instruction with photography while the author was a graduate student at The University of Iowa. Most, if not all, conodont workers of the last several decades are familiar with Gilbert's work ethic that has resulted in publication on a wide array of topics in paleontology and stratigraphy. With a cautionary eye on the recent comments that have been expressed on CONNEXUS towards the future of Paleontology, I would like to point out a facet of Gil's career that may be overlooked by some, and that is his dedication to the classroom. While cognizant that I will never have a published record to match that of my advisor, I take pride in the fact that as Gil's last Ph.D. student I may continue part of his tradition of excellence with a commitment to that noblest of professions: teaching.

B. J. Witzke provided field assistance collecting the Delhi samples, allowed access to collections from the other localities in this study, and provided critical review of an early version of the manuscript. M. Kleffner provided assessment and insight on several taxonomic identifications. A portion of the page charges for publication of this manuscript have been provided by the Southwestern Oregon Community College Geology Club. Thanks to James Barrick and Mark Kleffner for constructive reviews of the manuscript; of course they are not responsible for any errors of interpretation.

INTRODUCTION

Silurian carbonate rocks of eastern Iowa have been the subject of extensive lithostratographic study for over the past 150 years. The study area includes both outcrop and subsurface samples from eastern Iowa (Text-fig. 1). Earlier biostratigraphic analysis of the section has focused on brachiopod faunas, with limited attention being focused on conodont analysis for the sequence. The lowest occurrence of the brachiopods *Pentameroides subrectus* and *Costistricklandia castellana* in Iowa are suggestive of a mid- to late Telychian (late Llandovery; C_5 to C_6) age (Johnson, 1979). The graptolite *Monograptus priodon* has been reported from the middle of the Scotch Grove in the Garrison Core (Witzke, 1981a). Unfortunately, the long range of this species (Telychian to Homerian) does not allow a correlation to the Silurian graptolite zonation.

A paucity of conodont work can be attributed to the dominance of nearshore carbonates and pervasive dolomitization. The sample coverage for most sections is minimal (Text-fig. 2), with the Delhi West Roadcut (DLH) having the most complete sample coverage for the section. Average sample sizes for the Delhi (DLH) section is 4 kilograms (core sample sizes were not available) and provided yields of, at most, one to two well-preserved platform elements per kilogram. The sample coverage includes samples from the lower and middle section of the LaPorte City Formation, and the Johns Creek Quarry, Welton, Buck Creek Quarry, and Waubeek members of the Scotch Grove Formation. Additionally, a sample from the overlying Gower Formation is included. Although conodont yields are minimal, the presence of some biostratigraphically diagnostic species establishes an age for the Scotch Grove–LaPorte City sequence of *eopennatus* Zone through *Ozarkodina sagitta rhenana* Superzone of the Silurian Standard Conodont Zonation (Text-fig. 3). Further, this



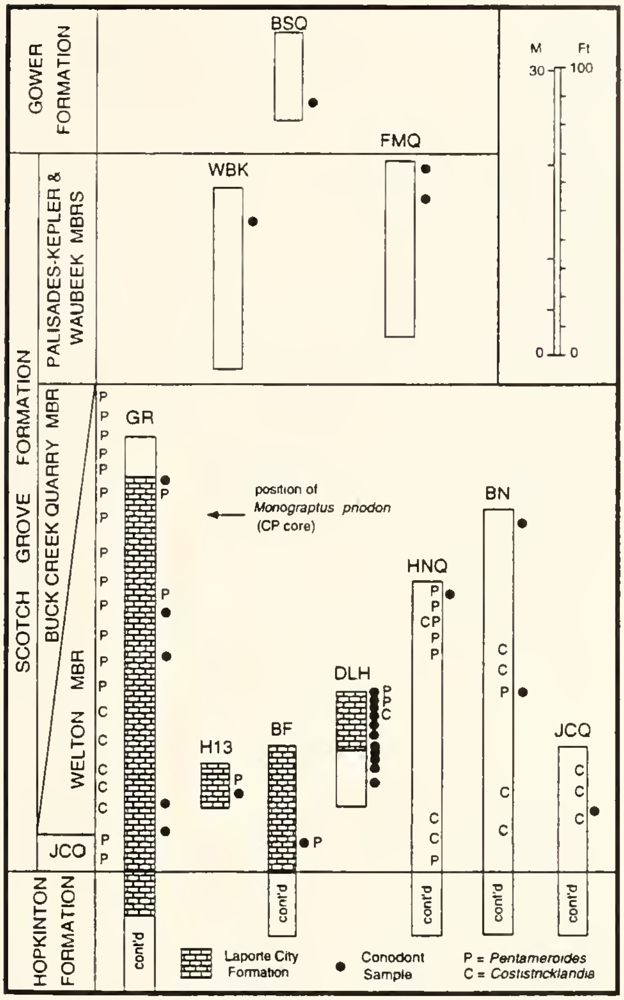
Text-figure 1.—Locality Map. Locality abbreviations: GR (Garrison Core), H13 (Highway 13 section), BF (Bailey's Ford section), DLH (Delhi West Section), JCQ (Johns Creek Quarry), WBK (Waubeek section), HNQ (Hanken Quarry), BN (Baldwin North), FMQ (Freeman Quarry) and BSQ (Beuse Quarry). See appendix for detailed locality information.

study will allow for preliminary correlations to be made with sections in basins further east that have been part of continuing work by Kleffner (1987, 1990, 1991, 1994).

STRATIGRAPHY

Study of the Silurian sequence in Iowa dates back to work by David Dale Owen in the 1840s and 1850s when he correlated strata to the Clinton and Niagara groups of New York state. The stratigraphic units continued to be defined by New York nomenclature until the late 1890s, with the exception of the LeClaire Limestone (Hall and Whitney, 1858). During the late 1890s and into the early twentieth century, the Iowa Geological Survey published new formal and informal stratigraphic units for the Silurian thereby developing a regional startigraphy removed from the New York based nomenclature.

This study focuses on the Scotch Grove Formation (Text-fig. 4), a unit that was informally introduced by Witzke (1981a, 1983) and formally introduced by Witzke (1985) for the "cherty dolomite interval above the Picture Rock Member and below the base of the laminated and mounded dolomites of the Gower Formation." The LaPorte City Formation is dominated by limestone units in central Iowa that are correlative to



Text-figure 2.—Stratigraphy, position of conodont samples, occurrence of brachiopod and graptolite taxa. GR (Garrison Core), H13 (Highway 13), BF (Bailey's Ford), DLH (Delhi West road cut), HNQ (Hanken Quarry), BN (North Baldwin), JCQ (Johns Creek Quarry), WBK (Waubeek), BSQ (Beuse Quarry) and FMQ (Freeman Quarry). Brick pattern represents limestone (LaPorte City Formation), lack of pattern represents dolostone (Scotch Grove Formation).

the dolomitized upper Hopkinton and Scotch Grove formations (Text-fig. 5) and (Witzke, 1981a). These units all were deposited in open marine conditions in subtidal environments and are associated with skeletal wackestone and packstone fabrics. The relationship between the limestone units of the LaPorte City and the dolostone facies of the Hopkinton and Scotch Grove have been described as resulting from diagenetic alteration. With subaerial exposure of the basin margins, an early influx of meteoric phreatic water displaced original marine pore fluids to prevent pervasive dolomitization of the LaPorte City Formation (Witzke, 1981b; Ludvigson *et al.*, 1992).

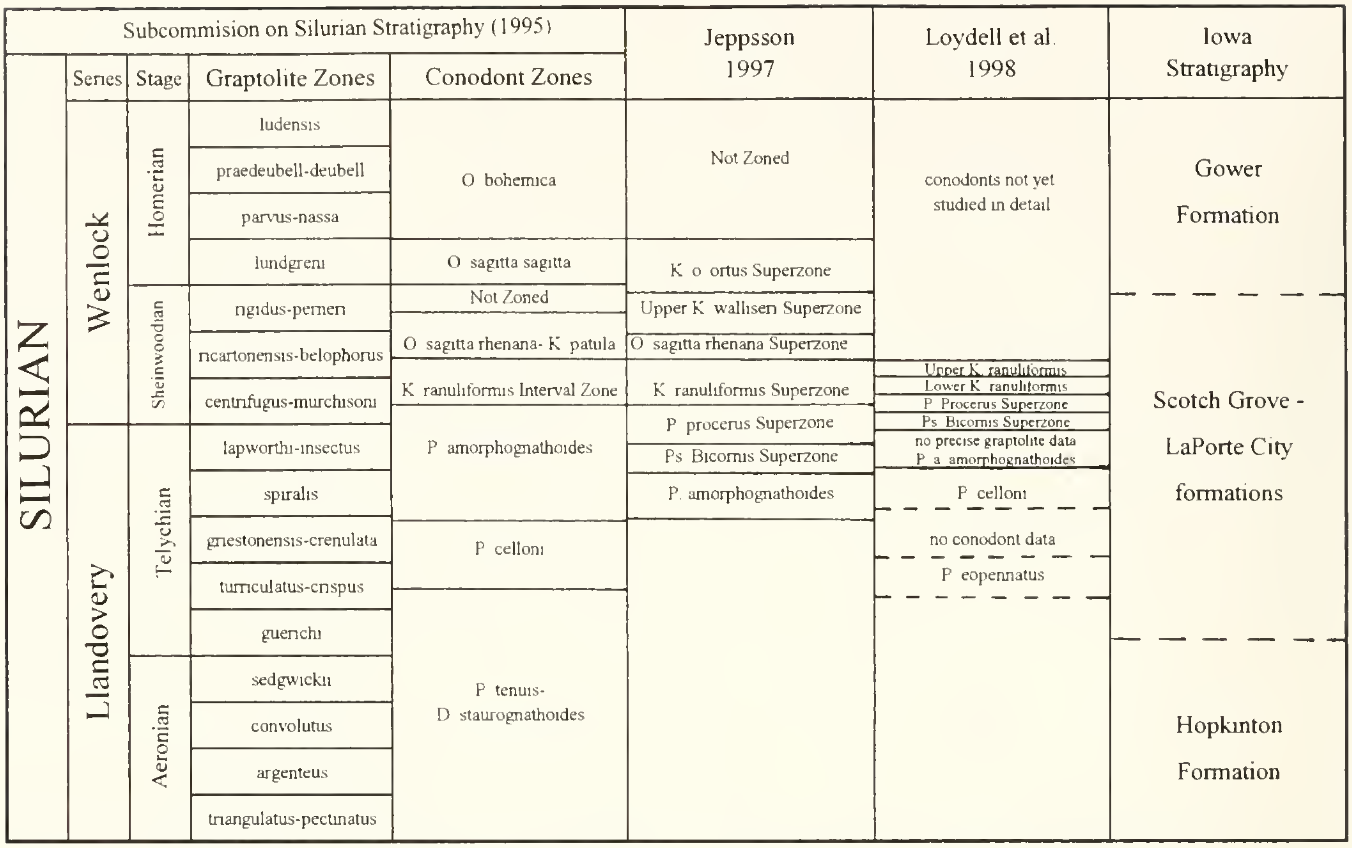
The Scotch Grove Formation is divided into the Johns Creek Quarry, Welton, Buck Creek Quarry, Waubeek and Palisades-Kepler members (Text-figs. 4 and 5). The Johns Creek Quarry Member is a thin (0.5–5.5 meters) dolomitic unit that includes thicker (5–15 meters) mound facies at the base of the Scotch Grove. The Johns Creek Quarry is overlain by fossiliferous dolostones of the Welton Member (12.5–75 meters) in the east and chert-rich dolostones of the Buck Creek Quarry Member (1–52 meters) in the west. There is also a facies relationship between the Palisades-Kepler Member (9–60 meters) that is comprised of carbonate mound complexes and skeletal facies that were shed from these "reefs" and the intermound facies of the Waubeek Member (12–17 meters).

The Scotch Grove interval is associated with a major transgressive-regressive event at its base (Text-fig. 4) and a second, lesser transgressive-regressive cycle in the upper Scotch Grove concurrent with deposition of the Waubeek and Palisades-Kepler members. The overlying Gower Formation is associated with deposition of laminated subtidal carbonates which formed during a mid-Wenlock regression.

BIOSTRATIGRAPHY

The Hopkinton Formation which underlies the Scotch Grove/LaPorte City formations in the study area has been assigned a Llandovery age (mid- to late Aeronian through early to mid-Telychian) based on occurrence of pentamerid and stricklandid brachiopod faunas (Witzke, 1992). The low diversity conodont faunas in this study (Text-figs. 6 and 7) tend to be dominated by *Panderodus*. The Scotch Grove–LaPorte City formations span a range from Llandovery (early to mid-Telychian) through early Wenlock (mid- to late Sheinwoodian). The overlying Gower Formation does not contain biostratigraphically diagnostic faunas and has been suggested to have an age of mid-Wenlock at its base and ranging up to late Wenlock-Ludlow age at its top based on brachiopod faunas (Witzke, 1992).

Faunas in the basal LaPorte City Formation are assigned to the *eopennatus* Zone of Männik (1998) based on the occurrence of *Aulacognathus bullatus* and *A. kuehni* in the Garrison Core (GR) in a sample that also contains elements of *Ozarkodina polinclinata polinclinata*. Samples from the lower LaPorte City from the Highway 13 outcrop (H13) and Bailey's Ford (BF) are assigned to the *eopennatus* Zone on the occurrence of *Pterospathodus eopennatus*. Both faunas also include elements of *Ozarkodina polinclinata polinclinata*. The lower Scotch Grove–LaPorte City at the Delhi (DLH) outcrop contain faunas assigned to the *eopennatus* Zone based on occurrence of *Apsidognathus tuberculatus* and *Pterospathodus eopennatus*. This interval also contains *Ozarkodina polinclinata*



Subcommision on Silurian Stratigraphy (1995)					Jeppsson 1997	Loydell et al. 1998	Iowa Stratigraphy
	Series	Stage	Graptolite Zones	Conodont Zones			
SILURIAN	Wenlock	Homerian	ludensis	O bohemica	Not Zoned	conodonts not yet studied in detail	Gower Formation
			praedeubell-deubell				
			parvus-nassa				
			lundgreni	O sagitta sagitta	K o ortus Superzone		
		Sheinwoodian	rigidus-perneri	Not Zoned	Upper K walliseri Superzone		Scotch Grove - LaPorte City formations
			ricartonensis-belophorus	O sagitta rhenana- K patula	O sagitta rhenana Superzone		
			centrifugus-murchisoni	K ranuliformis Interval Zone	K ranuliformis Superzone	Upper K ranuliformis Lower K ranuliformis P Procerus Superzone Ps Bicornis Superzone	
	Llandovery	Telychian	lapworthi-insectus	P amorphognathoides	P procerus Superzone Ps Bicornis Superzone	no precise graptolite data P a amorphognathoides	
			spiralis		P. amorphognathoides	P celloni	
			griestonensis-crenulata	P celloni		no conodont data	
			turriculatus-crispus	P tenuis- D staurognathoides		P eopennatus	
			guerichi				
		Aeronian	sedgwickii				Hopkinton Formation
			convolutus				
			argenteus				
			triangulatus-pectinatus				

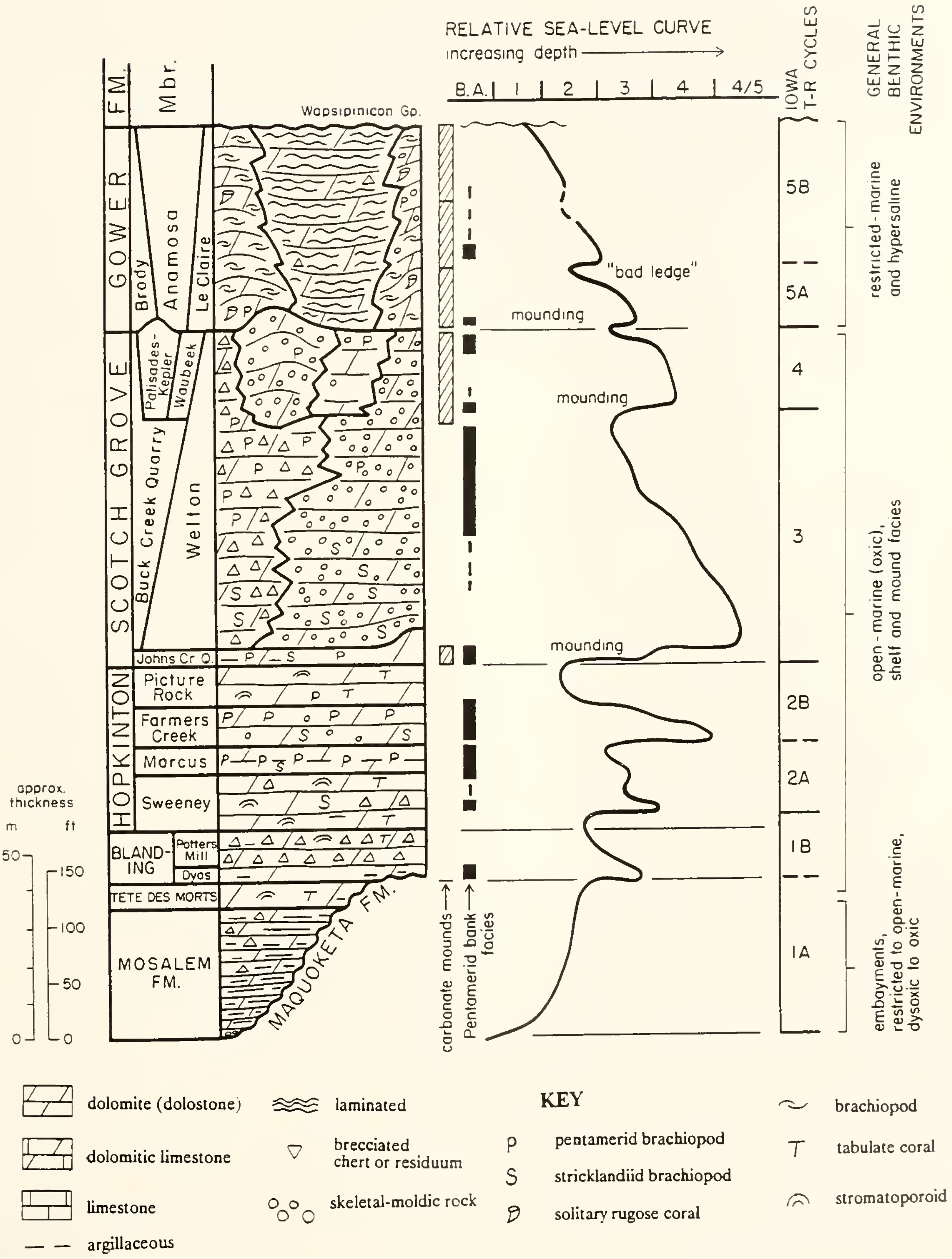
Text-figure 3.—Selected zonations for the late Llandovery and Wenlock with comparison to Iowa formations.

polinclinata, Kockelella cf. *K. abruptus* and *Distomodus staurognathoides*. The Delhi section includes a transition from the dolostone Scotch Grove Formation into the limestone LaPorte City Formation without noticeable changes in conodont faunas. The sample at DLH 6 contains platform (Pa) elements of both *P. eopennatus* and *P. amorphognathoides angulatus* resulting in assignment of a *celloni* Zone age as redefined by Männik (1998), for the middle portion of the Delhi section. The co-occurrence of these two taxa may be a result of the sample interval or slightly different ranges in the mid-continent of North America in comparison with Estonia. The occurrence of *Ozarkodina polinclinata polinclinata* raises questions based on its occurrence with elements from distinctly *eopennatus* and *celloni* zone faunas. Männik (1992) identified two subspecies of *Ozarkodina polinclinata*: *Ozarkodina polinclinata estonica* that is restricted to the *celloni* zone and the nominal subspecies that is restricted to the *amorphognathoides* Zone. Only the nominal species is identified in these faunas, and it occurs at a significantly lower biostratigraphic level than that reported by Männik (1992) in Estonia. The recovery of *Pterospathodus amorphognathoides* from the middle Scotch Grove at the Hanken Quarry (HNQ) indicates that at least part of the formation correlates with the *amorphognathoides* Zone. The Welton Member at the Baldwin North (BN) section contains *Ozarkodina excavata excavata* which can be assigned a Wenlock to Ludlow age (Lower *K. ranuliformis* Zone) of Jeppsson (1997). Samples from the Waubeek Member (upper Scotch Grove Formation) at the Freeman Quarry (FMQ) are placed in the *Ozarkodina sagitta rhenana* Superzone of Jeppsson (1997) based on the occurrence of the nominal subspecies.

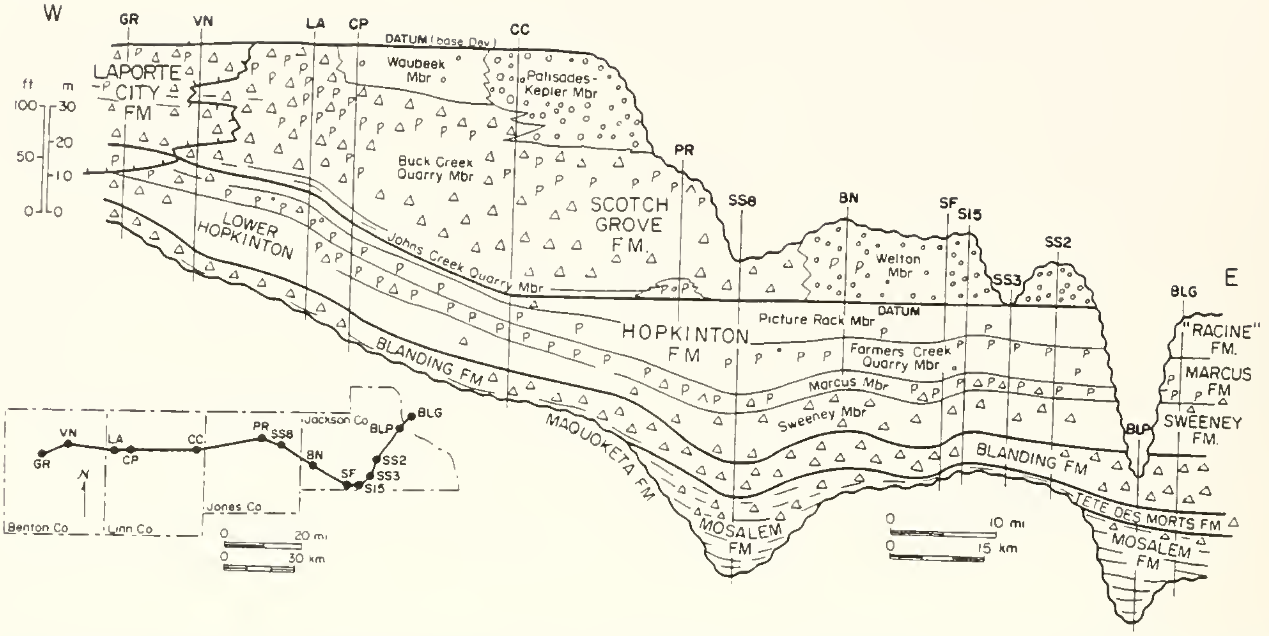
The limited faunas that have been recovered from the Scotch Grove–LaPorte City interval allow initial assessment of ages for these units. It is also noted that the Llandovery-Wenlock boundary falls within the middle to upper portion of this sequence. The boundary occurs somewhere below the base of the Waubeek and Palisades-Kepler and in the middle of the Welton members of the Scotch Grove Formation.

SYSTEMATIC PALEONTOLOGY

The suprageneric classification in this report follows that of Sweet (1988). Illustrated specimens are housed



Text-figure 4.—Stratigraphic relationship between formations and members for the Iowa Silurian compared to relative sea-level curve (adapted from Witzke, 1992).



Text-figure 5.—Stratigraphic cross-section of Silurian units in east-central Iowa. Control points include both core and outcrop sections. Datum shifts from base of Devonian in the west to base of Scotch Grove Formation in the east (adapted from Witzke, 1992). For lithologic symbols, see Text-figure 4.

FORMATION		SCOTCH GROVE / LAPORTE CITY												
SAMPLE NUMBER		DLH 1	DLH 2	DLH 3	DLH 4	DLH 5	DLH 6	DLH 7	DLH 8	DLH 9	DLH 10	DLH 11	DLH 12	DLH 13
SAMPLE WEIGHT (in kilograms)		5.4	4.6	4.2	4.6	3	5.1	2.8	4.7	5.7	5.7	5.4	2	5.7
Panderodus sp.		6	1	12	18	12	29	6	23	19	3	23	4	10
Apsidognathus tuberculatus	Pa	1												
Ozarkodina polinclinata polinclinata	Pa	1			2		2	2	1?				1	
	Pb				1	2	1	1?	1?					
	M					2?	3	1	3					
	Sa						1	2	1		1			
	Sb					2	1		1		1			
	Sc			2	1	2	5	1		2	1			1
Pterospathodus sp.	Pa	1												
Pterospathodus eopennatus	Pa				2		2			1				
	Pb	1				3	2			1		1?		
	M					1	1							
	S					1	1		2					
Kockelella cf. K. abruptus	Pa				1				1					
Distomodus staurognathoides	Pa					1								
	Sa					1?						1		
	Sb												1	
P. amorphognathoides angulatus	Pa						5	2?				1?		
	Pb						1	3?						
Pseudooneotodus bicornis							1							
Oulodus sp.	Pa								1					
Indeterminate Platform Element					1					1	1			1
Indeterminate Ramiform Element					2	2	4	3				1		1

Text-figure 6.—Conodont distribution within the Scotch Grove/LaPorte City formations at the Delhi West section (DLH). See Text-figure 2 and appendix for sample levels.

FORMATION		SCOTCH GROVE / LAPORTE CITY																	GOWER
SAMPLE NUMBER		GR 453	GR 444	GR 437	GR 408	GR 404	GR 392.5	GR 384	GR 369.6	GR 362	H13 1	BF 1	JCQ 2	BN 4	HNQ IS-1	WBK 5f	FMQ 3	FMQ top	BSQ bb
Panderodus sp.		2	124	9	1	4	10	1	38	7	78	97	4	22	1	14		34	10
Aulacognathus bullatus	Pa		3																
	Pb		1																
	Sa		1																
Aulacognathus? bullatus	Pa		1																
Aulacognathus kuehni	Pa		1																
Oz. polinclinata polinclinata	Pa		2								3	1?	1						
	Pb		2						2		2								
	M		1						1		1	5							
	Sa		3								2	1							
	Sb		7	1?															
	Sc		19			1?					4	1							
Walliserodus sp.			1																
Distomodus staurognathoides	Pa			1			1												
Oulodus sp	Pa											1							
	Pb											1							
	Sa											1							
	Sb											1							
	Sc											1							
Pseudooneotodus bicornis																			12
P. a. amorphognathoides	Pa														1				
	Pb						1								1				
Pterospathodus eopennatus	Pa										1								
	Pb										2	4							
	S										3	1							
Icriodella sp	Pa										1								
Ozarkodina excavata excavata	Pa													1					
	Pb													1					
Kockelella sp.	Sa															1			
Ozarkodina sagitta rhenana	Pa																	3	
	Pb																	2	
	M															1?		1	
	Sa																	4	
Kockelella ranuliformis	Pa																1		
Indeterminate Platform Element			16	1							1							2	3
Indeterminate Ramiform Element											5	9	1			3		3	9

Text-figure 7.—Conodont distribution within the Scotch Grove/LaPorte City and Gower formations at GR (Garrison Core), H13 (Highway 13), BF (Bailey's Ford), JCQ (Johns Creek Quarry), BN (North Baldwin), HNQ (Hanken Quarry), WBK (Waubeek), FMQ (Freeman Quarry also known as Pleasant Hill Quarry), and BSQ (Beuse Quarry). See Text-figure 2 and appendix for sample levels.

in The University of Iowa Paleontology Repository (SUI).

Phylum **CONODONTA** Pander, 1856

Class **CONODONTI** Branson, 1938

Order **OZARKODINIDA** Dzik, 1976

Family **SPATHOGNATHODONTIDAE** Hass, 1959

Genus **OZARKODINA** Branson and Mehl, 1933

Type species.—Ozarkodina confluens (Branson and Mehl, 1933) [=*Ozarkodina typica* Branson and Mehl, 1933].

Ozarkodina polinclinata polinclinata (Nicoll and Rexroad, 1969)

Plate 1, figures 24–26

Spathognathodus polinclinatus Nicoll and Rexroad, 1969, p. 60, pl. 2, fig. 19, 20.

Ozarkodina polinclinata (Nicoll and Rexroad) Klapper *in* Ziegler, 1977, p. 57–58, *Ozarkodina* pl. 3, figs. 5, 6; Kleffner, 1987, p. 87, fig. 5, PM 17–22.

Ozarkodina polinclinata polinclinata (Nicoll and Rexroad). Männik, 1992, p. 56–58, fig. 4. 1–28, fig. 5, 1–7, plate figs. 8, 10–20 (see synonymy).

Discussion.—The most abundant platform taxa in these collections, representative elements from the entire apparatus as reconstructed by Cooper (1977), Kleffner (1987) and Männik (1992) are present. The Pa element conforms to the description of the nominal subspecies of Männik (1992) by exhibiting less fused denticles and a well-developed posteriorly inclined cusp.

Collections.—14 and 2 questionable Pa elements, 10 and 2 questionable Pb elements, 15 and 2 questionable M elements, 11 Sa elements, 12 and 1 questionable Sb element, 39 and 1 questionable Sc element from the

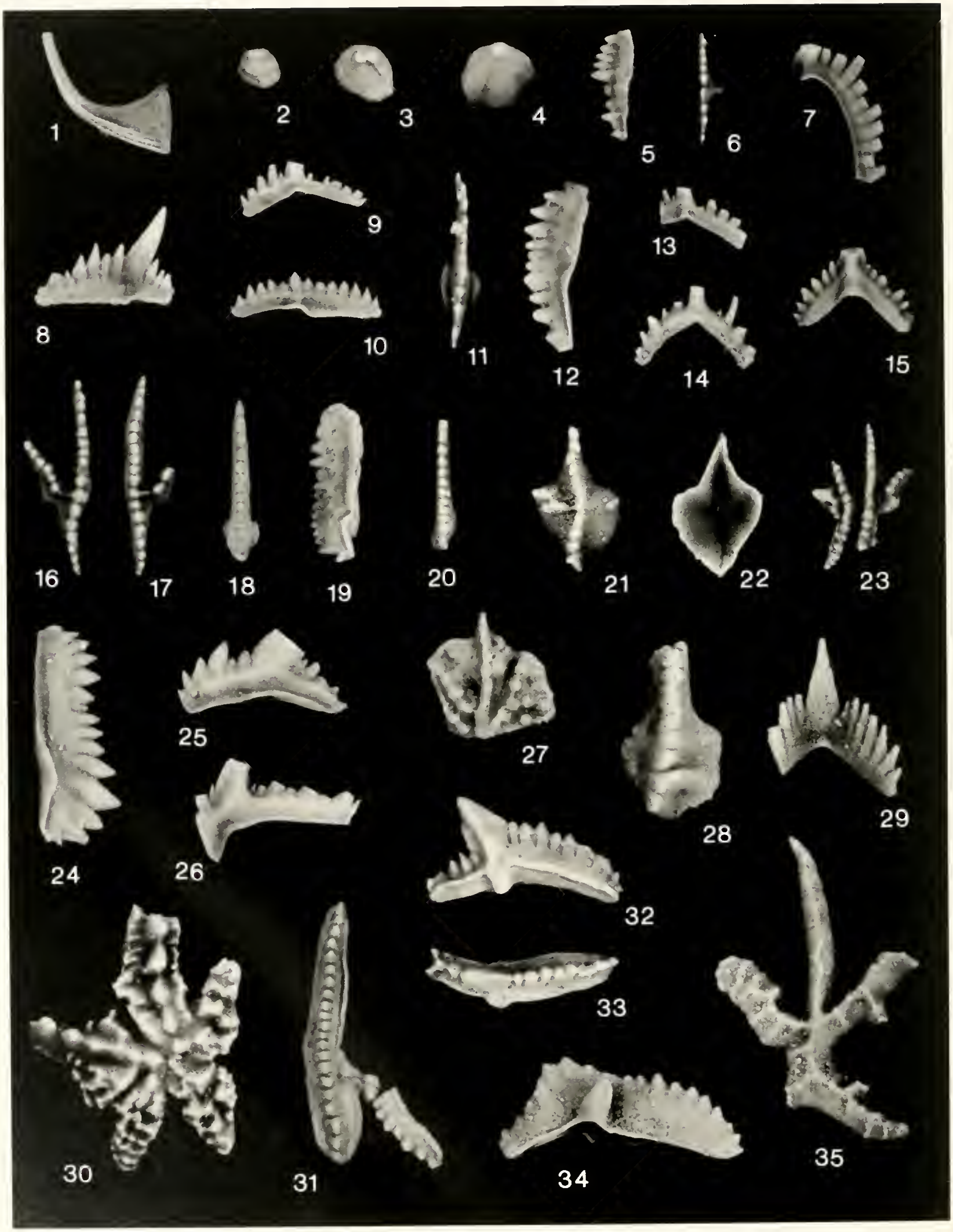

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PLATE I

1. *Walliserodus* sp.
    1. Coniform element, lateral view. GR-444. SUI 94708.

2–4. *Pseudooneotodus bicornis* Drygant, 1974
    2. Conical element, upper oblique view. BSQ-bb. SUI 94709.
    3. Conical element, upper oblique view. BSQ-bb. SUI 94710.
    4. Conical element, upper oblique view. DLH-6. SUI 94711.

5, 6. *Pterospathodus eopennatus* ssp. nov. 2 morphotype 4 Männik, 1998
    5. Pa element, lateral view. H13-1. SUI 94712.
    6. Pa element, upper view. H13-1. SUI 94712.

7. *Ozarkodina excavata excavata*? (Branson and Mehl, 1933)
    7. M element, inner lateral view. WBK-5F. SUI 94713.

8, 16, 17. *Pterospathodus amorphognathoides angulatus* (Walliser, 1964)
    8. Pb element, inner lateral view. DLH-6. SUI 94714.
    16. Pa element, upper view. DLH-6. SUI 94721.
    17. Pa element, upper view. DLH-6. SUI 94722.

9, 10. *Ozarkodina excavata excavata* (Branson and Mehl, 1933)
    9. Pb element, inner lateral view. BN-4. SUI 94715.
    10. Pa element, lateral view. BN-4. SUI 94716.

11–14. *Ozarkodina sagitta rhenana* (Walliser, 1964)
    11. Pa element, upper view. FMQ-top. SUI 94717.
    12. Pa element, lateral view. FMQ-top. SUI 94717.
    13. Sb element, inner lateral view. FMQ-top. SUI 94718.
    14. Sa element, inner lateral view. FMQ-top. SUI 94719.

15. *Kockelella*? sp.
    15. Sa element, inner lateral view. WBK-5F. SUI 94720.

18–20. *Kockelella* cf. *K. abruptus* (Aldridge, 1972)
    18. Pa element, upper view. DLH-4. SUI 94723.
    19. Pa element, lateral view. DLH-4. SUI 94723.
    20. Pa element, upper view. DLH-8. SUI 94724.

21, 22. *Aulacognathus*? *bullatus* (Nicoll and Rexroad, 1969)
    21. Pa element, upper view. GR-444. SUI 94725.
    22. Pa element, lower view. GR-444. SUI 94725.

23. *Aulacognathus kuehni* Mostler, 1967
    23. Pa element, upper view. GR-444. SUI 94726.

24–26. *Ozarkodina polinclinata polinclinata* (Nicoll and Rexroad, 1969)
    24. Pa element, inner lateral view. DLH-7. SUI 94727.
    25. Pb element, inner lateral view. DLH-5. SUI 94728.
    26. Sc element, inner lateral view. DLH-3. SUI 94729.

27. *Apsidognathus tuberculatus* Walliser, 1964
    27. Pa element, upper view. DLH-1. SUI 94730.

28. *Kockelella ranuliformis* (Walliser, 1964)
    28. Pa element, upper view. FMQ-3. SUI 94731.

29, 34, 35. *Aulacognathus bullatus* (Nicoll and Rexroad, 1969)
    29. Sa element, inner lateral view. GR-444. SUI 94732.
    34. Pb element, inner lateral view. GR-444. SUI 94736.
    35. Pa element, upper view. GR-444. SUI 94737.

30. *Distomodus staurognathoides* (Walliser, 1964)
    30. Pa element, upper view. GR-392.5. SUI 94733.

31–33. *Pterospathodus amorphognathoides amorphognathoides* Walliser, 1964
    31. Pa element, upper view. IS-1. SUI 94734.
    32. Pb element, inner lateral view. IS-1. SUI 94735.
    33. Pb element, upper view. IS-1. SUI 94735.

Magnifications all ×40.

Delhi West (DLH), Garrison Core (GR), Highway 13 road cut (H13), Bailey's Ford (BF) and John's Creek Quarry (JCQ).

Family **KOCKELELLIDAE** Klapper *in* Clark *et al.*, 1981

Genus **KOCKELELLA** Walliser, 1957

Type species.—Kockelella variabilis Walliser, 1957.

Kockelella cf. K. abruptus (Aldridge, 1972)

Plate 1, figures 18–20

Spathognathodus cf. *S. abruptus* Aldridge, 1972, p. 212, pl. 4, fig. 8.

Discussion.—Specimens in this study are similar to the specimen illustrated as *Spathognathodus* cf. *S. abruptus* by Aldridge (1972). Specimens may be ancestral to *Kockelella ranuliformis*, only lacking development of large basal cavity.

Collections.—2 Pa elements from the Delhi West section.

Family **PTEROSPATHODONTIDAE** Cooper, 1977

Genus **PTEROSPATHODUS** Walliser, 1964

Type species.—Pterospathodus amorphognathoides Walliser, 1964.

Pterospathodus amorphognathoides angulatus (Walliser, 1964)

Plate 1, figures 8, 16, 17

Spathognathodus pennatus angulatus Walliser, 1964, p. 79, pl. 14, figs. 19–22.

Pterospathodus amorphognathoides angulatus (Walliser). Mannik 1998, p. 1015–1019, pl. 2, figs. 1–22, 24–31, text-figs. 7–8 (see synonymy).

Discussion.—With revision of the *Pterospathodus* lineage, Männik (1998) identified *P. amorphognathoides angulatus* as the initial member of the *P. amorphognathoides* lineage. Specimens in this study exhibit a long blade with platform containing approximately 20 denticles. Specimens in this study are most similar to the Männik (1998) morphotype with tall denticles.

Collections.—5 Pa elements, 3 questionably assigned Pa elements, 1 Pb element and 3 questionably assigned Pb elements, all from the Delhi West section.

Pterospathodus eopennatus Männik, 1998

Plate 1, figures 5, 6

Pterospathodus eopennatus Männik, 1998, p. 1007–1013, pl. 1, figs. 1–46, pl. 2, figs. 23, 32–41, text-figs. 4–6 (see synonymy).

Discussion.—Specimens in this study are most closely related to *Pterospathodus eopennatus* ssp. nov. 2 morphotype 4 of Männik (1998, pl. 2, figs. 33, 38, 41; text-fig. 6, L, O–P, U). The most characteristic feature of this morphotype is a sharp decrease in denticle height just behind the cusp and posterior denticles being considerably shorter. The short, almost triangular, Pb element associated with *P. eopennatus* is also present in these faunas.

Collections.—6 Pa elements, 13 and 1 questionably assigned Pb element, 2 M elements and 8 symmetry elements from Delhi West, H13, and Bailey's Ford.

CONCLUSIONS

Conodont faunas in this study allow assignment of the LaPorte City/Scotch Grove formations to an interval correlative to the *eopennatus* Zone through *Ozarkodina sagitta rhenana* Superzone of the Silurian standard conodont zonation (Text-fig. 3). There is a complicated stratigraphic relationship between the units in this study, due both to initial facies relationships between members of the Scotch Grove Formation, and due to diagenetic alteration of the Scotch Grove compared to the limestones of the LaPorte City Formation. The conodont faunas are sparse in both lithologies. The presence of biostratigraphically diagnostic taxa gives some promise to more intensive study of this interval in the future, although this will involve the utilization of large sample sizes to get sufficient conodont faunas.

REFERENCES CITED

Aldridge, R.J.

1972. Llandovery conodonts from the Welsh Borderland. Bulletin of the British Museum (Natural History), Geology, vol. 22, pp. 127–231.

Branson, E.B.

1938. Stratigraphy and paleontology of the Lower Mississippian of Missouri. Part 1. The University of Missouri Studies, vol. 13, no. 3, 208 pp.

Branson, E.B., and Mehl, M.G.

1933. Conodonts from the Bainbridge (Silurian) of Missouri. University of Missouri Studies, vol. 8, pp. 39–52, pl. 3.

Calvin, S.

1896. Geology of Jones County. Iowa Geological Survey, Annual Report, vol. 8, pp. 121–192.

Clark, D.L., Sweet, W.C., Bergström, S.M., Klapper, G., Austin, R.L., Rhodes, F.H.T., Müller, K.J., Ziegler, W., Lindström, M., Miller, J.F., and Harris, A.G.

1981. Conodonta. *in* Treatise on invertebrate paleontology, Part W. Miscellanea. Supplement 2. R.A. Robison, *ed.*, Geological Society of America and the University of Kansas Press, Lawrence, 202 p.

Cooper, B.J.

1977. Toward a familial classification of Silurian conodonts. Journal of Paleontology, vol. 51, pp. 1057–1071.

Drygant, D.M.

1974. Simple cones from the Silurian and lowermost Devonian of the Volyno-Podolian area. Paleontologicheskiy Sbornik, vol. 10, pp. 64–70.

Dzik, J.

1976. Remarks on the evolution of Ordovician conodonts. Acta Palaeontologica Polonica, vol. 21, pp. 395–455.

Hall, J., and Whitney, J.D.

1858. Report on the Geological Survey of the State of Iowa: Iowa State Legislature, vol. 1, 472 pp.

Hass, W.H.

1959. Conodonts from the Chappel Limestone of Texas. United States Geological Survey Professional Paper 294J, pp. 365–400.

Jeppsson, L.

1997. A new latest Telychian, Sheinwoodian and Early Homerian (Early Silurian) standard conodont zonation. Transactions of the Royal Society of Edinburgh: Earth Sciences, vol. 88, pp. 91–114.

Johnson, M.E.

1975. Recurrent community patterns in epeiric seas: the Lower Silurian of eastern Iowa. Proceedings of the Iowa Academy of Science, vol. 82, pp. 130–139.

1977. Community succession and replacement in Early Silurian platform seas: the Llandovery Series of eastern Iowa. Unpublished Ph.D. thesis, University of Chicago, 237 pp.

1979. Evolutionary brachiopod lineages from the Llandovery Series of eastern Iowa. Palaeontology, vol. 22, pp. 549–567.

Kleffner, M.A.

1987. Conodonts of the Estill Shale and Bisher Formation (Silurian, southern Ohio): biostratigraphy and distribution. Ohio Journal of Science, vol. 87, pp. 78–89.

1990. Wenlockian (Silurian) conodont biostratigraphy, depositional environments, and depositional history along the eastern flank of the Cincinnati Arch in southern Ohio. Journal of Paleontology, vol. 64, pp. 319–328.

1991. Conodont biostratigraphy of the upper part of the Clinton Group and the Lockport Group (Silurian) in the Niagara Gorge region, New York and Ontario. Journal of Paleontology, vol. 65, pp. 500–511.

1994. Conodont biostratigraphy and depositional history of strata comprising the Niagaran sequence (Silurian) in the northern part of the Cincinnati Arch region, west-central Ohio, and evolution of *Kockelella walliseri* (Helfrich). Journal of Paleontology, vol. 68, pp. 141–153.

Loydell, D.K., Kaljo, D., and Männik, P.

1998. Integrated biostratigraphy of the lower Silurian of the Ohesaare core, Saaremaa, Estonia. Geological Magazine, vol. 135, pp. 769–783.

Ludvigson, G.A., Witzke, B.J., and González, L.A.

1992. Observations on the diagenesis and stable isotopic compositions of Silurian carbonates in Iowa. *in*: Silurian Stratigraphy and carbonate mound facies of eastern Iowa: Field trip guidebook to Silurian exposures in Jones and Linn Counties. Iowa Department of Natural Resources, Guidebook Series No. 11, pp. 73–83.

Männik, P.

1992. Taxonomy of the conodont species *Ozarkodina polinclinata* (Nicoll and Rexroad) in the Silurian of Estonia. Proceedings of the Estonian Academy of Science, Geology, vol. 41, pp. 54–62.

1998. Evolution and taxonomy of the Silurian conodont *Pterospathodus*. Palaeontology, vol. 41, pp. 1001–1050.

Mostler, H.L.

1967. Conodonten aus dem tieferen Silur der Kitzbühler Alpen (Tirol). Annalen des Naturhistorischen Museums in Wien, vol. 71, pp. 295–303.

Nicoll, R.S., and Rexroad, C.B.

1969. Stratigraphy and conodont paleontology of the Salamonie Dolomite and Lee Creek Member of the Brassfield Limestone (Silurian) in southeastern Indiana and adjacent Kentucky. Indiana Geological Survey Bulletin 40, 73 p.

Pander, C.H.

1856. Monographie der fossilen Fische des silurischen Systems der russich-baltischen Gouvernements. Akademie der Wissenschaften, St. Petersburg, 91 p.

Shaver, R.H., Ault, C.H., Ausich, W.I., Droste, J.B., Horowitz, A.S., James, W.C., Okla, S.M., Rexroad, C.B., Suchomel, D.M., and Welch, J.R.

1978. The search for a Silurian reef model, Great Lakes area. Indiana Department of Natural Resources, Geological Survey, Special Report 15, 36 pp.

Sweet, W.C.

1988. The Conodonta: morphology, taxonomy, paleoecology, and evolutionary history of a long-extinct animal phylum. Oxford Monographs on Geology and Geophysics, 10, 212 p.

Walliser, O.H.

1957. Conodonten aus dem oberen Gotlandium Deutschlands und der Karnischen Alpen. Hessisches Landesamtes für Bodenforschung Notizblatt, vol. 85, pp. 28–52.

1964. Conodonten des Silurs. Abhandlungen des Hessischen Landesamtes für Bodenforschung, 41, 106 p.

Witzke, B.J.

1976. Echinoderms of the Hopkinton Dolomite (Lower Silurian), eastern Iowa. Unpublished M.S. thesis, University of Iowa, 224 pp.

1981a. Stratigraphy, depositional environments, and diagenesis of the eastern Iowa Silurian sequence. Unpublished Ph.D. thesis, University of Iowa, 574 pp.

1981b. Silurian stratigraphy of eastern Linn and western Jones counties, Iowa. Geological Society of Iowa, Guidebook 35, 38 pp.

1983. Silurian benthic invertebrate associations of eastern Iowa and their paleoenvironmental significance. Transactions Wisconsin Academy of Sciences, Arts, and Letters, vol. 71, pp. 21–47.

1985. Silurian System. *in* The Plum River Fault Zone and the structural and stratigraphic framework of eastern Iowa. B.J. Bunker, G.A. Ludvigson, and B.J. Witzke, *eds.*, Iowa Geological Survey, Technical Information Series, no. 13, pp. 18–41.

1992. Silurian stratigraphy and carbonate mound facies of eastern Iowa. *in* Silurian stratigraphy and carbonate mound facies of eastern Iowa: Field trip guidebook to Silurian exposures in Jones and Linn Counties. Iowa Department of Natural Resources, Guidebook Series No. 11, pp. 3–63.

Ziegler, W., *ed.*

1977. Catalogue of Conodonts, III. E. Schweizerhart'sche Verlagsbuchhandlung, Stuttgart, 574 p.

APPENDIX

COLLECTING LOCALITIES AND SAMPLE INTERVALS

Abbreviations used for stratigraphic units: Maq (Maquoketa Formation), Bl (Blanding Formation), Hop (Hopkinton Formation), SG (Scotch Grove Formation), LPC (LaPorte City Formation), Gwr (Gower Formation), Wap (Wapsipinicon Group); BCQ (Buck Creek Quarry Member), WL (Welton Member), FC (Farmers Creek Member), PR (Picture Rock Member), JCQ (Johns Creek Quarry Member), Wbk (Waubeek Member), An-LC (Anamosa-LeClaire members undifferentiated).

BF: Baileys Ford, Logan Quarry, Kuhlman Construction Co., SE sec. 9, T 88 N, R 5 W, Delaware County; sample BF-1 taken 50 cm above base of LaPorte City Fm.; Hop (FC, PR), LPC. Ref: unpublished DOT log.

BN: Baldwin North, roadcuts and bluff exposures along Maquoketa River, NE sec. 3, T 84 N, R 1 E, Jackson County; sample BN-4 from 1.5 meters above the *Callipentamerus*-bearing bed in the succession; Hop (FC, PR), SG (WL). Refs: Witzke (1976, 1981a), Johnson (1977).

BSQ: Beuse Quarry, old quarry workings, NE SW NW sec. 28, T 80 N, R 5 E, Scott County; sample BSQ-bb from 1.2 meters above the base of quarry section; Gwr (An-LC). Ref: Witzke (1981a).

DLH: Delhi West Roadcut, SW SW SW SW sec. 18, T 88 N, R 4 W, Delaware Co.; Sample intervals from the base of outcrop in meters are: DLH-1, 1.50–1.75; DLH-2, 2.47–2.57; DLH-3, 2.67–2.82; DLH-4, 3.30–3.37; DLH-5, 3.71–3.76; DLH-6, 3.86–3.98; DLH-7, 4.43–4.48; DLH-8, 5.23–5.38; DLH-9, 5.63–5.68; DLH-10, 6.41–6.50; DLH-11, 7.07–7.17; DLH-12, 7.72–7.82; DLH-13, 7.97–8.02; SG, (BCQ), LPC.

FMQ: Freeman Quarry, old quarry bordering Plum River Fault Zone, NE SE SW sec. 20, T 83 N, R 2 W, Jones County; sample FMQ-3 is from 75 cm below top of quarry, sample FMQ-top is the uppermost bed exposed at the quarry; SG (Wbk). Ref: Witzke (1981a).

GR: Garrison core, Carbonate Hydrology Project, SW NW SW SW sec. 33, T 85 N, R 11 W, Benton County; Sample intervals are indicated as depth in core (feet) in Text-figure 5; Maq, Bl, Hop, LPC, Wap. Ref: Witzke (1981a, p. 504–506).

HNQ: Hanken Quarry, abandoned, NW NW NE sec. 6, T 85 N, R 2 W, Jones County; sample 1S-1 is from the upper 1 meter in the quarry; adjacent geest localities (fields and ravines), SW NE and NE NE sec. 6; SG (BCQ). Refs: Calvin (1896), Johnson (1977), Witzke (1976, 1981a, 1992).

JCQ: Johns Creek Quarry, Kuhlman Construction Co., type locality of Johns Creek Quarry Member, c E ½ SW sec. 36, T 88 N, R 2 W, Dubuque County; sample JCQ-2 from lower Scotch Grove Fm.; Hop (FC, PR), SG (JCQ, WL, BCQ geest). Refs: Johnson (1975, 1977, p. 140), Witzke (1976), Shaver *et al.* (1978).

WBK: Waubeek exposures, roadcuts and bluffs along Wapsipinicon River upstream from Waubeek, type locality for Waubeek Member, NE sec. 17, T 85 N, R 5 W, Linn County; sample WBK-5f is from the top of the exposure. Refs: Witzke (1981a, 1981b).

THE SILURIAN-DEVONIAN BOUNDARY AND THE KLONK EVENT IN THE FRAME FORMATION, SUBSURFACE WEST TEXAS

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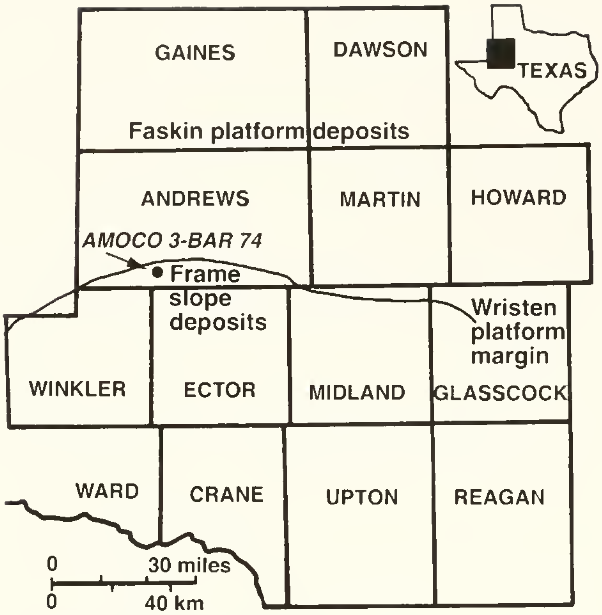
ABSTRACT

The Frame Formation (Wristen Group) in southern Andrews County, Texas, comprises fine-grained carbonate slope deposits that span the Silurian-Devonian boundary. Conodont faunas from a core of the upper Frame in the Amoco Three Bar 74 well range in age from Pridoli (*detorta* Zone) into the middle Lochkovian (*omoalpha* Zone). The Klonk event of Jeppsson (1998) may be represented by an extinction or replacement event in the Frame Formation, as well as in equivalent shelf strata in southern Oklahoma, where diagnostic late Silurian conodont species, mostly coniform taxa, are abruptly replaced by characteristic Early Devonian species. This event precedes the appearance of *Icriodus postwoschmidti* and may coincide with the Silurian-Devonian boundary.

INTRODUCTION

The Silurian-Devonian stratigraphic section in the Permian Basin region of West Texas and eastern New Mexico comprises over 2500 feet (760 m) of carbonates and shales that include prolific reservoirs and source rocks for hydrocarbons. Despite their economic importance, the time relations of the complex series of intergrading lithofacies that constitute this section are poorly known. The main reason for the paucity of chronostratigraphic control is the rarity of well cores from which well-constrained biostratigraphic data can be obtained. Previous works utilizing shelly fossils (Wilson and Majewski, 1960) and graptolites (Decker, 1942, 1952) have placed these strata in a general time frame (COSUNA Project, Hills and Kottlowski, 1983). More recent research on conodont faunas has begun to clarify the ages of some Silurian and Devonian units (Barrick and others, 1993; Barrick, 1995; Meyer and Barrick, 2000; Meyer, 2002), but details of the placement of major chronostratigraphic boundaries, in particular the Silurian-Devonian boundary, have remained unclear.

Recent studies of depositional and diagenetic facies in Silurian and Devonian rocks in the Permian Basin region have developed a new understanding of the spatial distribution of major lithofacies units in the carbonate-dominated Silurian to Lower Devonian section and an improved reconstruction of the depositional history (Ruppel, 1993; Ruppel and Holtz, 1994; Ruppel and Hovorka, 1995; Ruppel and Barnaby, 2001). As part of a program to characterize hydrocarbons reservoirs on lands owned by the University of Texas, cores from the Three Bar Field in southern Andrews County, Texas (Text-fig. 1), which produces from the Lower Devonian Thirtyone Formation, were made available for study (Ruppel and Hovorka, 1995). In the course of this research, a core that includes over 150 feet (46 m) of the underlying Frame Formation was obtained and has been processed for conodonts. Data



Text-figure. 1.—Locality map showing location of the Amoco Three Bar 74 well in West Texas. Position of the edge of the Wristen (Fasken) platform margin from Ruppel and Holtz (1994, fig. 5).

from this core permit resolution of the placement of the Silurian-Devonian boundary in this region as well as information on the significant changes in conodont faunas that occur during the "Klonk event" of Jeppsson (1998).

ACKNOWLEDGMENTS

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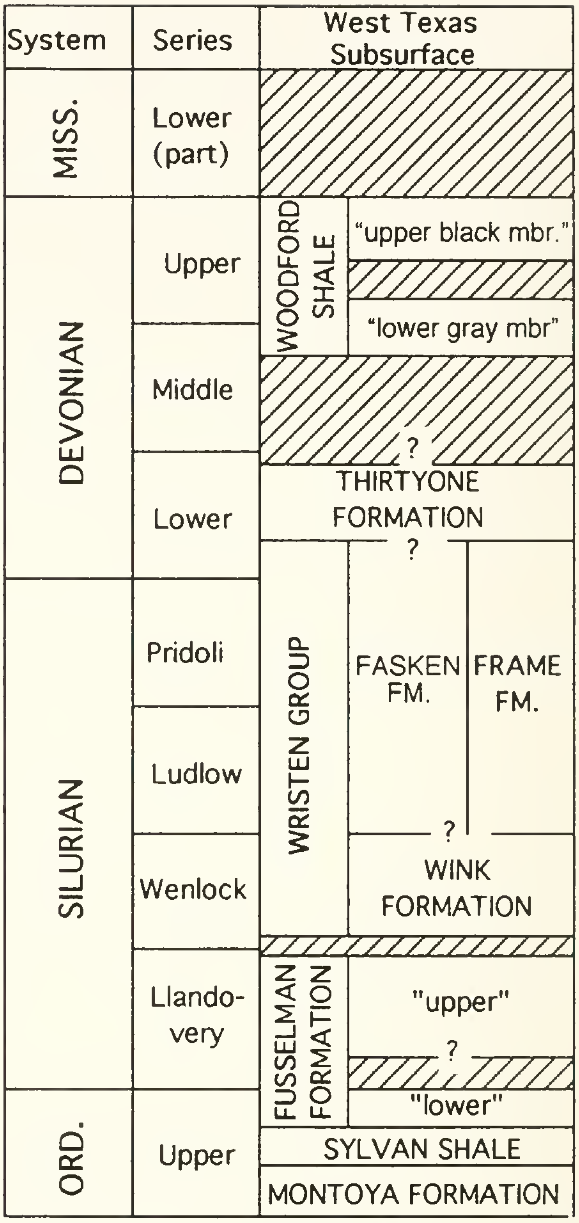
STRATIGRAPHIC SETTING

Ruppel and Holtz (1994) outlined the overall geological setting and depositional history of upper Silurian and Lower Devonian strata in the Permian Basin region (Text-fig. 2). During the Wenlock, tectonic subsidence transformed the Llandovery carbonate platform (Fusselman Formation) into a ramp that deepened to the south. In the outer ramp setting, nodular carbonate wackestones of the Wink Formation are overlain by the more distal, deeper water carbonates and shales of the Frame Formation. Continued subsidence during the late Silurian produced a deeper water basin to the present-day south, which was flanked on the north by shelf platform to steep ramp that sloped into the basin. Aggradation of the platform in central Andrews County, Texas, and northward, as represented by the Fasken Formation produced a shelf margin in central Andrews County, from which skeletal debris was delivered by downslope transport into the Frame basin. Facies and geometries in the Fasken Formation show that the platform-margin buildups were primarily aggradational, and that relatively little progradation of the shelf margin occurred during the late Silurian and Early Devonian.



Text-figure. 2.—Stratigraphic column of latest Ordovician (ORD.) through Devonian strata in the subsurface of West Texas. Ages of strata based largely on conodont faunas discussed in Barrick (1995), Meyer and Barrick (2000) and Meyer (2002). MISS. = Mississippian.

The Wink Formation and possibly the lower part of the Fasken Formation are Wenlock in age (Barrick, 1995), but the ages of the Frame Formation in the basin and the upper part of the Fasken Formation on the shelf are poorly known. Sparse Ludlow to Pridoli conodont faunas have been reported from dolostones assigned to the Fasken Formation well north of the basin margin (Barrick, 1995), but no Devonian taxa have been recovered from beds assigned to the Fasken. No evidence of breaks in deposition and related diagenetic alteration have been reported from the Fasken, and deposition appears to have continued without significant interruption from the Silurian into the Early Devonian on the platform.

Decker (1942, 1952) described Silurian graptolites from dark shales that we assign to the Frame Formation from two wells in Crane County, Texas (Text-fig. 1). Finney (*in* Barrick *et al.*, 1993) restudied Decker's collections and reported that the graptolites ranged in age from late Silurian (no older than Ludlow) to as young as the Early Devonian (Pragian). Fragments of *Icriodus* Pa elements were obtained from dark shales of the Frame just above the Wink Formation in the Pegasus core in Midland County, Texas (Barrick *et al.*, 1993). These biostratigraphic data suggest that deposition of dark shales and carbonates of the Frame continued from the Ludlow into the Early Devonian and that the Silurian/Devonian boundary should lie within the Frame Formation in the basin.

Ruppel and Holtz (1994) indicated that a major rise in sea level took place in West Texas and eastern New Mexico during the Early Devonian, which is reflected in the distinctly deeper water character of the basal deposits of the Thirtyone Formation, especially on the shelf margin area in Andrews County. There, deeper water Thirtyone chert deposits overlie Fasken reef deposits (F. J. Lucia, cited in Ruppel and Holtz, 1994). The Thirtyone Formation represents a thick wedge of cherts and siliceous carbonates that prograded southward into the basin during the Early Devonian (Ruppel and Holtz, 1994). The timing of the filling of the Thirtyone basin is unclear. Shelly faunas suggest that the unit was deposited during the Early to Middle Devonian (Wilson and Majewski, 1960), but conodont faunas indicate only a Pragian age for the unit (Barrick, 1995; Meyer, 2002).

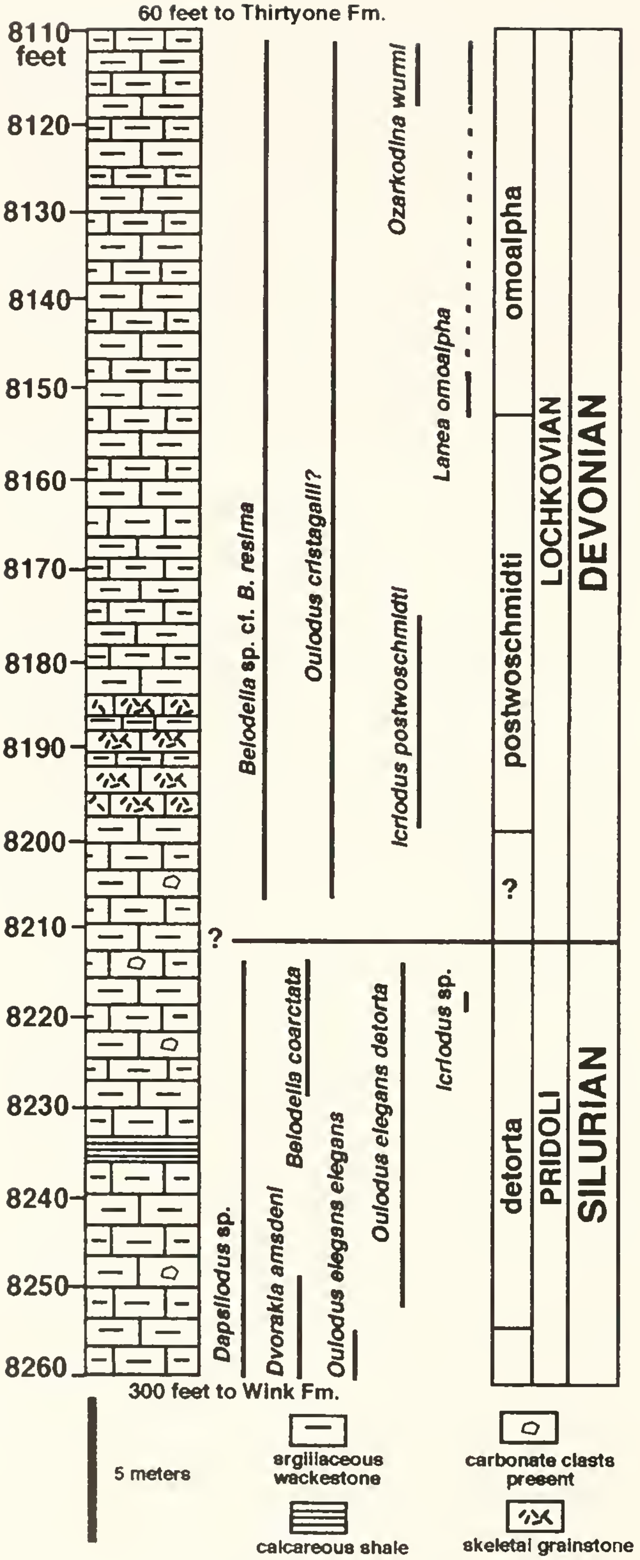
THE AMOCO THREE BAR 74 CORE

In southern Andrews County (Text-fig. 1), the shelf facies of the Fasken shelf grade into the outer ramp to slope facies of the Frame Formation (Ruppel and Holtz, 1994, fig. 4). The Amoco Three Bar 74 well lies just south of the transition, where nearly 500 feet (152 m) of the Frame Formation is recorded by cuttings and petrophysical logs. The base of the Thirtyone Formation is readily identified by its distinctive log signature (Ruppel and Holtz, 1994, fig. 10) at a depth of 8051 feet (2454 m) below sea level. Approximately 150 feet (45.7 m) of shale and carbonate assigned to the Frame Formation were cored in the Amoco Three Bar 74 (Text-fig. 3). The top of the core lies at 8112 feet (2472.5 m), 61 feet (18.6 m) below the top of the Frame, and extends down to 8258 feet (2517 m), nearly 300 feet (91.4 m) above of the base of the formation. The lithologic sequence of the cored interval is shown on Text-figure 3. In subsequent discussions, depth measurements are presented as feet below sea level, as this is the convention for subsurface work in the Permian Basin region of west Texas and eastern New Mexico.

The lower portion of the cored interval (8258′ to 8196′) consists of argillaceous and silty, slightly dolomitic carbonate mudstones and wackestones. Below 8235′ limestones are nodular bedded and interbedded with minor amounts of calcareous shale. From 8235′ to 8196′ the limestones are locally parallel-laminated or burrowed. At irregular intervals, angular clasts of skeletal to pelloidal carbonate mudstone occur. In contrast to the matrix, the clasts appear to contain little terrigenous material. The clasts are most prominent in three intervals (8251.5′–8247′; 8224′–8221′; and 8206′–8200′), but clasts occur as thin layers or individually at other levels. The clasts appear to represent lithified carbonate material that was eroded off the shelf margin and carried deeper onto the slope region by downslope transport.

Thin crinoid-brachiopod packstone/grainstone beds appear at 8196′ and occur up to 8178′. The poorly sorted, slightly abraded skeletal grains are dominated by echinoderm and brachiopod debris and include ostracods, trilobite and bryozoan grains, as well as peloids. The grainstone beds are interbedded with the typical Frame carbonate mudstones and wackestones, and may represent skeletal sands derived from the shelf margin. Above 8178′, slightly dolomitic laminated carbonate mudstones, wackestones, and rare packstones constitute the Frame Formation. In the upper parts of the core, brachiopods, corals, and bryozoans are more common, and the matrix becomes more argillaceous and silty. At 8116′, a few clasts of peloidal skeletal grainstone, like those found lower in the Frame, occur. Log responses indicate no significant additional change in lithology in the uppermost part of the Frame Formation in the Three Bar 74 well.

The overall succession of facies in the Three Bar 74 core suggests only a possible slight shallowing upward pattern for the Frame Formation, probably moderated by sea-level fluctuations. This could be a result of moderate progradation of the shelf margin during the



Text-figure. 3.—Generalized lithologic column of the Frame Formation in the Amoco Three Bar 74 core, Andrews County, Texas and ranges of important conodont species. Conodont zones and age assignments discussed in text.

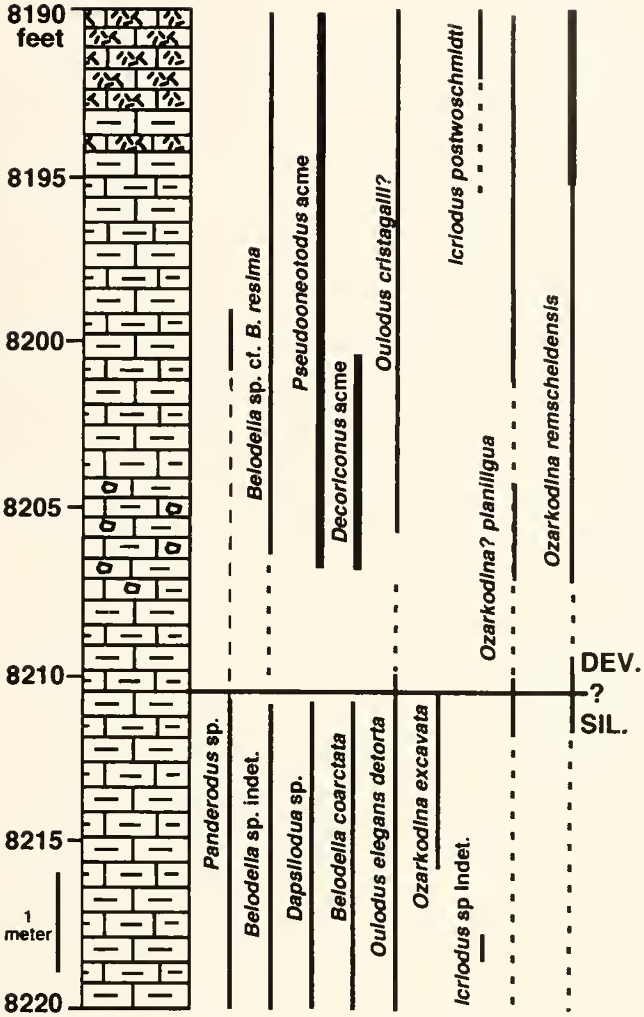
time the Frame was being deposited. However, it is unlikely that *in situ* shelf carbonates comprise any part of the Frame in this core, and we interpret the Frame here to represent a carbonate slope setting near the shelf margin.

CONODONT FAUNA

The core of the Frame Formation in the Amoco Three Bar 74 well was sampled for conodonts at one-foot (30 cm) and three-foot (90 cm) intervals. Previous handling of the core had obscured some footage indicators, which prevented sampling the entire core at one-foot intervals. Where the exact level in the core could be identified to the foot, a sample was taken and processed. Where the exact position of a core fragment was unclear, the material could be only be located within the three-foot interval given on the core box. In some instances, smaller one-foot samples and a larger sample including material from the three-foot interval were processed separately. As a result, numerous one-foot samples and fewer three-foot samples were processed. Ranges of significant conodont taxa are plotted on Text-figures 3 and 4. In only a few instances did the one-foot sampling reveal greater biostratigraphic resolution than the three-foot samples; these cases are noted below. Table 1 shows the number of conodonts recovered, recorded in three-foot intervals, and the relative abundance diagram (Text-fig. 5) is plotted at three-foot intervals.

The presence of carbonate clasts and possibly skeletal sands derived from an adjacent shelf margin suggests that minor admixing of conodont elements of different ages is possible. However, as the summary of faunas presented below indicates, we have not seen any evidence of conodonts of different zones occurring together. The carbonate material that was transported from the shelf setting into the slope environment of Frame deposition in the Three Bar 74 core must have been carried onto the slope soon after deposition, and in the case of the clasts, soon after early lithification.

The lowest part of the core contains the typical late Silurian (Pridoli) fauna of *Dvorakia amsdeni*, *Dapsilodus* sp., *Decoriconus fragilis*, *Belodella anfracta*, and *Panderodus* sp. (Text-figs. 3 and 4; Table 1). Unusual Pa elements that belong to an *Ozarkodina excavata*-type apparatus occur as do a few Pa elements that are assigned to the *O. remscheidensis* group. *Oulodus elegans detorta*, indicative of the latest Silurian *detorta* Zone, appears at 8252′. *Ozarkodina*? *planilingua* appears at 8233′ and ranges higher. *Belodella coarctata* appears and becomes relatively abundant at 8231′; this species is characteristic of the upper *detorta* Zone in the Henryhouse Formation in Oklahoma (Bar-



Text-figure. 4.—Detailed lithologic column and conodont ranges across the Silurian-Devonian boundary interval in the Amoco Three Bar 74 core, Andrews County, Texas. See text for details about faunal changes and placement of the systemic boundary. Lithologic symbols given on Text-figure 3.

rick and Klapper, 1992). An indeterminate, juvenile Pa element of *Icriodus* occurs at 8219′.

The most dramatic shift in conodont faunas occurs from 8213′ to 8207′ (Text-fig. 5). The three most characteristic species of the upper *detorta* Zone, *Belodella coarctata, Dapsilodus* sp., and *Panderodus* sp. disappear at 8211′–8212′. Only a single specimen of *Panderodus* occurs higher in the core (8197′–8200′). The highest collection with *Oulodus elegans detorta* (8213′–8210′) includes Sc elements with two small denticles between some of the large denticles. This subspecies may disappear at this level, or just higher (8209′–8210′), where a few poorly preserved ramiform elements occur. At 8213′ *Dvorakia philipi?* appears and at 8207′ *Belodella* cf. *B. resima* appears and becomes abundant. The low abundance of the ancestral species, *D. amsdeni* and *B. anfracta*, and poor preservation make the position of the faunal transitions in *Dvorakia* and *Belodella* difficult to locate exactly. *Ozarkodina remscheidensis*, which was uncommon in the underlying beds, becomes a persistent part of the fauna at 8213′ and *Ozarkodina*? *planilingua* occurs in small numbers. *Decoriconus fragilis* becomes more abundant than below, and *Pseudooneotodus beckmanni*, which occurred sparingly below, rises to moderate abundance at 8207′. Robust ramiform elements that may be referred questionably to *Oulodus cristagalli?* appear in small numbers at 8207′ and range higher.

Although a few indeterminate Pa elements and coniform elements of *Icriodus* appear lower, the first identifiable species is *I. postwoschmidti*, which appears with the first skeletal grainstone layer at 8195′. Elements of *Icriodus postwoschmidti* are moderately common through the grainstone interval, but are less common higher in the core. Associated with *Icriodus* in the grainstone interval are variable proportions of *Belodella* sp. cf. *B. resima, Pseudooneotodus beckmanni, Decoriconus fragilis, Ozarkodina remscheidensis, O. excavata*?, *O.*? *planilinuga*, and *Oulodus* elements.

Barrick and Klapper (1992) interpreted the appearance of *Icriodus postwoschmidti* in Oklahoma to represent the level of the Cordilleran *eurekaensis* Zone, based on the co-occurrence of this species with *Pedavis biexoramus*, which is known from the *eurekaensis* Zone in Nevada (Murphy and Matti, 1983). *Icriodus woschmidti*, the diagnostic species of the *woschmidti* Zone, was not recovered from the core, nor is it known from Oklahoma (Barrick and Klapper, 1992). Because of the broad geographic distribution of *Icriodus postwoschmidti* (see synonymy in Barrick and Klapper, 1992), a zone based on this species has broader application than the Cordilleran *eurekaensis* Zone and we employ it here (Text–fig. 3). The base of the *postwoschmidti* Zone is well correlated with the graptolite succession, because *I. postwoschmidti* appears in the middle of the *Monograptus uniformis* Zone in the Barrandian succession in Bohemia (Schönlaub, 1980) and in the upper range of the *M. uniformis* Zone in Podolia (Mashkova, 1970; Drygant, 1984).

The conodont fauna of the skeletal grainstones persists into the carbonate wackestones and mudstones that lie above it, but *Icriodus* declines in abundance. *Icriodus eolatericrescens*? occurs at only one level, at 8165′–8162′. *Lanea omoalpha* first appears at 8150′ and recurs in the highest samples from the core, 8117′–8111′. This species is the zonal index for the *omoalpha* Zone as used by Murphy and Valenzuela-Ríos (1999), which lies at the base of the middle Lochkovian.

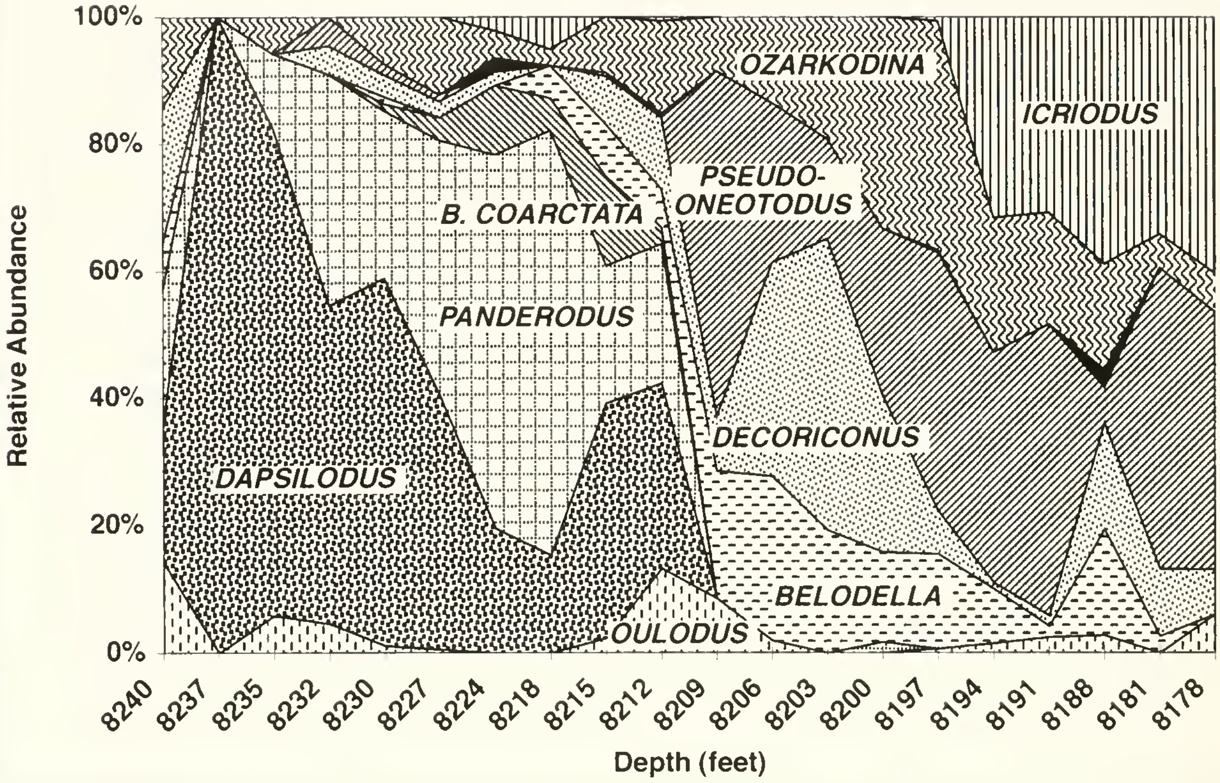
In summary, the conodont fauna of the Frame For-

Table 1.—Distribution of conodonts in the Amoco Three Bar 74 core, Andrews County, Texas. Data are given in three-foot increments unless otherwise indicated. Weights for all samples were not available and cocodont abundance for some samples could not be calculated. No cocodonts were obtained from intervals 8186′–8183′ and 8231′–8228′.

Sample interval (feet)		8256	8252	8249	8248	8245	8242	8239	8233	8233	8231	8228	8225	8222	8216	8213	8210	8207	8204	8201
		8259	8256	8252	8249	8248	8245	8242	8239	8236	8233	8231	8228	8225	8219	8216	8213	8210	8207	8204
Abundance (c/kg)		38	10	26	9	1	2	6	1	9	9	70	92	24	12	81	40	17	27	33
Ozarkodina remscheidensis rem-	Pa	1															3		1	1
scheidensis indet	Pa	1										4	2				3	1	10	3
	Pb												3				4		5	3
	M	1															1			2
	S	3									2	2	1				3	2	6	3
O. planilingua	Pa										3						3		1	
O. excavata excavata	Pa	2											3							
subspecies A	Pa	3		2																
subspecies B	Pa					1						1	2							
subspecies C	Pa															1	2			
	Pb	1		2									4			3	2			
	M	1	2										3		1					
	S	2	4	15	1		1						7	2		5	2			
Oulodus elegans elegans	Pb		2																	
	Sa/Sb		1																	
	Sc		2																	
Ou. elegans detorta	Pa							1		1	1						3			
	Pb						1	1									6			
	M			2												1	3			
	Sa/Sb			2			1	2									1			
	Sc			3	1		1			1		2				2	5			
Oulodus? species	Pb						1											1		
	M												1							
	Sa/Sb						2					1						1		
	Sc	1																1		
Oulodus cristigalli	M																		1	
	Sc																		1	
Icriodus sp. indet.	Pa														1					
Pelekysgnathus sp. indet.														2	1			1		
Dapsilodus species		3		1	2			3	3	12	11	101	78	9	6	65	44			
Panderodus unicostatus		10	7	6	2			3		2	8	46	78	27	26	37	33			
Dvorakia amsdeni		3	3?	5	3	2														
D. philipi?														1?			1			
Belodella anfracta		17	3?	4?			2?	1?				2?			2?	11?				
B. coarctata												2	7	5	2	23	9			
B. sp. cf. *resina*																	9?	4?	40	16?
Decoriconus fragilis		37	6	3	1			3			1	6	5	1		13	17	3	52	38
Pseudooneotodus beckmanni					1						1	3	2			1	1	19	39	13

Table 1.—Continued.

Sample interval (feet)		8198	8195	8192	8189	8186	8179	8177	8174	8171	8168	8165	8162	8159	8156	8152	8149	8146	8143	8141	8139	8136	8133	8130	8125	8122.5	8120	8117	8114	8111
		8201	8198	8195	8192	8189	8183	8179	8177	8174	8171	8168	8165	8162	8159	8156	8152	8149	8146	8143	8141	8139	8136	8133	8128	8125	8122 5	8120	8117	8114
Abundance (c/kg)			130	65	48	12	9			21		90	16		3	4	33	14	16	46	17	10	16	6	1	3	8	15	36	75
Ozarkodina remscheidensis remscheidensis	Pa	1	9	1		1		1	1		2	3				1	1	2	2	4	5	1	1	1			2	3		1
Ozarkodina sp. 1		2									3	2	3	2		2	1	1		3	2		1	1					1	
indet.	Pa		21	6	7	1	1	1	1		3	10	6	2			6	4	2	8	5			2			2	3	9	4
	Pb	1	16	6	4		1		2		4	3	4					2	1	2	3			1		2	1	1	7	2
	M		14	5	4						2	5	2				4	2		1	7			1		1	1	0	3	5
	S	11	33	23	5	2		4			2	11	17				16	3	3	3	10		1			1	5	11	10	4
O.? planilingua	Pa	2	4	1	1																								1	
Lanea omoalpha	Pa																1												2	1
Ozarkodina excavata	Pa									1?	1		2							1?										
	Pb		1																	1?										
	M										1																			
	S										2																1?	1?		
O. wurmi	Pa																												15	11
	Pb																												15	16
	M																												9	3
	S																												28	23
Icriodus postwoschmidti	Pa		1	8	5	2		2		1			4																	
I. eolatericrescens	Pa												1							1?										
Icriodus indet.	Pa			3	6	4	2	2	0	2	2	1	2																1	
Other elements			2	27	32	7	6	22	2	4	14	2	8		1					4	4							3		
Pedavis biexoramus	Pa																													1
sp. indet.	Pa							1		1																				
Other elements																					1		2							
Oulodus cristigalli?	Pa		1	2	1			2									1										1	1	1	
	Pb				1																									
	M					1		1			1																	1	2	
	Sa/Sb				1			3									1	1?											3	1
	Sc								1			1										1				1				
Panderodus unicostatus		1																												
D. philipi?						1?							1	1?				1								1				
B. resima?		8	42	17	2	6	1						2				11	6		1	8	1	19	2	1			9		9
Decoriconus fragilis		14	29	2	2	6	4	7	1	2	55	59	14		1				1	3	5							1	8	11
Pseudooneotodus beckmanni		15	115	72	55	2	18	40	16	29	4	30	23	2	1	1	6	12	12	7	6	9	2	5			7	8	11	9



Text-figure. 5.—Relative abundance of major conodont taxa across the Silurian-Devonian boundary interval in the Amoco Three Bar 74 core, Andrews County, Texas. Abundances plotted at three-foot intervals. Thin black areas between *Pseudooneotodus* and *Ozarkodina* represent the abundance of *Dvorakia* species. *Belodella* = *B. anfracta* and *B.* sp. cf. *B. resima*; *coarctata* = *Belodella coarctata*. See text for details about change in faunal abundance. Intervals without conodonts, 8186′–8183′ and 8231′–8228′, are omitted from text-figure.

mation in the Three Bar 74 core ranges in age from the Pridoli (late Silurian) into the middle Lochkovian (Early Devonian). Approximately 300 feet (91.4 m) of the Frame Formation lie below the cored section; these strata should be Ludlow to early Pridoli in age by stratigraphic position above the Wink Formation and below the cored interval. The base of the Thirtyone Formation lies some 60 feet (18.6 m) above the cored interval; the top of the Frame may span the middle and late Lochkovian and even extend into the Pragian.

THE SILURIAN–DEVONIAN BOUNDARY AND THE KLONK EVENT

The faunal transition across the Silurian-Devonian in the Frame Formation is similar to that reported by Barrick and Klapper (1992) from the Henryhouse-Haragan formations in southern Oklahoma. Despite a distinct, sharp faunal change near the inferred position of the Silurian-Devonian boundary, the exact position of this boundary is difficult to place. In Oklahoma and west Texas, at least four steps in the faunal transition occur in the same order though a thin stratigraphic interval and may represent steps in the Klonk event of Jeppsson (1998).

Step 1: Acme of *Belodella coarctata* in the upper part of the *detorta* Zone.

Step 2: Extinctions of *Belodella coarctata, Dapsilodus* sp., *Panderodus* sp., *B. anfracta*, and *Dvorakia amsdeni*. Appearance of *B.* cf. *B. resima* and *D. philipi*?. These events occur so close in the sections that their order has not been resolved.

Step 3: Extinction of *Oulodus elegans detorta*. A biofacies shift to *Decoriconus*- and *Pseudooneotodus*-dominated faunas, with common *Ozarkodina remscheidensis* group elements. Appearance of *Oulodus cristagalli*-like elements.

Step 4: Appearance of *Icriodus postwoschmidti*.

Barrick and Klapper (1992) found it difficult to locate the Silurian-Devonian boundary exactly in the Henryhouse-Haragan section using these faunas, and the same is true for the Frame Formation in the Three Bar 74 core. Part of the problem is that the base of the Devonian cannot be precisely placed using conodonts alone. *Icriodus woschmidti*, which is often used to help recognize basal Devonian strata, is well documented to occur in uppermost Silurian strata, perhaps as low as the *Monograptus transgrediens* Interzone (Jeppsson, 1988). However, in Oklahoma and West Texas, only the presumed descendent of *I. woschmidti, I. postwoschimdti* is present. It appears just above the base of the Devonian (middle *M. uniformis* Zone). *Oulodus elegans detorta*, the first appearance of which defines the highest Silurian conodont zone, appears to range into the lowest Devonian beds at the Devonian stratotype section at Klonk and elsewhere (Jeppsson, 1988, 1989). Jeppsson (1988, 1989) indicated that ramiform elements of *O. e. detorta* having two to three small denticles interspaced with major denticles may serve to distinguish latest Silurian from earliest Devonian forms. However, the preservation of ramiform elements in the uppermost samples of the range of *O. e. detorta* in the Frame samples is poor and such elements are known from only one sample (8113′–8110′).

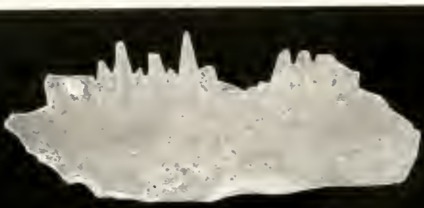
Jeppsson (1998) proposed the "Klonk Secundo Event" for the oceanic event that affected a variety of organisms, in particular graptolites and conodonts, at the end of the Silurian. He did not select a reference area, but indicated that it is best known in Bohemia, and that it could be recognized in Oklahoma, using data of Barrick and Klapper (1992). The Klonk event started at or near the replacement of *Oulodus elegans elegans* by *O. e. detorta*, based on observations of the conodont succession at Klonk (Jeppsson, 1988, 1989). Jeppsson (1998) also noted that *Ozarkodina excavata* dominates just before the end of the Silurian at Klonk and in the first Devonian fauna. He compared the dominance of *Ozarkodina excavata* in the Klonk Event with a similar dominance of this species in the last fauna just before recovery during the severe Mulde Event (Wenlock), which suggests that the recovery phase of the Klonk Event spanned the Silurian-Devonian boundary.

If the Klonk Event starts near the first appearance of *Oulodus elegans detorta* and extends into the earliest Devonian, then strata in the Three Bar 74 core and the Oklahoma sections span the entire event. No conodont faunal changes are evident in the lower part of the range of *O. e. detorta* in either area; all the faunal transitions occur in the uppermost part of the *detorta* Zone. The short range and acme of *Belodella coarctata* is the most conspicuous feature of the upper part of the *detorta* Zone in the Three Bar 74 core and the Oklahoma sections. Jeppsson (1988) records a comparable acme of this species (*B. mira* in his papers) that ranges from the upper part of the *Monograptus trangrediens* Interzone (Bed 10 at Klonk) and apparently peaks in the Post-*M. trangrediens* Interregnum (Bed 14). There, the *B. coarctata* acme lies below the first occurrence of *Oulodus elegans detorta* in Interbed 16/17, but the latter species occurs at only two levels, 16/17 and 19 in the Klonk section. The sparse occurrences of *B. mira (B. coarctata)* reported in Interbed 16/17 and 19 at Klonk by Jeppsson (1988) are based on very poor material that is not considered to be diagnostic. At U topolu, Bed 3 (Chlupác *et al.*, 1972; Jeppsson, 1988), *B. coarctata* does dominate a sample bearing *Oulodus e. detorta* within the upper range of *M. transgrediens*.

Conodont species comprising coniform elements from the Cellon section in Austria (Walliser, 1964) have never been described, but it is possible to make some observations about the range of *Belodella* species using comparative collections obtained by Jeppsson and Barrick from Cellon. *Belodella coarctata* occurs in samples 42A, 43C, and 47, ranging from well below the first occurrence of *Oulodus elegans detorta* (sample 45) as reported by Jeppsson (1988). *Belodella* cf. *B. resima* appears in sample 47 with the acme of *B. coarctata* and ranges higher, but the latter species is absent in samples 47A and 47B. *Icriodus woschmidti* appears in sample 47B, and *Monograptus uniformis* in sample 50.

The data from Klonk, U topolu, and Cellon place the acme of *Belodella coarctata* as ranging from the uppermost part of the *Monograptus transgrediens* Interzone into the lower part of the latest Pridoli Post-*Monograptus transgrediens* Interregnum. This may mark the first major step of the Klonk Event. Jeppsson (1988, 1989) indicated that *Oulodus e. detorta* appears high in the *Monograptus transgrediens* Interzone. However, because *Oulodus e. detorta* ranges well below the *Belodella coarctata* acme in our sections, we infer that the base of the *detorta* Zone lies somewhat lower, but still within the *trangrediens* Interzone.

The extinction of *Belodella coarctata* and the appearance of *B.* cf. *B. resima* occur during the Post-*Monograptus transgrediens* Interregnum. Because *Icriodus woschmidti* may occur as low as the *M. transgrediens* Interzone in the Barrandian (Jeppsson, 1988), the faunal events in West Texas and Oklahoma listed in Step 2 (above) may lie closer to the base of the Devonian than the first appearance of *I. woschmidti*. Note that juvenile, undiagnostic Pa elements of an *Icriodus* species occur at 8216′–8219′ in the Three Bar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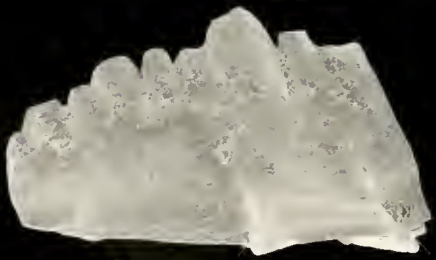
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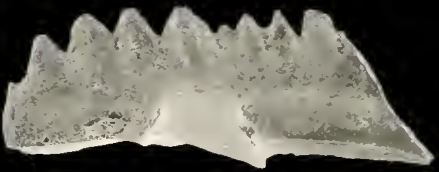
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74 core and at Highway 77 in Oklahoma (Barrick and Klapper, 1992, table 3), below the faunal change of Step 2.

The rise to dominance of *Ozarkodina excavata* reported by Jeppsson (1998) to mark the pre-recovery phase of the Klonk Event occurs in Bed 19 at Klonk, just below the base of the Devonian, the middle of Bed 20. In contrast, elements assigned now to *Ozarkodina excavata* disappear just before the first appearance of *Icriodus woschmidti* at Cellon (Walliser, 1964, table 2). In Oklahoma, *Ozarkodina excavata* is uncommon in the *detorta* Zone but becomes moderately abundant in one sample just before Step 2, but locally disappears with the extinctions of Step 2. In the Frame Formation in the Three Bar 74 core, however, *Ozarkodina excavata* is rare both below and above the potential boundary level.

If the faunal transition discussed here is reliable for detailed biostratigraphic correlation, then the base of the Devonian should lie just above the faunal events of Step 2. Faunas characterized by *Belodella anfracta, Dvorakia amsdeni, Dapsilodus* and the acme of *B. coarctata* would be latest Pridoli in age. Faunas bearing *Belodella* sp. cf. *B. resima* and *Dvorakia philipi* and *Oulodus elegans detorta* elements with two or more small denticles alternating with large denticles would be earliest Lochkovian in age. Both faunas may lie within the time represented by the *Icriodus woschmidti* Zone in the existing conodont zonation. If this interpretation is correct, then the base of the Devonian in the Frame Formation in West Texas can be placed at approximately 8211′ in the Three Bar 74 core.

The dramatic biofacies shift to *Decoriconus*- and *Pseudoonoetodus*-dominated faunas, which occurs at about the same level as the extinction of *Oulodus elegans detorta* (Step 3; at 8209 feet in the Frame), lies within the time interval represented by the *Icriodus woschmidti* Zone, but above the base of the Devonian. No change in lithology or evidence of a disconformity coincides with this biofacies shift, which may represent some later recovery step in the Klonk event. Step 4 is the appearance of *Icriodus postwoschmidti*, the first occurrence of which is a definitive indicator for the earliest Lochkovian (middle of the *Monograptus uniformis* Zone; see above).

Application of this argument to sections in Oklahoma indicates that the placement of the Silurian-Devonian boundary by Barrick and Klapper (1992) should be changed. These authors placed the base of the Devonian to coincide with the conodont biofacies shift of Step 3, which matches approximately the abrupt turnover in the shelly faunas reported by Amsden and Barrick (1988 and references cited therein) to coincide with the Henryhouse-Haragan formational boundary. Step 2 occurs slightly lower in their sections, and using this as the correlated boundary places the base of the Devonian at sample 2B instead of 2D at the I-35 section, or 0.50 m lower (Barrick and Klapper, 1992, text-fig. 3; table 1).

SYSTEMATIC PALEONTOLOGY

Most species discussed and illustrated in this paper have been well described in the literature, in particular in the paper by Barrick and Klapper (1992) on conodont faunas across the Silurian-Devonian boundary in Oklahoma. The species discussed below, however, are ones that have been subsequently described or revised, or represent forms that are not well known. The revisions recommended by Murphy *et al.* (2004), however, have not been incorporated. All illustrated specimens are reposited at the University of Iowa (SUI numbers).

←

PLATE 1

All specimens are from the Frame Member, Wristen Formation, Amoco Three Bar 74 well, Andrews County, Texas. All illustrations are 60×.

1. *Ozarkodina remscheidensis* (Ziegler, 1960)?
    1. SUI 98144, 8258 feet: lateral view of needle denticle Pa element morphotype.

2, 9, 10. *Ozarkodina remscheidensis* (Ziegler, 1960)
    2. SUI 98145, 8195–8198 feet, lateral view of Pa element.
    9, 10. SUI 98146, 8258 feet, 9, upper view of broken Pa element; 10, lateral view.

3, 4, 11, 12. *Ozarkodina? planilingua* Murphy and Valenzuela-Ríos, 1999
    3, 4. SUI 98147, 8210–8213 feet; 3, upper view of Pa element; 4, lateral view.
    11, 12. SUI 98148, 8210–8213 feet, 11, upper view of Pa element with broken basal cavity rim; 12, lateral view.

5–8, 13, 14. *Lanea omoalpha* Murphy and Valenzuela-Ríos, 1999
    5, 6. SUI 98149, 8117 feet; 5, upper view of Pa element; 6, lateral view (specimen broken during photography).
    7, 8. SUI 98150, 8114 feet, 7, upper view of broken Pa element; 8 lateral view.
    13, 14. SUI 98151, 8150 feet, 13, upper view of Pa element, 14, lateral view.


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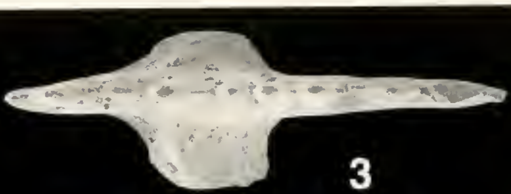
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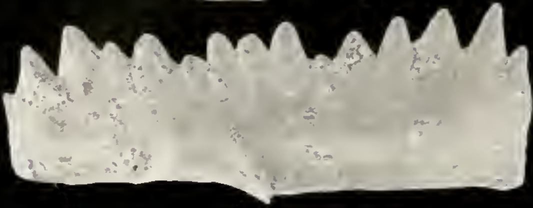
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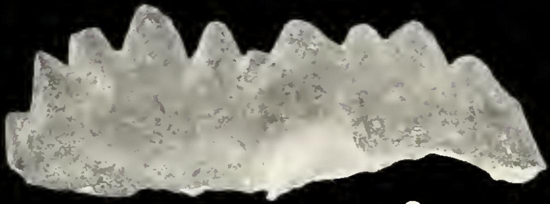
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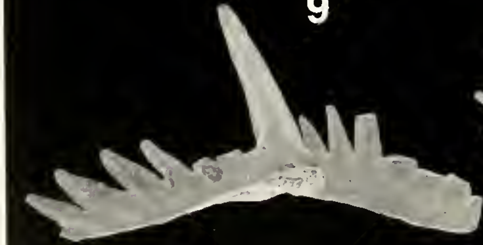
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Class **CONODONTI** Branson, 1938

Order **PRIONIODINIDA** Sweet, 1988

Family **PRIONIODINIDAE** Bassler, 1925

Genus **OULODUS** Branson and Mehl, 1933b

Oulodus elegans detorta (Walliser, 1964)

Plate 3, figures 1–3

Remarks.—The identification of *Oulodus elegans detorta* depends on the recognition of the presence of small denticles interspersed between large denticles on the processes. This feature appears gradually in populations of *O. elegans*, and alternating denticulation appears in the Sc elements before in the other elements. Jeppsson (1988) recommends that if 10% of the *O. elegans* elements in a collection possess alternating denticulation, then the population should be assigned to *O. elegans detorta*. The small numbers and variable preservation of elements of *O. elegans* from the Three bar 74 core makes application of the 10% rule problematic. The first Sc element with alternating denticulation appears low in the core, 8252–8249 feet, but collections in which several of the elements clearly possess alternating denticulation occur much higher, at 8213–8210 feet. The position of the base of the *detorta* Zone in the core is placed at 8252 feet, where the first Sc element with clearly alternating denticulation appears.

Order **OZARKODINIDA** Dzik, 1976

Family **SPATHOGNATHODONTIDAE**, Hass 1959

Genus **LANEA** Murphy and Valenzuela-Rios, 1999

Type species.—*Ozarkodina eleanorae* Lane and Ormiston, 1979.

Remarks.—Murphy and Valenzuela-Rios (1999) distinguish Pa elements of *Lanea* from those of similar taxa like *Ozarkodina*, by the presence of a distinct, broad terrace, a raised area extending from the blade, flanked by a sulcate brim, on the upper surface of the relatively large basal platform lobe. Unlike species of *Ancyrodelloides*, Pa elements of *Lanea* typically lack ridges or tubercules on the basal platform lobes.

Lanea omoalpha Murphy and Valenzuela-Rios, 1999

Plate 1, figures 5–8, 13, 14

Ancyrodelloides omus alpha morph Murphy and Matti, 1983, p. 17, pl. 2, figs. 18–20 [imprint 1982]; Valenzuela-Rios, 1994, pl. 1, fig. 10.

Lanea omoalpha Murphy and Valenzuela-Rios, 1999, p. 327, pl. 1, figs. 10–19, 23, 27–29, pl. 2, figs. 12–14.

Remarks.—The Pa element of *Lanea omoalpha* has large basal platform lobes with the area of the platform terrace equal to greater than that of the brim. The basal cavity is unrestricted. The four Pa elements assigned here to this species possess the relatively large terrace characteristic of the species. Other Pa elements that

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PLATE 2

All specimens are from the Frame Member, Wristen Formation, Amoco Three Bar 74 well, Andrews County, Texas. All illustrations are 60×.

1–4, 7. *Ozarkodina* sp. 1
  1, 2. SUI 98152, 8195–8198 feet. 1, upper view of Pa element; 2, lateral view.
  3, 4. SUI 98153, 8141–8143 feet. 3, upper view of Pa element; 4, lateral view.
  7. SUI 98154, 8141–8143 feet. 7, lateral view of Pa element.
5, 6. *Ozarkodina* sp. 1?
  5, 6. SUI 98155, 8148 feet. 5, upper view of Pa element; 6, lateral view.
8. *Ozarkodina remscheidensis* (Ziegler, 1960)?
  8. SUI 98156, 8198 feet. Lateral view of Pa element.
9, 10. *Ozarkodina excavata* subspecies C
  9. SUI 98157, 8213–8216 feet. Lateral view of Pa element.
  10. SUI 98158, 8213–8216 feet. Inner lateral view of Pb element.
11. *Ozarkodina excavata* subspecies A?
  11. SUI 98159, 8258 feet. Lateral view of Pa element.
12–14. *Ozarkodina excavata* subspecies A
  12. SUI 98160, 8249–8252 feet. Inner view of Pb element.
  13. SUI 98161, 8249–8252 feet. Lateral view of Pa element.
  14. SUI 98162, 8249–8252 feet. Lateral view of Pa element.
15. *Ozarkodina wurmi* (Bischoff and Sannemann, 1958)
  15. SUI 98163, 8116 feet. Lateral view of Pa element.
16. *Ozarkodina excavata* subspecies B
  16. SUI 98164, 8228–8231 feet. Lateral view of Pa element.


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have a terrace that approaches that of *L. omoalpha* in size were placed in the closely related species *Ozarkodina? planilingua*. *Lanea omoalpha* appears at 8152 feet in the Three Bar 74 core and occurs in the highest two samples of the core at 8117–8114 and 8114–8111 feet.

Genus **OZARKODINA** Branson and Mehl, 1933a

Ozarkodina excavata excavata Branson and Mehl, 1933a

Remarks.—Elements that can be assigned to *Ozarkodina excavata* in the broadest sense occur sporadically through the Three Bar 74 core. Despite their rarity, a variety of forms occur that are described here in open nomenclature. Murphy *et al.* (2004) discuss the nomenclatural and taxonomic problems associated with the *O. excavata* group. A few Pa and Pb elements resembling "typical" *Ozarkodina excavata excavata* occur only at the base of the core, at 8256′–8259′ and in the *postwoschmidti* Zone (8171′–8165′).

Ozarkodina excavata subspecies A
Plate 2, figures 12–14

Remarks.—This form includes small compressed Pa elements in which the lower margin of the element rises at mid-length and the posterior blade is elevated. A shallow, open basal cavity underlies entire posterior half of element. The anterior process bears 5 to 8 discrete, triangular, compressed denticles that are highest in the middle of the process and decline in height toward the cusp and anteriorly. The cusp is no larger than, or may be slightly smaller than, the 3 to 5 broadly triangular discrete denticles that lie on the posterior process. An associated Pb element is similar to Pb elements found with typical *Ozarkodina excavata*, but the processes are more widely spaced and denticles are triangular like those found on the associated Pa elements. S elements associated with these Pa and Pb elements are typical for *O. excavata*, except that denticles are discrete and more widely spaced. These elements occur only in the interval from 8259–8249 feet in the Three Bar 74 core.

Ozarkodina excavata subspecies B
Plate 2, figure 16

Remarks.—This form has large Pa elements in which the lower margin of the element rises at midlength like that of subspecies A. The open basal cavity, though, is very shallow, almost flat. Breakage obscures the nature of the denticulation, but at least the lower parts of nearly equally sized denticles appear to be fused together. Subspecies B could represent a larger version of subspecies A, or a modified somewhat younger form. This form occurs in samples from 8249–8245 and 8231–8225 feet in the Three Bar 74 core.

Ozarkodina excavata subspecies C
Plate 2, figures 9, 10

Remarks.—Subspecies C has a small strongly compressed Pa element that possesses a large reclined triangular cusp and a short posterior process. Only three to five relatively large denticles lie on the anterior pro-

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PLATE 3

All specimens are from the Frame Member, Wristen Formation, Amoco Three Bar 74 well, Andrews County, Texas. All illustrations are 60×.

- 1–3. *Oulodus elegans detorta* (Walliser, 1964)
  - 1. SUI 98165, 8210–8213 feet. Inner view of Sc element.
  - 2. SUI 98166, 8210–8213 feet. Anterior-lateral view of detortiform element.
  - 3. SUI 98167, 8249–8252 feet. Inner view of Sc element.
- 4–6. *Oulodus cristagalli* (Ziegler, 1960)?
  - 4. SUI 98168, 8178 feet. Inner view of walliseriform element.
  - 5. SUI 98169, 8178 feet. Inner view of Sb element.
  - 6. SUI 98170, 8178 feet. Inner view of M element.
- 7. *Ozarkodina* sp. 1?
  - 7. SUI 98171, 8148 feet. Inner view of Pb element.
- 8. *Ozarkodina remscheidensis or O.? planilingua*
  - 8. SUI 98172, 8210–8213 feet. Inner view of Pb element.
- 9, 10, 12. *Icriodus postwoschmidti* Mashkova, 1968
  - 9. SUI 98173, 8192 feet. Upper view of Pa element.
  - 10. SUI 98174, 8192–8195 feet. Upper view of Pa element.
  - 12. SUI 98175, 8192 feet. Upper view of Pa element.
- 11. *Icriodus eolatericrescens* Mashkova, 1968
  - 11. SUI 98176, 8162–8165 feet. Upper view of Pa element.

cess, and three to four smaller denticles lie on the short posterior process. An associated Pb element is of the *Ozarkodina excavata* type, but is strongly compressed like the Pa element. S elements occurring with the Pa and Pb elements are small, and have delicate, closely spaced denticles. Subspecies C occurs in samples from 8216 to 8210 feet in the Three Bar 74 core.

Ozarkodina? planilingua Murphy and Valenzuela-Ríos, 1999
Plate 1, figures 3, 4, 11, 12

[?]*Ozarkodina remscheidensis remscheidensis* (Ziegler, 1960) Uyeno, 1981, pl. 3, fig. 21–23, 29–33.
Ozarkodina? planilingua Murphy and Valenzuela-Ríos, 1999, p. 326, pl. 1, fig. 1–9.

Remarks.—*Ozarkodina? planilingua* was erected by Murphy and Valenzuela-Rios (1999) to include Pa elements that are similar to those of the *Ozarkodina remscheidensis* group of species, but differ in the possession of a small raised area, the terrace, that extends from the blade. The surface of the brim, the lower area of the upper surface of the basal cavity, is larger in area than the terrace. Pa elements assigned here to *O.? planilingua* grade into Pa elements lacking a terrace/brim that are placed here in *O. remscheidensis*, and confident identification of some specimens is problematic without SEM images. Pa elements assigned to *O.? planilingua* range through most of the cored interval, from the late Pridoli *detorta* Zone (8233–8231 feet) through the *omoalpha* Zone near the top of the Three Bar 74 core (8117–8114 feet).

Ozarkodina remscheidensis (Ziegler, 1960)
Plate 1, figures 2, 9, 10

Remarks.—Pa elements that had formerly been referred to *Ozarkodina remscheidensis* can now be assigned to a number of species depending on the author. See Murphy *et al.* (2004) for discussion about this group of species. Specimens assigned to this species in this paper lack the attributes that characterize forms that have been separated from it. Considerable variation exists among the Pa elements extracted from the core, but small size, breakage and poor preservation inhibits a thorough analysis of the group. Jeppsson (1988) restricted the use of the name *O. r. eosteinhornensis* to Pa elements that possess a rectangular basal cavity, one side of which bears a denticle or short process. No Pa elements of this type were recovered from the Three Bar 74 core.

Most elements assigned to *Ozarkodina remscheidensis* have relatively even denticulation and a heart-shaped to subquadrate basal cavity. The white matter occupies the denticles and extends down into the blade as peg-like extensions from the centers of the denticles. Commonly, the white matter extends further down into the blade in the center of the element than towards the extremities of the processes. Diagnostic features of *O. remscheidensis*, according to Jeppsson (1988), are that the denticles on the anterior blade rise toward the anterior, as does the base of the white matter below the denticles. The size and position of the basal cavity varies, but most specimens have a somewhat restricted basal cavity that is located just posterior of midlength. These forms appear to grade into *Ozarkodina? planilingua*, but differ in that they lack the brim and terrace of that species. Specimens with a pinch zone on the blade show some constriction of the upper surface of the basal cavity where it joins the blade, but it does not extend around the outer margin of the basal cavity.

Some specimens differ from the typical morphology and are included with question. In the lower part of the core (8258 feet), a few specimens occur with numerous needle-like denticles and a somewhat restricted basal cavity (Pl. 1, fig. 1). At the other extreme of variation are a few specimens that possess arched processes and extremely irregular coarse denticulation (Pl. 2, fig. 8; 8198 feet).

Ozarkodina species 1
Plate 2, figures 1–4, 7

Remarks.—A group of Pa elements occurs in lower Lochkovian beds in the Three Bar 74 core that differs from the typical *Ozarkodina remscheidensis* morphology. These Pa elements have a larger, more quadrate basal cavity that extends further to the posterior and lacks a brim on the upper basal cavity surface. The few older examples of this form from the *postwoschmidti* Zone (8201–8195 feet) possess the same type of denticulation and white matter distribution as co-occurring specimens of *O. remscheidensis*. In younger beds, from 8171 feet and higher into the *omoalpha* Zone (Pl. 2, figs. 3, 4, 7), specimens assigned to *Ozarkodina* species 1 are slightly more robust and possess fewer stout to triangular denticles than *O. remscheidensis*. The most obvious difference is that the Pa element is mostly hyaline and the white matter is restricted to the cores of denticles in the middle of the blade. One specimen bears a short ridge on the posterior surface of the outer basal cavity surface (Pl. 2, figs. 3, 4). However, in the same lower Lochkovian beds occur a few Pa elements that have a similar restriction of white matter, but possess a more *O. rem-*

scheidensis-like basal cavity (*Ozarkodina* sp. 1?, Pl. 2, figs. 5, 6; 8148 feet). The Pb elements associated with *O.* species 1. (Pl. 3, fig. 7) possess a larger cusp and lower processes than Pb elements occurring in faunas with *O. remscheidensis* and *O.? planilingua* (Pl. 3, fig. 8).

REFERENCES CITED

Amsden, T.T., and Barrick, J.E.

1988. Late Ordovician through Early Devonian annotated correlation chart and brachiopod range charts for the southern Midcontinent region, U.S.A., with a discussion of Silurian and Devonian conodont faunas. Oklahoma Geological Survey Bulletin 143, 66 pp.

Barrick, J.E.

1995. Biostratigraphy of uppermost Ordovician through Devonian depositional sequences in the Permian Basin, west Texas and southeastern New Mexico. *in* Carbonate facies and sequence stratigraphy: Practical application of carbonate models. P.H. Pausé and M.P. Candelaria, *eds.*, Permian Basin Section–SEPM Publication 95-36, pp. 207–216.

Barrick, J.E., Finney, S.C., and Haywa-Branch, J.N.

1993. Revision of ages of the Fusselman, Wristen, and Thirty-one Formations (Late Ordovician–Early Devonian) in the subsurface of West Texas based on conodonts and graptolites. Texas Journal of Science, vol. 45, pp. 231–247.

Barrick, J.E., and Klapper, G.

1992. Late Silurian–Early Devonian conodonts from the Hunton Group (Upper Henryhouse, Haragan, and Bois d'Arc Formations), south-central Oklahoma. Oklahoma Geological Survey Bulletin 145, pp. 19–65.

Bassler, R.S.

1925. Classification and stratigraphic use of conodonts. Geological Society of America Bulletin, vol. 36, pp. 218–220.

Bischoff, G.C.O., and Sannemann, D.

1958. Unterdevonische Conodonten aus dem Frankenwald. Notizblatt des hessischen Landesamtes für Bodenforschung, vol. 86, pp. 87–110.

Branson, E.B.

1938. Stratigraphy and paleontology of the Lower Mississippian of Missouri. Part I. University of Missouri Studies, vol. 13, no. 3, 208 pp.

Branson, E.B., and Mehl, M.G.

1933a. Conodonts from the Bainbridge (Silurian) of Missouri. University of Missouri Studies, vol. 8, no. 1, pp. 39–52.

1933b. Conodonts from the Plattin (Middle Ordovician) of Missouri. University of Missouri Studies, vol. 8, no. 2, pp. 101–119.

Chlupác, I., Jaeger, H., and Zikumundova, J.

1972. The Silurian-Devonian boundary in the Barrandium. Bulletin of Canadian Petroleum Geology, vol. 20, pp. 104–174.

Decker, C.E.

1942. A Silurian graptolite zone in Crane County, Texas. American Association of Petroleum Geologists Bulletin, vol. 26, pp. 857–861.

1952. Texas graptolites change supposed Devonian zone to Silurian. American Association of Petroleum Geologists Bulletin, vol. 36, pp. 1639–1641.

Drygant, D.M.

1984. Korreliatsiia i konodonty Siluriiskikh-Nizhnedevonskikh otlozhenii Volyno-Podolii. Akademiia Nauk Ukrainskoi SSR, Institute Geologii i Geokhimii Goriuchikh Iskopaemykh, Kiev, 192 pp.

Dzik, J.

1976. Remarks on the evolution of Ordovician conodonts. Acta Palaeontologica Polonica, vol. 21, pp. 395–455.

Hass, W.H.

1959. Conodonts from the Chappel Limestone of Texas. U. S. Geological Survey Professional Paper 294J, pp. 365–400.

Hills, J.H., and Kottlowski, F.E. *(coordinators).*

1983. SSMC—Southeast/Southwest Mid-Continent Region. Correlation of Stratigraphic Units in North America (COSUNA). American Association of Petroleum Geologists, Tulsa, Oklahoma.

Jeppsson, L.

1988. Conodont biostratigraphy of the Silurian-Devonian boundary stratotype at Klonk, Czechoslovakia. Geologica et Palaeontologica, vol. 22, pp. 21–31.

1989. Latest Silurian conodonts from Klonk, Czechoslovakia. Geologica et Palaeontologica, vol. 23, pp. 21–37.

1998. Silurian oceanic events: Summary of general characteristics. *in* Silurian cycles: Linkages of dynamic stratigraphy with atmospheric, oceanic, and tectonic changes. Ed Landing and M.E. Johnson, *eds.*, New York State Museum Bulletin 491, pp. 239–257.

Lane, H.R., and Ormiston, A.R.

1979. Siluro-Devonian biostratigraphy of the Salmontrout River area, east-central Alaska. Geologica et Palaeontologica, vol. 13, pp. 39–70.

Mashkova, T.V.

1968. Conodonts of the genus *Icriodus* Branson and Mehl, 1938, from the Borshchov and Chortkov horizons, Podolia. Doklady Akademii Nauk SSSR, vol. 182, pp. 941–944. [in Russian]

1970. Ob utochnenii ob"ema zony *woschmidti* v Podolii. Doklady Akademii Nauk SSSR, vol. 190, pp. 654–657.

Meyer, B.

2002. Conodont biostratigraphy of Devonian strata of West Texas and eastern New Mexico and the apparatus of Early Devonian Icriodus species. Unpublished Ph.D. thesis, Texas Tech University, Lubbock, Texas, 164 pp.

Meyer, B.D., and Barrick, J.E.

2000. Conodonts from the Woodford Formation (Late Devonian) and adjacent units, subsurface West Texas and eastern New Mexico. *in* The Permian Basin: Proving ground for tomorrow's technologies. W.D. DeMis, M.K. Nelis and R.C. Trentham, *eds.*, West Texas Geological Society Publication 00-19, pp. 229–237.

Murphy, M.A., and Matti, J.C.

1983. Lower Devonian conodonts (*herperius-kindlei* Zones), central Nevada. University of California Publications in Geological Sciences, vol. 123, 83 pp.

Murphy, M.A., and Valenzuela-Ríos, J.I.

1999. *Lanea* new genus, lineage of Early Devonian conodonts. Bollettino della Societa Paleontologica Italiana, vol. 37, pp. 321–334.

Murphy, M.A., Valenzuela-Ríos, J.I., and Carls, P.

2004. On classification of Pridoli (Silurian)-Lochkovian (Devonian) Spathognathodontidae (conodonts). University of

California, Riverside Campus Museum Contribution 6, pp. 1–25, 3 figs.

Ruppel, S.C.

1993. Depositional and diagenetic character of Hunton-equivalent rocks in the Permian Basin of west Texas. *in* Hunton Group core workshop and field trip. K.S. Johnson *ed.*, Oklahoma Geological Survey Special Publication 93-4, pp. 91–106.

Ruppel, S.C., and Barnaby, R.J.

2001. Contrasting styles of reservoir development in proximal and distal chert facies: Devonian Thirtyone Formation, Texas. American Association of Petrtoleum Geologists Bulletin, vol. 85, pp. 7–33.

Ruppel, S.C., and Holtz, M.H.

1994. Depositional and diagenetic facies patterns and reservoir development in Silurian and Devonian rocks in the Permian Basin. The University of Texas, Bureau of Economic Geology, Report of Investigations 216, 89 pp.

Ruppel, S.C., and Hovorka, S.D.

1995. Chert reservoir development in the Devonian Thirtyone Formation: Three Bar Field, West Texas. The University of Texas, Bureau of Economic Geology, Report of Investigations 230, 50 pp.

Schönlaub, H.P.

1980. Conodont biostratigraphy for Stop 1, Stop 2, and Stop 9 *in* I. Chlupác and others, Silurian and Devonian conodont localities of the Barrandium. *in* Second European conodont symposium (ECOS II), Guidebook, Abstracts. H.P. Schönlaub, *ed.*, Abhandlungen der Geologischen Bundesanstalt, 128, pp. 153–159, 175–177.

Sweet, W.C.

1988. The conodonta. Oxford monographs on geology and geophyics. Oxford University Press, New York, 212 pp.

Uyeno, T.T.

1981. Systematic study of conodonts. *in* Stratigraphy and conodonts of Upper Silurian and Lower Devonian rocks in the environs of the Boothia Uplift, Canadian Arctic Archipelago. R. Thorsteinsson and T.T. Uyeno, *eds.*, Geological Survey of Canada, Bulletin 292, pp. 39–75 [imprint 1980].

Valenzuela-Ríos, J.I.

1994. Conodontos del Lochkoviense y Praguiense (Devónico Inferior) del Pirino central español. Memorias del Museo Palaeontólogico de la universidad de Zaragoza, vol. 5, 192 pp.

Walliser, O.H.

1964. Conodonten des Silurs. Abhandlungen Hessischen Landesamtes für Bodenforschung, vol. 41, 106 pp.

Wilson, J.L., and Majewske, O.P.

1960. Conjectured middle Paleozoic history of central and west Texas. University of Texas, Bureau of Economic Geology, Publication 6017, pp. 65–86.

Ziegler, W.

1960. Conodonten aus dem Rheinischen Unterdevon (Gedinnian) des Remscheider Sattels (Rheinisches Schiefergebirge). Paläontologische Zeitschrift, vol. 34, pp. 169–201.

THORNTON CREEK MEMBER (NEW) OF THE FLUME FORMATION AND THE INITIAL MIDDLE DEVONIAN ONLAP OF THE WEST ALBERTA ARCH: CANADIAN ROCKY MOUNTAINS

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ABSTRACT

The name Thornton Creek Member (Flume Formation) is proposed for the mixed clastic-carbonate stratigraphic package that onlaps Cambrian rocks and is overlain by typical carbonate ramp deposits of the upper Flume Formation beneath the isolated Ancient Wall reef platform in the Alberta Rocky Mountains of western Alberta, Canada. At Ancient Wall, the Thornton Creek Member is nearly 10 meters thick, records a single Transgressive-Regressive (T-R) cycle, and consists of three coarsening upward parasequences. Bioturbated clastic mudstones in parasequence 1 contain a restricted monospecific inner-shelf brachiopod fauna (*Athyris* sp.). Middle shelf sediments of parasequence 2 signify deposition during maximum flooding. The lower part of parasequence 2 yields a low-diversity *Athyris*-dominated assemblage. The middle part of parasequence 2 yields the conodont *Icriodus subterminus*, associated with a diverse brachiopod fauna consisting of abundant shells of *Eleutherokomma*, *Schizophoria* (*S.*), and *Athyris*, with less common *Cyrtina*, *Desquamatia* (*Independatrypa*), *Pseudoatrypa*, *Cranaena*, *Strophodonta*, and ichnofossils suggestive of the *Cruziana* ichnofacies. Low-angle cross-stratified dolomitic sandstones capping parasequence 3 indicate shallow inner-shelf conditions and maximum shoaling. Faunal data indicate that deposition of this unit coincided with part of the Slave Point and lower Waterways formations elsewhere in central and northern Alberta, respectively, and Devonian T-R cycle IIa-2 of Day *et al.* (1996). Proposed new species of brachiopods from the Thornton Creek Member at Ancient Wall include *Eleutherokomma wendtei* n.sp. and *Schizophoria* (*S.*) *stelcki* n.sp.

INTRODUCTION

In this study we document the stratigraphy and fauna from late Givetian age deposits of the Thornton Creek Member (new) of the Flume Formation at the Ancient Wall reef platform in the Alberta Rocky Mountains. These deposits yield faunas that suggest a correlation with the upper part of Devonian T-R cycle IIa of Johnson *et al.* (1985), designated as Devonian T-R cycle IIa-2 by Day *et al.* (1996) and Uyeno (1998), and central Alberta subsurface Beaverhill Lake Group Lower T-R Cycle A of Wendte *et al.* (1995). The late Givetian marine onlap of the West Alberta Arch represented by the Thornton Creek Member predated the more widespread sea level rise that initiated upper Flume Formation carbonate ramp deposition in the Alberta Rocky Mountains and Swan Hills reef development in the Beaverhill Lake Group (see Uyeno and Wendte, this volume) in the subsurface of central and eastern Alberta during in the late Givetian–early Frasnian.

Stratigraphic analysis of these previously unnamed deposits indicates that they make up a single third order depositional sequence comprised of three parasequences. Sandy dolomitic mudstones of parasequence 2 yield a moderately diverse brachiopod fauna associated with the conodont *Icriodus subterminus* which suggests correlation with the upper part of the *Icriodus subterminus* Fauna (Upper *subterminus* Fauna or the Upper *disparilis* Zone).

Facies-stacking patterns within the Thornton Creek Member indicate progradation of mixed carbonate-siliciclastic deposits of middle and inner-shelf environments prior to a latest Givetian-early Frasnian sea-level rise that initiated Devonian T-R cycle IIb of Johnson *et al.* (1985). The most likely siliciclastic sediment source for the Thornton Creek Member is the West Alberta Arch that was ultimately onlapped and buried during the subsequent late Givetian transgression of Devonian T-R cycle IIb-1 of Day *et al.* (1996) that initiated carbonate ramp development of the upper part of the Flume Formation, and the Lower T-R cycle A of the Beaverhill Lake Group of Uyeno and Wendte (this volume).

Responsibility for the biostratigraphic interpretations and systematic descriptions and authorship of new brachiopod taxa rests with J. Day. Other portions of the text are entirely co-authored.

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REGIONAL GEOLOGIC SETTING OF WESTERN ALBERTA

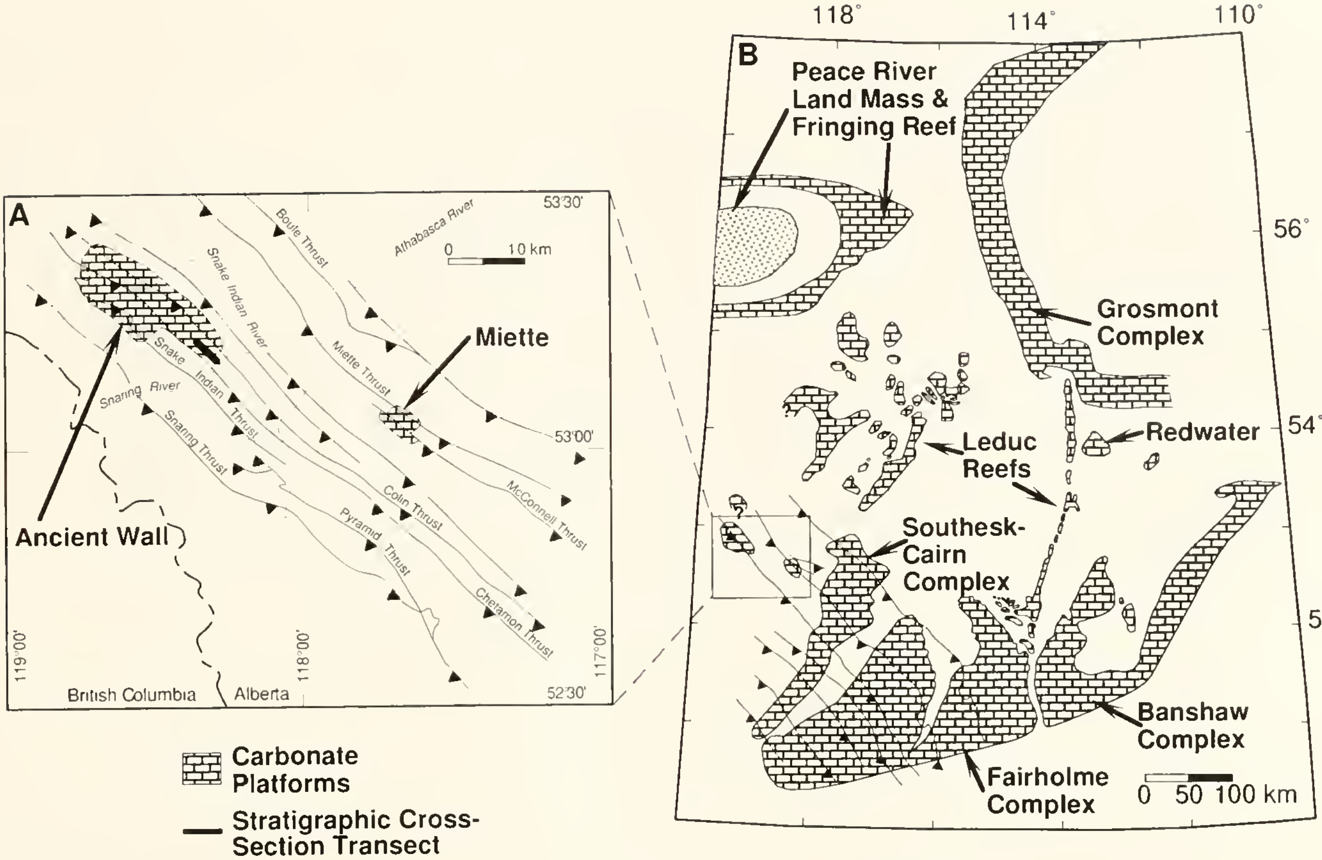
During the Middle Devonian, Western Canada was located at near-equatorial latitudes, within the southeast trade wind belt, along the meridionally oriented western margin of Laurussia (Heckel and Witzke, 1979; Witzke and Heckel, 1989; Scotese and McKerrow, 1990). Major paleotectonic elements that influenced patterns of sedimentation in Alberta include the West Alberta and Peace River Arches (Text-fig. 1). These have been interpreted as passive tectonic features after the Middle Devonian but the West Alberta Arch was apparently tectonically active during the Late Cambrian and in the Early and Middle Devonian (Aitken, 1993).

Middle Devonian carbonate sedimentation began east of the West Alberta Arch during the "Taghanic onlap event" (Switzer *et al.*, 1994). A broad open to restricted marine carbonate ramp represented by the Slave Point and lower part of the Waterways formations was deposited across eastern and central Alberta (Text-fig. 2; Braun *et al.*, 1989; Switzer *et al.*, 1994; Norris and Uyeno, in Day *et al.*, 1996; Uyeno and Wendte, this volume). Incised valley fill and sabkha deposits of the Yahatinda Formation were deposited on the eastern flank of the West Alberta Arch (Text-fig. 2; Aitken, 1966; Elliott and Johnson, 1997; Elliott *et al.*, 2000). The first isolated carbonate platforms, the Swan Hills reefs, aggraded atop the Slave Point or Watt Mountain formations and basinal facies (shales and mixed carbonate-siliciclastics) of the Waterways Formation filled in around the reefs (Text-fig. 2; Switzer *et al.*, 1994). Overlying the Swan Hills reefs and Waterways Formation are deposits of the Cooking Lake platform and Leduc reefs (Text-fig. 2; Campbell, 1992; Wendte, 1992, 1994; Switzer *et al.*, 1994).

A regionally extensive carbonate ramp first developed on the west side of the West Alberta Arch during the latest Givetian (*Skeletognathus norrisi* Zone) to early Frasnian and is represented by the overlying shelf carbonates of the upper Flume Formation above the Thornton Creek Member at Ancient Wall (Text-fig. 2; Whalen *et al.*, 2000a). The Flume Formation appears to correlate with the Swan Hills reefs (Cook, 1972; McLean and Klapper, 1998; Whalen *et al.*, 2000a). Subsequently early-late Frasnian carbonate platform and reefal facies of the Cooking Lake and Leduc equivalent Cairn and Southesk formations accumulated on the Flume Formation ramp (Text-fig. 2; Weissenberger, 1994; McLean and Klapper, 1998; Whalen *et al.*, 2000a). These younger units record isolated and attached early-middle Frasnian carbonate platform development in the vicinity of the West Alberta Arch (Text-fig. 1).

The isolated Ancient Wall platform is one of the westernmost detached carbonate platforms in Alberta (Text-fig. 1) and it experienced greater differential subsidence due to its paleogeographic position on the continental shelf with respect to the continental margin hingeline (McLean and Mountjoy, 1993; Whalen *et al.*, 2000b). The Thornton Creek Member comprises the basal Devonian unit underlying the Ancient Wall platform and constrains the timing of the initial Givetian onlap of the West Alberta Arch in the Canadian Rocky Mountains of Alberta.

Previous sequence stratigraphic analyses of the



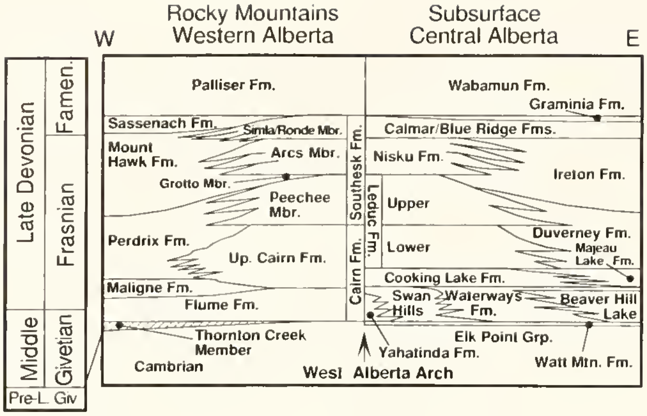
Text-figure 1.—Location maps. A. Detailed location map of the overthrust belt in western Alberta illustrating the locations of the Miette and Ancient Wall platforms (after Mountjoy, 1965). The thick black line indicates the location of the stratigraphic cross section along the southeast margin of the Ancient Wall platform (Text-fig. 3). B. Map illustrating the location of Upper Devonian isolated and attached carbonate platforms in the Alberta basin. Buildups located west of the barbed line (=eastern limit of Laramide thrusting) are exposed in the Canadian Rocky Mountains. The type section of the Thornton Creek Member of the Flume Formation is located along the southeastern margin of the Ancient Wall platform (after Mountjoy, 1980; Geldsetzer, 1989; Switzer *et al.*, 1994).

Miette and Ancient Wall platforms documented six Frasnian depositional sequences that were interpreted as 3rd order cycles (Text-fig. 3; van Buchem *et al.*, 1996; Whalen *et al.*, 2000a,b). These sequences record different styles of platform development, from aggrading ramp to prograding, backstepping and aggrading isolated platforms, to a prograding ramp phase, that were controlled by episodic continental margin subsidence and the 2nd order eustatic sea-level trend (van Buchem *et al.*, 1996; Whalen *et al.*, 2000b). Major sea level rises that initiated deposition of these six sequences coincide with Devonian T-R cycle IIb, IIc and IId sea-level events of the Johnson curve (Johnson *et al.*, 1985, 1991; McLean and Mountjoy, 1993; Whalen *et al.*, 2000a,b). Faunal evidence suggests that deposition of the Thornton Creek Member appears to correlate with the upper subcycle of Johnson *et al.*'s (1985, 1991) T-R cycle IIa, designated as T-R cycle IIa-2 by Day *et al.* (1996).

STRATIGRAPHY OF THE THORNTON CREEK MEMBER AT ANCIENT WALL

The type section of the Thornton Creek Member of the Flume Formation (Section A in cross-section of Text-figs. 3 and 4-A) consists of approximately 10 m of mixed carbonates and siliciclastics overlying the Cambrian Lynx Formation and underlying ramp carbonates typical of the remainder of the lower Flume Formation on the southeast margin of the Ancient Wall platform along the western flank of the West Alberta Arch (Text-figs. 1, 3, 4 and 5). Faunal data outlined below suggest correlation of this new member with part of the Slave Point Formation in northern Alberta and the southern Northwest Territories (NWT) and the late Givetian lower part of the basin-filling Waterways Formation in the subsurface of eastern Alberta.

At Ancient Wall, the Thornton Creek Member overlies five meters of unfossiliferous dolomitic siltstone

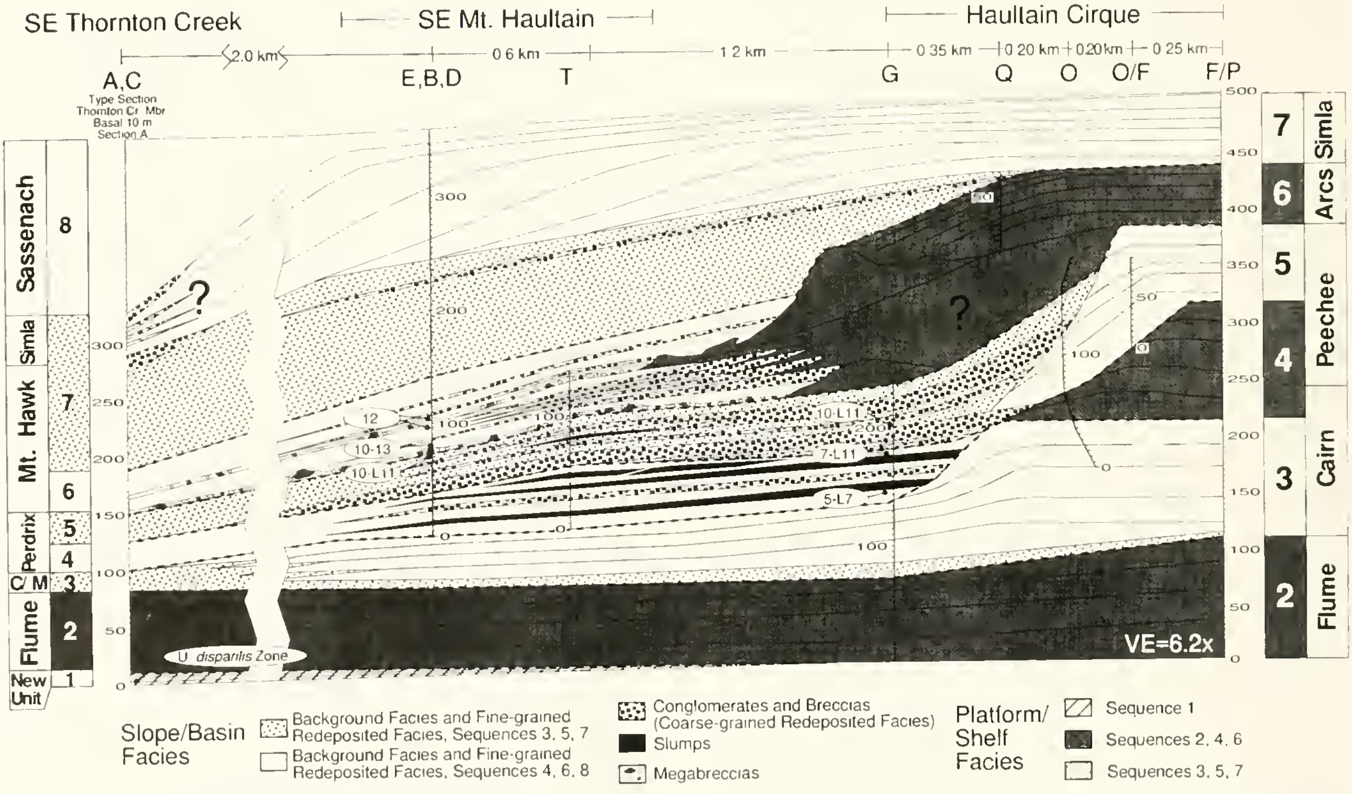


Text-figure 2.—Upper Devonian stratigraphic nomenclature for the Rocky Mountains, western Alberta and the central Alberta subsurface (after Switzer *et al.*, 1994). The Thornton Creek Member of the Flume Formation in the Alberta Rocky Mountains is equivalent to the basal Waterways Formation in the central Alberta subsurface (=Lower T-R cycle A of Wendte *et al.*, 1995, and Uyeno and Wendte, this volume).

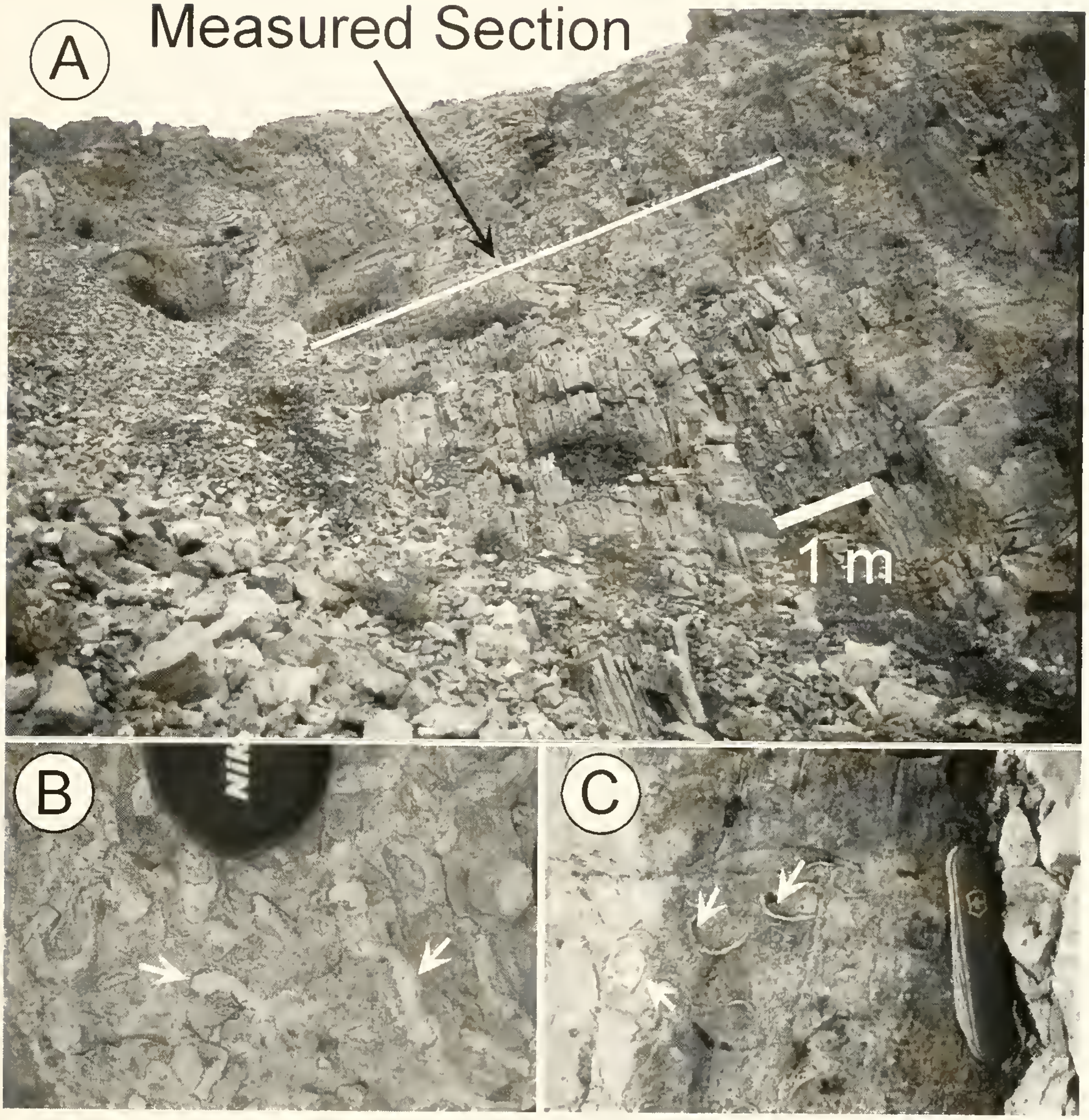
to fine-sandstone of indeterminate age that overlays finely laminated Upper Cambrian dolomitic mudstones of the Lynx Formation (Text-figs. 4 and 5; Aitken, 1966). The contact between the Devonian and older Paleozoic rocks, locally a disconformity, is regionally an angular unconformity with progressively younger Paleozoic rocks underlying Devonian rocks to the east and west of the West Alberta Arch (McLaren, 1953; Pugh, 1973).

FACIES

Three major lithofacies comprise the Thornton Creek Member at its type section (Text-figs. 3, 4 and 5). These are: 1) laminated to burrowed argillaceous dolo-mudstone and calcareous shale, 2) fossiliferous, bioturbated, quartzose (silty to sandy) dolo-mud/wack/packstones, and 3) dolomitic sandstones (Text-figs. 4 and 5). The laminated to burrowed argillaceous dolo-mudstone and calcareous shale are dark gray to dark brown, laminated to thin bedded, dominantly unfossil-



Text-figure 3.—Cross-section of Middle and Upper Devonian strata along the southeast margin of the Ancient Wall platform illustrating lithostratigraphy, the sequence stratigraphic subdivision, and general lithofacies. Locations of measured stratigraphic sections are indicated by letters and graduated lines. The type section of the Thornton Creek Member of the Flume Formation of this report (indicated by diagonal ruled pattern at the base of the cross section) is the lower part of stratigraphic section A. Conodont sample locations and zones are indicated within ovals next to measured sections. Conodonts from Thornton Creek Member suggest a correlation with the late Givetian Upper *subterminus* Fauna, younger conodont samples are correlated with Frasnian Montagne Noire (M.N.) zones of Klapper (1989). Ancient Wall platform sequences are indicated by alternating dark and light shades of gray. Slope and basin sequences are indicated by alternating white and stippled patterns. Thick, dashed black lines indicate sequence boundaries. Thin black lines within platform sequences indicate parasequence boundaries. The abbreviation C/M in the lithostratigraphy column on the left stands for the Cairn and Maligne formations (after Whalen *et al.*, 2000a,b).

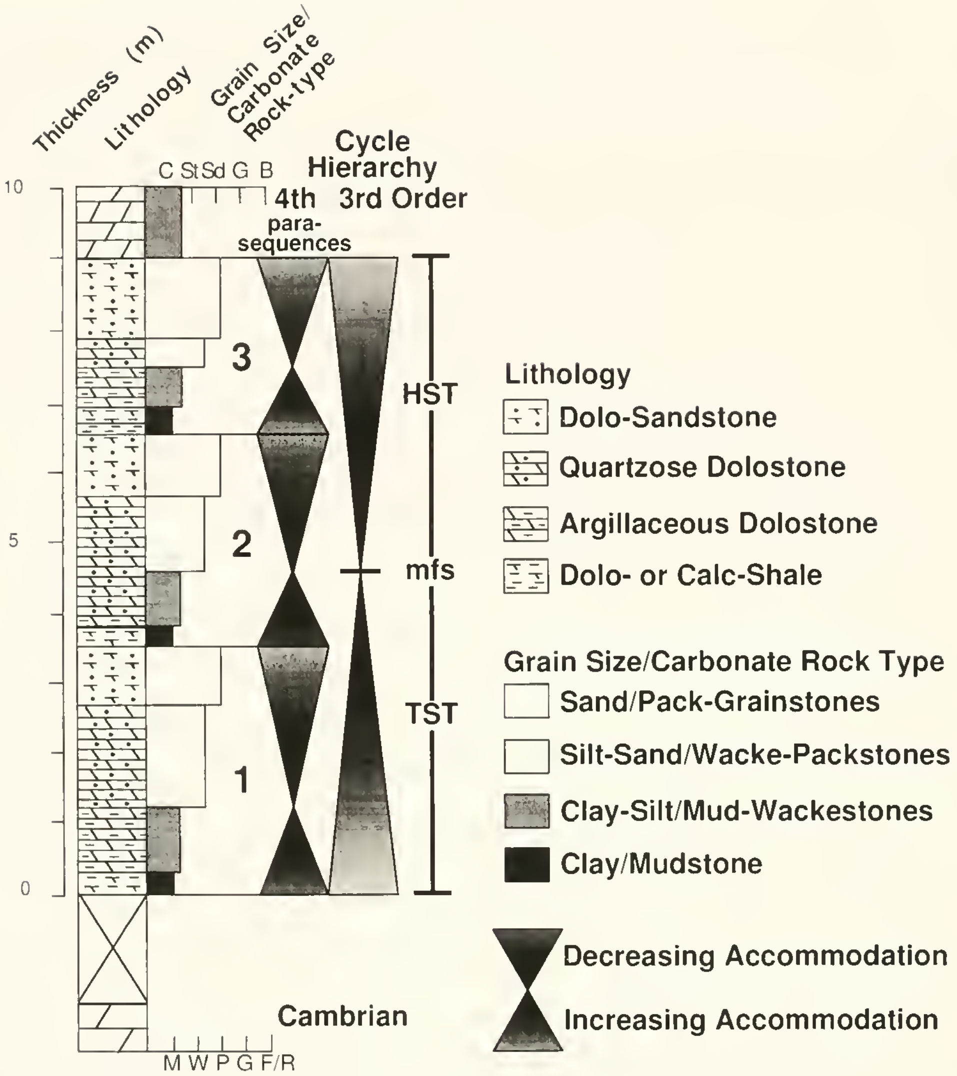


Text-figure 4.—*A.* Outcrop photograph of the type section of the Thornton Creek Member of the Flume Formation (=section A illustrated in Text-fig. 5). Note the cyclic pattern of three parasequences comprising calcareous shale and argillaceous dolo-mudstones, overlain by quartzose dolo-mud/wackestones, and capped by dolomitic sandstones. Parasequences thin upward but internally facies coarsen and beds thicken upward. *B.* Field photograph of abundant *Thallasinoides* burrows (arrows) observed in argillaceous dolo-mudstones of the second 4th order parasequence. *C.* Field photograph of abundant silicified fossils (arrows) present in the quartzose dolo-mudstones and wackestones of the second parasequence.

iferous except for locally abundant trace fossils consisting of simple indeterminate sub-horizontal burrows and burrow complexes of the ichnogenus *Thallasinoides.* The quartzose dolo-mud/wackestones are medium gray to brown, thin to medium bedded, commonly thoroughly bioturbated, but locally contain abundant *Thallasinoides* burrows. Locally, this facies also contains monospecific to moderately diverse brachiopod assemblages described below. The dolomitic sandstone facies is medium to light gray or brown, thick bedded, well sorted, and either bioturbated or contains low-angle tabular sets of tangential cross-laminae.

Parasequences

The facies described above comprise three shallowing-upward cycles or parasequences (Text-figs. 4 and 5). Within each parasequence facies coarsen and beds thicken upward while individual parasequences thin upward. Facies grade upward from calcareous shale and argillaceous dolo-mudstones, to quartzose dolo-

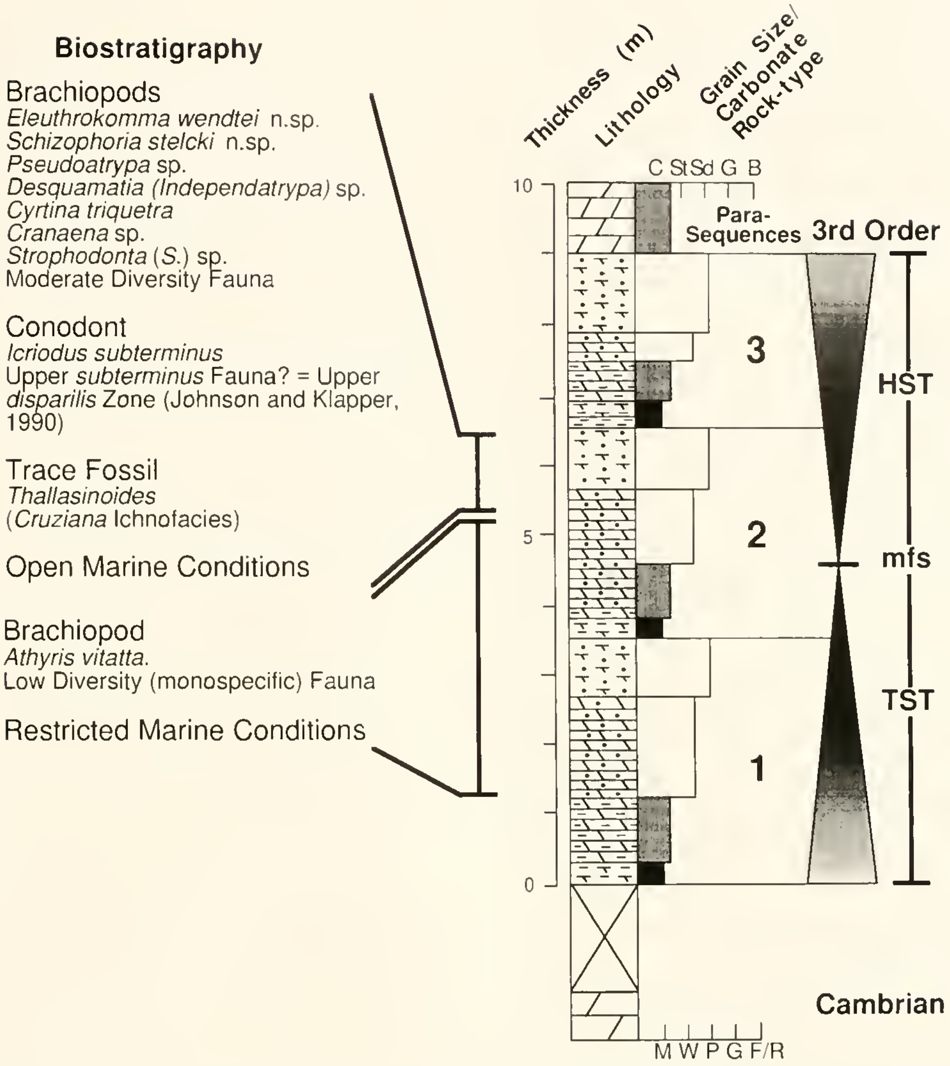


Text-figure 5.—Base of stratigraphic section A measured in 1998 (Text-fig. 3) illustrating the type section of the Thornton Creek Member (new unit) of the Flume Formation. Diagram illustrates thickness, grain-size, and clastic and carbonate lithologies, and third and fourth order cycle hierarchy. Shaded triangles illustrate variations in accomodation space in third (sequence) and fourth order (parasequence) cycles. Key to abbreviations in grain size/carbonate rock type column: C, St, Sd, G, B indicate clay, silt, sand, gravel, and boulder respectively, where M, W, P, G, F/R indicate mudstone, wackestone, packstone, grainstone, and floatstone/rudstone respectively.

mud/wackestones, to dolomitic sandstones. Facies stacking within each parasequence is gradational and thinning-upward shales and argillaceous dolo-mudstones are interbedded with quartzose dolo-mud/wackestones. Marine flooding surfaces are indicated by the abrupt juxtaposition of argillaceous dolo-mudstone or calcareous shale above one or more parasequence-capping beds of dolomitic sandstone. The dolomitic sandstones increase in thickness and represent a greater proportion of each parasequence upsection.

Depositional Environments and Sequence Stratigraphy

The sedimentologic and paleontologic data provide criteria for interpretation of depositional environments and sequence stratigraphy. The laminated to thin-bedded, sparsely fossiliferous, argillaceous dolo-mudstones and calcareous shales contain little evidence of wave and current activity and record restricted to open marine conditions. The quartzose dolo-mud/wackestones yield both brachiopods and ichnofossils (*Thallasinoides*), and record dominantly open marine conditions. The lack of wave- and current-generated structures might be attributed to intense bioturbation, therefore position with respect to fair-weather wave base is equivocal. The bioturbated to cross-bedded dolomitic sandstones are interpreted to indicate deposition above fair-weather wave base, most likely in the middle to upper shoreface. The facies-stacking pattern within each parasequence records a change from restricted



Text-figure 6.—Faunal data from stratigraphic section A illustrating the stratigraphic positions of the low-diversity restricted-marine *Athyris* Fauna (Table 1, samples 1F and 2F) and moderate diversity, open marine *Eleutherokomma-Schizophoria* brachiopod Fauna (Table 1, sample 3F), conodont, and trace fossils. Abbreviations as in Text-figure 5.

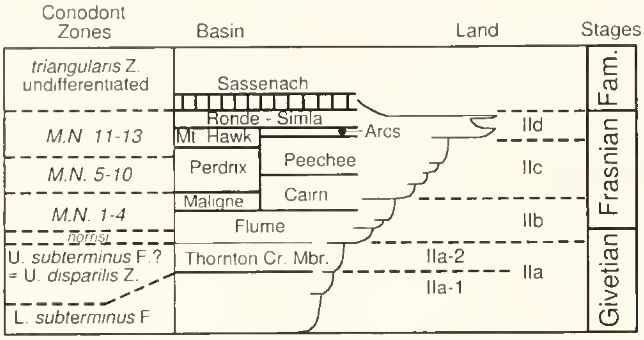
shallow marine conditions to subtidal open marine conditions below fair-weather wave base, to shallow open-marine conditions within fair-weather wave base.

The sedimentologic and faunal data imply that the three parasequences represent one genetic sequence (Text-figs. 5 and 6). Parasequence 1 and the lower portion of parasequence 2 are interpreted as a Transgressive System Tract (TST) recording initially restricted and then open marine conditions (Text-fig. 5). The low-diversity *Athyris*-dominated faunas recovered from those intervals support this interpretation. Maximum flooding occurs within the upper part of parasequence 2 as indicated by the diverse and open-marine brachiopod fauna dominated by *Eleutherokomma*, *Athyris*, and *Schizophoria* (Text-figs. 5 and 6). The uppermost part of parasequences 2 and all of parasequence 3 (Text-fig. 5) are interpreted as High-Stand System Tract (HST). The thinning-upward nature of the parasequences and the increase in thickness and proportion of dolomitic sandstone upsection (Text-figs. 4 and 5) indicate progradation and decreasing accommodation space.

CONODONT AND BRACHIOPOD FAUNAS OF THE THORNTON CREEK MEMBER

Conodonts

The base of the ramp carbonates of the Flume Formation at the Ancient Wall reef complex is correlated by McLean and Klapper (1998) with the *norrisi* Zone (=Lowermost *asymmetricus* Zone of the older conodont zonation) (Text-fig. 7). Uyeno (1987) recovered



Text-figure 7.—Diagram illustrating the Middle to Late Devonian conodont zonation, western Alberta lithostratigraphy, and a second order sea level curve. The second order curve also illustrates a series of higher-frequency transgressive-regressive (T-R) cycles documented in North America and Europe (IIa-d of Johnson *et al.*, 1985). Transgressive-Regressive Cycle IIa was subdivided into T-R cycles IIa-1 and IIa-2 by Day *et al.* (1996). Conodonts recovered from the Thornton Creek Member of the Flume Formation suggest correlation with the Upper *subterminus* Fauna was deposited during T-R cycle IIa-2 (after Johnson *et al.*, 1985; Day *et al.*, 1996; McLean and Klapper, 1998).

Pandorinellina insita in the basal Flume Formation at the Cold Sulphur Spring section (see his fig. 28, GSC samples 12NBd and 12Nbe) approximately 25 km southeast of the Ancient Wall reef complex.

At the type section of the Thornton Creek Member, the conodont *Icriodus subterminus* was recovered in sample 3F (parasequence 2) in association with brachiopods of the *Eleutherokomma-Schizophoria* Fauna described below. The position of the Thornton Creek Member (with *Icriodus subterminus*) below the base of the ramp carbonate succession of the remainder of the Flume suggests a pre-*norrisi* Zone correlation within the interval of the late Givetian Upper *subterminus* Fauna. *Pandorinellina insita* or other species of the late Givetian *norrisi* Zone have not been recovered in sequence from Flume carbonates overlying the Thornton Creek Member in our samples from section A at Thornton Pass.

The Upper *subterminus* Fauna is a shallow-water conodont fauna considered to be equivalent to all or part of the Upper *disparilis* Zone of the Devonian conodont zonation (Johnson and Klapper, *in* Johnson, 1990). The first occurrence of *Polygnathus angustidiscus* with *Icriodus subterminus*, below the first occurrence of *Pandorinellina insita* and/or *Skeletognathus norrisi*, defines the interval of the Upper *subterminus* Fauna of Witzke *et al.* (1985).

BRACHIOPODS

At the proposed type section (section A, Text-figs. 3–6) at Thornton Pass south of the Ancient Wall, reef platform brachiopods were recovered from parasequences 1 and 2 of the Thornton Creek Member (Text-fig. 6; Table 1). The low-diversity assemblages of samples 1F and 2F (Table 1; Text-fig. 6) consisting of *Athyris* sp. or *A. vittata* are designated as the *Athyris* Fauna. The moderately diverse fauna of sample 3F (Table 1; Text-fig. 6) from the upper part of parasequence 2 is referred to as the *Eleutherokomma-Schizophoria* Fauna.

Athyris Fauna

Mudstones in the lower part of parasequence 1 (Table 1, sample 1F) yield shells (partially decalcified) of *Athyris* sp. Dark gray dolomitic mudstones in the lower part of parasequence 2 (Table 1, sample 2F) yield a similar low-diversity brachiopod assemblage consisting entirely of *Athyris vittata* from 4.9–5.1 meters. This monospecific assemblage suggests restricted marine conditions during initial transgression, and is sim-

Table 1.—Late Givetian brachiopod faunas in the Thornton Creek Member (samples 1F–3F) and overlying carbonates of the Flume Formation (sample 4F) at the type section of the Thornton Creek Member, Thornton Pass, Jasper National Park, Alberta.

Sample number	1F	2F	3F	4F
Sample elevation (m above base of Devonian)	1.9	4.9	5.2–6.5	
Athyris sp.	29	0	0	0
A. vittata	0	25	210	0
Eleutherokomma wendtei n.sp.	0	0	266	0
Schizophoria (S.) stelcki n.sp.	0	0	98	0
Desquamatia (Independatrypa) sp.	0	0	3	0
Pseudoatrypa sp. cf. *P. gigantea*	0	0	18	0
Cyrtina triquetra	0	0	54	0
Cranaena sp.	0	0	7	0
Strophodonta (S.) sp.	0	0	1	0
Athyris sp. cf. *A. simplex*	0	0	0	27
Total specimens per sample	29	25	657	27
Weight of sample acidized			8 kg	1 kg
Parasequence	1	2	2	4

ilar to other coeval inner-shelf, shallow-water brachiopod associations dominated by *Athyris* and shallow-water conodont associations of the Upper *subterminus* Fauna. These include athyroid faunas reported from the Devils Gate Limestone at Devils Gate (Drake, 1978; Johnson *et al.*, 1980, p. 89) in central Nevada, and the Gizzard Creek Member of the Coralville Formation in central Iowa (upper part of the *Tecnocyrtina* Fauna of Day, 1992, p. 75).

Eleutherokomma-Schizophoria Fauna

The overlying, moderately diverse brachiopod assemblage in the middle and upper parts of parasequence 2 is referred to as the *Eleutherokomma-Schizophoria* Fauna (Table 1, sample 3F). This fauna occurs in quartzose dolo-mud/wackestones from 5.2 to 6.5 meters above the base of the type section. Elements of the *Eleutherokomma-Schizophoria* Fauna are associated with the conodont *Icriodus subterminus* and trace fossils including *Thallasinoides*. The *Eleutherokomma-Schizophoria* Fauna is dominated by the spiriferid *E. wendtei* n. sp. and the orthoid *Schizophoria* (*S.*) *stelcki* n. sp.; less abundant are: *Athyris vittata* Hall (1850), *Cyrtina triquetra* Hall (1860), the atrypoids *Pseudoatrypa* sp. cf. *P. gigantea* and *Desquamatia* (*Independatrypa*) sp., the terebratuloid *Cranaena* sp., and a single poorly preserved specimen of *Strophodonta* (*S.*) sp. The middle-shelf brachiopod fauna and ichnofossils in the middle and upper parts of parasequence 2, above the sparse faunas of parasequence 1 and lower part of 2, support the interpretation of maximum flooding (highstand) during deposition of this part of parasequence 2.

Our proposed correlation of the Thornton Creek Member of the Flume Formation with the Upper *subterminus* Fauna suggests that *Eleutherokomma wendtei* n. sp. is the oldest species of the genus known in western Canada. The only North American species that is older than *E. wendtei* n.sp. is *E. extensa* described from the late Givetian Oñate Formation in the northern Sacramento Mountains of southern New Mexico by Cooper and Dutro, 1982). The slightly older clastic shelf and basinal deposits of the Oñate were deposited during the initial transgression of Devonian T-R cycle IIa, or T-R cycle IIa-1 of Day *et al.* (1996), based on data and correlations presented in Day (1988, 1989b, 1992, 1998). All previously described species of genus *Eleutherokomma* Crickmay, 1950, in western Canada are from deposits spanning the interval correlated with the *norrisi* Zone (latest Givetian) through Montagne Noire Zone 9–10 (upper part of middle Frasnian).

The occurrence of *Pseudoatrypa* sp. aff. *P. gigantea* (Webster, 1921) in the Thornton Creek Member (Table 1, sample 3F) in western Alberta is slightly younger than occurrences of *P. gigantea* in the upper part of the Little Cedar Formation of central and eastern Iowa. There it occurs in the interval of the *Neatrypa waterlooensis* Zone (Day, 1992, 1996) associated with conodonts of the Lower *subterminus* Fauna. Similar forms reported by Warren and Stelck (1956) and Norris (1963, in Norris and Uyeno, 1981) are all from the younger latest Givetian and early Frasnian deposits of the Waterways Formation in northeastern Alberta (see below).

The subtidal marine brachiopod fauna of the Thornton Creek Member indicates development of fully open marine conditions along the western margin of the West Alberta Arch, associated with a major transgression in the interval of the Upper *subterminus* Fauna in the late Givetian, prior to the widespread transgression that initiated Devonian T-R cycle IIb of Johnson *et al.* (1985). The overlying carbonates of the remainder of the Flume were deposited during T-R cycle IIb.

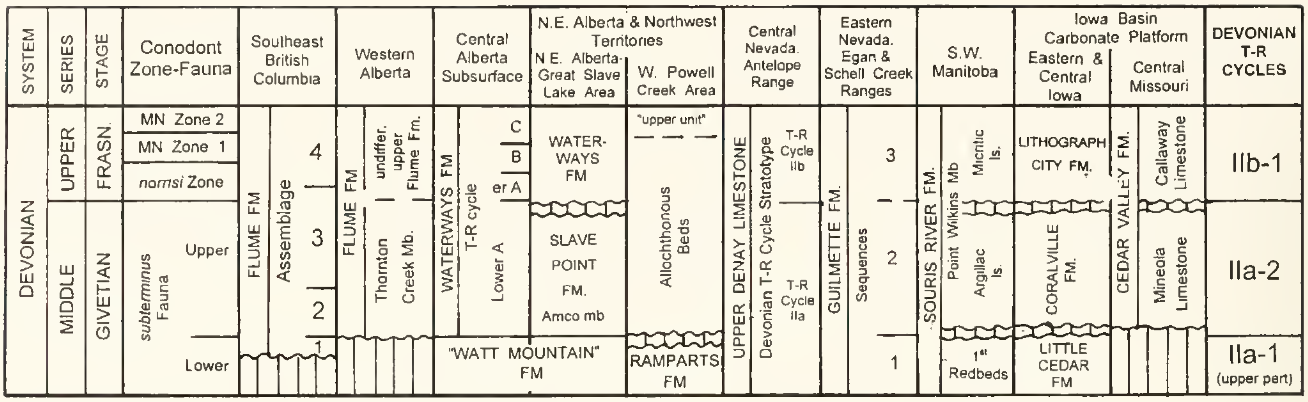
Athyroid, atrypoid, rhynchonellioid and spiriferoid brachiopods have been described from carbonate facies making up most of the Flume Formation at a variety of locations in the Alberta Rocky Mountains (McLaren, 1954, 1962; McLaren *et al.*, 1962), and the undifferentiated Flume Formation of southeastern British Columbia (Maurin and Raasch, 1972). Brachiopod assemblages from the lower part of the undifferentiated Flume Formation at the Kawka and Cecelia lakes areas of eastern British Columbia (illustrated in Maurin and Raasch, 1972) are dominated by atrypoid brachiopods and are of similar age to the Thornton Creek Member whose fauna is dominated by athyrioid, spiriferoid, and orthoid brachiopods, and smaller proportion of atrypoids.

North and northeast of the West Alberta Arch, sparse brachiopod faunas consisting of two to three species are reported from coeval deposits of the late Givetian Slave Point Formation in northern Alberta and the southern N.W.T (Text-fig. 8). The low diversity of the Slave Point brachiopod fauna associated with conodonts of the *subterminus* Fauna indicates more restricted conditions in those parts of the Western Canadian Sedimentary basin.

CORRELATION OF THE THORNTON CREEK MEMBER, FLUME FORMATION

NORTHEASTERN BRITISH COLUMBIA

The lower part of the Flume Formation in the Kakwa-Cecilia lakes area of eastern British Columbia (B.C.) has been correlated with the Slave Point Formation of northeastern Alberta and the Pine Point area of the southern NWT (Text-fig. 8) by Norris and



Text-figure 8.—Correlation chart for late Givetian and early Frasnian units in western and central North America showing proposed correlations of the Thornton Creek Member (new unit) of the Flume Formation. See text discussion for references on the stratigraphy and biostratigraphy of units shown. Transgressive-Regressive Cycles IIa and IIb after Johnson *et al.* (1985), and subdivisions after Day *et al.* (1996) and Uyeno (1998). Conodont zones after Klapper (1989), and Klapper and Johnson, *in* Johnson (1990). Abbreviations, from left to right: FRASN. = Frasnian; MN = Frasnian Montagne Noire conodont zones of Klapper (1989); FM. = Formation; Mb. = Member; N.E. = Northeast; S.W. = Southwest.

Uyeno (in Braun *et al.*, 1989, see area 8 of their text-fig. 2), and other coeval late Givetian units in central Canada and the central and western United States by Day (1997, 1998). The brachiopod sequence in the Flume at the Kakwa Lake and Wallbridge Mountain sections of Maurin and Raasch (1972) indicates that the faunas that include the brachiopods *Tecnocyrtina missouriensis raaschi*, *Cyrtina triquetra*, *Schizophoria* (*S.*) "*meeki*," with species of *Desquamatia* (*Independatrypa*), *Pseudoatrypa*, and possibly *Desquamatia* (*Seratrypa*) of their Assemblage II and most of Assemblage III, are correlative with the Slave Point Formation of northern Alberta and the southern NWT, and the Thornton Creek Member of the Flume Formation in the Rocky Mountains of western Alberta. The conodont fauna and biostratigraphy and detailed analysis of the carbonate sedimentology and sequence stratigraphy of the Flume Formation in the Kakwa Lake and Wallbridge Mountain sections of northeastern British Columbia have yet to be fully documented.

CENTRAL ALBERTA

Based on the conodont and brachiopod faunas, the Thornton Creek Member can be correlated with strata making up the basal Waterways Formation in the subsurface of central Alberta (Text-fig. 8). There shales and carbonates make up the basal Beaverhill Lake Group Transgressive-Regressive (T-R) cycle Lower A of Wendte *et al.* (1995, fig. 2) and Uyeno and Wendte (this volume, Text-fig. 6) that yields conodonts of the Upper *subterminus* Fauna. Consequently, deposition of the Thornton Creek Member and the lower Waterways Formation in the subsurface of eastern and central Alberta (Uyeno and Wendte, this volume, Text-fig. 4) coincided with the deepening event initiating Devonian T-R cycle IIa-2 of Day *et al.* (1996). A recent sequence stratigraphic analysis by Potma *et al.* (2001) defined three depositional sequences within the Beaverhill Lake Group. Based on the limited biostratigraphic data provided in Potma *et al.* (2001), the Thornton Creek Member seems to correlate with the lower part of their Beaverhill Lake Group Sequence 1.

WESTERN ALBERTA SUBSURFACE

Based on information summarized in Elliott and Johnson (1997, pp. 183–184) and Elliott *et al.* (2000, pp. 123–124), it is possible that part of the Yahatinda Formation in parts of western Alberta may represent peritidal or terrestrial coastal plain equivalents of the Thornton Creek Member of the Flume Formation (Text-fig. 2). Spore and vertebrate data cited in Elliott *et al.* (2000) are equivocal and do not permit precise correlation with the marine conodont sequence, and hence could be somewhat older than the Flume Formation and the basal Waterways Formation in the central Alberta subsurface. Recent study of the Yahatinda Formation in south-central Alberta identified a series of twelve intertidal-supratidal dolostone couplets, nine of which were interpreted as paleosol chronosequences (Williams and Krause, 2000). The base of the Yahatinda section is a shallow subtidal to intertidal wackestone that unconformably overlies the Cambrian Eldon Formation (Williams and Krause, 2000). The lower seven Yahatinda couplets display carbon isotopic signatures that reflect a marine carbon source, but the signature abruptly changes to a continental source in couplet eight (Williams and Krause, 2000). Overlying couplets contain green friable shales interpreted as marine or restricted marine mudstones, implying renewed marine influence and possibly transgression (Williams and Krause, 2000). The marine succession of the Thornton Creek Member may correlate with the all or a portion of the first seven Yahatinda couplets and the underlying wackestone identified by Williams and Krause (2000). The continental influence recorded in couplet eight of Williams and Krause (2000) could represent either the relative fall of sea level that terminated the Thornton Creek Member (*i.e.*, T-R cycle IIa-2) deposition or, perhaps, the early Frasnian exposure surface reported at the top of the Utopia Member of the Flume Formation by Noble (1970) and Cook (1972).

NORTHEASTERN ALBERTA

In the Wood Buffalo National Park area in northeastern Alberta, conodonts recovered from the Slave Point Formation include *Polygnathus angustidiscus* and *Icriodus subterminus* (=Upper *subterminus* Fauna) below strata of the Waterways Formation (Text-fig. 8) with conodonts of the *Pandorinellina insita* Fauna (Norris and Uyeno, 1983; Norris and Uyeno, *in* Day *et al.*, 1996). In outcrop, the Slave Point Formation of northern Alberta yields a sparse brachiopod fauna that suggests more restricted conditions in this region of the northern platform than in western Alberta and eastern British Columbia. Norris (1965; *in* Norris and Uyeno, 1981, 1983; *in* Day *et al.*, 1996) and Day (1998) reported a sparse megafauna from the Slave Point Formation in both northern Alberta and equivalents in the southern NWT that includes *Desquamatia* (*Independatrypa*) sp. cf. *D.* (*I.*) *independensis*, *Emanuella vernilis*, and the coral *Grypophyllum mackenziense*, associated with ostracodes of the late Givetian DM 9 Biozone of Braun (see discussion of ostracode faunas and correlations by Braun, *in* Braun *et al.*, 1989).

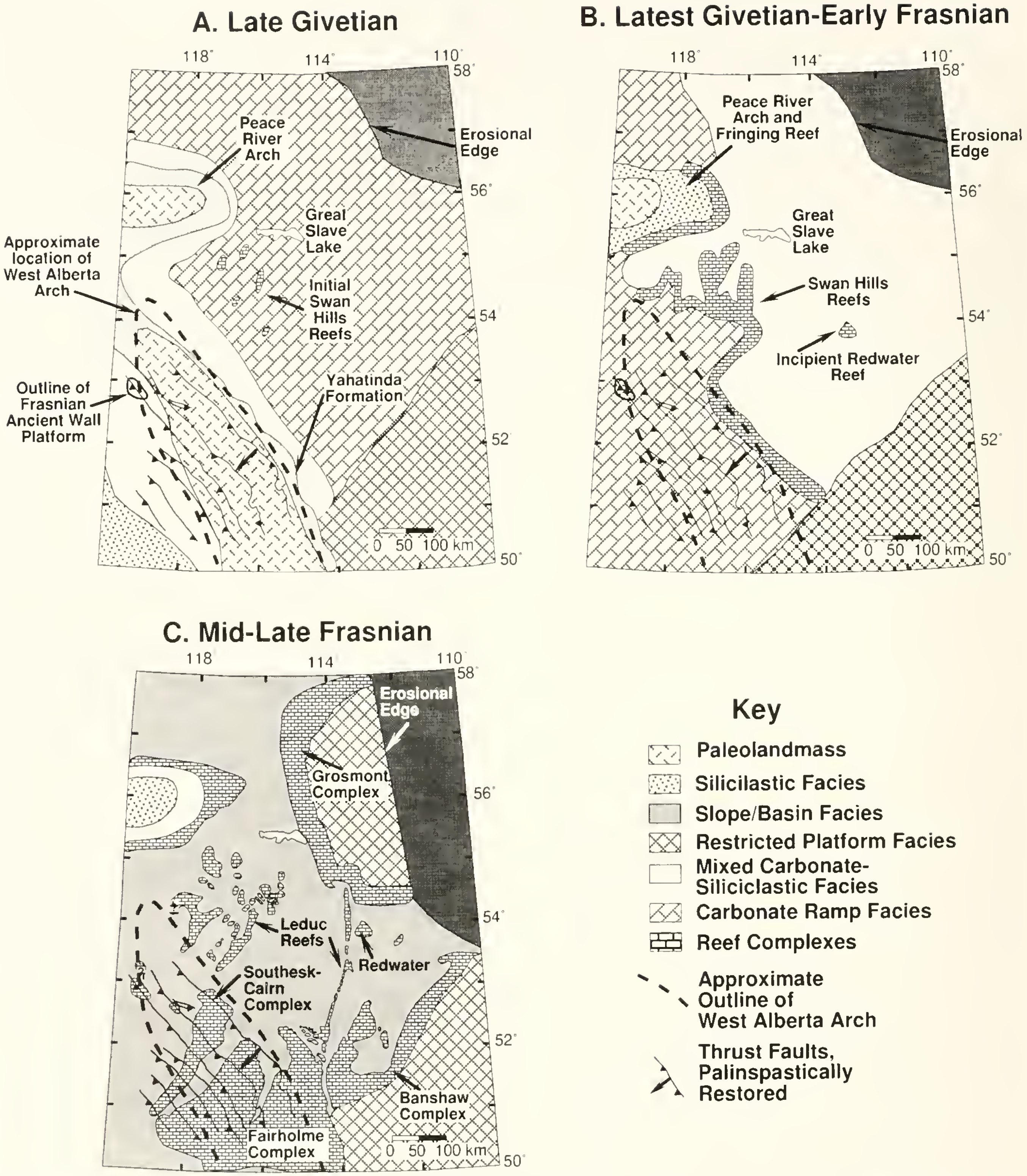
NORTHWEST TERRITORIES—GREAT SLAVE LAKE AND POWELL CREEK AREA

In the Pine Point area along the south shore of Great Slave Lake, the Amco Member of Slave Point Formation unconformably overlies the "Watt Mountain" Formation (Text-fig. 8) and consists of blue-gray, highly argillaceous skeletal mudstone and wackestones, and variably fossiliferous sandy mudstones (Braun *et al.*, 1989; Norris and Uyeno, *in* Day *et al.*, 1996; Norris, 1998). Lantos (1983) reported *Polygnathus* aff. *P. brevilaminus* (=*P. angustidiscus*) from the Amco Member in the Pine Point in the subsurface of the area, which permits correlation with the Upper *subterminus* Fauna (see discussion by Uyeno *in* Day *et al.*, 1996; Uyeno, 1998). Uyeno's (1998, p. 156) samples from the undivided Slave Point there did not yield conodonts. The Thornton Creek Member would correlate with the lower part of the Allochthonous Beds in the Powell Creek area of the central Mackenzie River Valley, based on the occurrence of conodonts of the Lower *subterminus* Fauna by Uyeno (1979, 1998) and McLean and Klapper (1998).

GREAT BASIN—CENTRAL AND EASTERN NEVADA

Equivalents of the Thornton Creek Member in the Great Basin of the western United States (Text-fig. 8) include part of the Upper Denay Limestone and Guilmette Formation of central and eastern Nevada, respectively, and part of the Devils Gate Limestone at its type section near Eureka, Nevada (not shown in Text-fig. 8). Brachiopod faunas of the Lower *Tecnocyrtina* Community of Johnson (1990, figs. 2 and 35) are associated directly with conodonts of the Upper *disparilis* Zone in the Upper Denay Limestone in measured sections III, IV, V, and X in the Antelope Range of central Nevada (see Johnson *et al.*, 1980, fig. 4; Johnson *et al.*, 1996, fig. 3). The associated brachiopod and conodont faunas above characterize late Givetian Great Basin Devonian Faunal Interval (F.I.) 27 of Johnson (1977, 1990), Johnson *et al.* (1980), and Johnson and Trojan (1982). The Devonian (Pragian-Famennian) succession in the Antelope Range of central Nevada was selected as the principal reference succession (Johnson *et al.*, 1996) for global eustatic sea level cycles (Devonian Transgressive-Regressive Cycles Ia to IIb of Johnson *et al.*, 1985). Although Johnson *et al.* (1996, p. 8, fig. 3) did not formally subdivide Devonian T-R cycle IIa of Johnson *et al.* (1985), they outlined lithologic evidence for an intra T-R cycle IIa deepening event coinciding with the first occurrence of brachiopods and conodonts of Great Basin Devonian F.I. 27 just above bed 1340 in their "Upper V" section. Day *et al.* (1996) designated this intra T-R cycle IIa deepening event as Devonian T-R cycle IIa-2, based on stratigraphic and biostratigraphic analysis of cratonic carbonate platform successions in Iowa, Manitoba, and northern Alberta and the southern NWT of western Canada.

LaMaskin and Elrick (1997) identified eleven Givetian through early Famennian sequences within the Guilmette Formation of eastern Nevada and western Utah. Their analysis suggested that the second sequence (sequence 2 of their figs. 2, 10, 11) was deposited during the *disparilis* Zone and may have been initiated by T-R cycle IIa-2 of Day *et al.* (1996). Correlation of this sequence is equivocal because samples through that interval are zonally indeterminate. How-



Text-figure 9.—Paleogeographic maps showing facies distributions in western and central Alberta during the upper Middle (late Givetian) to lower Upper Devonian (Frasnian). Palinspastically restored thrust faults in the Rocky Mountains are shown in southwestern parts of each map. A. Late Givetian: the West Alberta Arch was emergent and served as a sediment source for the Yahatinda Formation and the Thornton Creek Member of the Flume Formation. The area underlying the southeast margin of the Ancient Wall platform was inundated by the late Givetian transgression of T-R cycle IIa-2 of Day *et al.* (1996), followed by open marine waters where mixed carbonate-siliciclastic units of the Thornton Creek Member were deposited. East of the West Alberta Arch initial Swan Hills reefs were deposited surrounded by carbonate ever, their sequence 2 is bracketed by sequences that yield diagnostic conodont faunas (LaMaskin and Elrick, 1997), and based on its stratigraphic position it appears to be correlative with the Thornton Creek Member of the Flume Formation.

CENTRAL CANADA—WILLISTON BASIN OF MANITOBA AND SASKATCHEWAN

In southwestern Manitoba, equivalents of the Thornton Creek Member of the Flume Formation are the argillaceous limestone beds of the Point Wilkins Member of the Souris River Formation (Text-fig. 8). The diagnostic megafossils of the argillaceous limestone beds of the Point Wilkins Member (see Norris, *in* Norris *et al.*, 1982; fig. 5 of Norris, Uyeno, and Day, *in* Day *et al.*, 1996; Day, 1997) include *Desquamatia* (*Independatrypa*) cf. *D.* (*I.*) *independensis*, *Athyris vittata*, *Emanuella* cf. *E. subumbona*, *Cyrtina triquetra*, *Tecnocyrtina missouriensis missouriensis*, and *Cranaena* sp. cf. *C. iowensis*. Conodonts of the Upper *subterminus* Fauna occur with the brachiopod *Desquamatia* (*I.*) *independensis* in Unit B of the Davidson Member of the Souris River Formation of Saskatchewan. The associated conodont and brachiopod faunas indicate correlation with the Slave Point Formation of northern Alberta and, by extension, with the Thornton Creek Member of the Flume Formation of western Alberta.

IOWA BASIN OF THE CENTRAL UNITED STATES

The Thornton Creek Member of the Flume Formation of western Alberta can be correlated with the Coralville Formation and Mineola Limestone of the Cedar Valley Formation of the central and southern parts of the Iowa Basin, respectively (Text-fig. 8). The Coralville Formation of the central and northern part of the Iowa Basin makes up a single carbonate-dominated depositional sequence aligned with the upper part of T-R cycle IIa of Johnson *et al.* (1985), or T-R cycle IIa-2 by Day *et al.* (1996). Transgressive facies of the Coralville (Gizzard Creek and lower Cou Falls members) yield conodonts of the Upper *subterminus* Fauna (Witzke *et al.*, 1985; Witzke *et al.*, 1989; Witzke and Bunker, 1997; Bunker and Witzke, 1992; Day *et al.*, 1996; Day, 1996, 1997), and brachiopod faunas of the *Tecnocyrtina johnsoni* Zone (Day, 1997). Equivalent deposits along the southern margin of the Iowa Basin in central Missouri are skeletal grainstones and packstones of the Mineola Limestone of the Cedar Valley Formation (Thompson, 1993; Day, 1997). Day (1997) reported conodonts of the Upper *subterminus* Fauna from the Mineola, directly associated with a moderately diverse brachiopod fauna that includes *Tecnocyrtina missouriensis missouriensis*, *Cyrtina triquetra*, *Tylothyris* sp., *Athyris* sp., *Schizophoria* sp., *Cranaena* sp. cf. *C. iowensis*, *Strophodonta* (*S.*) sp., and *Pentamerella* sp.

INITIAL FLUME FORMATION ONLAP OF THE WESTERN ALBERTA ARCH AND IMPLICATIONS FOR LATE GIVETIAN SEA LEVEL HISTORY OF NORTH AMERICA

Previous stratigraphic analyses have documented deepening events coincident with the timing of sea level rises initiating eustatic Devonian T-R cycle IIb-IIf of Johnson *et al.* (1985, 1991) in the Rocky Mountains of western Alberta (Moore, 1989; McLean and Mountjoy, 1993; van Buchem *et al.*, 1996; Whalen *et al.*, 2000a,b). Correlations and distribution of strata deposited during the major eustatic sea level rise of Devonian T-R cycle IIa-2 are documented in the subsurface on the east flank of the West Alberta Arch by Wendte (1992), Campbell (1992) and Wendte *et al.*, (1995), and Uyeno and Wendte (this volume); in northeastern Alberta by Norris and Uyeno (*in* Day *et al.*, 1996), Norris (1998), and Uyeno (1998); and in the lower and upper Mackenzie River Valley by Uyeno (1998). As outlined above, equivalent strata have also been documented in the Great Basin of the western U.S. (Johnson *et al.*, 1996; LaMaskin and Elrick, 1997), the U.S. mid-continent and central Canada (Day, Witzke and Bunker, *in* Day *et al.*, 1996; Witzke and Bunker, 1997). The Thornton Creek Member of the Flume Formation represents the first documentation of strata deposited during Devonian T-R cycle IIa-2 of Day *et al.* (1996) in the Canadian Rocky Mountains of western Alberta (Text-fig. 8).

Correlations of the Thornton Creek Member outlined above (Text-figs. 7 and 8) provide new constraints on the timing and pattern of onlap of the West

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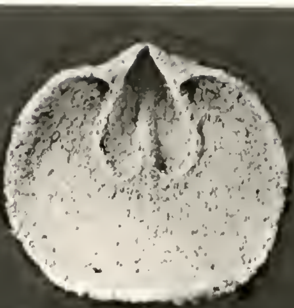
ramp deposits of the Slave Point Formation. *B*. Latest Givetian to early Frasnian time: the West Alberta Arch was inundated by marine transgression (T-R cycle IIb of Johnson *et al.*, 1985, 1991; T-R cycle IIb-1 of Day *et al.*, 1996) and blanketed by distal deposits of the regionally extensive upper Flume Formation carbonate ramp. Swan Hills reefs reached their maximum development along the eastern margin of the submerged West Alberta Arch, central and eastern Alberta were sites of mixed carbonate-siliciclastic shallow marine deposition. *C*. Remainder of the Frasnian: western and central Alberta were sites of isolated carbonate platform and associated basinal sedimentation. After Mountjoy (1980), Moore (1989), Morrow and Geldsetzer (1988), Oldale and Munday (1994), Switzer *et al.* (1994), and Whalen *et al.* (2000a,b).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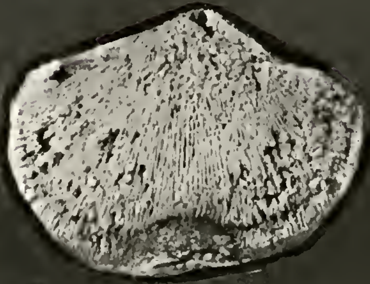
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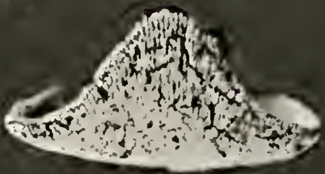
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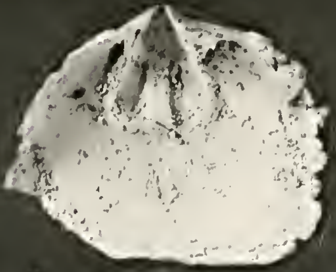
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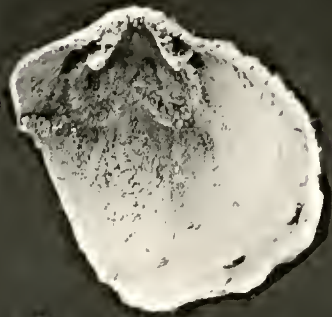
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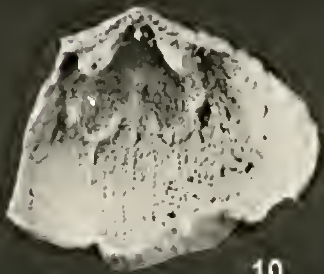
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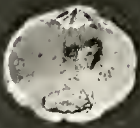
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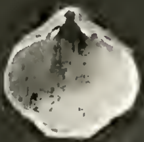
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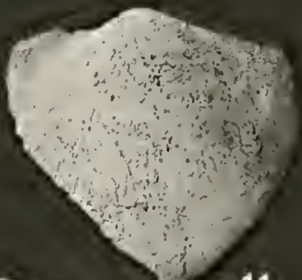
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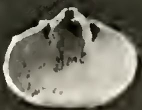
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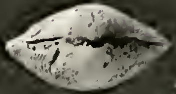
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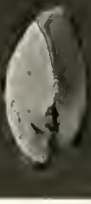
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Alberta Arch (Text-figs. 7–9). Prior biostratigraphic data indicated that onlap along the western flank of the Arch began no earlier than the latest Givetian (*norrisi* Zone). Our new data indicate a late Givetian age for the initial onlap during the interval of the Upper *subterminus* Fauna (Text-figs. 7 and 8). The high siliciclastic content of the Thornton Creek Member, and the lack of all but very fine-grained siliciclastics throughout the Frasnian units in the area, imply that the West Alberta Arch was partially exposed and probably served as a source for locally derived siliciclastic sediments of the Thornton Creek Member and its possible equivalent to the southeast (Yahatinda Formation; Text-fig. 9). By earliest Frasnian time, this local source had been onlapped and buried beneath the regionally extensive Flume ramp (Text-fig. 9).

SYSTEMATIC PALEONTOLOGY

Illustrated specimens and additional material from samples A98-1 to 3 from the Thornton Creek Member of the Flume Formation are housed in the Geological Survey of Canada (GSC) repository in Ottawa, Ontario. Preparation of standard serial sections of shells was not possible because all specimens recovered from the Thornton Creek Member are silicified. The single fragmental specimen (GSC 122846) of *Strophodonta* (*S.*) sp. Hall, 1852, discussed above (see Table 1) is too poorly preserved to warrant illustration. The systematic classification of the order Orthida follows Williams and Harper (2000), Alvarez *et al.* (1998) for the Order Athryida, and Carter *et al.* (1994) for the spiriferid brachiopods.

Phylum **BRACHIOPODA** Dumeril, 1806

Subphyllum **RHYNCHONELLIFORMEA** Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class **RHYNCHONELLATA** Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order **ORTHIDA**Schuchert and Cooper, 1932

Suborder **DALMANELLIDINA** Moore, 1952

Superfamily **ENTELETOIDEA** Waagen, 1884

Family **SCHIZOPHORIIDAE** Schuchert and Levene, 1929

Genus **SCHIZOPHORIA** King, 1850

Subgenus **SCHIZOPHORIA (SCHIZOPHORIA)** King, 1850

Type species.—*Conchyliolithus* (*Anomites*) *resupinatus* Martin, 1809, pl. 49, figs. 13–14.

Schizophoria (Schizophoria) stelcki new species
Plate 1, figures 1–10

Diagnosis.—Medium to large species of *Schizophoria* (up to 34 mm in width), width exceeds length. Subcircular shell outline with minor, or lacking, anterior indentation. Anterior commissure unisulcate with high subangular ventral tongue of sulcus strongly deflected at almost 90° relative to commissural plane.

Description.—Medium to large dorsibiconvex shell (up to 34 mm in width), width greater than length, anterior commissure broadly unisulcate with relatively

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PLATE 1

Brachiopods from the Thornton Creek Member of the Flume Formation. All specimens from sample 3F from section A at GSC Thornton Pass locality, Ancient Wall Reef Platform, Jasper National Park, Alberta, Canada. All specimens ×1.5 unless otherwise indicated.

1–10. *Schizophoria* (*Schizophoria*) *stelcki* new species.
  1–4. GSC 122847 (syntype): internal, external (upper), lateral, and anterior views of complete ventral valve.
  5, 6. GSC 122848 (syntype): internal and external views of complete dorsal valve.
  7. GSC 122849 (paratype): upper view of relatively complete ventral valve embedded in matrix.
  8. GSC 122851 (paratype): internal view of ventral valve.
  9. GSC 122852 (paratype): internal view of dorsal valve.
  10. GSC 122853 (paratype): internal view of dorsal valve.
11, 12. *Desquamatia* (*Independatrypa*)? species.
  Figured specimen. GSC 122871. External and internal views, respectively of partial dorsal valve showing socket plates and damaged bases of crura.
13–24. *Athyris vittata* Hall, 1860.
  13–17. GSC 122862.
    13. Internal view of dorsal valve.
    14, 15, 17. External (normal to commissural plane), standard and oblique internal views, respectively of ventral valve; 16. anterior view of articulated valves showing gape.
  18–20. GSC 122863. Right lateral, anterior, and dorsal views, respectively, of complete shell.
  21–24. GSC 122864. Dorsal, posterior, anterior, and left-lateral views, respectively of complete shell.

high subangular ventral tongue strongly deflected at almost 90° relative to commissural plane. Anterior dorsal sulcus deep, originating anterior of midlength. Shell subcircular in outline, rounded outline along anterior margin lacking medial anterior indentation at position of medial sulcus and tongue, maximum width at midlength. Dorsal valve highly convex with planoconvex ventral valve. Exterior of both valves with poorly preserved fine radial costellae.

Dorsal valve strongly convex, and in anterior view maximum lateral convexity at midline with shell surface sloping to lateral margins, in lateral view maximum longitudinal convexity just posterior of midlength. Short triangular anacline dorsal interarea, short open triangular notothyrium formed by convergence of the short dental and crural plates of cardinalia. Dental plates diverge anteriorly at approximately 70° immediately below the beak from medial cardinal margin. Dorsal interior with poorly preserved cardinal process consisting of simple short elongate ridge originating from valve floor immediately below beak. Short socket plates diverge from cardinal margin below beak at 65–75°, fulcral plates flooring sockets join socket plates along postero-lateral forming two shallow lateral cavities as seen in most species of the genus. Stout crura arise from socket plates and are strongly recurved ventrally diverging anteriorly at same angle as dental plates and bound the notothyrial cavity. Bilobed adductor muscle scars extending anteriorly from notothyrial cavity approximately along 20% of the arc length of valve floor, the two adductor lobes separated by low weakly developed medial ridge or myophragm, bounded at their lateral and anterior margins by weakly to moderately developed ridges originating as extensions of bases of socket plates along margins of muscle field. Four weakly to strongly impressed pallial trunks extend anterior of forward edge of the ridge bounding muscle field as is typical for most species of the genus (see Schuchert and Cooper, 1932, pl. 23).

Ventral valve with open triangular delthyrium; slightly concave apsacline interarea, width averages 65% of maximum valve width. Gently convex with maximum convexity at 20% of shell length just anterior of beak. Sulcus originates anterior of midlength (at 60% length anterior of beak), becomes strongly deflected at almost 90° relative to commissural plane close to anterior margin (75–85% of length anterior of beak), medial anterior tongue subangular in outline, width of deflected shell margin of tongue 60–65% of maximum shell width. Ventral interior with deep delthyrial cavity, strong teeth arising from well-developed dental plates that extend anteriorly on floor of the valve to along the margins of the muscle field. Adductor muscle field bilobed, divided medially along its length by strong medial diductor ridge with anterior end of ridge often thickened and elevated slightly above ridge bounding muscle field, forward lobate ridges along margins of adductor scars extend anterior of shorter diductor ridge. Lacks a medial ridge anterior of edge of muscle field. Muscle field longer than wide extending on floor of valve 25–35% of length.

Types.—Syntypes are the isolated ventral valve GSC 122847 and the dorsal valve GSC 122848. Four illustrated paratypes including GSC 122849, 122851, to 122853. Nine unfigured paratypes numbered GSC 122850, 122854 to 122861.

Other material examined.—Includes 87 unnumbered valves consisting of 23 partial dorsal valves and 64 partial ventral valves from the type locality.

Type stratum and locality.—The type stratum is the 1.5 meter interval of sample 3, section A, at Thornton Pass, in Jasper National Park, Alberta Rocky Mountains, with type locality coinciding with the type section of the Thornton Creek Member of the Flume Formation, GSC Thornton Pass locality.

Etymology.—Named in honor of Dr. Charles Stelck (Professor of Geology Emeritus, University of Alberta) for his pioneering contributions to the knowledge and understanding of the Paleozoic and Mesozoic stratigraphy and paleontology of western Canada.

Occurrence.—As currently known, it is restricted to the late Givetian *Eleutherokomma-Schizophoria* Fauna (Table 1, sample 3F; Text-fig. 6) of the Thornton Creek Member of the Flume Formation of the Alberta Rocky Mountains.

Discussion.—Schizophoria (*S.*) *stelcki* is similar to both *S.* (*S.*) *athabaskensis* Warren, 1944, and *S.* (*S.*) *allani* Warren, 1944, described from the latest Givetian and early Frasnian Waterways Formation of northern Alberta. All three forms have prominent medial ventral tongues, although *S.* (*S.*) *stelcki* n.sp. differs in that its tongue is proportionally longer than that of *S.* (*S.*) *athabaskensis*, not as angular or V-shaped in outline as that of *S.* (*S.*) *allani*, and is deflected at the anterior margin at almost at 90° relative to the commissural plane. When viewed dorsally, the outline of the anterior margin of *S.* (*S.*) *stelcki* is rounded and is not indented medially, versus the somewhat lobate-indented anterior outlines of both of the Waterways species. It also differs from *S.* (*S.*) *allani* in its larger adult size. It differs from *S.* (*S.*) *athabaskensis* by its somewhat smaller adult shell size, internally in its proportionally narrower ventral adductor muscle field and bounding ridges, and it lacks the medial ridge of the Waterways form that extends anterior of the ventral muscle platform and medial adductor ridge. The internal shell features of *S.* (*S.*) *allani* are unknown (Norris, 1983, p. 10).

Order **ATHYRIDIDA** Boucot, Johnson and Staton, 1964

Suborder **ATHYRIDIDINA** Boucot, Johnson and Staton, 1964

Superfamily **ATHYRIDOIDEA** Davidson, 1881

Family **ATHYRIDIDAE** Davidson, 1881

Subfamily **ATHYRIDINAE** Davidson, 1881

Genus **ATHYRIS** M'Coy, 1844

Type species.—*Terebratula concentrica* Buch, 1834, p. 123 [see discussion of new lectotype for *Athyris concentrica* (Buch, 1834) by Grunt and Racki, 1998, pp. 365–366]

Athyris vittata Hall, 1860
Plate 1, figures 13–24

Athyris vittata Hall, 1860, pp. 89–90; Hall, 1867, p. 289, pl. 46, figs. 1–4; Hall and Clark, 1893, p. 90, pl. 2, figs. 62 and 63, pl. 45, figs. 1–4; Branson, 1923, p. 110, pl. 17, figs. 8–10, 15, 16; Stainbrook, 1942, pp. 616–617, pl. 89, figs. 19–22. [non: *A. vittata* Nettleroth, 1889, p. 87, pl. 16, figs. 25–32; Savage, 1931, pl. 30, figs. 4–5].

Athyris fultonensis (Swallow), Cleland, 1911, pp. 83–84, pl. 14, figs. 1–4 [non *A. fultonensis* Savage, 1930, pl. 4, figs. 3–4].

Material examined.—The figured specimens: GSC 122862 to 122864. Additional material includes GSC 122844, 45 unnumbered complete shells, and 110 ventral and dorsal valves.

Occurrence.—*Athyris vittata* occurs in all three samples (Table 1, samples 1F–3F) taken in parasequences 1 and 2 in section A of the Thornton Creek Member of the Flume Formation in the Alberta Rocky Mountains. It is a highly variable species and is widespread in carbonate platform deposits of central and western North America during the late Givetian (lowest occurrences known from the Middle *varcus* Subzone) to early Frasnian (known to range into deposits correlated with Montagne Noire Zone 4). We have also recovered this species in subtidal carbonate lagoonal facies of the upper Flume Formation at the Miette Reef platform, and it is reported by Maurin and Raasch (1972) from the "Flume Formation" (undifferentiated) in the interval of their Assemblage 4 (early Frasnian) in their Wapati Mountain and Kakwa Lake sections. Its occurrences in the late Givetian and early Frasnian of Manitoba, Iowa, and Missouri are outlined in the discussion of Thornton Creek brachiopod faunas above.

Discussion.—The 160 specimens recovered include a complete range of growth stages from small juveniles to medium sized adults. The Thornton Creek specimens are closest to the *Athyris vittata randalia* morphotype of Stainbrook (1942, pl. 89, figs. 1–6). The three varieties of *A. vittata* described by Stainbrook (1942, p. 616) are considered to be phenotypic variants of highly variable populations of one species.

Order **ATRYPIDA** Rzhonsnitskaya, 1960

Family **ATRYPIDAE** Gill, 1871

Subfamily **ATRYPINAE** Gill, 1871

Genus **PSEUDOATRYPA** Copper, 1973

Type species.—*Atrypa devoniana* Webster, 1921, p. 15 (see illustrations in Fenton and Fenton, 1935).

Pseudoatrypa aff. P. gigantea (Webster, 1921)
Plate 2, figures 1–13

Atrypa gigantea Webster, 1921, p. 16; Fenton and Fenton, 1935, p. 376; Stainbrook, 1938, p. 233, pl. 30, figs. 5, 13, 17.

Atrypa cf. *gigantea* Webster, Warren and Stelck, 1956, pl. 11, figs. 16–18.

Pseudoatrypa sp. cf. *P. gigantea* (Webster), Norris, in Norris and Uyeno, 1981, pp. 18–19, pl. 7, figs. 28–38.

Material examined.—A partial figured dorsal valve GSC 122816, two nearly complete figured adult shells (slightly crushed) GSC 122818 and GSC 122819, and 22 unnumbered fragments of dorsal and ventral valves.

Occurrence.—In the Alberta Rocky Mountains *Pseudoatrypa* sp. aff. *P. gigantea* (Webster, 1921) occurs in the late Givetian Thornton Creek Member of the Flume Formation at its type section in sample 3 (Table 1; Text-fig. 6) as an element of the *Eleutherokomma-Schizophoria* Fauna. Similar forms are known from older late Givetian deposits in Iowa and younger latest Givetian and early Frasnian deposits in northeastern Alberta (see below).

Discussion.—The same species, or closely similar forms, of *Pseudoatrypa* are widespread in late Givetian and early Frasnian carbonate platform and basinal deposits in central and western North America. *Pseudoatrypa gigantea* (Webster, 1921) was first described from late Givetian deposits in central and eastern Iowa. Webster's original types were lost, according to discussion by Fenton and Fenton (1935, p. 376). In his description of *P. gigantea*, Stainbrook (1938) designated two specimens as hypotypes and mentioned five additional comparative specimens (one lost, remaining material housed at the University of Iowa) from the upper part of the Rapid Member of the Cedar Valley Limestone (now Little Cedar Formation, see Witzke *et al.*, 1989, pp. 229–232) interval of his "*Atrypa waterlooensis* Zone." Stainbrook's specimens originate from the upper Rapid Member of the Little Cedar Formation that yields conodonts of the Lower *subterminus* Fauna (Day, 1992, 1996) and hence those specimens are slightly older than the material illustrated here from the Thornton Creek Member of the Flume Formation.

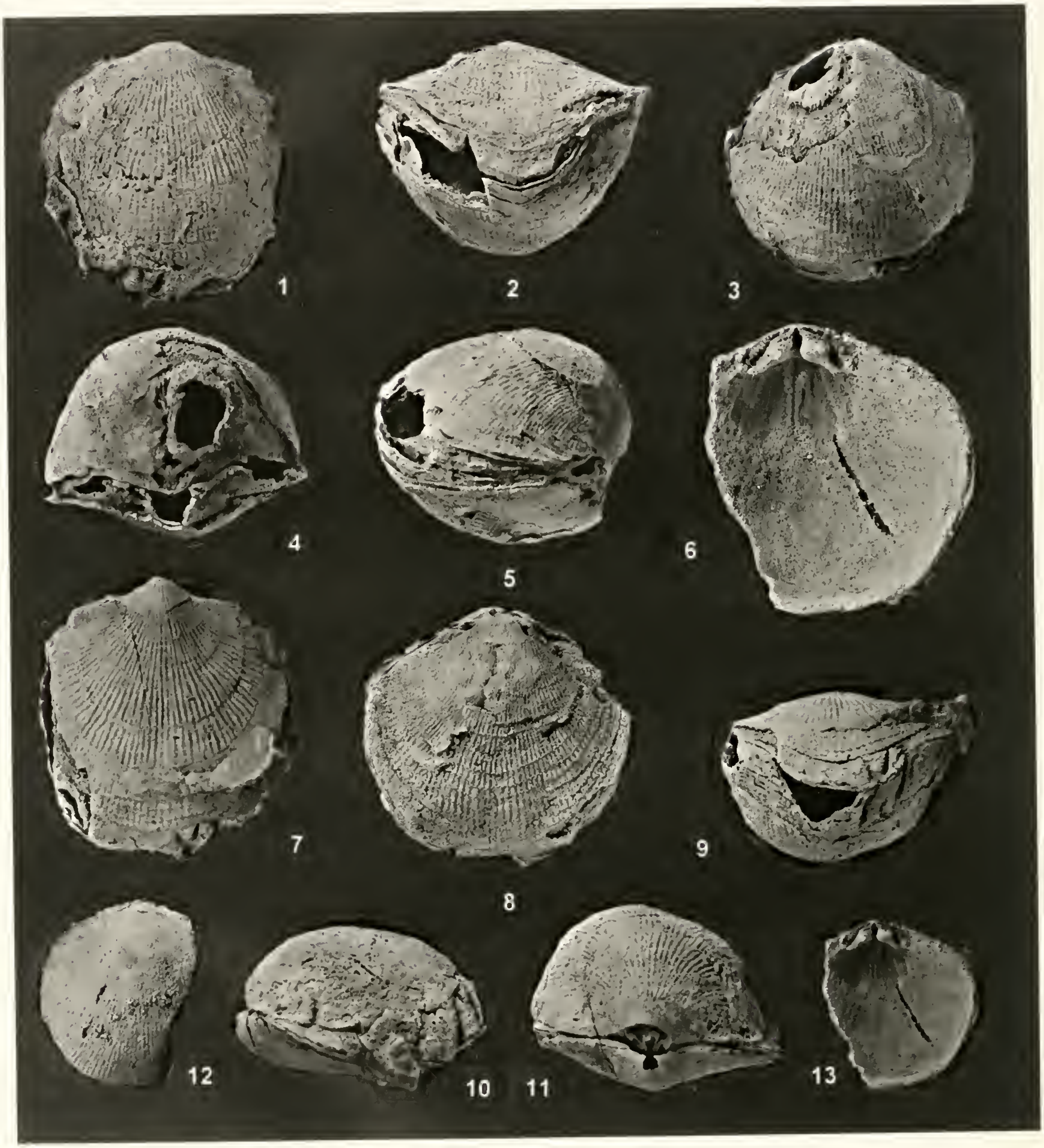

PLATE 2

Brachiopods from the Thornton Creek Member of the Flume Formation. All specimens from sample 3F from section A at GSC Thornton Pass locality, Ancient Wall Reef Platform, Jasper National Park, Alberta, Canada. All specimens ×1.5 unless otherwise indicated.

1–13. *Pseudoatrypa* aff. *P. gigantea* (Webster, 1921).

- 1–5. Figured specimen. GSC 122818: dorsal, anterior, ventral, posterior, and left-lateral views, respectively of damaged shell.
- 6, 12, 13. GSC 122816: 6, 13. internal view of dorsal valve showing lobate impressed adductor muscle field, oblique ridges and grooves on floor of sockets, and massive crural bases arising from inner socket ridges, ×3 and ×1.5 respectively; 12. external view showing abraded radial ribs.
- 7–11. GSC 122819: dorsal, ventral, anterior, right-lateral, and posterior views, respectively of relatively complete shell, showing damage to left anterior margin resulting from encrusting epibionts (epibionts not preserved).

Warren and Stelck (1956, pl. 11, figs. 16–18), illustrated a similar form under the name "*Atrypa*" cf. *gigantea* Webster, from the latest Givetian–early Frasnian Waterways Formation at McMurray, Alberta. Norris (*in* Norris and Uyeno, 1981, p. 18) illustrated *P.* sp. cf. *P. gigantea* (Webster, 1921) from the Calumet Member of the Waterways Formation on Birch River and along the Athabasca River near Fort McMurray, in northeastern Alberta. Norris (1963, text-figs. 6 and 8) noted "*Atrypa*" cf. *gigantea* Webster from the early Frasnian Calumet and Moberly members of the Waterways in the Clearwater-Athabasca Rivers outcrop belt.

Subfamily **VARIATRYPINAE** Copper, 1978

Genus **DESQUAMATIA** Aleskeeva, 1960

Subgenus **INDEPENDATRYPA** Copper, 1973

Type species.—Atrypa independensis Webster, 1921, p. 15 (see illustrations in Fenton and Fenton, 1935).

Desquamatia (Independatrypa)? sp.
Plate 1, figures 11, 12

Material examined.—The illustrated specimen GSC 122871, and six unnumbered valve fragments.

Occurrence.—This species occurs in the interval of sample 3F in the type section of the Thornton Creek Member at the GSC Thornton Pass locality (Text-figs. 3, 4, 6).

Discussion.—The limited material available does not permit a definitive assignment to any described species of *Desquamatia* (*Independatrypa*).

Suborder **DELTHYRIDINA** Ivanova, 1972

Superfamily **DELTHYRIDOIDEA** Phillips, 1841

Family **MUCROSPIRIFERIDAE** Boucot, 1959

Genus **ELEUTHEROKOMMA** Crickmay, 1950

Type species.—Eleutherokomma hamiltoni Crickmay, 1950, pp. 220–222, pl. 36, figs. 1–3. See internal features in Crickmay, 1953, pl. 3, figs. 6–9.

Eleutherokomma wendtei new species
Plate 3, figures 1–17

Diagnosis.—Medium sized *Eleutherokomma* up to 22 mm in width, with inflated subpyramidal ventral valve with gently concave nearly catacline to apsacline ventral interarea; eight to 15 simple plications per flank on adult shells (shells 13 mm and wider); dorsal and ventral interior with short medial myophragm (dorsal myophragm variably developed; absent or not preserved in 20% of specimens).

Description.—Medium sized *Eleutherokomma* with greatest width at hinge or at mid length (largest ventral valve width of 22 mm), width greater than length (Tables 2 and 3); acute cardinal extremities with very short mucronate extensions (see Plate 3, figures 7–9); subpyramidal ventral valve with greatest width along hinge in juvenile growth stages, in adult shells (width greater than 15 mm) greatest width is anterior of hinge along rounded flanks 50% to 60% of length anterior of cardinal margin. Shell ventribiconvex, in profile, with more inflated ventral valve up to 70% of shell thickness, transversely semicircular in outline in early growth stages (less than 14 mm in width), with greatest width at midlength at rounded lateral margins anterior of acute lateral cardinal margins in larger adult shells (>14 to 15 mm in width). Shell surface with simple-rounded radial plica on flanks (up to 15 per flank). Medially uniplicate with simple fold and sulcus. Sulcus broad with nearly flat to slightly concave lateral profile near anterior margin. Medial anterior margin of ventral sulcus extended dorsally to form prominent tongue in large adult shells. Concentric growth lamellae overlap anteriorly as seen in other species of the genus. Preserved micro-ornament consists of radial capillae on and parallel to plica and in intervening grooves.

Ventral valve with open triangular delthyrium extending from cardinal margin ventrally to just beneath apex of valve; slightly concave interarea nearly vertical to slightly apsacline in juvenile shells becoming strongly recurved (apsacline with area inclined up to 60° relative to commissural plane) in some adult shells. Ventral interior features short low myophragm or ridge arising at posterior margin of valve interior in the delthyrial cavity between and extends up to 50% of valve length, flanked on either side by weakly to moderately impressed adductor muscle scars; bases of dental plates extend anteriorly to form low rimmed margin around muscle scars where muscle scars moderately impressed. Short dental plates, extend anteriorly 10–15% of valve length, bounding and parallel to margin of delthyrium from posterior margin ventrally approximately 70% of shell depth, then diverge laterally beneath the apex away from margin of delthyrial opening joining floor of ventral valve beneath flanks. Simple short peg-like teeth.

Dorsal valve with simple fold averaging 37% of maximum valve width at anterior margin, with broad U-shaped lateral outline. Fold bounded by strong grooves, flanks with simple plica with rounded transverse profiles with simple grooves or interspaces, averaging nine per flank (range is 8 to 15 in shells greater than 13 mm in width), cardinal margin with extremely short (less than .06 mm) strongly apsacline dorsal interarea. Cardinalia in dorsal interior consist of simple ctenophoridium with up to a dozen vertical lamellae,

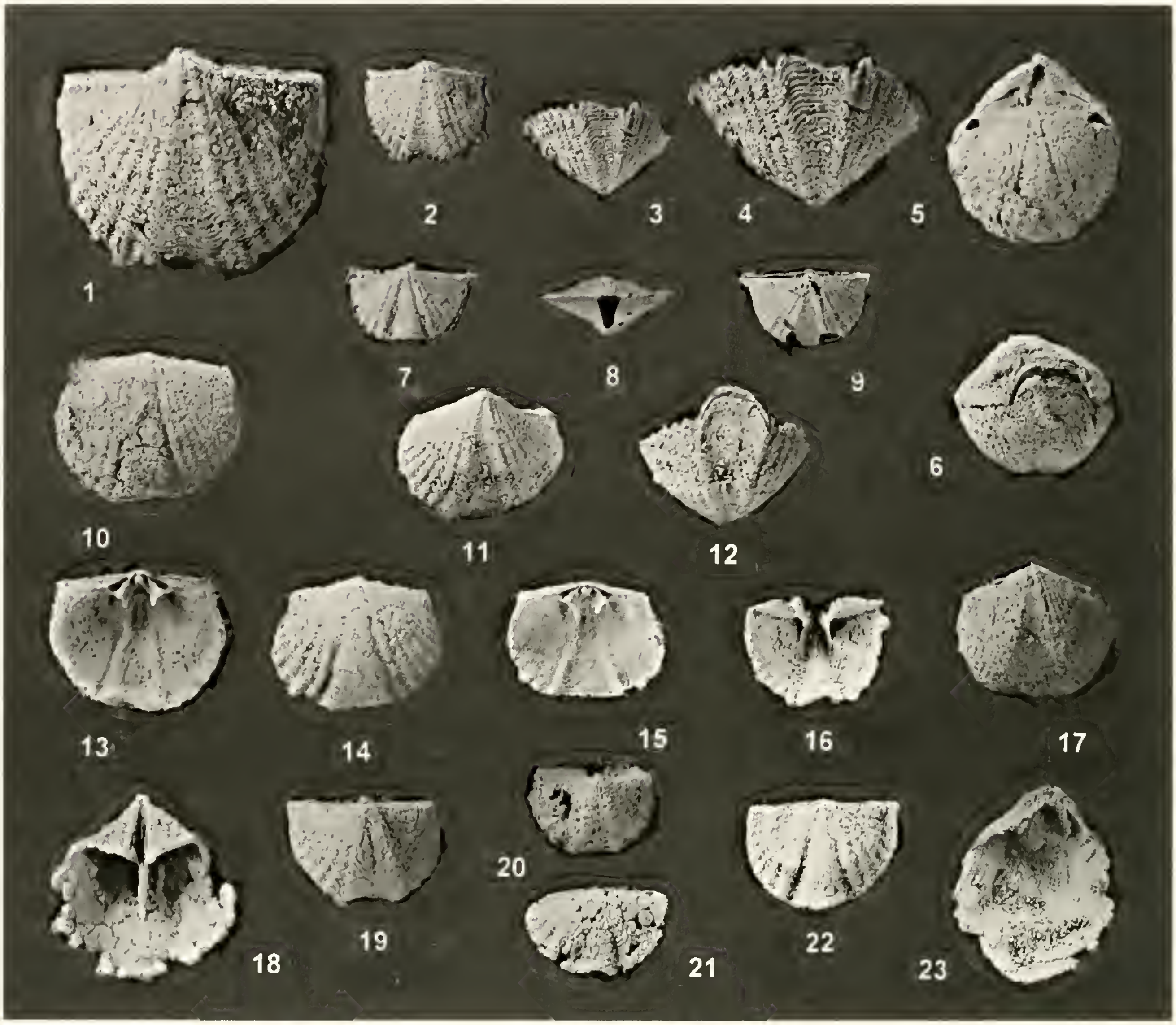

PLATE 3

Brachiopods from the Thornton Creek Member of the Flume Formation. All specimens from sample 3F from section A at GSC Thornton Pass locality, Ancient Wall Reef Platform, Jasper National Park, Alberta, Canada. All specimens ×1.5 unless otherwise indicated.

1–17. *Eleutherokomma wendtei* new species: 1–4, 16. GSC 122823 (syntype), 1, 2. upper views of ventral valve, at ×4 and 1.5 respectively; 3, 4. anterior views, at ×1.5 and ×3, respectively; 16. internal view showing dental plates, and medial ventral myophragm.

5, 6. GSC 122828 (paratype): dorsal and anterior views of complete adult with rounded profile and outline.

7–9. GSC 122829 (paratype): dorsal, posterior, and ventral views, respectively of large juvenile growth stage.

10, 13. GSC 122835 (syntype): external and internal views of dorsal valve. Internal view shows low medial myophragm, flanked by impressed adductor scars, sockets, socket ridges, ctenophoridium, and bases of the crus arising from socket plates.

11, 12. GSC 122825 (paratype): ventral and anterior views of ventral valve.

14, 15. GSC 122830 (paratype): exterior and internal views, respectively of dorsal valve.

17. GSC 122822 (syntype): upper view of ventral valve.

18–22. *Cyrtina triquetra* (Hall, 1858).

18. GSC 122839: Oblique view from posterior of partial ventral valve (showing strong medial septum fused to dental plates to form posterior chamber, delthyrial covering not preserved.

19, 22. GSC 122841: ventral and dorsal views, respectively, of complete shell showing external ornament. Ventral view shows trace of ventral medial septum preserved on surface of specimen.

20, 21. GSC 122840: ventral and dorsal views, respectively, of a relatively complete small adult shell showing external ornament.

23. *Cranaena* species. GSC 122845: internal view of damaged adult ventral valve.

lamellae rarely preserved in the available material. Ctenophoridium positioned medially on floor of dorsal valve immediately anterior of and below dorsal beak in space between socket plates and crural bases. Sockets oriented at approximately 35° relative to cardinal margin, preserved socket plates simple with angular edges between socket and cardinal margin. Short blade-like crura parallel to inner margins of fold, arise from and fused with bases of socket plates on inner valve surface just below commissure of medial cardinal margin. Very low medial myophragm extends up to 50% of valve length on floor of valve, some shells with impressed adductor muscle pits flanking myophragm near apex of valve interior.

Types.—Three syntypes GSC 122822, 122823 122835, the figured paratypes GSC 122825, 122828 to 122830; and 12 unfigured paratypes GSC 122827, 122831 to 122834, 122836 to 122838, 122874 to 122877.

Other material examined.—248 unnumbered whole and fragments of dorsal and ventral valves from sample 3F at the type locality.

Type stratum and locality.—The type stratum is the 1.5 meter interval of sample 3, type section of the Thornton Creek Member of the Flume Formation at Thornton Pass, in Jasper National Park, Alberta Rocky Mountains (Text-figs. 2, 3, 4, 6; GSC Thornton Pass locality).

Occurrence.—*Eleutherokomma wendtei* is restricted to late Givetian age Thornton Creek Member of the Flume Formation at its type section in the Alberta Rocky Mountains. In western Alberta, it is the dominant species of the *Eleutherokomma-Schizophoria* Fauna of the Thornton Creek Member described above.

Discussion.—The material on hand displays well-preserved internal features consistent with the genus as first defined by Crickmay (1950, pp. 219–220). These include a cardinal process consisting of simple ctenophoridium, a low myophragm in the dorsal interior, and a low myophragm and lack of a delthyrial plate in the ventral interior. Thus far, no delthyrial covering (pseudodeltidium or stegidium) is known from any species described from Givetian–middle Frasnian strata of western and central North America. The related genus *Mucrospirifer* Grabau, 1931, has a well-developed delthyrial covering as shown in illustrations of the type species *M. mucronatus* in Tillman (1964, pl. 153) and Cowen (1968), and lacks well-developed dental plates. Those features readily distinguish it from *Eleutherokomma.*

The juvenile growth stages of *Eleutherokomma wendtei* are closely similar to, although proportionally thicker than, adult shells of *E. impennis* Crickmay, 1950 (see: Crickmay, 1950, pl. 2; Warren and Stelck, 1956, pl. 120; McLaren *et al.*, 1962, pl. 10; Harrington, 1971, pl. 4, figs. 12–16 only; and Norris, *in* Norris and Uyeno, 1983, pls. 7, 8). *Eleutherokomma wendtei* is easily distinguished from *E. impennis* by its much larger (up to 22 mm in width) proportionally thicker (greater shell thickness) adult shell, more numerous flank plications, greater range in the angle of inclination of the nearly catacline to apsacline ventral interarea, and its greatest shell width anterior of the hinge. Nearly all other described species of *Eleutherokomma* are distinguished from *E. wendtei* by their less inflated ventral valves, and short and highly recurved concave ventral interareas, with mucronate or extended cardinal margins.

Order **SPIRIFERINIDA** Ivanova, 1972

Suborder **CYRTINIDINA** Carter and Johnson, 1994
(*in* Carter *et al.*, 1994)

Superfamily **CYRTINOIDEA** Frederiks, 1912

Family **CYRTINIDAE** Frederiks, 1912

Genus **CYRTINA** Davidson, 1858

Type species.—*Calceola heteroclita* Defrance, 1828, p. 306.

Cyrtina triquetra (Hall, 1858)
Plate 3, figures 18–22

Cyrtia triquetra Hall, 1858, p. 513
Cyrtina triquetra Meek and Worthen, 1868, p. 436, pl. 13, fig. 4; Hall and Clarke, 1894, pl. 28, figs. 34 and 35;
Cyrtina triquetra (Hall) Stainbrook, 1943, pp. 446–447, pl. 22–29.
Cyrtina cf. *triquetra* Hall, Maurin and Raasch, 1972, pl. 9, figs. 5–7.
not *Cyrtina triquetra* Warren and Stelck, 1956, pl. 15, figs. 22–24.

Material examined.—The illustrated specimens GSC 122839 to122841; two unfigured shells GSC 122842 and 122843; six unnumbered whole juvenile and adult shells; and 36 unnumbered fragments of ventral valves.

Occurrence.—The range of this form in the Givetian of North America is from the Upper *varcus* Subzone to *norrisi* Zone. In western and central Canada, this species is known from the "Flume" Formation of northeast British Columbia (Maurin and Raasch, 1972), the Thornton Creek Member of the Flume at Ancient Wall in the Alberta Rocky Mountains (this report); and the lower part of the argillaceous limestone beds of the Point Wilkins Member of the Souris River Formation of southwestern Manitoba (Norris and Day, *in* Day *et al.*, 1996, text-fig. 5). In the central United States it is known from its type locality in the Little Cedar Formation in northwestern Illinois and eastern Iowa, and ranges into the Coralville Formation of Iowa and Illinois (Stainbrook, 1943; Day, 1989a, 1992, 1996, 1997).

Discussion.—*Cyrtina triquetra* is widespread in carbonate and mixed clastic-carbonate platform deposits in central and western North America as outlined above. In northeast British Columbia, this form is illustrated from the brachiopod fauna of Assemblage 4 of the Flume Formation by Maurin and Raasch (1972), and was reported by Norris and Day (*in* Day *et al.*, 1996, fig. 5) from the argillaceous limestone beds of the Point Wilkins Member of the Souris River Formation.

Hall (1858) erected this form based on specimens from Rapid Member of the Little Cedar Formation and Cou Falls Member of the Coralville Formation in eastern Iowa and western Illinois. Other species of *Cyrtina* known from late Givetian deposits in North America include *C. caroline* Johnson (1978) and *C. umbonata* (Hall, 1858). *Cyrtina caroline* Johnson (1978, p. 131, pl. 8, figs. 1–31), described from the late Givetian of the Great Basin, differs from *C. triquetra* (Hall, 1858) by its more numerous flank plications and angular sinus. *Cyrtina umbonata* (Hall, 1858) from the late Givetian of the Iowa Basin differs from *C. triquetra* by its larger adult shell size, fewer flank plications, highly concave (apsacline to anacline) interarea, and shallow U-shaped ventral sinus.

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATULIDINA** Waagen, 1883

Superfamily **DIELASMATATOIDEA** Schuchert, 1913

Family **CRANAENIDAE** Cloud, 1942

Subfamily **CRANAENINAE** Cloud, 1942

Genus **CRANAENA** Hall and Clarke, 1893

[=*Eunella* Hall and Clarke, 1893, and *Cranaenella* Fenton and Fenton, 1924]

Type species.—*Terebratula romingeri* Hall, 1863, p. 48, text-figs. 22–23.

Cranaena sp.

Plate 3, figure 23

Material examined.—Figured damaged ventral valve of large adult GSC 122845, unfigured small adult shell GSC 122863, one unnumbered juvenile shell, and five unnumbered partial ventral valves.

Occurrence.—*Cranaena* sp. of this study is known only from sample 3F from section A (type section of the Thornton Creek Member) of the Flume Formation at Thornton Pass (GSC Thornton Pass locality).

Discussion.—The present material on hand—single juvenile shell, small adult shell (GSC 122863), and poorly preserved fragments of ventral valves (figured specimen GSC 122845)—does not permit identification of the Thornton Creek species or accurate comparisons with other late Givetian species of *Cranaena*. The small adult shell is similar in outline and profile to small adult specimens of *C. iowensis* (Calvin, 1890) and *C.* sp. cf. *C. iowensis* known from coeval deposits in eastern Iowa and central Missouri (see species listed in Day, 1996, 1997), and southwestern Manitoba (see fig. 5 of Norris, Day, and Uyeno, in Day *et al.*, 1996), respectively. The partial ventral valve of the large adult (GSC 122845) suggests a maximum size similar to that of *C. iowensis*.

REFERENCES CITED

Aitken, J.D.

1966. Sub-Fairholme Devonian rocks of the eastern Front Ranges, southern Rocky Mountains, Alberta. Geological Survey of Canada Paper 64–33, pp. 1–88.

1993. Tectonic evolution and basin history. Chapter 5 *in* Sedimentary Cover of the North American Craton in Canada. D.F. Stott and J.D. Aitken, *eds.*, Geological Survey of Canada, Geology of Canada, no. 5, pp. 483–504.

Aitken, J.D., and Greggs, R.G.

1967. Upper Cambrian formations, southern Rocky Mountains of Alberta, an interim report. Geological Survey of Canada Paper 66-49.

Aleskeeva, R.E.

1960. A new subgenus Atrypa (Desquamatia) of the family Atrypidae Gill (Brachiopoda). Akademiya Nauk SSSR, Dolkady, vol. 131, no. 2, pp. 421–424 [in Russian].

Alvarez, F., Rong, J.-Y., and Boucot, A.J.

1998. The classification of the athyridid brachiopods. Journal of Paleontology, vol. 72, pp. 827–855.

Boucot, A.J.

1959. Brachiopods of the Lower Devonian rocks at Highland Mills, New York. Journal of Paleontology, vol. 33, pp. 727–769.

Boucot, A.J., Johnson, J.G., and Staton, R.D.

1964. On some Atrypoid, Retzioid, and Athyidoid Brachiopoda. Journal of Paleontology, vol. 38, pp. 805–822.

Branson, E.B.

1923. The Devonian of Missouri. Missouri Bureau of Geology and Mines, vol. 17, Second Series, 279 pp.

Braun, W.K., Norris, A.W., and Uyeno, T.T.

1989. Givetian to early Frasnian biostratigraphy of western Canada: the Slave Point-Waterways boundary and related events. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 3, pp. 93–112.

Buch, L.

1834. Über Terebrateln, mit einem Versuch, sie zu klassifizieren und zu beschreihwn. Abhandlungen der Königlichen Academie der Wissenschaften. vol. 6, pp. 21–144.

Bunker, B.J., and Witzke, B.J.

1992. An upper Middle through lower Upper Devonian lithostratigraphic and conodont biostratigraphic framework of the Midcontinent Carbonate Shelf area, Iowa. *in* The stratigraphy, paleontology, depositional and diagenetic history of the Middle-Upper Devonian Cedar Valley Group of central and eastern Iowa. J. Day and B.J. Bunker, *eds.*, Iowa Department of Natural Resources, Guidebook 16, pp. 3–26.

Calvin, S.

1890. Iowa State University Laboratory of Natural History Bulletin, vol. 1, p. 174.

Campbell, C.V.

1992. Upper Elk Point megasequence. *in* Devonian-Early Mississippian Carbonates of the Western Canada Sedimentary Basin: A Sequence Stratigraphic Framework. J.C. Wendte, F.A. Stoakes, and C.V. Campbell, *eds.*, SEPM, Short Course 28, pp. 145–162.

Carter, J.L., Johnson, J.G., Gourvennec, R., and Hou, H.-F.

1994. A revised classification of the Spiriferid brachiopods. Annals of the Carnegie Museum, vol. 63, no. 4, pp. 327–374.

Cleland, H.F.

1911. The fossils and stratigraphy of the Middle Devonic of Wisconsin. Wisconsin Geological and Natural History Survey Bulletin 21, Science Series, no. 6, 222 pp.

Cloud, P.E.

1942. Terebratuloid Brachiopoda of the Silurian and Devonian. Geological Society of America, Special Paper 38, 182 pp.

Cook, H.E.

1972. Miette platform evolution and relation to overlying bank ("reef") localization, Upper Devonian, Alberta. Bulletin of Canadian Petroleum Geology, vol. 20, pp. 275–311.

Cooper, G.A.

1944. Chapter 9. Phylum Brachiopoda. *in* Index fossils of North America. H.W. Shimer and R.R. Shrock, *eds.*, The M.I.T. Press (Massachusetts Institute of Technology, Cambridge, Massachusetts), pp. 277–365.

Cooper, G.A., and Dutro, J.T., Jr.

1982. Devonian brachiopods of New Mexico. Bulletins of American Paleontology, vols. 82–83, no. 315, 215 pp.

Copper, P.

1973. New Siluro-Devonian atrypoid brachiopods. Journal of Paleontology, vol. 47, pp. 484–500.

1978. Devonian atrypoids from western and northern Canada. *in* Western and Arctic Canadian Biostratigraphy. C.R. Stelck and B.D.E. Chatterton, *eds.*, Geological Association of Canada Special Paper 18, pp. 289–331.

Cowen, R.

1968. A new type of delthyrial cover in the Devonian brachiopod *Mucrospirifer*. Palaeontology, vol. 11, pp. 317–327.

Crickmay, C.H.

1950. Some Devonian Spiriferidae from Alberta. Journal of Paleontology, vol. 24, pp. 219–225.

1953. New Spiriferidae from the Devonian of western Canada. Imperial Oil Limited [published by the author], 11 pp.

Davidson, T.

1858. British Carboniferous Brachiopoda, part 5. Paleontological Society of London, vol. 11, pp. 49–80.

1881. On genera and species of spiral-bearing Brachiopoda from specimens developed by Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire. Geological Magazine (new series, Decade II), vol. 8, no. 1, pp. 1–13.

Day, J.E.

1988. Stratigraphy, biostratigraphy, and depositional history of the Givetian and Frasnian strata in the San Andres and Sacramento Mountains of southern New Mexico. Unpublished Ph.D. dissertation, University of Iowa, Iowa City, 238 pp.

1989a. The brachiopod succession of the late Givetian-Frasnian of Iowa. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 3, pp. 303–326.

1989b. Biostratigraphy of the Middle and Upper Devonian Strata (Givetian & Frasnian) of south-central New Mexico. Geological Society of America, Abstracts with Programs, vol. 21, no. 7, p. 384.

1992. Middle-Upper Devonian (late Givetian–early Frasnian) brachiopod sequence in the Cedar Valley Group of central and eastern Iowa. *in* The stratigraphy, paleontology, depositional and diagenetic history of the Middle-Upper Devonian Cedar Valley Group of central and eastern Iowa. Iowa Department of Natural Resources, Guidebook 16, J. Day, and B.J. Bunker, *eds.*, pp. 53–105.

1996. Faunal signatures of Middle-Upper Devonian depositional sequences and sea level fluctuations in the Iowa Basin: U.S. midcontinent. *in* Paleozoic Sequence Stratigraphy: Perspectives from the North American Craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America Special Paper 306, pp. 277–299.

1997. Phylogeny and biogeography of *Tecnocyrtina* (Brachiopoda-Spiriferinida) in the Devonian (Givetian-Frasnian) of North America. *in* Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. G. Klapper, M.A. Murphy, and J.A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 245–262.

1998. Middle-Late Devonian Transgressive-Regressive cycles in cratonic platform & platform-to-basin settings: San Andres and Sacramento Mountains—southern New Mexico. Geological Society of America, Abstracts with Programs, vol. 30, no. 2, pp. 13.

Day, J., Uyeno, T.T., Norris, A.W., Witzke, B.J., and Bunker, B.J.

1996. Middle-Upper Devonian relative sea-level histories of central and western North American interior basins. *in* Paleozoic Sequence Stratigraphy: Views from the North American Craton: B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of American Special Paper 306, pp. 259–275.

Defrance, M.J.L.

1828. Térébratules fossils. Dictionary of Natural Science, vol. 53, 147 pp.

Drake, E.A.

1978. Paleozoic Stratigraphy of the Devils Gate—northern Mahogany Hills area, Eureka County, Nevada. Unpublished M.S. thesis, Oregon State University, Corvallis, 110 pp.

Dumeril, A.M.C.

1806. Zoologie analytique ou méthode naturelle de classification des animaux. Allais (Paris), 344 pp.

Elliot, D.K., and Johnson, H.G.

1997. Use of vertebrates to solve biostratigraphic problems: examples from the Lower and Middle Devonian of western North America. *in* Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. G. Klapper, M.A. Murphy, and J.A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 179–188.

Elliott, D.K., Dineley, D.L., and Johnson, H.G.

2000. A vertebrate fauna from the Middle Devonian Yahatinda Formation of southwestern Canada. Journal of Paleontology, vol. 74, pp. 123–132.

Fenton, C.L., and Fenton, M.D.

1924. The stratigraphy and fauna of the Hackberry stage of the Upper Devonian. University of Michigan Museum of Geology Contribution, vol. 1. The MacMillan Company, New York. 260 pp.

1935. Atrypae described by Clement L. Webster and related forms (Devonian, Iowa). Journal of Paleontology, vol. 9, pp. 369–384.

Frederiks, G.N.

1912. Bemerkugen uber eigige oberpalaozoische Fossilien von Krasnoufimsk. Kazan University, Protocols of the Sessions of the Natural History Society, vol. 269, pp. 1–9.

Geldsetzer, H.H.J.

1987. Stop 5-Cold Sulphur Spring. *in* Devonian of Alberta Rocky Mountains between Banff and Jasper. International Union of Geological Sciences, Subcommission on Devonian Stratigraphy, Geological Survey of Canada. A.W. Norris and A.E.H. Pedder, *eds.*, pp. 59–61.

1989. Ancient Wall reef complex, Frasnian age, Alberta. *in* Reefs, Canada and Adjacent Areas. H.H.J Geldsetzer, N.P. James, and G.E. Tebbutt, *eds.*, Canadian Society of Petroleum Geologists, Memoir 13, pp. 431–439.

Gill, T.

1871. Arrangement of the families of mollusks prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections, no. 227, pp. 1–49.

Grabau, A.W.

1931. Studies for students. The Brachiopoda [part 2]. The Science Quarterly of the National University of Peking, vol. 2, pp. 247–248.

Grunt, T.A., and Racki, G.

1998. Late Frasnian Athyridida (Brachiopoda) from Poland and the Late Devonian biotic turnover. Acta Palaeontologica Polonica, vol. 43, pp. 361–378.

Hall, J.

1850. On the Brachiopoda of the Silurian Period: particularly the Leptaenidae. American Association for the Advancement of Science, vol. 2, pp. 347–351.

1851. Containing descriptions of the organic remains of the lower middle division of the New York System (equivalents in part of the Silurian rocks of Europe). New York State Geological Survey, Paleontology, 353 pp.

1858. Report on the Geological Survey of the State of Iowa, embracing the results of investigations made during 1855, 1856, and 1857. Iowa Geological Survey, 1: Part 2, pp. 473–724.

1860. Descriptions of new species of fossils, from the Hamilton Group of western New York, with notices of others from the same horizon in Iowa and Indiana. New York State Cabinet of Natural History, Annual Report 13, pp. 76–94.

1863. Descriptions of new species of Brachiopoda from the Upper Helderberg, Hamilton, and Chemung groups. New York State Cabinet of Natural History, Annual Report 16, pp. 38–61.

1867. Descriptions of the fossil Brachiopoda of the Upper Helderberg, Hamilton, Portage, and Chemung groups. New York Natural History Survey, Paleontology, vol. 4, Part 1, 422 pp.

Hall, J., and Clarke, J.M.

1893. An introduction to the study of the genera of Palaeozoic Brachiopoda. Natural History, New York, Palaeontology, vol. 8, pt. 2, 217 pp.

1894. An introduction to the study of the genera of Paleozoic Brachiopoda. Geological Survey of the State of New York, Paleontology, vol. VIII, 393 pp.

Harrington, J.W.

1971. Brachiopods of the Melville Island Group (Upper Devonian), Banks Island, N.W.T. Bulletin of Canadian Petroleum Geology, vol. 19, pp. 782–798.

Heckel, P.H., and Witzke, B.J.

1979. Devonian world paleogeography determined from distribution of carbonates and related lithic paleoclimatic indicators. *in* The Devonian System. M.R. House, C.T. Scrutton, and M.G. Bassett, *eds.*, Palaeontological Association of London. Special Papers in Palaeontology, no. 23, pp. 99–123.

Ivanova, Ye. A.

1978. Main features of Spiriferid evolution. Paleontological Journal, 1972, no. 3, pp. 309–320.

Johnson, J.G.

1977. Lower and Middle Devonian faunal intervals in central Nevada based on brachiopods. *in* Western North America: Devonian. M.A. Murphy, W.B.N. Berry, and C.A. Sandberg, *eds.*, University of California, Riverside Campus Museum Contribution 4, pp. 16–32.

1978. Devonian, Givetian age brachiopods and biostratigraphy, central Nevada. Geologica et Palaeontologica, vol. 12, pp. 117–150.

1990. Lower and Middle Devonian brachiopod-dominated communities of Nevada, and their position in a biofacies-province-realm model, with a section on Revision of Middle Devonian conodont zones, by G. Klapper and J.G. Johnson. Journal of Paleontology, vol. 64, pp. 902–941.

Johnson, J.G., and Klapper, G.

1992. North American midcontinent T-R cycles. *in* Special Papers in Paleontology and Stratigraphy: A Tribute to Thomas W. Amsden. J.R. Chaplin and J.E. Barrick, *eds.*, Oklahoma Geological Survey Bulletin 145, pp. 127–136.

Johnson, J.G., Klapper, G., and Elrick, M.

1996. Devonian transgressive-regressive cycles and biostratigraphy, northern Antelope Range, Nevada: establishment of reference horizons for global cycles. Palaios, vol. 11, pp. 3–14.

Johnson, J.G., Klapper, G., and Sandberg, C.A.

1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, vol. 96, pp. 567–587.

Johnson, J.G., Klapper, G., and Trojan, W.R.

1980. Brachiopod and conodont successions in the Devonian of the Antelope Range, central Nevada. Geologica et Palaeontologica, vol. 14, pp. 77–116.

Johnson, J.G., and Sandberg, C.A.

1988. Devonian eustatic events in the eastern United States and their biostratigraphic responses. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Memoir 14, vol. 3, pp. 171–178.

Johnson, J.G., Sandberg, C.A., and Poole F.G.

1991. Devonian lithofacies of western United States. *in* Paleozoic Paleogeography of the Western United States II. J.D. Cooper and C.H. Stevens, *eds.*, Society of Economic Paleontologists and Mineralogists, Pacific Section, pp. 83–106.

Johnson, J.G., and Trojan, W.R.

1982. The *Tecnocyrtina* brachiopod fauna (?Upper Devonian) of central Nevada. Geologica et Palaeontologica, vol. 16, pp. 119–150.

King, W.

1850. A monograph of the Permian fossils of England. Palaeontological Society Monograph 3, pp. 1–258.

Klapper, G.

1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 3, pp. 449–468.

Klapper, G., and Lane, H.R.

1989. Frasnian (Upper Devonian) conodont sequence at Luscar Mountain and Mount Hualtain, Alberta Rocky Mountains. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 3, pp. 469–478.

LaMaskin, T.A., and Elrick, M.

1997. Sequence stratigraphy of the Middle to Upper Devonian Guilmette Formation, southern Egan and Schell Creek ranges, Nevada. *in* Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. G. Klapper, M.A. Murphy, and J.A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 245–262.

Lantos, J.A.

1983. Middle Devonian stratigraphy north of the Pine Point barrier complex, Pine Point, Northwest Territories. Unpublished M.Sc. thesis, University of Alberta, 202 pp., 4 pls.

Martin, W.

1809. Petrifacta Derbiensia; or figures and descriptions of petrifaction collected in Derbyshire. Printed for the author by Lyon and Atkinson, Wigan, 28 pp.

Maurin, A.F., and Raasch, G.O.

1972. Early Frasnian stratigraphy, Kakwa-Cecilia Lakes, British Columbia, Canada. Compagnie Française des Pètroles, Notes et Mèmoires, vol. 10, 80 pp.

McLaren, D.J.

1953. Summary of the Devonian stratigraphy of the Alberta Rocky Mountains. Alberta Society of Petroleum Geologists, Third Annual Field Conference, Guidebook, pp. 89–104.

1954. Upper Devonian rhynchonellid zones in the Canadian Rocky Mountains. *in* Western Canada Sedimentary Basin—A Symposium of the Alberta Society of Petroleum Geologists (Ralph Leslie Rutherford Memorial Volume). L.M. Clark, *ed.*, AAPG, Tulsa, Oklahoma, pp. 159–181.

1962. Middle and Early upper Devonian rhynchonellid brachiopods from western Canada. Geological Survey of Canada Bulletin 86, 122 pp.

McLaren, D.J., Norris, A.W., and McGregor, D.C.

1962. Illustrations of Canadian fossils—Devonian of western Canada. Geological Survey of Canada Paper 62-4, 34 pp.

McLean, D.J., and Mountjoy, E.W.

1993. Upper Devonian buildup-margin and slope development in the southern Canadian Rocky Mountains: Geological Society of America Bulletin, vol. 105, pp. 1263–1283.

McLean, R.A., and Klapper, G.

1998. Biostratigraphy of Frasnian (Upper Devonian) strata in western Canada, based on conodonts and rugose corals: Bulletin of Canadian Petroleum Geology, vol. 46, pp. 515–563.

M'Coy, F.

1844. A synopsis of the characters of the Carboniferous limestone fossils of Ireland. 207 pp., Dublin.

Meek, F.B., and Worthen, A.H.

1868. Paleontology of Illinois: Lower Silurian species; Upper Silurian species; Devonian species; Carboniferous species. Geological Survey of Illinois, vol. 3, no. 2, pp. 291–565.

Montjoy, E.W.

1965. Stratigraphy of the Devonian Miette complex and associated strata, eastern Jasper National Park, Alberta. Geological Survey of Canada Bulletin 110, 132 pp.

1980. Some questions about the development of Upper Devonian carbonate buildups (reefs), western Canada. Bulletin of Canadian Petroleum Geology, vol. 28, pp. 315–344.

Moore, P.F.

1989. Devonian reefs in western Canada and some adjacent areas. *in* Reefs, Canada and Adjacent Areas. H.W.J. Geldsetzer, N.P. James, and G.E. Tebbutt, *eds.*, Canadian Society of Petroleum Geologists Memoir 13, pp. 367–389.

Moore, R.C.

1952. Brachiopoda. *in* Invertebrate Fossils. R.C. Moore, C.G. Lalicker, and A.G. Fischer, *eds.*, McGraw-Hill, New York, pp. 197–267.

Morrow, D.W., and Geldsetzer, H.H.J.

1989. Devonian of the Eastern Canadian Cordillera. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 1, pp. 85–122.

Nettleroth, H.

1889. Kentucky fossil shells; a monograph on the fossil shells of the Silurian and Devonian rocks of Kentucky. Kentucky Geological Survey Memoir, 245 pp.

Noble, J.P.A.

1970. Biofacies analysis, Cairn Formation of Miette Reed complex (Upper Devonian), Jasper National Park, Alberta. Bulletin of Canadian Petroleum Geology, vol. 18, pp. 493–543.

Norris, A.W.

1963. Devonian stratigraphy of northeastern Alberta and northwestern Saskatchewan. Geological Survey of Canada Memoir 313, 168 pp.

1965. Stratigraphy of Middle Devonian and older Paleozoic rocks of the Great Slave Lake region, Northwest Territories. Geological Survey of Canada Memoir 322, pp. 1–180.

1983. Brachiopods [*Schizophoria, Strophodonta (Strophodonta), Nervostrophia, Eostrophalosia* and *Devonoproductus*] from the lower Upper Devonian Waterways Formation of northeastern Alberta. Geological Survey of Canada Bulletin 350, 45 pp., 7 pls., 4 figs.

1998. Brachiopod faunas of the Bituminous Limestone Member of the Pine Point Formation and Sulphur Point Formation (Middle Devonian), Pine Point area on south side of Great Slave Lake, District of Mackenzie; and a discussion of related Devonian stratigraphy and biostratigraphy of adjacent areas. Geological Survey of Canada Bulletin 522, Part 1, 144 pp.

Norris, A.W., and Uyeno, T.T.

1981. Stratigraphy and paleontology of the lowermost Upper Devonian Slave Point Formation on Lake Claire and the lower Upper Devonian Waterways Formation on Birch River, northeastern Alberta. Geological Survey of Canada Bulletin 334, 53 pp.

1983. Biostratigraphy and paleontology of the Middle-Upper Devonian boundary beds, Gypsum Cliffs area, northeastern Alberta. Geological Survey of Canada Bulletin 313, 65 pp.

Norris, A.W., Uyeno, T.T., and McCabe, H.R.

1982. Devonian rocks of the Lake Winnipegosis–Lake Manitoba outcrop belt, Manitoba. Geological Survey of Canada Memoir 392, 280 pp.

Phillips, J.

1841. Figures and descriptions of the Paleozoic fossils of Cornwall, Devon, and west Somerset. Geological Survey of Great Britain, Memoir 1. Longman & Co. London, 231 pp.

Potma, K., Weissenberger, J.A.W., Wong, P.K., and Gilhooly, M.G.

2001. Toward a sequence stratigraphic framework for the Frasnian of the Western Canada Basin. Bulletin of Canadian Petroleum Geology, vol. 49, pp. 37–85.

Pugh, D.C.

1973. Subsurface lower Paleozoic stratigraphy in northern and central Alberta. Geological Survey of Canada Paper 72-12.

Rzhonsnitskaya, M.A.

1960. Order Atrypida. *in* Mshanki, Brakhiopody [Bryozoa, Brachiopoda], T.G. Sarytcheva, *asst. ed.*, Osnovy Paleontologii, vol. 7, Y.A. Orlov, *ed.*, Akademia Nauk SSSR, Moscow, pp. 257–264, pls. 53–56.

Rogers, F.S., and Pitrat, C.A.

1986. Distribution of *Tylothyris* (Brachiopoda) and its occurrence in the Traverse Group (Middle Devonian) of Michigan. Journal of Paleontology, vol. 61, pp. 494–507.

Savage, T.E.

1930. Devonian rocks of Kentucky. Kentucky Geological Survey, Series VI, vol. 33, pp. 1–163.

1931. Paleontology of Kentucky, Symposium. The Devonian Fauna. Kentucky Geology Survey, vol. 36, pp. 215–247.

Schuchert, C.

1913. Class Brachiopoda. *in* K.A. von Zittel, Text-book of Palaeontology, vol. 1, part 1, 2d ed., translated and edited by Charles R. Eastman. MacMillan & Co., Ltd. London, pp. 355–420.

Schuchert, C., and Cooper, G.A.

1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. Memoirs of the Peabody Museum of Natural History, Vol. IV (pt. 1), 270 pp.

Schuchert, C., and Levene, C.M.

1929. Brachiopoda (Generum et genotyporum index et bibliographia). Fossilum Catalogus, vol. 1, Animalia, part 42, 140 pp.

Scotese, C.R., and McKerrow, W.S.

1990. Revised world maps and introduction. *in* Palaeozoic Palaeogeography and Biogeography. W.S. McKerrow and C.R. Scotese, *eds.*, Geological Society of London, Memoir 12, pp. 1–21.

Stainbrook, M.A.

1938. *Atrypa* and *Stropheodonta* from the Cedar Valley beds of Iowa. Journal of Paleontology, vol. 2, pp. 229–256.

1942. Brachiopods of the Cedar Valley Beds of Iowa, Inarticulata, Rhynchonellacea and Rostrospiracea. Journal of Paleontology, vol. 16, pp. 604–619.

1943. Spiriferacea of the Cedar Valley Limestone of Iowa. Journal of Paleontology, vol. 17, pp. 417–450.

Switzer, S.B., Holland, W.G., Christie, G.S., Graf, G.C., Hedinger, A.S., McAuley, R.J., Wierzbicki, R.A., and Packard, J.J.

1994. Devonian Woodbend-Winterburn strata of the western Canada sedimentary basin. *in* Geological Atlas of the Western Canada Sedimentary Basin. G. Mossop and I. Shetsen, *eds.*, Canadian Society of Petroleum Geologists and Alberta Research Council, pp. 165–202.

Thompson, T.L.

1993. Paleozoic succession in Missouri, Part 3, Silurian and Devonian systems. Missouri Department of Natural Resources, Report of Investigations no. 70, 228 pp.

Tillman, J.R.

1964. Variation in species of *Mucrospirifer* from Middle Devonian rocks of Michigan, Ontario, and Ohio. Journal of Paleontology, vol. 38, pp. 952–156.

Uyeno, T.T.

1979. Devonian conodont biostratigraphy of Powell Creek and adjacent areas, western District of Mackenzie. *in* Western and Arctic Canadian Biostratigraphy. C.R. Stelck and B.D.E. Chatterton, *eds.*, Geological Association of Canada Special Paper 18, pp. 223–257.

1987. Report on conodonts from Cold Sulphur Spring (Stop 5). *in* Devonian of Alberta Rocky Mountains between Banff and Jasper. A.W. Norris and A.E.H. Pedder, *eds.*, International Union of Geological Sciences, Subcommission on Devonian Stratigraphy, Geological Survey of Canada, pp. 62–63.

1998. Conodont faunas. *in* Middle Devonian brachiopods and conodonts, stratigraphy, and transgressive-regressive cycles, Pine Point area, south of Great Slave Lake, District of Mackenzie, Northwest territories. Geological Survey of Canada Bulletin 522, Part II, pp. 149–191.

Vail, P.R., Mitchum, R.M., Jr., Todd, R.G., Widmeri, J.W., Thomson, S., Sangree, J.B., Bubb, J.N., and Hatfield, W.G.

1977. Seismic stratigraphy and global changes of sea-level. *in* Seismic Stratigraphy–Applications to Hydrocarbon Exploration. C.E. Payton, *ed.*, American Association of Petroleum Geologists Memoir 26, pp. 49–212.

van Buchem, F.S.P., Chaix, M., Eberli, G.P., Whalen, M.T., Masse, P., and Mountjoy, E.W.

2000. Outcrop to subsurface correlation of the Upper Devonian (Frasnian) in the Alberta Basin (W. Canada) based on the comparison of Miette and Redwater Carbonate Buildup Margins. *in* Genetic stratigraphy on the exploration and production scales—Case studies from the Pennsylvanian of the Paradox Basin and the Upper Devonian of Alberta. P.W. Homewood and G.P. Eberli, *eds.*, Bulletin, Centre Recherche Elf Exploration-Production, Memoire 24, pp. 225–267.

van Buchem, F.S.P., Eberli, G.P., Whalen, M.T., Mountjoy, E.W., and Homewood, P.

1996. The basinal geochemical signature and platform margin geometries in the Upper Devonian mixed carbonate-siliciclastic system of western Canada. Bulletin of the Geological Society of France, vol. 167, pp. 685–699.

Waagen, W.H.

1883. Salt Range Brachiopoda (Terebratulidae). Palaeontologia Indica, Memoir Series 13, vol. 1, no. 4, fascicle 1, pp. 329–395.

1884. Salt Range fossils, Part 4 (2) Brachiopoda. Palaeontologia Indica, Memoir Series 13, vol. 1, no. 3, pp. 547–610.

Warren, P.S.

1944. Index brachiopods of the Mackenzie River Devonian. Transactions of the Royal Society of Canada, 3rd Series, vol. 38, pp. 105–135.

Warren, P.S., and Stelck, C.R.

1956. Devonian faunas of western Canada. Geological Association of Canada, Special Paper 1, 75 pp.

Webster, C.L.

1921. Notes on the genus *Atrypa*, with description of New Species. American Midland Naturalist, vol. 7, pp. 13–20.

Weissenberger, J.A.W.

1994. Frasnian reef and basinal strata of West Central Alberta: a combined sedimentological and biostratigraphic analysis. Bulletin of Canadian Petroleum Geology, vol. 42, pp. 1–25.

Wendte, J.C.

1992. Cyclicity of Devonian strata in the western Canada sedimentary basin. *in* Devonian-Early Mississippian Carbonates of the Western Canada Sedimentary Basin: A Sequence Stratigraphic Framework. J.C. Wendte, F.A. Stoakes, and C.V. Campbell, *eds.*, Society of Economic Paleontologists and Mineralogists Short Course 28, pp. 25–40.

1994. Cooking Lake platform evolution and its control on Late Devonian Leduc reef inception and localization, Redwater, Alberta. Bulletin of Canadian Petroleum Geology, vol. 42, pp. 499–528.

Wendte, J.C., Uyeno, T.T., and Abrahamson, B.

1995. Physical stratigraphy and conodont biostratigraphy of the Beaverhill Lake Group, Late Middle to Early Late Devonian, east-central Alberta. *in* Proceedings of the Oil and Gas Forum '95, Energy from Sediments. J.S. Bell, T.D. Bird, T.L. Heller, and P.L. Greener, *eds.*, Geological Survey of Canada Open File Report 3058, pp. 141–144.

Whalen, M.T., and Day, J.

2000. Initial Devonian Onlap of the West Alberta Arch, Canadian Rocky Mountains: Implications for paleogeography and sea-level history of western Alberta. American Association of Petroleum Geologists Bulletin, Annual Convention Program, vol. 84, no. 4, p. A156.

Whalen, M.T., Eberli, G.P., van Buchem, F.S.P., Mountjoy, E.W., and Homewood, P.W.

2000a. Bypass margins, basin-restricted wedges and platform-to-basin correlation, Upper Devonian, Canadian Rocky Mountains: Implications for Sequence Stratigraphy of Carbonate Platform System. Journal of Sedimentary Research, vol. 70, pp. 913–936.

Whalen, M.T., Eberli, G.P., van Buchem, F.S.P., and Mountjoy, E.W.

2000b. Facies architecture of Upper Devonian carbonate platforms, Rocky Mountains, Canada. *in* Genetic stratigraphy on the exploration and production scales—Case studies from the Pennsylvanian of the Paradox Basin and the Upper Devonian of Alberta. P.W. Homewood and G.P. Eberli, *eds.*, Bulletin, Centre Recherche Elf Exploration-Production, Memoire 24, pp. 141–180.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., and Popov, L.E.

1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London (Ser. B), vol. 351, pp. 1171–1193.

Williams, A., and Harper, D.A.T.

2000. Order Orthida. *in* Treatise on invertebrate paleontology. Part H, Brachiopoda. vol. 3. A. Williams, C.H.C. Brunton, and S.J. Carlson, *eds.*, Geological Society of America and University of Kansas Press, pp. H714–H844.

Williams, C.A., and Krause, F.F.

1999. Paleosol chronosequences and peritidal deposits of the Middle Devonian (Givetian) Yahatinda Formation, Wasootch Creek, Alberta, Canada. Bulletin of Canadian Petroleum Geology, vol. 48, pp. 1–18.

Witzke, B.J., and Bunker, B.J.

1996. Relative sea level changes during Middle Ordovician through Mississippian deposition in the Iowa area, North American Craton. *in* Paleozoic Sequence Stratigraphy: Perspectives from the North American Craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America Special Paper 306, pp. 307–330.

1997. Sedimentation and stratigraphic architecture of a Middle Devonian (late Givetian) transgressive-regressive carbonate-evaporite cycle, Coralville Formation, Iowa area. *in* Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. G. Klapper, M.A. Murphy, and J.A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 67–88.

Witzke, B.J., Bunker, B.J., and Klapper, G.

1983. Devonian stratigraphy in the Quad Cities area, eastern Iowa-northwestern Illinois. *in* Devonian & Pennsylvanian stratigraphy of the Quad-Cities Region Iowa-Illinois. W.R. Hammer, R.C. Anderson, and D.A. Schroeder, *eds.*, Great Lakes Section of the Society of Economic Paleontologists and Mineralogists, 15th Annual Field Conference Guidebook, pp. 19–64.

Witzke, B.J. Bunker, B.J., and Rogers, F.S.

1989. Eifelian through lower Frasnian stratigraphy and deposition in the Iowa area, Midcontinent, U.S.A. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 1, pp. 221–250.

Witzke, B.J. and Heckel, P.H.

1989. Paleoclimatic indicators and inferred Devonian paleolatitude of Euramerica. *in* Devonian of the World. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir 14, vol. 1, pp. 49–66.

CONODONT BIOSTRATIGRAPHY AND PHYSICAL STRATIGRAPHY IN TWO WELLS OF THE BEAVERHILL LAKE GROUP, UPPER MIDDLE TO LOWER UPPER DEVONIAN, CENTRAL ALBERTA, CANADA

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ABSTRACT

An integrated study of conodont biostratigraphy with transgressive-regressive sequence stratigraphy has related genetic successions of the Beaverhill Lake Group over a widespread area of south-central Alberta. The study area spans from the Eastern Shelf in eastern Alberta through an intervening Central Alberta Basin, to the Western Shelf in western Alberta. This paper primarily reports on the conodont biostratigraphy of basinal successions (Waterways Formation) from two wells, 32 km apart, near the Western Shelf, within a sequence-stratigraphic framework.

In the area of the two wells in central Alberta, the Waterways Formation consists of up to approximately 150 m of interstratified basinal limestones and calcareous shales. The entire Waterways succession is divided into nine genetic units, which have been correlated throughout the basin. These genetic successions are assignable to six conodont zones: in ascending order, the Upper *subterminus* Fauna (approximately equivalent to the Upper *disparilis* Subzone), the *norrisi* Zone, and Montagne Noire (MN) zones 1 to 4. This suggests that sedimentation was continuous across the Givetian-Frasnian (Middle-Late Devonian) boundary. The standard marker for the base of MN Zone 4, *Palmatolepis transitans*, makes a late entry within that zone. The base of MN 4 was determined by the first occurrence of *Ancyrodella postbinodosa* new species, a species that has been demonstrated to be restricted to that zone through graphic correlation (Klapper, pers. commun., 2000). Other new species introduced here include *Mesotaxis keithi*, *Palmatolepis paradisparilis*, and *Polygnathus tedi*.

The correlations made independently from physical sequence stratigraphy and conodont biostratigraphy parallel one another and thus corroborate each other.

INTRODUCTION

The Beaverhill Lake Group in the subsurface of south-central Alberta consists of limestones, dolostones, and calcareous shales, up to over 200 m thick. These strata overlie coastal plain and marginal marine shales, dolostones, and limestones of the Watt Mountain Formation and are overlain by either platform carbonates (Cooking Lake and Leduc formations) or basinal shales and limestones (Duvernay Formation) of the Woodbend Group (Text-fig. 1).

Beaverhill Lake strata were examined throughout an extensive area in south-central Alberta. The area of investigation extends from the Alberta-Saskatchewan boundary west to the Cordilleran thrust belt or the Sixth Meridian and from Township 24 north through Township 71 (Text-fig. 2). Within this area, the Beaverhill Lake Group is divided into two formations (Text-fig. 1). The Swan Hills Formation includes shallow-marine limestones and dolostones that occur in the western part of the study area. These carbonates were deposited on areally extensive carbonate platforms, and on both younger, backstepped carbonate platforms, hereinafter referred to as banks, and areally restricted, isolated reefs (Text-fig. 2). The Waterways Formation denotes basinal limestones and calcareous shales deposited throughout most of the study area, but also incorporates limestones and dolostones deposited on areally extensive carbonate platforms and isolated reefs in the eastern part of the study area.

SCOPE OF PAPER

This paper focuses on the results of an integrated study of the conodont biostratigraphy, physical stratigraphy, and sedimentology of the Beaverhill Lake Group from two wells in the northwestern part of the area of investigation (Text-fig. 2). The Pan American Home Archie well (4-1-66-8W5) (hereafter called the Archie well) lies just basinward of the Swan Hills platform and contains a continuous core through the entire basinal Waterways succession. The Imperial Forestry well (16-7-64-10W5) (hereafter called the Forestry well) occurs along the northeastern flank of the isolated Judy Creek reef complex. A core at this well penetrates the entire Waterways succession at this location, including both distal foreslope deposits shed from the reef and overlying basinal limestones and calcareous shales. Both cores were described in detail and systematically and extensively sampled for conodonts.

This paper also incorporates and summarizes aspects of both the physical and conodont biostratigra-

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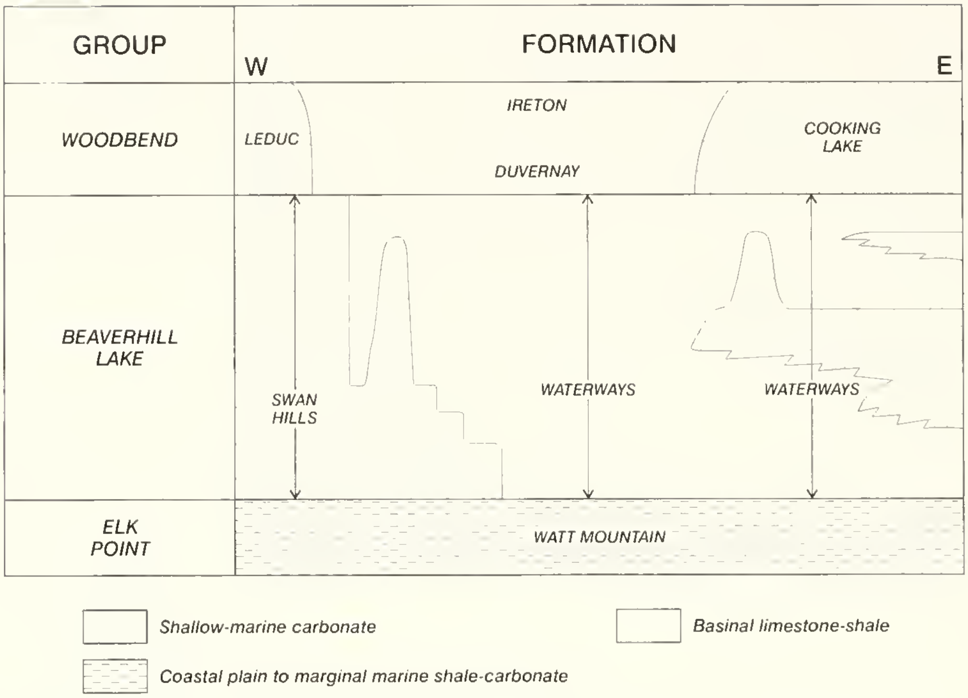
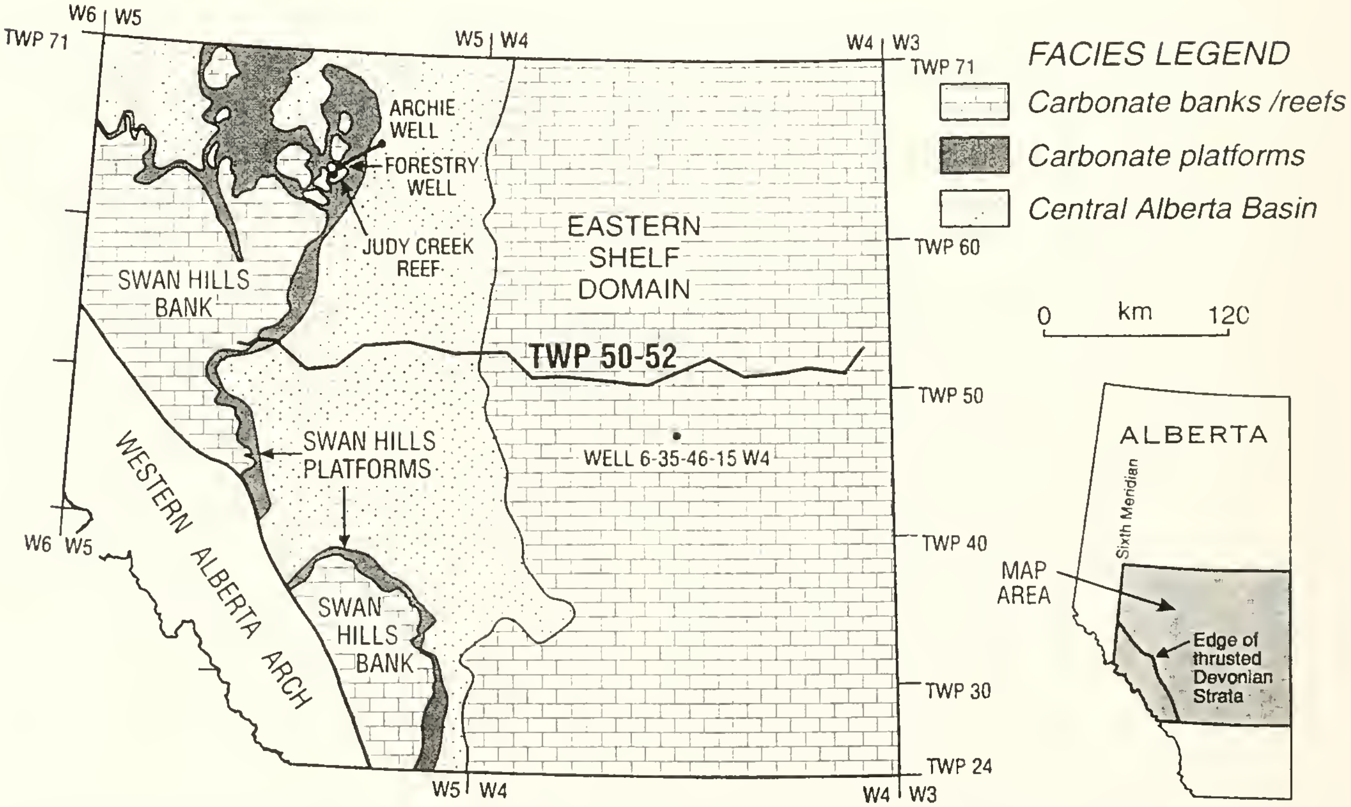


Text-figure 1.—Lithostratigraphy of the Elk Point, Beaverhill Lake, and Woodbend Groups of south-central Alberta.



Text-figure 2.—Map showing Beaverhill Lake domains in subsurface of south-central Alberta. The Pan American Home Archie 4-1-66-8W5 and Imperial Forestry 16-7-64-10W5 wells occur in the vicinity of the Judy Creek reef complex in the northwestern part of the map area. The transects at Townships 50–52 and from the Archie well to the Judy Creek reef complex correspond to the position of cross-sections on Text-figures 4 and 5, respectively. A small index map shows the location of the study area.

phy from wells throughout the entire area of investigation. The data base includes approximately 1300 wells, whose depositional cycles were correlated throughout a grid of wireline log cross-sections. Cores from approximately 150 of these wells were described, enabling a detailed interpretation of the depositional facies and depositional sequences. Cores from 49 of these wells were sampled for conodont biostratigraphy. This synthesis provides a more regional context to the physical and conodont biostratigraphy for the Archie and Forestry wells.

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DEPOSITIONAL SETTING

Beaverhill Lake strata comprise three depositional domains (Text-fig. 2). A Western Shelf consists of a succession up to 150 m thick of shallow-marine limestones and dolostones of the Swan Hills Formation. These carbonates were deposited on the carbonate platforms, banks, and isolated reefs situated along the eastern flank of the slowly subsiding Western Alberta Arch. A pronounced embayment at a latitude of approximately Township 40 separates the Western Shelf into northern and southern sub-domains.

An Eastern Shelf complex occurs in the eastern half of the area of investigation. The position of the margin of this shelf shifts during the deposition of Beaverhill Lake strata. During transgressive episodes the margin retreats or backsteps to the southeast. During regressive episodes the shelf margin progrades to the northwest. The position of the shelf margin depicted on Text-figure 2 corresponds to its most regressive, basinward position. For geographical reference the area of the shelf shown on Text-figure 2 is termed the Eastern Shelf Domain. As a result of these transgressive and regressive episodes, boreholes throughout most of the Eastern Shelf Domain encounter an interbedded succession of basinal limestones or calcareous shales and shallow-marine limestones and dolostones, deposited mainly on widespread carbonate platforms and to a lesser degree on isolated carbonate reefs. This Eastern Shelf Domain succession thickens to the northeast, away from the positive Western Alberta Arch, attaining a maximum thickness of approximately 240 m.

The Central Alberta Basin occurs between the eastern and western shelves. Deposits in the basin consist entirely of deep-water calcareous shales and limestones. These deposits vary in thickness from 75 to 210 m.

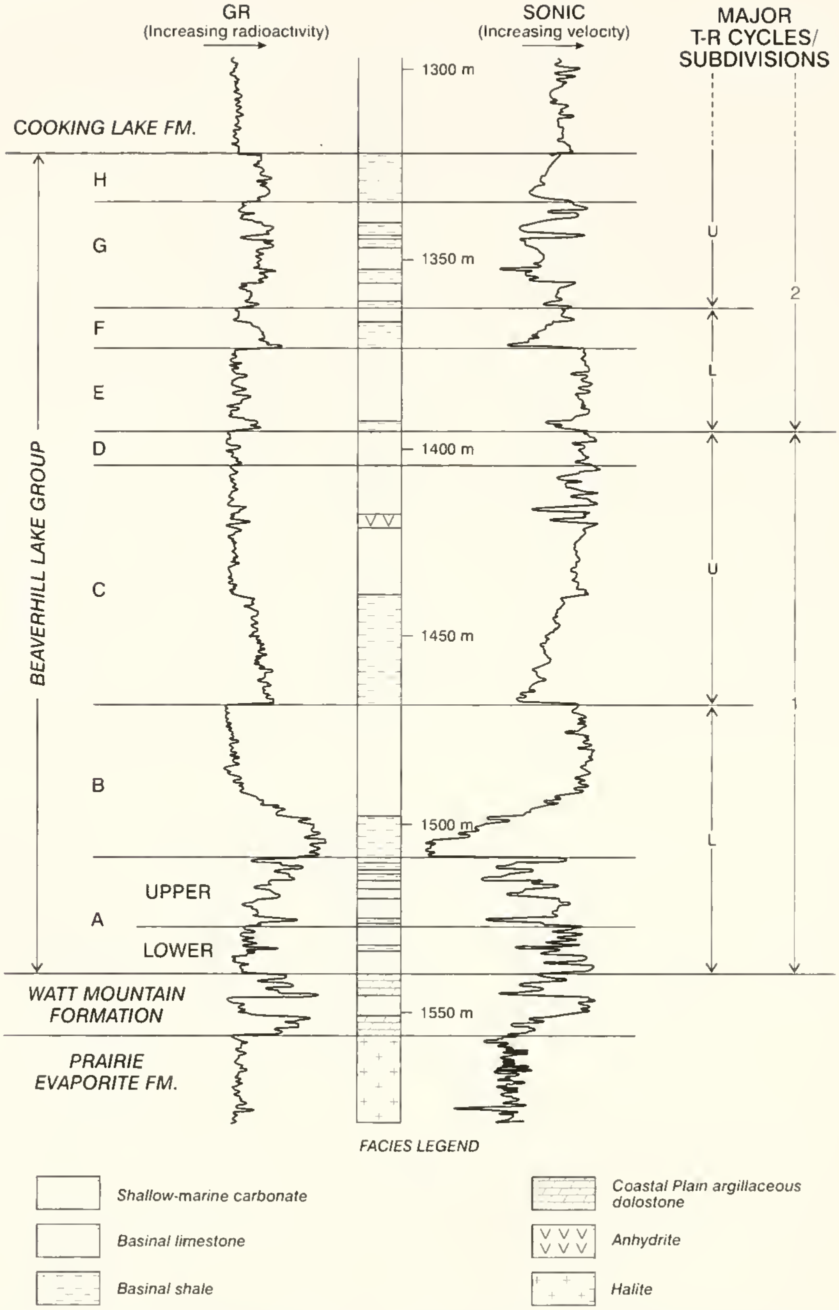
PHYSICAL STRATIGRAPHY

EASTERN SHELF AND CENTRAL ALBERTA BASIN

Beaverhill Lake strata on the Eastern Shelf and in the Central Alberta Basin consist of nine transgressive-regressive (T-R) cycles (termed A to H, with A subdivided into lower and upper parts). T-R cycle boundaries were determined from both core and wireline log examination. Text-figure 3 shows the gamma-ray log and sonic log signatures of these T-R cycles from a well (6-35-46-15W4) on the Eastern Shelf Domain. T-R cycle boundaries correspond to the position, within a given interval, that marks the change from progressively shallower-water facies to progressively deeper-water facies. This position is marked by an increase in argillaceous content. On wireline logs this level corresponds to an increase in the radiation count on gamma-ray logs and to decreased acoustic velocities on sonic logs. In either basinal successions or in successions that grade from basinal facies up into shallow-water facies, T-R cycles have a dominantly shoaling-upward aspect. This aspect corresponds to decreasing argillaceous content and is recorded by decreasing radiation on the gamma-ray logs and by increased acoustic velocities on the sonic logs. In these T-R cycles, such as cycle B, the transgressive part of the succession is either absent or thin. Some T-R cycles, however, may have either a significant transgressive basal portion (cycle G) or have an overall transgressive aspect (Upper A cycle).

On the Eastern Shelf Domain, it is important to recognize that the top of the Beaverhill Lake Group (top of succession H) is not a T-R cycle contact. Instead, it is a facies contact and, as illustrated on Text-figure 3, marks the position in a shoaling-upward cycle where shallower-water carbonate facies of the Cooking Lake Formation prograde over deeper-water, argillaceous facies of succession H.

Correlation of T-R cycle boundaries allows recognition of the change from regression to transgression. The cross-section on Text-figure 4 shows the correlation of the T-R cycle boundaries and the disposition of depositional facies within these cycles on an east-west transect across the basin, at the latitude of Township 50-52. The cross-section also shows the lower successions of the overlying Woodbend Group. On the eastern side of the basin, shallow-water lithofacies are

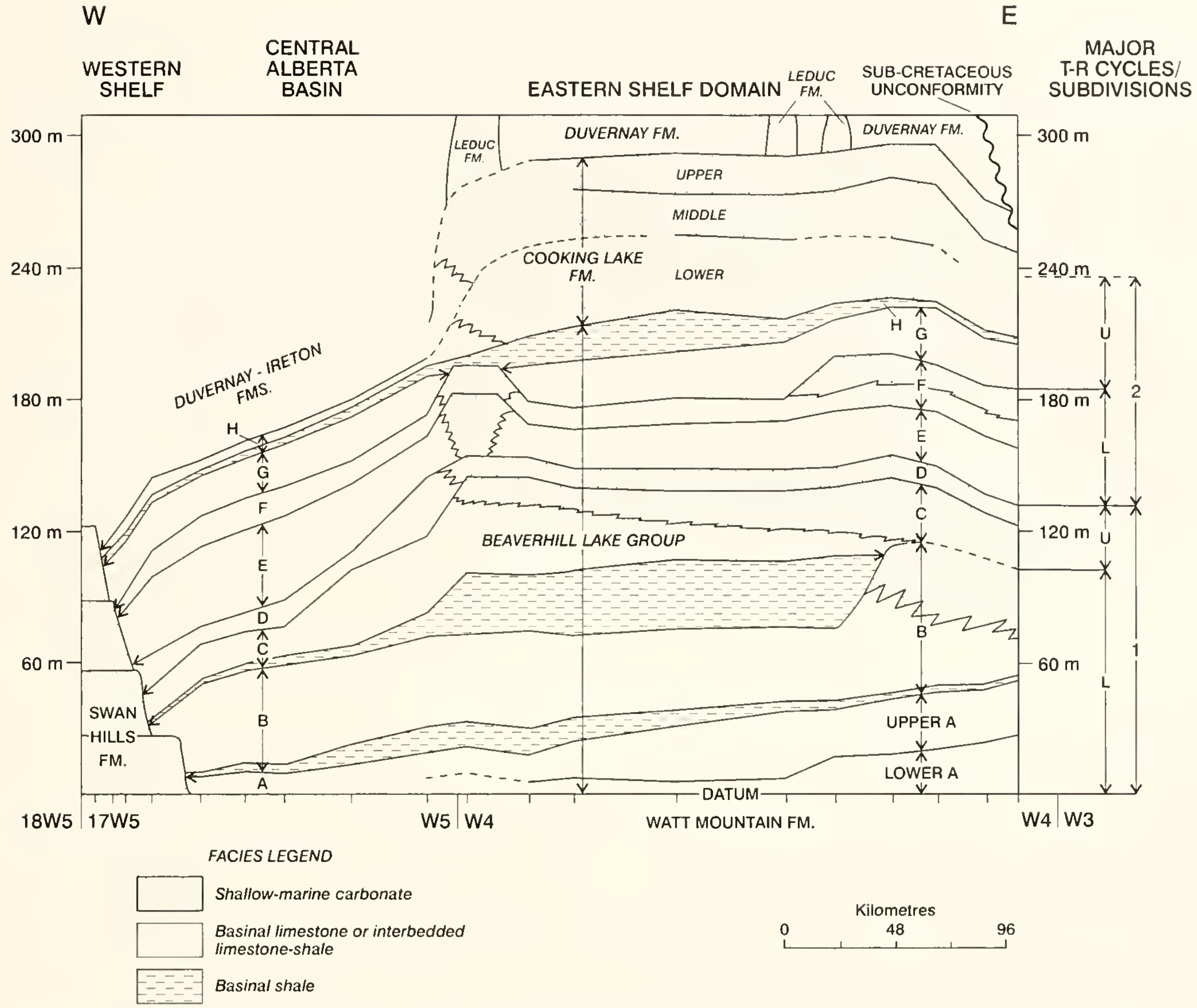


Text-figure 3.—Gamma-ray and sonic log signatures of the nine T-R cycles of the Beaverhill Lake Group and their lithofacies. These cycles are combined into two major T-R cycles (1 and 2), each of which is divided into two subdivisions (L and U). Well 6-35-46-15W4, Eastern Shelf Domain. Depths correspond to log depths. *See* Text-fig. 2 for location.

limited to the Eastern Shelf Domain, east of the Fifth Meridian. Basinal, deeper-water facies form clinoforms to the west and distally onlap the Swan Hills platform-bank complex on the Western Shelf.

The T-R cycles on the Eastern Shelf and in the Central Alberta Basin are split into two major T-R successions. Each of these T-R cycles, in turn, can be subdivided into two T-R cycle subdivisions. The major T-R cycles and their subdivisions are marked on the gamma-ray log and on the sonic log on Text-figure 3 as well as on the cross-section on Text-figure 4.

The lower T-R succession 1 extends from the base of the group to the top of cycle D. The transgressive phase of this succession extends up into the calcareous shales in the basal part of cycle B. The regressive phase culminates in the progradation of shallow-water



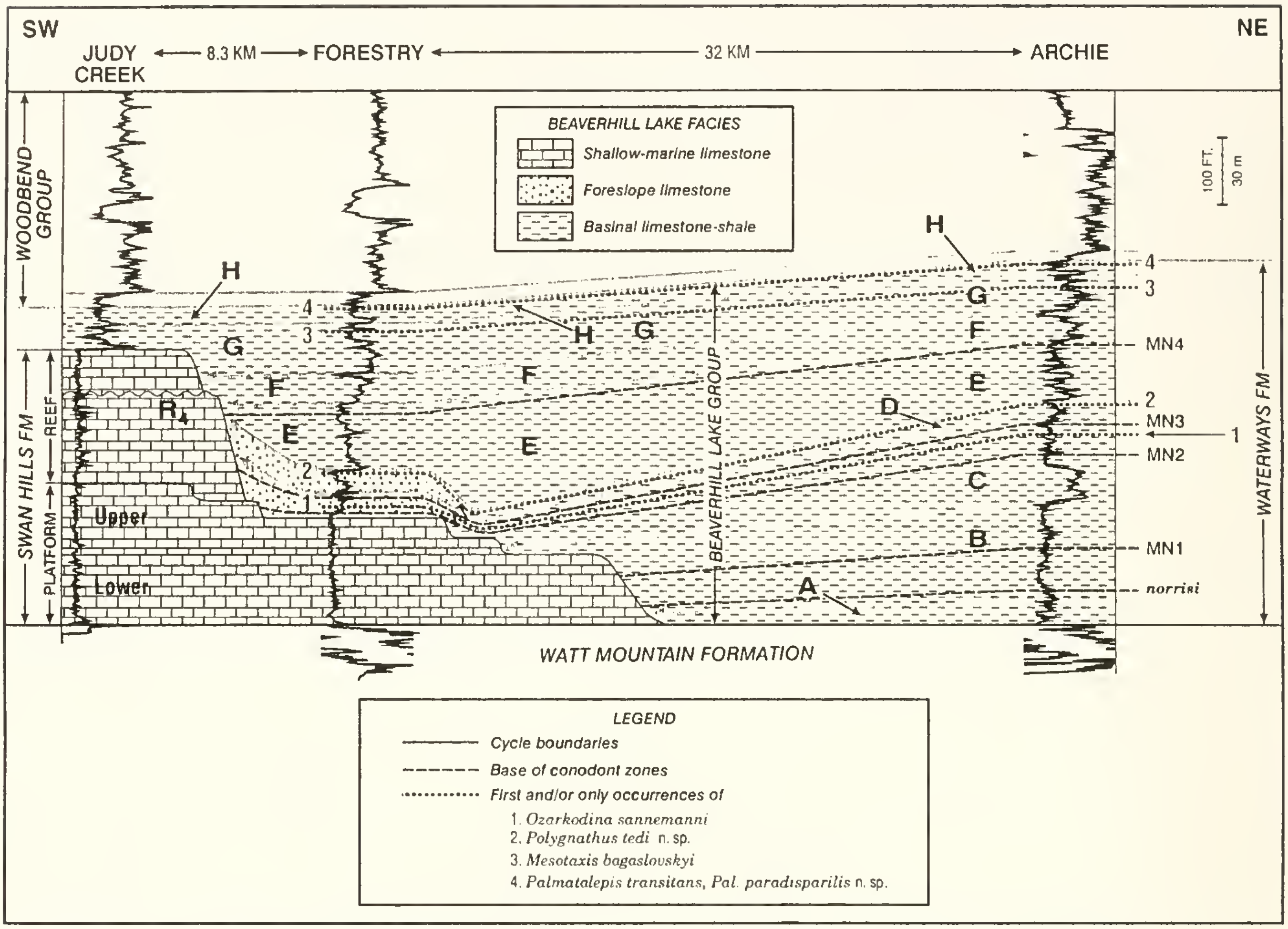
Text-figure 4.—Stratigraphic cross-section of the Beaverhill Lake Group showing the correlation of T-R cycles and the disposition of depositional facies, at a latitude of Township 50–52. The major T-R cycles and their subdivisions are labeled at the right end. Vertical ticks at the base of the cross-section correspond to the position of wells. *See* Text-fig. 2 for location of the transect.

platform carbonates of cycles C and D to approximately the Fifth Meridian.

T-R succession 1 can be split into two T-R cycle subdivisions (1L and 1U) at the top of cycle B. The onset of the T-R subdivision 1B is not marked by a significant shift in facies at the top of the cycle B platform, but by the deposition of a thick shale succession in the basin.

The upper T-R succession 2 extends from the top of cycle D to the top of cycle H in the Central Alberta Basin. The top of cycle H in the basin corresponds to the T-R cycle boundary that separates the Beaverhill Lake and Woodbend Group successions. Upslope, it correlates to the top of the lower Cooking Lake succession on Text-figure 4 (base of cycle 2, middle member of the Cooking Lake Formation of Wendte, 1994).

T-R succession 2 includes platform and isolated reefal carbonates of cycles E and F (cycle E platform facies occur south of the transect of the cross-section on Text-figure 4) and the argillaceous limestones and calcareous shales of cycles G and H. The position of maximum transgression occurs near the middle of cycle G. Calcareous shales in the upper part of cycle G and in cycle H sigmoidally prograde to the west, allowing for the outbuilding of the lower Cooking Lake platform succession to approximately the Fifth Meridian. The top of cycle F marks the division between the lower and upper T-R subdivisions (2L and 2U).



Text-figure 5.—Stratigraphic cross-section of the Beaverhill Lake Group from the Pan American Home Archie 4-1-66-8W5 well into the Judy Creek reef complex (well 4-35-63-11W5). T-R cycle boundaries correspond to the base of radioactive intervals on the gamma ray logs. The cross-section illustrates the parallelism of the T-R cycle and conodont zone boundaries. *See* Text-fig. 2 for location of the transect. The bases of conodont zones, *norrisi*, and MN 1 through MN 4, are marked. The numbers 1 through 4 mark the only and/or the first occurrences, of the cited conodont species.

WESTERN SHELF

Swan Hills carbonates on the Western Shelf consist of cyclic repetitions of shallow-marine limestones and dolostones. These carbonate successions lack the argillaceous limestones and calcareous shales that typify the basal portion of T-R cycles on the Eastern Shelf and in the Central Alberta Basin. As a result, cycle boundaries on the Western Shelf have no wireline-log signature and can only be identified by the examination of cores. Therefore, the cycle architecture of Swan Hills carbonates can only be discerned in areas with good well and core control. Also, lacking the log signature of T-R cycles on the Eastern Shelf Domain, the T-R cycle stratigraphy of the Western Shelf is independent of that on the Eastern Shelf Domain.

A synthesis of the T-R cycle stratigraphy of Swan Hills carbonates in the vicinity of the isolated Judy Creek reef complex is presented on the cross-section on Text-figure 5, along a transect from the Archie well southwest through the Forestry well into the Judy Creek reef complex (well 4-35-63-11W5). The T-R cycle stratigraphy of Swan Hills carbonates is a summary based on previous investigations of the Judy Creek reef complex (Wendte, 1992, and Wendte and Muir, 1995) as well as aspects from this regional study.

The Swan Hills Formation in the vicinity of the Judy Creek reef complex consists of four T-R cycles of growth, each with component sub-cycles, as described below.

(1) A widespread lower platform stage with the position of its margin depicted on Text-figure 2. Stratal relationships and conodont biostratigraphy suggest that this stage is coeval with the Lower A T-R cycle.

(2) A progressively more areally-restricted, upper platform stage.

(3) A rimmed reef complex stage with a peripheral reef rim and an interior lagoon (not illustrated on Text-fig. 5). The basal portion of this stage marks the change from transgression to progradation (regression) of the reef out over a previously drowned platform step. The top of this stage corresponds to a widespread subaerial unconformity (Wendte and Muir, 1995), termed R4 because it caps the top of the fourth reef cycle. Distinctive aspects of this unconformity have provided a basis for its widespread correlation, including to the Eastern Shelf. R4 corresponds to a level approximately at the middle of cycle C bankward of the underlying cycle B platform margin (Text-fig. 4). The position of the margin of isolated reefs and coeval banks on Text-figure 2 corresponds to an initial phase of this stage.

(4) An upper ramp-bounded shoal stage on the isolated reefs. The top of this stage is time-diachronous. Cycles of growth younger than that represented at the 4-35-63-11W5 well are present elsewhere on the Judy Creek reef and other isolated Swan Hills reefs, as well as on the Swan Hills banks.

CORRELATION OF WATERWAYS SUCCESSIONS IN THE PAN AMERICAN HOME ARCHIE AND IMPERIAL FORESTRY WELLS

The Archie and Forestry wells occur on the west side of the Central Alberta Basin (Text-fig. 2). The location of these wells is analogous to a distal position on the basinal clinoforms of the Waterways Formation on the regional cross-section on Text-figure 4.

The tops of T-R cycles A through H occur at the base of radioactive, argillaceous successions at the Archie well on the northeast end of the cross-section on Text-figure 5. These T-R cycle boundaries clinoform to the southwest, away from the position of the Archie well. The tops of cycles A and B onlap the flanks of the Lower and Upper Swan Hills platforms, respectively, northeast of the position of the Forestry well. The tops of cycles C and D correlate up into foreslope successions of the Forestry well before onlapping the flanks of the Judy Creek reef complex. These T-R cycle boundaries equate to positions in the ramp-bounded shoal above R4 at Judy Creek.

The tops of cycles E and F correlate to analogous positions in the Forestry well before onlapping against the flank of the Judy Creek reef complex. The tops of cycles G and H (top of Beaverhill Lake Group) correlate to analogous positions in the Forestry well and to the base of Waterways successions in the Imperial Judy Creek 4-35-63-11W5 well that overlie the Swan Hills Formation.

The close relationship between physical stratigraphy and conodont biostratigraphy is demonstrated on Text-figure 5. The positions of the base of the *norrisi* Zone and of MN zones 1 to 4 are shown for the Archie and Forestry wells. The biostratigraphic and T-R cycle boundaries are remarkably parallel. This close relationship is reinforced by correlations of the wells based on the single occurrences of (1) *Ozarkodina sannemanni* in MN Zone 2 and of (2) *Polygnathus tedi* in MN Zone 3, and on the lowest occurrences of (3) *Mesotaxis bogoslovskyi* and of (4) *Palmatolepis paradisparilis* and *Palmatolepis transitans* in MN Zone 4. These positions are marked on Text-figure 5.

In the Archie well, the base of the *norrisi* Zone occurs a thin interval (19–19.7 ft; 5.8–6.0 m) above the top of cycle A. Based on a more regional study, however, this is considered to be a late entry for this zone, as elsewhere the base of the *norrisi* Zone is found between Lower A cycle and Upper A cycle (Text-fig. 6).

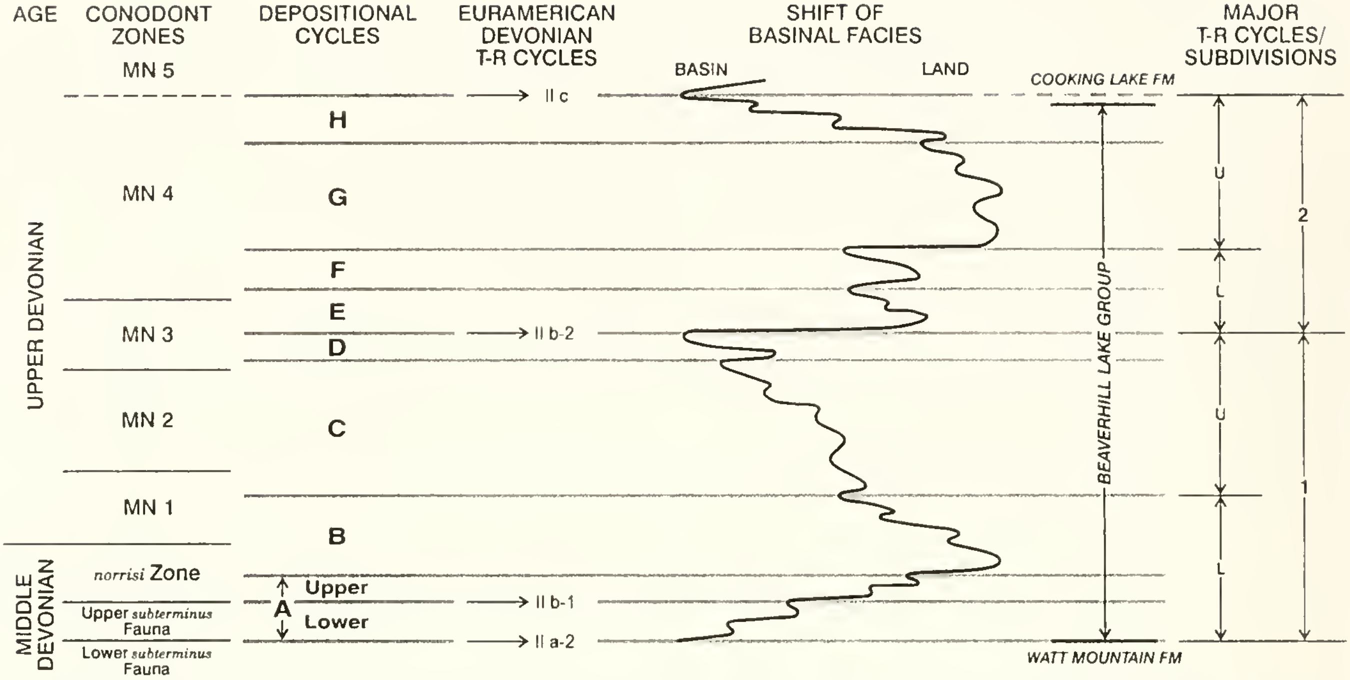
In the Archie well, the base of MN Zone 1 occurs about mid-way within the interval of cycle B. This relationship is found in the more regional coverage as well. The bases of MN Zones 2 and 3 are within cycle C in the Archie well, with Zone 3 close to the top of cycle C interval. In the Forestry well, the bases of both zones are found between the top of cycle C and the top of the Swan Hills Platform, and again with Zone 3 close to the cycle top. These relative positions of the bases of Zones 2 and 3 are also found in our more regional study.

The base of MN Zone 4 is located high up within cycle E in both wells. The base of MN Zone 5 is not found in the successions in these wells, but based on our regional coverage, it may occur extremely high in the Beaverhill Lake Group and certainly does so in the basal part of the overlying Duvernay Formation.

CORRELATION OF THE T-R CYCLES WITH CONODONT ZONES

Text-figure 6 shows the relationship between the conodont zones, depositional cycles, Euramerican Devonian T-R cycles (Johnson *et al.*, 1985; Johnson and Klapper, 1992; Day *et al.*, 1996), and the shift of basinal facies of the Beaverhill Lake Group in the Alberta Basin. The spacing of the conodont zones is based on values provided by Klapper (1997) from his work on the Frasnian Composite Standard.

As noted above, the Waterways Formation consists of two megacycles, with the lower T-R succession 1 ranging from the onset of cycle A to the top of cycle D. The upper T-R succession 2 ranges from the base



Text-figure 6.—A summary of the Beaverhill Lake Group from south-central Alberta, showing its conodont zones, depositional cycles, Euramerican Devonian T-R cycles, shift of basinal facies, and major T-R cycles and subdivisions. Conodont zones are after Bunker and Klapper (1984), Witzke *et al.* (1985), Klapper and Johnson (*in* Johnson, 1990), and Klapper (1989). Devonian T-R cycles are after Johnson *et al.* (1985), Johnson and Klapper (1992), and Day *et al.* (1996). Spacing of conodont zones is based on values in Klapper (1997).

of cycle E to the top of cycle H. The start of succession 1 coincides with the base of the Upper *subterminus* Fauna, and is at the start of cycle IIa-2. A major transgression preceding the Lowermost *asymmetricus* Zone (=*norrisi* Zone) was suggested earlier by Talent and Yolkin (1987) for the Canning Basin, Western Australia, and for southern West Siberia. A fourth order cycle, labelled 3B, was suggested to start in the Late *disparilis* Zone (=Upper *subterminus* Fauna) during the Timan Horizon in West Bashkortostan (Yunusov *et al.*, 1997). This may be an equivalent of cycle IIa-2. Racki (1993, 1997) discussed the global significance of this post-*Stringocephalus* transgression, and the presence of the transgression at or near the *norrisi* Zone in western New York State was discussed by Kirchgasser *et al.* (1997). The peak of the lower succession 1 occurs in the lower part of cycle B, which occurs in the upper part of the *norrisi* Zone.

Elsewhere, the start of T-R cycle IIa-2 is present at the base of the Argillaceous limestone of the Point Wilkins Member of the Souris River Formation in central and southern Manitoba, at the base of the Amco Member of the Slave Point Formation at Great Slave Lake, District of Mackenzie, Northwest Territories, and at the base of the Allochthonous Beds in the Powell Creek area in District of Mackenzie, western Northwest Territories (Uyeno, 1998).

T-R cycle IIb-1 (IIb of Johnson *et al.*, 1985) is placed at the base of the *norrisi* Zone, and in the Waterways sequence occurs at the base of Upper A cycle. In terms of the Waterways Formation nomenclature, this is at the base of the Firebag Member (Uyeno, 1974) or the base of the Peace Point Member (Uyeno *in* Norris and Uyeno, 1983), in Alberta. In central and southern Manitoba it coincides with the base of the Micritic limestone of the Point Wilkins Member of the Souris River Formation, and in central and eastern Iowa with the base of the Lithograph City Formation (Day *et al.*, 1996).

The start of the upper T-R succession 2 occurs at mid-way of MN Zone 3, and coincides with the base of T-R cycle IIb-2. This cycle represents an intra-IIb cycle deepening event (Day *et al.*, 1996). It is also observed in the Lithograph City Formation, within the Andalusia and Idlewild members, in central and eastern Iowa. In central and southern Manitoba, this event may occur at the base of the Dolomitic limestone of the Point Wilkins Member, Souris River Formation (Day *et al.*, 1996).

The maximum transgression of the upper T-R succession 2 is in cycle G, and lies within MN Zone 4. As noted above, the top of the upper megacycle is at the top of cycle H, and correlates to the top of the lower Cooking Lake succession. This level is in MN

Zone 5 (=*Palmatolepis punctata* Zone) (Klapper, 1989, 1997; Klapper and Becker, 1999). It coincides with the start of T-R cycle IIc, the beginning of the next major deepening event, and the deposition of the Woodbend Group. This cycle has been recognized over a large area (Johnson *et al.*, 1985; Racki, 1993, 1997; Racki and Bultynck, 1993; among others).

CONODONTS

CONODONT FAUNA

The studied conodont fauna is generally well preserved and has color alteration index (CAI) of 2 (Epstein *et al.*, 1977). The Archie well was sampled at 75 intervals, with each sample averaging 448 g, whereas the 51 Forestry well samples averaged 702 g. The sampled intervals are shown on Text-figures 7 and 8, with listings of selected species only.

Of some interest is the concentration of conodonts in allochthonous carbonate sands in the foreslope succession in the Forestry well, from samples number 5 through 13 (interval from 8564.5 ft, 2610.5 m to 8624.5 ft, 2628.7 m). The conodont animals may have inhabited a more proximal foreslope environment, and were concentrated when the sand was episodically shed down the reef foreslope and deposited in and around the well-site.

CONODONT BIOSTRATIGRAPHY

Five, and possibly six, conodont zones are recognized in the Beaverhill Lake Group as represented in the two wells. In ascending order, they are the Upper *subterminus* Fauna, the *norrisi* Zone, and MN (Montagne Noire) zones 1 to 4. The first interval is tentatively recognized in the lowest parts of the Archie well, and is succeeded by the *norrisi* Zone in the same well. Zone MN1 may possibly be present in the lowest parts of the Forestry well. The higher zones are present in both wells. In the following discussion, refer to Text-figures 7 and 8. It should be noted that the Archie well was independently sampled by McLean and Klapper (1998), and they recognized exactly the same zonal succession.

The history of the *subterminus* Fauna was succinctly summarized by Rogers (1998), so suffice it to say here that Bunker and Klapper (1984) and Witzke *et al.* (1985) had proposed the *subterminus* Fauna as the shallow-water carbonate shelf equivalent of the *disparilis* Zone of the standard conodont zonation. However, the exact relationship of the *subterminus* Fauna to the standard zonation was found to be not entirely clear in a study of the Little Cedar and lower Coralville formations of Iowa, by Rogers (1998). The refined definition of the fauna, as subsequently proposed by Witzke *et al.* (1989), is inapplicable to the Beaverhill Lake collection in these wells. The Upper *subterminus* Fauna has been recognized, however, in some wells included in the overall study, of which this is a part (*see* Wendte *et al.*, 1995).

In the Archie well, the lowest interval of 2313.0 to 2320.7 m, below the first occurrence of *Pandorinellina insita* (Stauffer), is possibly assignable to the *norrisi* Zone (*see* below). This is based on our more regional correlations, where the base of the *norrisi* Zone occurs much lower. The following species that appear in this interval and continue on higher include *Polygnathus angustidiscus*, *P. xylus xylus*, *P. dubius*, *P. alatus*, and *Icriodus subterminus*.

The *norrisi* Zone, proposed by Klapper and Johnson (*in* Johnson, 1990), is the youngest Middle Devonian conodont zone. This zonal interval was previously referred to the Lowermost *asymmetricus* Zone of Ziegler (1971) (Klapper and Johnson [*ibid.*]). Although the entry of *Skeletognathus norrisi* marks the base of the zone, in its absence the zonal base is approximated with the entry of *Pandorinellina insita*. The zone is recognized in the Archie well, within the interval of 2291.8 to 2310.1 m. Herein, *S. norrisi* was recovered only from an interval assigned to MN Zone 2 in the Forestry well. That this species ranges as high as MN Zone 2 has been demonstrated by means of graphic correlation by Klapper (1997).

The Frasnian Stage of the Upper Devonian was divided by Klapper (1989) into 13 conodont zones at the Montagne Noire in southern France. Of these, the lowest four zones, MN zones 1 to 4, are recognized in the Beaverhill Lake sequence. The interval of MN zones 1 to 4 was previously referred to the Lower *asymmetricus* Zone of Ziegler (1971). It should also be noted that the interval, including the *norrisi* Zone, and MN zones 1 to 3, was placed in the *falsiovalis* Zone by Sandberg *et al.* (1989) (Klapper and Johnson *in* Johnson, 1990).

The base and the top of MN Zone 1 are at the first appearances of the early and late forms of *Ancyrodella rotundiloba* (Klapper, 1985), respectively. In the Archie well, MN Zone 1 occurs in the interval of 2253.2 to 2291.3 m, and may be present in the lowest parts of the Forestry well, in the interval of 2630.1 to 2634.1 m. The only occurrence of *A. binodosa* is within MN Zone 1 in the Archie well. *Polygnathus incompletus* makes its first appearance within this zone and continues up to MN Zone 2, also in the Archie well.

MN Zone 2 has its base and top at the first appearances of the late form of *Ancyrodella rotundiloba* and *A. rugosa*, respectively (Klapper, 1989). In the Archie well, it is in the interval of 2236.3 to 2249.1 m, and in the Forestry well, 2622.3 to 2629.7 m. The only

Sample No	Interval (ft)	Interval (m)	Pol. angustidiscus	Pol xylus xylus	Polygnathus alatus	Polygnathus dubius	Icriodus subterminus	Pandorinellina insita	Anc rotundiloba early	Pol. incompletus	Ancyrodella binodosa	Anc rotundiloba late	Ozark sannemanni	Polygnathus pennatus	Icriodus expansus	Ancyrodella rugosa	Ancyrodella alata	Pol cf P decorosus	Meso. asymmetrica	Ancyrodella recta	Ancyrodella triangulata	Polygnathus tedi	Ozarkodina brevis	Mesotaxis ovalis	Anc postbinodosa	Ancyrodella africana	Meso. bogoslovskyi	Pal paradisparilis	Pol cf P webbi	Palmatolepis transitans	Conodont zones	Cycles
75	7103.0-7104.5	2165.0-2165.5				X													X					X				X	X	X	MN 4	H
74	7104.5-7107.5	2165.5-2166.4																?														
73	7113.0-7114.5	2168.0-2168.5																X	X					?								
72	7122.0-7125.5	2170.8-2171.9																X					X				X					G
71	7133.5-7136.0	2174.3-2175.1																	X								X					
70	7142.6-7145.1	2177.1-2177.8																X														
69	7148.5-7150.8	2178.9-2179.6														?	?		X													
68	7161.3-7163.5	2182.7-2183.4																X	X													
67	7163.8-7166.3	2183.5-2184.3														X			X													
66	7169.5-7171.0	2185.3-2185.7						?								X			X							X						F
65	7176.0-7178.0	2187.2-2187.9														X			X					X		X						
64	7180.0-7183.0	2188.5-2189.4														X			X				X									
63	7184.0-7186.5	2189.7-2190.4						X										?														
62	7202.0-7206.0	2195.2-2196.4																X	X													
61	7212.3-7214.3	2198.3-2198.9														X		X	X													E
60	7218.3-7220.3	2200.1-2200.7															X	X	X						X							
59	7228.5-7230.5	2203.2-2203.9	X		?											X	X	X	X						?						MN 3	
58	7232.3-7233.3	2204.4-2204.7	X															X	X			X										
57	7235.5-7237.5	2205.4-2206.0																	X													
56	7239.5-7241.0	2206.6-2207.1																?	X													
55	7243.5-7245.5	2207.8-2208.4														?		X														
54	7248.5-7250.5	2209.3-2210.0																X	X													
53	7253.5-7255.5	2210.9-2211.5																X	X													
52	7256.0-7258.0	2211.6-2212.2														?			X													
51	7262.5-7264.5	2213.6-2214.2						X																								
50	7270.5-7271.5	2216.0-2216.4					X												?													
49	7278.3-7279.8	2218.4-2218.9	X				X									X							X									
48	7281.5-7284.0	2219.4-2220.2	X				X									?																
47	7286.0-7288.0	2220.8-2221.4					X										?	X					X									
46	7291.0-7293.3	2222.3-2223.0														X	X															
45	7298.0-7299.8	2224.4-2225.0														X	X		X		?	X	X	X								D
44	7303.0-7305.0	2226.0-2226.6					X										X			X												
43	7316.5-7318.5	2230.1-2230.7					X												X													
42	7323.0-7325.0	2232.1-2232.7				X	X										X	X	X													C
41	7333.0-7334.5	2235.1-2235.6	cf													X																
40	7337.0-7339.0	2236.3-2236.9	X			cf	X	X						X	X																MN 2	
39	7346.5-7348.5	2239.2-2239.8		X										X																		
38	7351.0-7352.5	2240.6-2241.0			X		X	X				X	X																			
37	7357.0-7359.5	2242.4-2243.2								X																						
36	7363.5-7365.0	2244.4-2244.9		X			X					X																				
35	7371.5-7373.5	2246.8-2247.4					X			X		X																				
34	7377.5-7379.0	2248.7-2249.1					X	X		X		X																				
31	7392.5-7394.5	2253.2-2253.8								X																					MN 1	
30	7396.5-7398.5	2254.5-2255.1		X	X					X																						
28	7416.8-7418.0	2260.6-2261.0								X																						
27	7420.3-7422.8	2261.7-2262.5			X					X																						
26	7429.8-7431.5	2264.6-2265.1		X			X		?	X																						
24	7444.5-7446.0	2269.1-2269.5					X	X	X	X																						
23	7454.0-7455.5	2272.0-2272.4			X		X			X																						B
22	7460.0-7461.5	2273.8-2274.3					X																									
21	7462.3-7464.0	2274.5-2275.0					X		X	X																						
20	7472.0-7473.5	2277.5-2277.9					X				X																					
19	7483.0-7484.8	2280.8-2281.4		?			X	X		X																						
18	7488.0-7489.5	2282.3-2282.8					X																									
17	7499.0-7500.5	2285.7-2286.2					X																									
16	7509.0-7510.5	2288.7-2289.2					X	X		X																						
15	7516.0-7517.5	2290.9-2291.3			X	X	X		X	X																						
14	7519.0-7520.5	2291.8-2292.2					X																								norrisi	
13	7531.0-7532.5	2295.4-2295.9				?																										
11	7553.0-7554.0	2302.2-2302.5				X		X																								
10	7566.0-7567.5	2306.1-2306.6				X	X																									
9	7576.5-7577.5	2309.3-2309.6			X	X	X	X																								
8	7578.3-7579.0	2309.9-2310.1						X																								
6	7588.5-7590.0	2313.0-2313.4		X			X																									A
5	7594.0-7595.5	2314.7-2315.1		X	cf	X																										
4	7598.5-7599.5	2316.0-2316.3		X																												
3	7602.3-7603.5	2317.2-2317.5		X																												
2	7613.0-7614.0	2320.4-2320.7	X																													

Text-figure 7.—Distribution of conodonts in the Beaverhill Lake Group in the Pan American Home Archie 4-1-66-8W5 well. *Anc.* = *Ancyrodella*, *Meso.* = *Mesotaxis*, *Ozark.* = *Ozarkodina*, *Pal.* = *Palmatolepis*, *Pol.* = *Polygnathus*. SWP = Swan Hills Platform, D. Fm. = Duvernay Formation, MN = Montagne Noire. Note: The sampled intervals that were barren of conodonts, or those that yielded only indeterminate fragments, have been omitted.

Sample No.	Interval (ft)	Interval (m)	*Icriodus subterminus*	*Polygnathus alatus*	*Polygnathus dubius*	*Anc. rotundiloba late*	*Pandorinellina insita*	*Ozark. sannemanni*	*Ozarkodina brevis*	*Skeletognathus norrisi*	*Polygnathus webbi*	*Mesotaxis distinctus*	*Ancyrodella triangulata*	*Mesotaxis keithi*	*Ancyrodella rugosa*	*Meso. asymmetrica*	*Mesotaxis ovalis*	*Pol. cf. P. decorosus*	*Mehlina gradata*	*Playfordia primitiva*	*Ancyrodella recta*	*Ancyrodella alata*	*Polygnathus tedi*	*Anc. postbinodosa*	*Ancyrodella africana*	*Pol. angustidiscus*	*Meso. bogoslovskyi*	*Pol. xylus xylus*	*Pal. paradisparilis*	*Palmatolepis transitans*	*Icriodus expansus*	Conodont zones	Cycles/Formations
50	8319.5-8320.5	2535.8-2536.1			X																								X	X	X	MN 4	D Fm
49	8323.5-8325.0	2537.0-2537.5			X																									X	X		
48	8329.5-8332.0	2538.8-2539.6																										X	X	X			H
47	8335.5-8337.5	2540.7-2541.3	X																									X					
46	8341.0-8343.0	2542.3-2542.9																										X					
45	8344.5-8347.0	2543.4-2544.2																		X					X			X					
44	8351.0-8353.0	2545.4-2546.0																	X	X								X					
43	8356.5-8358.0	2547.1-2547.5							X																		X						G
42	8359.5-8360.5	2548.0-2548.3																aff	X														
41	8363.0-8365.0	2549.0-2549.7																aff									X						
40	8368.5-8370.5	2550.7-2551.3																															
39	8374.5-8377.0	2552.5-2553.3																aff/X															
38	8384.0-8385.5	2555.4-2555.9																	X	X													
34B	8420.3-8421.0	2566.5-2566.7	cf												X	X	X	aff							X	cf							F
34A	8423.5-8424.0	2567.5-2567.6													X	X		aff								cf							
33	8426.0-8428.5	2568.2-2569.0													X	X		X															
32	8436.0-8438.0	2571.3-2571.9													X	X		X							X								
31	8439.0-8441.0	2572.2-2572.8													X	X									X								
30	8444.0-8445.0	2573.7-2574.0													X	X		X	X						X								
29	8449.0-8451.0	2575.3-2575.9	?													X																	
28	8453.5-8456.0	2576.6-2577.4													X	X		X	X														
27	8461.0-8463.0	2578.9-2579 5														?		X							?								
26	8464.5-8466.5	2580.0-2580.6							X						X	X		X							X								E
25	8468.0-8470.5	2581.0-2581.8	cf						X						X	X		X						X									
24	8473.0-8475.5	2582.6-2583.3																X															
23	8482.0-8484.5	2585.3-2586.1									X					X		X						X									
22	8488.0-8490.5	2587.1-2587.9														X																MN 3	
21	8493.0-8495.5	2588.7-2589.4									X							X															
20	8500.5-8503.0	2591 0-2591.7														X		?															
19	8510.5-8513 0	2594 0-2594.8	X	X					X						X			X		X													
18	8519.0-8521.5	2596.6-2597.4	X													X																	
17	8527.0-8529.5	2599.0-2599.8														X																	
16	8536.5-8539.0	2601.9-2602.7	X						X																								
15	8546.5-8549.0	2605.0-2605 7														X																	
14	8559.5-8562.0	2608.9-2609.7																?															
13	8564.5-8567.0	2610.5-2611.2									X				X	X		X			X	X	X										D
12	8571.5-8574.0	2612.6-2613.4	X				X		X		X		X	X	X	X	X	X	X		X	X											
11	8576.0-8578.5	2614.0-2614.7							X		X			X		X			X	X													
10	8583.0-8585.5	2616.1-2616.9							X																								
9	8590.0-8592.5	2618.2-2619.0					X									cf		X	X														
8	8595.5-8598.0	2619 9-2620.7		X			X				X	X	X	X	X	X	X	X	X														
7	8603.5-8605.5	2622.3-2623.0	cf	X			X			X	X																					MN 2	C
6	8613.0-8615.5	2625.2-2626.0	cf		X		X																										
5	8621.5-8624.5	2627.8-2628.7	cf/X	X		X	X	X	X																								
4	8625.5-8627.5	2629.1-2629.7				X	X																										
3	8629.0-8632.0	2630.1-2631.0		?																													
2	8634.0-8636.0	2631.6-2632.3		X	cf																												
1	8639.5-8642.0	2633 3-2634 1	cf																														SWI

Text-figure 8.—Distribution of conodonts in the Beaverhill Lake Group in the Imperial Forestry 16-7-64-10W5 well. (See caption to Text-fig. 7 for abbreviation and notes.)

occurrences of *Ozarkodina sannemanni* in both wells are within MN Zone 2.

MN Zone 3 is defined with its base and top at the first appearances of *Ancyrodella rugosa* and *Palmatolepis transitans*, respectively (Klapper, 1989). In the Beaverhill Lake sequence, *P. transitans* makes a late appearance, based on graphic correlation by Klapper (pers. commun., 1995). The top of the zone is instead marked by the first occurrence of *A. postbinodosa*, which is restricted to Zone 4, again based on graphic correlation by Klapper (pers. commun., 2000). Using this revised base of MN Zone 4 (and therefore, the top of MN Zone 3), the zone is present in the Forestry well within the interval of 2587.1 to 2620.7 m, and in the Archie well, 2203.2 to 2235.6 m. The species confined to this zone include *A. recta*, possibly *A. trian-*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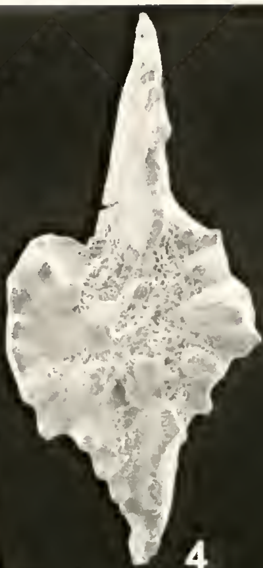
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gulata, and *Polygnathus tedi* in both wells, and in the Forestry well only, *Mesotaxis distinctus* and *M. keithi*. The species with their lowest occurrences within this zone include *Polygnathus* cf. *P. decorosus* of Uyeno (1974), *A. alata*, *M. asymmetrica*, and *M. ovalis* in both wells, and *Playfordia primitiva* in the Forestry well only.

As noted above, the base of MN Zone 4 in the present study is at the first occurrence of *Ancyrodella postbinodosa*. Using this definition, the zone is present in the Forestry well within the interval of 2535.8 to 2586.1 m, and in the Archie well, 2165.0 to 2200.7 m. In the Forestry well, *Palmatolepis transitans* makes its first appearance at 2539.6 m, and in the Archie well, at 2165.5 m. That the occurrences in the Forestry well are high in MN Zone 4, and approaching MN Zone 5, is suggested by a form of *P. transitans* that may be transitional to *P. gutta* (*see* under *P. transitans* in the Systematics section). *Mesotaxis bogoslovskyi* and *P. paradisparilis* also occur high within the zone, while *A. africana* has a longer range within the zonal interval. No conodonts to suggest the presence of MN Zone 5 were found in either of these wells.

SYSTEMATIC PALEONTOLOGY

All of the genera listed in this section belong to the Polygnathidae, in the sense used by Klapper, Kuz'min, and Ovnatanova (1996, p. 137). The distribution of the listed conodonts is given in Text-figures 7 and 8.

The primary type and figured specimens are deposited in the collection of the Geological Survey of Canada (GSC), 601 Booth Street, Ottawa, Ontario.

Family **POLYGNATHIDAE** Bassler, 1925

Genus **ANCYRODELLA** Ulrich and Bassler, 1926

Type species.—*Ancyrodella nodosa* Ulrich and Bassler, 1926, p. 48.

Ancyrodella postbinodosa, new species

Plate 1, figures 16–19

Diagnosis.—Pa element with two distinctly large nodes on either side of platform; nodes may be accompanied by up to three much smaller nodes on one side, or both sides, of platform. Platform outline asymmetrical, with straight outer that is parallel with keel, and a rounded inner. Upper surface may have faint anteriorly-pointed ridges running from central node. Free blade and carina form very gentle curve. Denticles on free blade and posterior part of carina higher than those on mid-carina. Basal pit moderate-sized, with traces of laterally- or anteriorly-directed secondary keels.

Remarks.—Pa element is similar to *Ancyrodella binodosa* Uyeno, from which it differs primarily in its asymmetrical platform outline. The latter has rounded platform margins on both sides, and also a larger basal pit at similar growth stages. Based on graphic correlation (Klapper, pers. commun., 2000), the new species makes its first appearance in MN Zone 4. In this study, the lowest occurrence is taken as the base of that zone.

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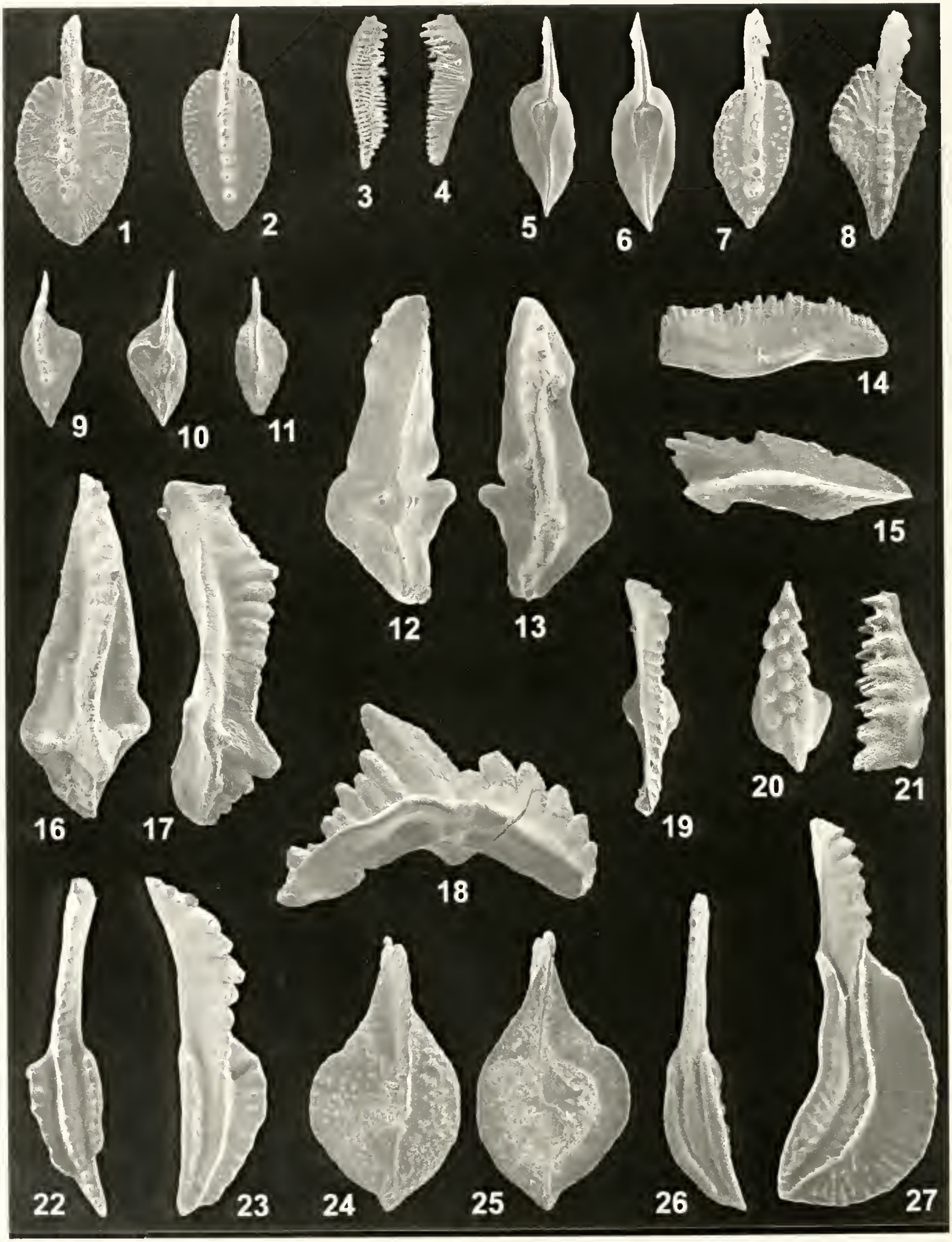
PLATE 1

All specimens of Pa elements. All figures ×50. All depth intervals have been corrected to logs. "Archie well" cited below is the Pan American Home A-1 Archie 4-1-66-8W5 well, GSC locality number C-222352; "Forestry well" is the Imperial Forestry 16-7-64-10W5 well, GSC locality number C-222353.

1, 2. *Ancyrodella rotundiloba* (Bryant, 1921), early form of Klapper (1985)
    1, 2. GSC 122721: Upper and lower views. Archie well, sample 15 (7516.0–7517.5 ft; 2290.0–2291.3 m).
3, 8, 9. *Ancyrodella alata* Glenister and Klapper (1966)
    3. GSC 122722: Lower view. Forestry well, sample 12 (8571.5–8574.0 ft; 2612.6–2613.4 m).
    8, 9. GSC 122723: Lower and upper views. Archie well, sample 45 (7298.0–7299.8 ft; 2224.4–2225.0 m).
4, 5. *Ancyrodella rotundiloba* (Bryant, 1921), late form of Klapper (1985)
    4, 5. GSC 122724: Upper and lower views. Forestry well, sample 5 (8621.5–8624.5 ft; 2627.8–2628.7 m).
6, 7. *Ancyrodella triangulata* Kralick (1994)
    6, 7. GSC 122725: Upper and lower views. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
10, 11. *Ancyrodella rugosa* Branson and Mehl (1934)
    10, 11. GSC 122726: Upper-lateral and lower views. Archie well, sample 45 (7298.0–7299.8 ft; 2224.4–2225.0 m).
12, 13. *Ancyrodella recta* Kralick (1994)
    12, 13. GSC 122727: Lower and upper views. Forestry well, sample 13 (8564.5–8567.0 ft; 2610.5–2611.2 m).
14, 15. *Ancyrodella africana* García-López (1981)
    14, 15. GSC 122728: Upper and lower views. Archie well, sample 66 (7169.5–7171.0 ft; 2185.3–2185.7 m).
16–19. *Ancyrodella postbinodosa*, n.sp.
    16, 17. GSC 122729 (holotype): Upper and lower views. Archie well, sample 60 (7218.3–7220.3 ft; 2200.1–2200.7 m).
    18, 19. GSC 122730 (paratype): Upper and lower views. Forestry well, sample 25 (8468.0–8470.5 ft; 2581.0–2581.8 m).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Stratum typicum and locus typicus.—Beaverhill Lake Group, Archie well, sample 60 (7218.3–7220.3 ft; 2200.1–2200.7 m).

Type series.—Holotype, the specimen illustrated in Plate 1, figures 16, 17 (GSC 122729). Paratype, GSC 122730.

Derivation of name.—In reference to the close similarity of the species to *Ancyrodella binodosa* Uyeno, 1967.

Genus **MESOTAXIS** Klapper and Philip, 1972

Type species.—*Polygnathus asymmetricus* Bischoff and Ziegler, 1957, pp. 88–89.

Mesotaxis distinctus Ovnatanova and Kuz'min, 1991

Plate 2, figures 1, 2

Mesotaxis distinctus Ovnatanova and Kuz'min (1991, p. 45, 47, pl. 1, figs. 11, 12).

Remarks.—One of the key characteristics of this species is the carina that terminates before the posterior end of the platform. There are two forms in the present material, one with a broad platform, and the other with narrow platform. The latter form may have adcarinal areas that are free of nodes, and in this respect differs from the holotype specimen. There seems to be no biostratigraphic significance to the forms

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PLATE 2

All specimens of Pa elements, unless otherwise indicated. All figures ×50. All depth intervals have been corrected to logs. "Archie well" cited below is the Pan American Home A-1 Archie 4-1-66-8W5 well, GSC locality number C-222352; "Forestry well" is the Imperial Forestry 16-7-64-10W5 well, GSC locality number C-222353.

1, 2. *Mesotaxis distinctus* Ovnatanova and Kuz'min (1991)
  1. GSC 122731: Upper view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
  2. GSC 122732: Upper view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
3, 4. *Skeletognathus norrisi* (Uyeno, 1967)
  3, 4. GSC 122733: Upper and lateral views. Forestry well, sample 7 (8603.5–8605.5 ft; 2622.3–2623.0 m).
5–7. *Mesotaxis keithi*, n.sp.
  5. GSC 122734 (paratype): Lower view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
  6. GSC 122735 (paratype): Lower view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
  7. GSC 122736 (holotype): Upper view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).
8. *Mesotaxis bogoslovskyi* Ovnatanova and Kuz'min (1991)
  8. GSC 122737: Upper view. Archie well, sample 72 (7122.0–7125.5 ft; 2170.8–2171.9 m).
9–11. *Palmatolepis paradisparilis*, n.sp.
  9. GSC 122738 (paratype): Upper view. Archie well, sample 75 (7103.0–7104.5 ft; 2165.0–2165.5 m).
  10. GSC 122739 (holotype): Lower view. Forestry well, sample 48 (8329.5–8332.0 ft; 2538.8–2539.6 m).
  11. GSC 122740 (paratype). Upper view. Archie well, sample 75 (7103.0–7104.5 ft; 2165.0–2165.5 m).
12, 13, 16–18. *Polygnathus tedi*, n.sp.
  12, 13. GSC 122741 (paratype): Lower and upper views. Archie well, sample 45 (7298.0–7299.8 ft; 2224.4–2225.0 m).
  16, 17. GSC 122742 (holotype): Upper and lateral views. Forestry well, sample 13 (8564.5–8567.0 ft; 2610.5–2611.2 m).
  18. GSC 122743 (paratype): Lateral view of Pb element. Forestry well, sample 13 (8564.5–8567.0 ft; 2610.5–2611.2 m).
14. *Mehlina gradata* Youngquist (1945)
  14. GSC 122744: Lateral view. Forestry well, sample 12 (8571.5–8574.0 ft; 2612.6–2613.4 m).
15. *Playfordia primitiva* (Bischoff and Ziegler, 1957)
  15. GSC 122745: Lateral view. Forestry well. sample 38 (8384.0–8385.5 ft; 2555.4–2555.9 m).
19. *Ozarkodina sannemanni* (Bischoff and Ziegler, 1957)
  19. GSC 122746: Upper view. Forestry well, sample 5 (8621.5–8624.5 ft; 2627.8–2628.7 m).
20, 21. *Icriodus subterminus* Youngquist (1947)
  20, 21. GSC 122747: Upper and lateral views of I element. Forestry well, sample 5 (8621.5–8624.5 ft; 2627.8–2628.7 m).
22, 23. *Polygnathus* cf. *P. decorosus* Stauffer (1938) of Uyeno (1974)
  22. GSC 122748: Upper view. Archie well, sample 58 (7232.3–7233.3 ft; 2204.4–2204.7 m).
  23. GSC 122749: Upper view. Forestry well, sample 23 (8482.0–8484.5 ft; 2585.3–2586.1 m).
24, 25. *Palmatolepis transitans* Müller (1956)
  24, 25. GSC 122750: Upper and lower views. Forestry well, sample 48 (8329.5–8332.0 ft; 2538.8–2539.6 m).
26. *Polygnathus incompletus* Uyeno (1967)
  26. GSC 122751: Upper view. Archie well, sample 15 (7516.0–7517.5 ft; 2290.0–2291.3 m).
27. *Polygnathus alatus* Huddle (1934)
  27. GSC 122752: Upper view. Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).

since they occur in similar intervals. Similar variations were noted by Klapper (1989) in *Polygnathus dengleri* Bischoff and Ziegler.

Mesotaxis keithi, new species
Plate 2, figures 5–7

Diagnosis.—Pa element with symmetrical to slightly asymmetrical platform. Platform upper surface covered with fine nodes, with free blade and carina forming straight line. Carina extends to posterior end of platform. Free blade about half of platform length. Pit small, surrounded by large, symmetrical basal cavity, located mid-way between mid-length and anterior end of platform.

Remarks.—In its symmetrical platform outline, the new species resembles *Mesotaxis ovalis* (Ziegler and Klapper), although it tends to be more slender. It differs from the latter primarily in the shape and position of the basal cavity; in *M. ovalis,* the basal cavity is more asymmetrical and located in mid-length of platform.

Stratum typicum and locus typicus.—Beaverhill Lake Group, Forestry well, sample 8 (8595.5–8598.0 ft; 2619.9–2620.7 m).

Type series.—Holotype, the specimen illustrated in Plate 2, figure 7 (GSC 122736). Paratypes, GSC 122734 and 122735.

Derivation of name.—From proper noun, Keith.

Genus **PALMATOLEPIS** Ulrich and Bassler, 1926

Type species.—*Palmatolepis perlobata* Ulrich and Bassler, 1926, p. 49.

Palmatolepis paradisparilis, new species
Plate 2, figures 9–11

Palmatolepis disparilis Ziegler and Klapper?. Uyeno, 1991, p. 144, pl. 3, figs. 20, 21.

Diagnosis.—Pa element with asymmetrical platform, the outer lobe slightly to moderately developed; lobe oriented laterally to slightly anteriorly. Upper surface smooth to sparsely nodose. Free blade-carina outline straight to slightly curved, with carina terminating before posterior end of platform. Basal pit large, asymmetrical, L-shaped, and clearly raised above surrounding platform.

Remarks.—The basal pit of the present species is similar in shape and size to that of *Palmatolepis disparilis* Ziegler and Klapper. The principal difference is in the outline of the platform, which in *P. paradisparilis* is more slender, with a narrow inner side, and a lobe on the outer. Platform of *P. disparilis* is also more robust and its upper surface more nodose.

Stratum typicum and locus typicus.—Beaverhill Lake Group, Forestry well, sample 48 (8329.5–8332.0 ft; 2538.8–2539.6 m).

Type series.—Holotype, the specimen illustrated in Plate 2, figure 10 (GSC 122739). Paratypes, GSC 122738 and 122740.

Derivation of name.—In reference to the close similarity of the species to *Palmatolepis disparilis* Ziegler and Klapper.

Palmatolepis transitans Müller (1956)
Plate 2, figs. 24, 25

Palmatolepis transitans Müller, 1956, pp. 18–19, pl. 1, fig. 1; Klapper, Kuz'min, and Ovnatanova, 1996, pp. 149–150, fig. 9.14 [see for further synonymy]; Kuz'min, 1998, pl. 7, fig. 1, pl. 8, figs. 1, 6, 7; Ding, Jiang, and Bai, 2000, pl. 1, fig. 18.

Remarks.—The specimen in Pl. 2, figs. 24, 25 herein differs slightly from the holotype in having a small sinus at the outer margin immediately adjacent to the posterior end of the platform. Its slightly rounded outer posterior margin is similar to the specimen illustrated by Kuz'min (1998, pl. 8, fig. 6), a form which he considered to be transitional to *Palmatolepis gutta* Kuz'min. *P. gutta,* a name given to a species that was left in open nomenclature by Uyeno (1991, pl. 3, figs. 24, 25; pl. 4, figs. 1, 2), is associated with *Polygnathus timanicus* Ovnatanova in the eastern Canadian Cordillera. *P. timanicus* has its lowest occurrences within MN Zone 5 (Klapper, 1997).

Genus **POLYGNATHUS** Hinde, 1879

Type species.—*Polygnathus dubius* Hinde, 1879, pp. 361–362.

Polygnathus tedi, new species
Plate 2, figures 12, 13, 16–18

Ozarkodina(?) aff. *proxima* (Pollock, 1968). Racki and Bultynck, 1993, pl. 3, fig. 12.

Diagnosis.—Pa element with an extended platform on either side, reaching to or almost to, the anterior and posterior ends. Free blade may therefore be extremely short. Platform widest adjacent to the basal cavity and main cusp. Upper surface of platform smooth; the widest part may have a node on one or both sides. The free/fixed blade-carina outline almost straight to gently incurved or sinuous. Unit gently arched as laterally viewed. Anterior of the cusp, the carina-free/fixed blade outline rises gently or steeply, with highest point near anterior end, followed by 2 or 3 small denticles. Basal pit moderately large, located about one-third of unit length from posterior end, with keels extending to both ends.

Remarks.—Some specimens with sinuous free/fixed blade-carina outline superficially resemble *Tortodus* sp. A of Sparling (1999). The latter differs in several aspects, however, including absence of any free blade, more central position of basal cavity and lack of large nodes on platform. *Polygnathus beckmanni* Bischoff and Ziegler similarly has fixed blade, but displays strong ridges on the platform.

The Pa element of the genus *Polygnathellus* Ulrich and Bassler (1926), as exemplified by its type species, *P. typicalis*, differs from *Polygnathus tedi* in its denticulation pattern: as laterally viewed, the outline of the denticles slopes downward from the main cusp, located over the pit, towards both ends.

The Pa element with fixed blade superficially resembles *Ancyrognathus ancyrognathoideus* (Ziegler). The latter differs from the present species in displaying a platform that is more uniformly tapering, with no abrupt widening adjacent to the cusp; also, there are no nodes on the platform.

A large Pb element was recovered with the Pa element of *Polygnathus tedi*. It is similar to some Pb elements assigned to *Ancyrognathus*, and illustrated by Klapper (1990, figs. 7.13 and 8.14). It has morphological similarities to the Pa elements in its general robustness, and large cusp, the wide ledge, and moderately large pit.

Stratum typicum and locus typicus.—Beaverhill Lake Group, Forestry well, sample 13 (8564.5–8567.0 ft; 2610.5–2611.2 m).

Type series.—Holotype, the specimen illustrated in Plate 2, figures 16, 17 (GSC 122742). Paratypes, GSC 122741 and 122743.

Distribution.—Found in MN Zone 3. Also in MN Zone 3 equivalent in the Kielce area, Holy Cross Mountains of southern Poland (Racki and Bultynck, 1993).

Derivation of name.—From proper noun, Ted, a derivative of Theodore.

Polygnathus cf. **P. decorosus** Stauffer of Uyeno, 1974

Plate 2, figures 22, 23

Polygnathus cf. *P. decorosus* Stauffer. Uyeno, 1974, p. 38–39, pl. 4, figs. 2, 7; pl. 5, fig. 2.

Diagnosis.—The free blade of the Pa element about half of unit length, and is extremely high at its midpoint, and abruptly or gradually sloping downward at anterior end. Unit straight to gently incurved. Lateral outline shows lower margin of unit gently and continuously arched. Pit narrow, of moderate size, surrounded by inverted basal cavity. Platform saggitate, rimmed with subdued nodes, or abbreviated, not reaching the posterior end.

Remarks.—The specimen illustrated by Uyeno (1974, pl. 4, fig. 7C) displays a wide inverted basal cavity; its full platform development is similar to the specimen in Plate 2, figure 23. The specimen in Plate 2, figure 22, with abbreviated platform, is similar to that in Uyeno (1974, pl. 4, fig. 2).

REFERENCES CITED

Bai, S.L., Bai, Z.Q., Ma, X.P., Wang, D.R., and Sun, Y.L.

1994. Devonian events and biostratigraphy of South China. Peking University Press, 303 pp.

Baliński, A.

1979. Brachiopods and conodonts from the Frasnian of the Debnik Anticline, southern Poland. Palaeontologia Polonica, no. 39, pp. 3–95.

Bassler, R.S.

1925. Classification and stratigraphic use of conodonts. Geological Society of America Bulletin, vol. 36, pp. 218–220.

Bischoff, G., and Ziegler, W.

1957. Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. Abhandlungen des Hessischen Landesamtes für Bodenforschung, Heft 22, 136 pp.

Branson, E.B., and Mehl, M.G.

1934. Conodonts from the Grassy Creek Shale of Missouri. University of Missouri Studies, vol. 8, pp. 171–259.

Bryant, W.L.

1921. The Genesee conodonts, with descriptions of new species. Bulletin of Buffalo Society of Natural Sciences, vol. 13, no. 2, 59 pp.

Bultynck, P.

1983. Origin and development of the conodont genus *Ancyrodella* in the late Givetian–early Frasnian. Fossils and Strata, no. 15, pp. 163–168.

Bultynck, P., and Hollard, H.

1980. Distribution comparée de conodontes et goniatites dévoniens des plaines du Dra, du Ma'der et du Tafilalt (Maroc). Aardkundige Mededelingen, vol. 1, 73 pp.

Bunker, B.J., and Klapper, G.

1984. Conodont zones and correlation of the Cedar Valley–State Quarry interval of eastern Iowa. *in* Underburden-Overburden, An examination of Paleozoic and Quaternary strata at the Conklin Quarry near Iowa City, B.J. Bunker and G.R. Hallberg, *eds.*, Geological Society of Iowa, Guidebook 41, pp. 15–18.

Day, J., Uyeno, T., Norris, W., Witzke, B.J., and Bunker, B.J.

1996. Middle-Upper Devonian relative sea-level histories of central and western North American interior basins. *in* Paleozoic sequence stratigraphy: views from the North American craton. B.J. Witzke, G.A. Ludvigson, and J. Day, *eds.*, Geological Society of America Special Paper 306, pp. 259–275.

Ding, G., Jaing, D.Y., and Bai, S.L.

2000. Evolution lineage of conodont *Ancyrodella* and the Middle-Upper Devonian boundary at Liujing, Guangxi. Acta Palaeontologica Sinica, vol. 39, pp. 197–204.

Epstein, A.G., Epstein, J.B., and Harris, L.D.

1977. Conodont color alteration—an index to organic metamorphism. U.S. Geological Survey Professional Paper 995, 27 pp.

García-López, S.

1981. Nueva especie de *Ancyrodella* (Conodonta) del Devónico superior de la Cordillera Cantábrica (no. de España). Estudios Geológicos, v. 37, pp. 263–267.

1987. Los conodontos y su aplicacion al estudio de las divisiones cronostratigraficas mayores del Devonico Asturleones (España). Publicaciones especiales del Boletín Geológico y Minero, vol. 97, nos. 3–5, 112 pp.

Glenister, B.F., and Klapper, G.

1966. Upper Devonian conodonts from the Canning Basin, Western Australia. Journal of Paleontology, vol. 40, pp. 777–842.

Hinde, G.J.

1879. On conodonts from the Chazy and Cincinnati Group of the Cambro-Silurian, and from the Hamilton and Genesee-Shale divisions of the Devonian, in Canada and the United States. Quarterly Journal of the Geological Society of London, vol. 35, pp. 351–369.

Huddle, J.W.

1934. Conodonts from the New Albany Shale of Indiana. Bulletins of American Paleontology, vol. 21, pp. 1–136.

Iudina, A.B.

1995. Frasnian conodonts of the northern Chernyshev Swell. *in* Ecostratigraphy and communities of Palaeozoic and Mesozoic of the European north-east. V.A. Molin and V.S. Tsyganko, *eds.*, Syktyvkar, pp. 31–40.

Johnson, J.G.

1990. Lower and Middle Devonian brachiopod-dominated communities of Nevada, and their position in a biofacies-province-realm model (with a section on revision of Middle Devonian conodont zones, by G. Klapper and J.G. Johnson). Journal of Paleontology, vol. 64, pp. 902–941.

Johnson, J.G., and Klapper, G.

1992. North American Midcontinent Devonian T-R cycles. *in* Special papers in paleontology and stratigraphy: a tribute to Thomas W. Amsden. J.R. Chaplin and J.E. Barrick, *eds.*, Oklahoma Geological Survey, Bulletin 145, pp. 127–135.

Johnson, J.G., Klapper, G., and Sandberg, C.A.

1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, vol. 96, pp. 567–587.

Kirchgasser, W.T.

1994. Early morphotypes of *Ancyrodella rotundiloba* at the Middle-Upper Devonian boundary, Genesee Formation, west-central New York. *in* Studies in stratigraphy and paleontology in honor of Donald W. Fisher. E. Landing, *ed.*, New York State Museum, Bulletin no. 481, pp. 117–134.

Kirchgasser, W.T., Over, D.J., and Woodrow, D.L.

1997. Upper Devonian facies, strata, and cycles in western New York State. *in* Devonian cyclicity and sequence stratigraphy in New York State, Field trip guidebook, July 1997. C.E. Brett and C.A. Ver Straeten, *eds.*, University of Rochester, pp. 131–146.

Klapper, G.

1985. Sequence in conodont genus *Ancyrodella* in Lower *asymmetricus* Zone (earliest Frasnian, Upper Devonian) of the Montagne Noire, France. Palaeontographica, Abt. A, vol. 188, Lfg. 1–1, pp. 19–34.

1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *in* Devonian of the World, Proceedings of the Second International Symposium on the Devonian System, vol. III, Paleontology, paleoecology and biostratigraphy. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Memoir 14, pp. 449–468 [imprint 1988].

1990. Frasnian species of the Late Devonian conodont genus *Ancyrognathus*. Journal of Paleontology, vol. 64, pp. 998–1025.

1997. Graphic correlation of Frasnian (Upper Devonian) sequences in Montagne Noire, France, and western Canada. *in* Paleozoic sequence stratigraphy, biostratigraphy, and biogeography: studies in honor of J. Granville ("Jess") Johnson. G. Klapper, M.A. Murphy, and J.A. Talent, *eds.*, Geological Society of America Special Paper 321, pp. 113–129.

Klapper, G., and Becker, R.T.

1999. Comparison of Frasnian (Upper Devonian) conodont zonations. *in* Studies on conodonts, Proceedings of the Seventh European Conodont Symposium. E. Serpagli and C. Corradini, *eds.*, Bolletino della Società Paleontologica Italiana, vol. 37, pp. 339–348.

Klapper, G., Kuz'min, A.V., and Ovnatanova, N.S.

1996. Upper Devonian conodonts from the Timan-Pechora region, Russia, and correlation with a Frasnian composite standard. Journal of Paleontology, vol. 70, pp. 131–152.

Klapper, G., and Lane, H.R.

1985. Upper Devonian (Frasnian) conodonts of the *Polygnathus* biofacies, N.W.T., Canada. Journal of Paleontology, vol. 59, pp. 904–951.

Klapper, G., and Philip, G.M.

1972. Familial classification of reconstructed Devonian conodont apparatuses. Geologica et Palaeontologica, Sonderband 1, pp. 97–114.

Kralick, J.A.

1994. The conodont genus *Ancyrodella* in the middle Genesee Formation (Lower Upper Devonian, Frasnian), western New York. Journal of Paleontology, vol. 68, pp. 1384–1395.

Kuz'min, A.V.

1998. New species of early Frasnian *Palmatolepis* (Conodonta) from southern Timan. Paleontologicheskii Zhurnal, vol. 1998, no. 2, pp. 70–76. (English translation in Paleontological Journal, 1998, vol. 32, pp. 174–184.)

Kuz'min, A.V., Yatskov, S.V., Orlov, A.N., and Ivanov, A.O.

1997. "Domanik Crisis" in faunal development in the Frasnian sea basin at South Timan (north-eastern Russian Platform). Paleontologicheskii Zhurnal, vol. 1997, no. 3, pp. 3–9. (English translation in Paleontological Journal, 1997, vol. 31, pp. 251–258.)

McLean, R.A., and Klapper, G.

1998. Biostratigraphy of Frasnian (Upper Devonian) strata in western Canada, based on conodonts and rugose corals. Bulletin of Canadian Petroleum Geology, vol. 46, pp. 515–563.

Metzger, R.A.

1989. Upper Devonian (Frasnian-Famennian) conodont biostratigraphy in the subsurface of north-central Iowa and southeastern Nebraska. Journal of Paleontology, vol. 63, pp. 503–524.

Müller, K.J.

1956. Die Gattung *Palmatolepis*. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, vol. 494, pp. 1–70.

Norris, A.W., and Uyeno, T.T.

1983. Biostratigraphy and paleontology of Middle-Upper Devonian boundary beds, Gypsum Cliffs area, northeastern Alberta. Geological Survey of Canada, Bulletin 313, 65 pp.

Norris, A.W., Uyeno, T.T., and McCabe, H.R.

1982. Devonian rocks of the Lake Winnipegosis–Lake Manitoba outcrop belt, Manitoba. Geological Survey of Canada Memoir 392, Manitoba Mineral Resources Division Publication 771, 280 pp.

Ovnatanova, N.S., and Kuz'min, A.V.

1991. Conodonts from type sections of the Domanik Suites in South Timan. Seriya Geologicheskiya, Izvestiya Akademii Nauk SSSR, 1991, no. 3, pp. 37–50.

Perri, M.C., and Spalletta, C.

1981. Conodonti e biozonatura del Frasniano (Devoniano sup.) di Pramosio, Alpi Carniche. Bolletino della Società Paleontologica Italiana, vol. 19, pp. 281–310 [imprint 1980].

Pollock, C.A.

1968. Lower Upper Devonian conodonts from Alberta. Journal of Paleontology, vol. 42, pp. 415–433.

Racki, G.

1993. Evolution of the bank to reef complex in the Devonian of the Holy Cross Mountains. Acta Palaeontologica Polonica, vol. 37, pp. 87–182.

1997. Devonian eustatic fluctuations in Poland. *in* On sea-level fluctuations in the Devonian. M.R. House and W. Ziegler, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 199, pp. 1–12.

Racki, G., and Bultynck, P.

1993. Conodont biostratigraphy of the Middle to Upper Devonian boundary beds in the Kielce area of the Holy Cross Mts. Acta Geologica Polonica, vol. 43, pp. 1–25.

Rogers, F.S.

1998. Conodont biostratigraphy of the Little Cedar and lower Coralville formations of the Cedar Valley Group (Middle Devonian) of Iowa, and significance of a new species of *Polygnathus*. Journal of Paleontology, vol. 72, pp. 726–737.

Sandberg, C.A., Ziegler, W., and Bultynck, P.

1989. New standard conodont zones and early *Ancyrodella* phylogeny across Middle-Upper Devonian boundary. *in* Contributions to Devonian palaeontology and stratigraphy, Part II: various Devonian topics. O.H. Walliser and W. Ziegler, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 110, pp. 195–230.

Sparling, D.R.

1999. Conodonts from the Prout Dolomite of north-central Ohio and Givetian (upper Middle Devonian) correlation problems. Journal of Paleontology, vol. 73, pp. 892–907.

Stauffer, C.R.

1938. Conodonts of the Olentangy Shale. Journal of Paleontology, vol. 12, pp. 411–443.

Talent, J.A., and Yolkin, E.A.

1987. Transgression-regression patterns for the Devonian of Australia and southern West Siberia. *in* Neue daten zur biostratigraphie, paläogeographie und paläontologie des Devons in Eurasien und Australien. R. Werner and W. Ziegler, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 92, pp. 235–249.

Ulrich, E.O., and Bassler, R.S.

1926. A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species. Proceedings of the United States National Museum, vol. 68, art. 12, 63 pp.

Uyeno, T.T.

1967. Conodont zonation, Waterways Formation (Upper Devonian), northeastern and central Alberta. Geological Survey of Canada, Paper 67-30, 20 pp.

1974. Conodonts of the Waterways Formation (Upper Devonian) of northeastern and centralAlberta. Geological Survey of Canada, Bulletin 232, 93 pp.

1991. Pre-Famennian Devonian conodont biostratigraphy of selected intervals in the eastern Canadian Cordillera. *in* Ordovician to Triassic conodont paleontology of the Canadian Cordillera. M.J. Orchard and A.D. McCracken, *eds.*, Geological Survey of Canada, Bulletin 417, pp. 129–161.

1998. Conodont faunas. *in* Middle Devonian brachiopods, conodonts, stratigraphy, and transgressive-regressive cycles, Pine Point area, south of Great Slave Lake, District of Mackenzie, Northwest Territories. Geological Survey of Canada, Bulletin 522, Part II, pp. 149–191.

Vandelaer, E., Vandormael, C., and Bultynck, P.

1990. Biofacies and refinement of conodont succession in the lower Frasnian (Upper Devonian) of the type area (Frasnes-Nismes, Belgium). *in* 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V) Contributions III, Papers on Ordovician to Triassic conodonts. W. Ziegler, *ed.*, Courier Forschungsinstitut Senckenberg, vol. 117, pp. 321–351 [imprint 1989].

Weary, D.J., and Harris, A.G.

1994 Early Frasnian (Late Devonian) conodonts from the Harrell Shale, Western Foreland Fold-and-Thrust Belt, West Virginia, Maryland, and Pennsylvania Appalachians, U.S.A. Courier Forschungsinstitut Senckenberg, vol. 168, pp. 195–225.

Wendte, J.C.

1992. Evolution of the Judy Creek Complex, a late Middle Devonian isolate platform–reef complex in west-central Alberta. *in* Devonian–Early Mississippian carbonates of the Western Canada Sedimentary Basin: a sequence stratigraphic framework, Chapter 4. SEPM Short Course no. 28, Calgary, pp. 89–125.

1994. Cooking Lake platform evolution and its control on Late Devonian Leduc reef inception and localization, Redwater, Alberta. Bulletin of Canadian Petroleum Geology, vol. 42, pp. 499–528.

Wendte, J., and Muir, I.

1995. Recognition and significance of an intraformational unconformity in Late Devonian Swan Hills Reef Complexes, Alberta. *in* Unconformities and porosity in carbonate strata. D.A. Budd, A.H. Saller, and P.M. Harris, *eds.*, American Association of Petroleum Geologists Memoir 63, Chapter 13, pp. 259–278.

Wendte, J.C., Uyeno, T.T., and Abrahamson, B.

1995. Physical stratigraphy and conodont biostratigraphy of the Beaverhill Lake Group, late Middle to early Late Devonian, east-central Alberta. *in* Proceedings of the Oil and Gas forum '95, Energy from Sediments. J.S. Bell, T.D. Bird, T.L. Hillier, and P.L. Greener, *eds.*, Geological Survey of Canada, Open File 3058, pp. 141–144.

Witzke, B.J., Bunker, B.J., and Klapper, G.

1985. Devonian stratigraphy in the Quad Cities area, eastern Iowa–northwestern Illinois. *in* Devonian and Pennsylvanian stratigraphy of the Quad Cities region, Illinois-Iowa. W.R. Hammer, R.C. Anderson, and D.C. Schroeder, *eds.*, Society of Economic Paleontologists and Mineralogists, Great Lakes Section, 15th Annual Field Conference Guidebook, pp. 19–64.

Witzke, B.J., Bunker, B.J., and Rogers, F.S.

1989. Eifelian through lower Frasnian stratigraphy and deposition in the Iowa area, central midcontinent, U.S.A. *in* Devonian of the World, vol. I, Regional Syntheses. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists, Calgary, Alberta, Proceedings of the Second International Symposium on the Devonian System, pp. 221–250 [imprint 1988].

Youngquist, W.L.

1945. Upper Devonian conodonts from the Independence Shale (?) of Iowa. Journal of Paleontology, vol. 19, pp. 355–367.

1947. A new Upper Devonian conodont fauna from Iowa. Journal of Paleontology, vol. 21, pp. 95–112.

Yunusov, M.A., Masagutov, R.K., Arkhipova, V.V., and Yunusova, G.M.

1997. Devonian sea-level changes in the platform region of Bashkortostan. *in* On sea-level fluctuations in the Devonian. M.R. House and W. Ziegler, *eds.*, Courier Forschungsinstitut Senckenberg, vol. 199, pp. 65–73.

Ziegler, W.

1971. Conodont stratigraphy of the European Devonian. *in* Symposium on Conodont Biostratigraphy. W.C. Sweet and S.M. Bergström, *eds.*, Geological Society of America Memoir 127, pp. 227–284.

Ziegler, W., *ed.*

1975. Catalogue of Conodonts. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, vol. 2, 404 pp.

Ziegler, W., Ovnatanova, N., and Kononova, L.

2000. Devonian polygnathids from the Frasnian of the Rheinisches Schiefergebirge, Germany, and the Russian Platform. Senckenbergiana lethaea, vol. 80, pp. 593–645.

Ziegler, W., and Wang, Cheng-yuan.

1985. Sihongshan section, a regional reference section for the Lower-Middle and Middle-Upper Devonian boundaries in east Asia. Courier Forschungsinstitut Senckenberg, vol. 75, pp. 17–38.

APPENDIX

For those species that are illustrated but not discussed in the Systematic Paleontology section, a brief synonymy is provided. Unlike conventional synonymy style, no attempt is made to trace the history of nomenclatural changes; rather, to conserve space, the names used in the references are omitted. The name preferred herein, however, is at the head of each entry.

Ancyrodella africana García-López (1981)
Plate 1, figures 14, 15

García-López, 1981, pp. 264–265, pl. 1, figs. 1–14; Klapper, 1985, pp. 28–29, pl. 8, figs. 11–22; pl. 9, figs. 1–16; text-figs. 3S, T, AA, BB; García-López, 1987, pp. 57–58, pl. 2, figs. 8–19; Vandelaer *et al.*, 1990, p. 329, pl. 1, figs. 6, 7.

Ancyrodella alata Glenister and Klapper (1966)
Plate 1, figures 3, 8, 9

Glenister and Klapper, 1966, pp. 799–800, pl. 85, figs. 1–8; Weary and Harris, 1994, pl. 2, figs. 11–14; Kralick, 1994, p. 1393, pl. 3, figs. 1, 2 [?]; pl. 4, figs. 5, 6 [?]; Bai *et al.*, 1994, pl. 2, figs. 1, 3; Ding *et al.*, 2000, pl. 1, figs. 9, 10, 13, 14.

Ancyrodella recta Kralick (1994)
Plate 1, figures 12, 13

Kralick, 1994, pp. 1387, 1390, figs. 3.5, 3.6, 3.11, 3.12, 4.11, 4.12, 6.1, 6.2, 6.5, 6.6, 6.9, 6.10; Racki and Bultynck, 1993, pl. 9, figs. 3, 6.

Ancyrodella rotundiloba (Bryant, 1921)
Plate 1, figures 1, 2, 4, 5

Bryant, 1921, pp. 26–27, pl. 12, figs. 1–6; Klapper, 1985, pp. 24, 26–27, pl. 1, figs. 1–20; pl. 2, figs. 1–12; pl. 3, figs. 1–12; pl. 4, figs. 9–12; pl. 8, figs. 9, 10; pl. 11, figs. 3, 4; text-fig. 3 A–J, M, N [synonymy]; Racki and Bultynck, 1993, pl. 6, fig. 8; Kralick, 1994, p. 1387, figs. 3.15–3.24, 4.7, 4.8, 5.3, 5.4, 5.7–5.11 [synonymy]; Weary and Harris, 1994, pl. 2, figs. 1–10, 19–21; Bai *et al.*, 1994, pl. 1, figs. 2, 3, 8.

Ancyrodella rugosa Branson and Mehl (1934)
Plate 1, figures 10, 11

Branson and Mehl, 1934, p. 239, pl. 19, figs. 15, 17; Racki and Bultynck, 1993, pl. 8, figs. 10, 11; Weary and Harris, 1994, p. 217, pl. 1, figs. 14, 15; Iudina, 1995, pl. 1, fig. 10.

Ancyrodella triangulata Kralick (1994)
Plate 1, figures 6, 7

Kralick, 1994, pp. 1390, 1393, figs. 3.3, 3.4, 3.9, 3.10, 4.1–4.4, 6.3, 6.4, 6.7, 6.8, 6.11, 6.12.

Icriodus subterminus Youngquist (1947)
Plate 2, figures 20, 21

Youngquist, 1947, p. 103, pl. 25, fig. 14; Racki and Bultynck, 1993, pl. 3, fig. 8; Rogers, 1998, p. 737, figs. 6.2–6.6 [synonymy].

Mehlina gradata Youngquist (1945)
Plate 2, figure 14

Youngquist, 1945, p. 363, pl. 56, fig 3; Klapper and Lane, 1985, p. 921, fig. 12.1 [synonymy]; Uyeno, 1991, pl. 5, fig. 27.

Mesotaxis bogoslovskyi Ovnatanova and Kuz'min (1991)
Plate 2, figure 8

Ovnatanova and Kuz'min, 1991, p. 45, pl. 1, figs. 8–10; Klapper *et al.*, 1996, p. 140, pl. 6, figs. 11, 12; Kuz'min *et al.*, 1997, fig. 1C.

Ozarkodina sannemanni (Bischoff and Ziegler, 1957)
Plate 2, figure 19

Bischoff and Ziegler, 1957, pp. 117–118, pl. 19, figs. 15, 19–23, 25; Pollock, 1968, p. 439, pl. 63, figs. 22, 24, 25; Bultynck and Hollard, 1980, pl. 10, figs. 1–3; Perri and Spalletta, 1981, p. 308, pl. 7, fig. 11; Bultynck, 1983, figs. 1.10, 1.11.

Playfordia primitiva (Bischoff and Ziegler, 1957)
Plate 2, figure 15

Bischoff and Ziegler, 1957, p. 83, pl. 21, figs. 5–9; Glenister and Klapper, 1966, p. 827, pl. 95, figs. 19, 20; Uyeno, 1974, p. 36, pl. 6, figs. 6, 7; Ziegler and Wang, 1985, pl. 3, fig. 14; Uyeno, 1991, pl. 5, fig. 12.

Polygnathus alatus Huddle (1934)
Plate 2, figure 27

Huddle, 1934, p. 100, pl. 8, figs. 19, 20; Klapper and Lane, 1985, p. 932, figs. 16.15–16.17 [synonymy]; Metzger, 1989, p. 518, figs. 15.1, 15.2; Uyeno, 1991, pl. 5, fig. 7; Racki and Bultynck, 1993, pl. 4, figs. 7, 8; Weary and Harris, 1994, pl. 1, fig. 12; Ziegler *et al.*, 2000, pl. 6, fig. 3.

Polygnathus incompletus Uyeno (1967)
Plate 2, figure 26

Uyeno, 1967, pp. 7, 10, pl. 2, figs. 6, 7; Klapper *in* Ziegler, *ed.*, 1975, pp. 291–292, *Polygnathus*-pl. 5, fig. 4; Baliński, 1979, p. 80, pl. 23, fig. 11.

Skeletognathus norrisi (Uyeno, 1967)
Plate 2, figures 3, 4

Uyeno, 1967, p. 10, pl. 2, figs. 4, 5; Perri and Spalletta, 1981, pp. 305–306, pl. 7, figs. 5, 6; Uyeno *in* Norris *et al.*, 1982, p. 75, pl. 36, figs. 23–30, 34–39; Sandberg *et al.*, 1989, p. 214, pl. 5, figs. 1–12 [synonymy]); Racki and Bultynck, 1993, pl. 3, figs. 9, 10; Kirchgasser, 1994, pl. 3, figs. C, K, M–O.

TIME ELAPSED IN THE COURSE OF CONODONT EVOLUTION AFTER THE KELLWASSER MASS EXTINCTION (EARLY FAMENNIAN, LATE DEVONIAN)

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ABSTRACT

The conodont stratigraphy of the early Famennian sequence of the Montagne Noire is compared with a time series analysis of sedimentological proxy data. The results of the time series analysis indicate that deposition of calcareous sediments was mainly triggered by surface water carbonate productivity. Thus, a cyclical pattern of carbonate sedimentation has been reconstructed that probably reflects the 0.1 Ma Milankovitch cycle. If correlated with the respective conodont zones, a highly unequal conodont zonal duration results for the time interval analyzed. Especially, the basal Famennian *triangularis* Zone has a very short duration which indicates a conodont faunal recovery after the Kellwasser mass extinction much shorter than estimated.

INTRODUCTION

The Late Devonian biotic crisis, which had its climax with the Kellwasser mass extinction at the Frasnian-Famennian boundary, is regarded as one of the five major mass extinctions in Phanerozoic life history (McLaren, 1970). It was named "Kellwasser event" by Walliser (1980, 1984). Numerous authors have since focused their investigations on the extinction and recovery of various faunal elements involved in this major faunal turnover and on the mechanisms and processes that lead to a mass extinction of the magnitude of the Kellwasser event. Significant articles that considered these topics include Schindler (1990) and Buggisch (1991). We do not wish to renew the discussion of all aspects of a global process as complex as the Kellwasser event, but to focus on an important single aspect, namely the timing and duration of faunal recovery of conodonts after the extinction.

Conodonts provide the best fossil record to justify such an analysis because they range continuously through the event horizon and are by far the most abundant fossil group below and above the mass extinction layer. In addition, their behaviour and faunal development across the Kellwasser event is extraordinarily well documented throughout the world (*e.g.*, Ziegler and Lane, 1987; Sandberg *et al.*, 1988; Ziegler and Sandberg, 1990; Schindler, 1990; Klapper *et al.*, 1993; Schülke, 1995, 1996, 1998, 1999a,b; Morrow and Sandberg, 1996; Morrow, 2000; Schindler *et al.*, 1998 and many others). Nevertheless, in only a few articles are estimates on the duration and timing of the faunal recovery given (*e.g.*, Sandberg and Ziegler, 1992; Morrow and Sandberg, 1996; Schülke 1998, 1999a,b).

These estimates are based chiefly on assumptions of average conodont zonal duration in the Late Devonian (*e.g.*, Sandberg *et al.*, 1988; Ziegler and Sandberg, 1990, 1998; Morrow and Sandberg, 1996; Sandberg and Ziegler, 1996; Schülke, 1998). The equal time intervals of Famennian conodont biozones (0.5 Ma) have been calculated by Sandberg and Ziegler (1996) by the division of the (possible) duration of the Famennian (10 Ma) by the number of conodont zones (20). These assumptions provide only a crude tool for time calibration—possibly the best exclusively based on biostratigraphy, but may not be used without further testing (Weddige, 1997). Such testing can be achieved by comparing conodont zones with small-scale chronological and periodical signals that are produced by cyclical or sequence stratigraphical approaches. In this study, we analyzed two early Famennian sections in the Montagne Noire: (1) Upper Coumiac quarry, the GSSP for the Frasnian-Famennian boundary, and (2) La Serre Trench C. Apart from the high conodont content, which allowed a high resolutional conodont biostratigraphy (Schülke 1995, 1997a, 1999a,b), these sections expose an alternating marl- and limestone sequence in the basal Famennian that is highly appropriate for cyclostratigraphical approaches based on its carbonate content. Some preliminary results of the sequence stratigraphical analysis presented here have been included in earlier publications on early Famennian high resolution conodont biostratigraphy (Schülke 1999a,b) and its implications have been discussed there. Because we now have complete data sets for both sections and the results of a time series analysis, the timing of conodont recovery and the duration of Late Devonian standard conodont zones need to be re-evaluated. A time series analysis of sedimentological data as has been realized here, involves the assumption that the sedimentation rate is relatively constant and that the sequence is continuous. These assumptions may be justified retrospectively by the positive results (Swan and Sandilands, 1995) which made time series analysis a standard technique in processing sedimentological proxy data. In our case, the results seem to justify the application of this method, but they will nevertheless be treated and their implications discussed with caution.

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We are indebted to the reviewers Jeff Over (Geneseo) and Catherine Girard (Lyon) for their constructive reviews. Also, we would like to thank Jim Barrick (Lubbock) for his kind improvement of the manuscript. This study was supported by the German Research Foundation (DFG; proj.-no.: Schu 1214/1-1,2).

GEOLOGICAL SETTING

The Variscan structures of the southern Massif Central comprise the Cevennes, the Albigeois, and, most southward, the Montagne Noire. Fossiliferous Paleozoic sedimentary sequences of the southern Massif Central range from the Lower Cambrian well into the Carboniferous.

Upper Devonian strata are best exposed in the southwestern and southeastern parts of the Montagne Noire area and belong to two tectonically separated units (*e.g.*, Feist, 1983, 1990), the "nappe unit" from the Mont Peyroux area and the "klippen unit" from the "Cabrières klippen." Both tectonic units represent slightly different facies conditions and are claimed to have been transported southward (Engel *et al.*, 1982), but paleogeographic reconstruction of Variscan depositional basins is far from settled and is beyond the scope of this paper (*e.g.*, Scotese, 1986; Young, 1987; Morzadec *et al.*, 1988; Schindler, 1990; Feist and Schindler, 1994).

The early Famennian sedimentary sequences of the Montagne Noire comprise alternating marlstones and limestones, mostly mud- to wackestones, with a mainly pelagic fossil content. They were deposited in an outer shelf environment that generally lacked large-scale siliciclastic influx or bottom currents, presumably on a widespread drowned carbonate platform. The bathymetric position of this carbonate platform is yet unsettled, but is assumed to have been below storm-wave base and above the base of the photic zone (Feist and Schindler, 1994). Our analysis of microfacies patterns and conodont faunas indicates a water depth between 100 and 200 m.

Locality 1: Abandoned Coumiac Quarry (Boundary Stratotype of the Frasnian/Famennian Stage Boundary)

Geographic Position

The abandoned Coumiac quarry is situated in the southeastern Montagne Noire, Département Hérault, about 1.5 km NE of Cessenon village and 0.175 km WSW of the Les Granges farmhouse near the road D 136 between Cessenon and Causses et Veyran (topographic mapsheet 1:25 000 Murviel lès Béziers) (Text-fig. 1).

The Frasnian part of the boundary stratotype section is exposed in the upper quarry (the northernmost of a series of three abandoned marble quarries) followed by the Frasnian/Famennian boundary above its eastern wall. The Famennian part of the section extends on the slope in a NE direction where it is exposed in natural outcrops and artificial trenches.

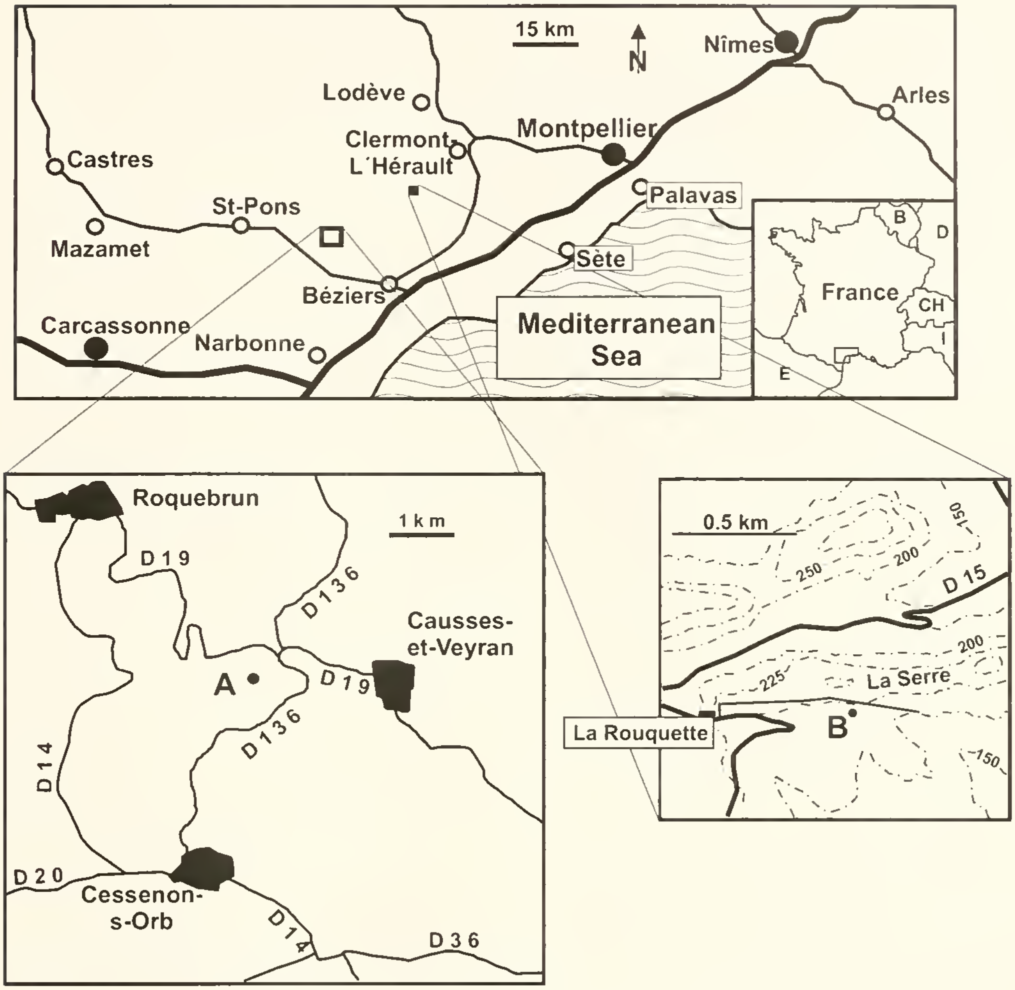
Tectonics and Lithology

Probably known to, but not reported by, former workers (*e.g.*, Klapper *et al.*, 1993), the most recent measuring of the Coumiac section during a field campaign late in 1997 revealed a small wrench fault that crosses the Famennian part of the section in a northward direction. The displacement amounts to about 0.80 m (Schülke, 1999b).

The early Famennian part of the section that is assigned to the Coumiac Formation consists mainly of reddish, marly, nodular cephalopod limestones with intercalated marls. The basal Famennian part of the section exposes evenly bedded, reddish strata. Subsequently, bed character changes to yellowish-red strata with knobby bedding planes. In the lowermost middle Famennian, the Coumiac Formation is overlain by the transgressive, red and partly yellow nodular limestones of the Griotte Formation.

References

The Coumiac section has been known as a locality for Frasnian goniatites since De Rouville (1887). The importance of this section for trilobite, goniatite and other faunal groups has been emphasized by House *et al.*, 1985; Becker *et al.*, 1989; Klapper, 1989; Schindler, 1990; Feist, 1990, 1991; Lethiers and Feist, 1991; Becker, 1993; Klapper *et al.*, 1993; Feist and Schindler, 1994; Girard, 1994a, 1994b, 1995; Girard and Feist, 1997; and Schülke, 1995, 1996, 1997b, 1999a,b. Chemostratigraphic investigations on this section have



Text-figure 1.—Locality map of the studied sections. A: Abandoned Coumiac quarry. B: La Serre Trench C.

been carried out by Joachimski and Buggisch, 1993, Grandjean *et al.*, 1993, and Girard and Albarède, 1996.

Locality 2: La Serre Trench C

Geographic Position

Trench C at La Serre hill is situated in the south-eastern Montagne Noire, Département Hérault (Text-fig. 1), about 2.5 km S of Cabrières village and 450 m E of the farmhouse "La Rouquette" on the southern slope of the hill (topographic mapsheet 1:25 000 Pezenas).

Middle Devonian to Carboniferous rocks on the southern slope of La Serre hill are barely covered by soil and are frequently exposed in small natural outcrops. The section of La Serre trench C was dug under the direction of R. Feist (Montpellier) in the late 1970s and early 1980s. It extends from the upper Frasnian to strata as young as Mississippian, with well-developed Frasnian/Famennian and Devonian/Carboniferous boundary intervals.

Lithology

The deposits of the La Serre trench C section consist of well-bedded grey limestone, dark grey shales, marls, nodular limestones, and partly black laminated limestone beds that belong to the La Serre Formation. The lithology differs strikingly from the sequence of the Coumiac quarry both in its higher amount of intercalated shales and marls and the typically light to medium grey colors of calcilutite beds. The black Kellwasser facies (black laminated limestones) is continuous across the Frasnian/Famennian boundary and extends into middle Famennian strata. In addition, large parts of these rocks have been recrystallized to microspar. When compared to Coumiac, significantly more benthic faunal elements can be recognized at La Serre (*e.g.*, Feist and Schindler, 1994).

Facies

The depositional environment of the deposits exposed at La Serre trench C is presumed to have been shallower than that of Coumiac (*e.g.*, Schindler, 1990; Feist and Schindler, 1994) because of its higher content of benthic faunal elements. This assumption is sustained by the generally higher content of *Icriodus*, a shallow water conodont taxon, although differences are not significant (Schülke, 1999a). Schindler (1990) proposed a middle to deep carbonate ramp environment, possibly situated in a slight depression.

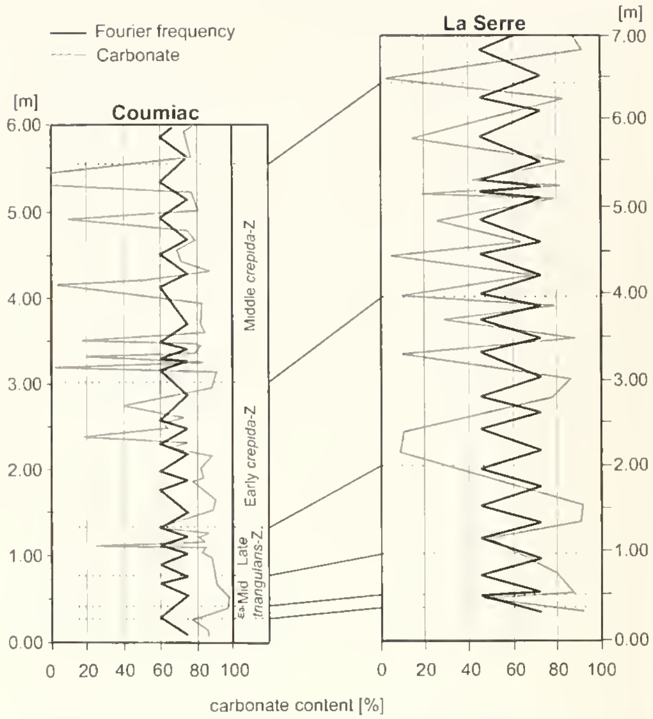
References

The La Serre section has been analyzed several times for its goniatite content, beginning late in the nineteenth century (v. Koenen, 1883a,b; Frech, 1887; Bergeron, 1889; Schindewolf, 1921; Böhm, 1935; v. Gaertner, 1937). Detailed investigations of the goniatite succession from this locality were published in House *et al.* (1985) and Becker (1993). As is the case with the abandoned Coumiac quarry (loc. 1), detailed studies of conodont faunas from La Serre began in the 1980s (Klapper, 1989; Feist, 1990; Klapper and Foster, 1993; Girard, 1994b, 1995; Schülke, 1996, 1997a, 1999a,b). Mega- and microfaunal content has been described by Flajs and Feist (1988), Schindler (1990), Feist and Schindler (1994), Derycke *et al.* (1995), and Levy (1999).

METHODS

The biostratigraphical correlation of the Coumiac and La Serre sections, based on the high-resolution conodont zonation, is presented in Schülke (1999a,b). The investigations led to a separate regional conodont zonation for the Montagne Noire early Famennian sections, which differs slightly from the Late Devonian "standard" conodont zonation (Ziegler and Sandberg, 1990). For differences and correlation of these zonations see Schülke (1999a,b).

The new results we discuss in the following paragraphs are based mainly on the processing of the sedimentological proxy data by Spiehl (1999) and Levy (1999). Apart from an extensive microfacies analysis of the early Famennian sections, which was aimed to support or reject the assumption of a continuous sedimentological record with no major distortion in the time dimension, we focused on a time series analysis of fine-scale carbonate content data of the deposits. We found no clear evidence for corruption of the sedimentological record (*e.g.*, reworking, bottom currents, high siliciclasic influx, calciturbidites and so on) and consequently assumed a depositional regime that was triggered mainly by carbonate productivity and "pelagic snowing." Otherwise, unequal "thicknesses" of the resulting cycles (Text-fig. 2) show minor changes of the sedimentation rate through time or differential effects of diagenesis on the respective deposits (*e.g.*, pressure solution), but without suppression of the evident cyclical character of the sequence.

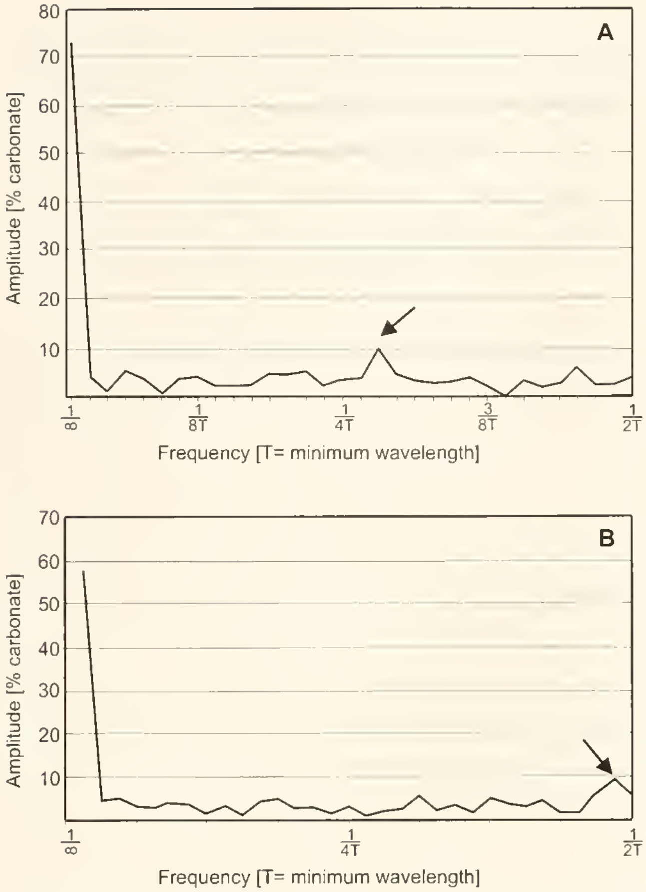


Text-figure 2.—Correlation of conodont biozones with carbonate content values (crossed hatched lines) and the resulting 0.1 Ma frequency (bold lines) of the measured sections.

The bulk samples that were analyzed for their carbonate content were taken bed by bed. If the thickness of a single bed exceeded 8 cm, the samples were taken every five centimeters of rock thickness. Samples were broken down using standard techniques (jaw breaker, mortar and pestle). The rock flour was processed using the "Carbonate bomb," following Müller and Gastner (1971) for calcimetry. All carbonate content samples (160: Coumiac quarry; 96: La Serre Trench C) were measured three times, and the determined values of each sample were averaged. The deviation of the carbonate content values was below 5% in all samples. The HCl-insoluble residue varied between 99% and 10%. Since bed-by-bed conodont data exist only for the early Famennian part of both sections, Early *triangularis* Zone to Late *crepida* Zone, the time series analysis of carbonate content data was run only for this interval (Text-fig. 2).

For time series analysis we chose to use the Fast Fourier Transform (FFT), which offers a rapid execution at the expense of the following constraints:

1. The data must be regularly spaced through time and the number of observations must be 2^n where n is an integer.
2. There should be no trend in the data.



Text-figure 3.—Power spectra showing the results of the "Fast Fourier Transform (FFT)" executed on carbonate proxy data from the early Famennian sections at Coumiac (A) and La Serre (B). Arrows indicating "dominant" waveform used for inverse Fourier transformation.

3. Only integer frequencies are calculated.

Fourier methods are aimed to decompose a time series into a suite of waveforms, the sum of which are regarded to form the sequence of data. The resulting power spectra (Text-fig. 3) show the amplitude of each of the integer frequencies. The cyclicity in a time series will normally be represented by a significant spike in the power spectra. As can be seen from Text-figure 3, both power spectra show that the possible cyclicity in the sections results from a variety of waveforms of similar and comparatively low amplitude, one of which has a slightly elevated spike. This means that even the most influential cyclical process in the sedimentation of the early Famennian deposits produces only a weak signal. For both sections the highest spike, indicating the most powerful single waveform, has been used to carry out an inverse Fourier transform in order to single out the most dominant cyclicity (Text-fig. 2) and remove noise from time series data.

POSSIBLE FREQUENCIES AND MISTAKES

The major processes forming marl-limestone alternations and black shale-carbonate alternations were summarized by Einsele and Ricken (1991) as follows:

1) Productivity cycles that are formed entirely by changes in organic surface water carbonate productivity.
2) Dilution cycles that are triggered by oscillating terrigenous input.
3) Dissolution cycles that are produced by rhythmic oscillation of lysocline and CCD.
4) Calcareous redox cycles indicate fluctuating oxygenation of bottom waters, which coincides with primary organic carbon productivity in surface water.
5) Diagenetic overprinting enhances original carbonate-clay differences between beds by carbonate redistribution.

The true mechanism, or the combination of mechanisms, that formed the early Famennian sequence in the Montagne Noire can only be determined by excluding or discounting the influence of others. A complete modification of originally homogeneous sediments exclusively by diagenetic redistribution of carbonate is unlikely, although diagenesis definitely played a role. Existing pressure solution phenomena (stylolites, clay seams) are significant, but far too obscure to lead to carbonate content values below 1% in black shale interbeds. Also, the influence of pre-diagenetic dissolution of the sediments by oscillations of the CCD or the lysocline can be excluded in environments with a water depth above 200 m—even in the middle Palaeozoic with its possibly different oceanographic conditions. Finally, we think that a fluctuating input of the detrital phase may have occurred, but carbonate content values below detection limits cannot be produced exclusively by this process. Either primary productivity of organic carbonate in surface water or bottom water oxygenation due to surface water organic carbon production presumably controlled the rate of pelagic carbonate mud production in this geological setting.

Most simply, changes in the surface water productivity are triggered by climatic changes and water temperature (Ricken, 1986; Hering, 1995). These changes can be caused by orbital forcing and global or regional-scale tectonics (Smith, 1994). During the time interval investigated, two large-scale T/R-events are recorded that are positioned in the Middle/Late *triangularis* Zone and the Middle *crepida* Zone (Johnson *et al.*, 1985; Schülke, 1999a,b). Both events are easily detectable in the early Famennian conodont record by a change in faunal composition (Schülke, 1999a,b), but do not necessarily represent cyclical processes. They are presumed to have been caused by global-scale tectonics and have been interpreted as third-order cycles with "average" durations of about 1.5 Ma (*e.g.*, Johnson *et al.*, 1985). Our cyclical signals show much higher frequencies and are, therefore, assumed to be produced by changes of orbital parameters (Milankovitch cycles).

In order to extract the maximum frequency resolvable (the Nyquist frequency) with the minimum wavelength, which is double the interval between the observations, we needed at least a crude estimation of the possible duration of the interval under consideration. The formerly best estimates are based on the calculations of average conodont zonal length in the Famennian of Sandberg and Ziegler (1996). These authors (and others) presume an average and almost constant conodont zonal duration of about 0.5 Ma during the whole Famennian, save a few zones with shorter durations in the middle Famennian. Consequently, our time interval would have lasted about 2.5 to 3 Ma following these assumptions. Therefore, the Nyquist frequency is calculated to have a minimum wavelength of about 30 ka, which corresponds with Milankovitch cyclicity. Other estimates of the possible duration of the time interval considered can be based on rock thickness, for example. The Montagne Noire Famennian succession in the Mont Peyroux area where the abandoned Coumiac quarry is situated (loc. 1) is about 70 m thick (Feist, 1990). The measured section has a thickness of 8 m (Schülke, 1999b; Spiehl, 1999) which is about 12% of the total thickness of the Famennian. Given a total duration of the Famennian of 10 Ma (Sandberg and Ziegler, 1996), the interval considered would have lasted about 1.2 Ma. Presumably, the above two estimates (3 and 1.2 Ma) are the limits between which the timespan may have varied.

Which of the orbital parameters had the highest influence on carbonate productivity on the Montagne Noire carbonate platform during the early Famennian can only be assumed. Usually, in areas at low latitudes between 20° and 30°, which is the paleogeographic position of the Montagne Noire during the early Famennian (Dineley, 1984; Sandberg *et al.*, 1988), the influence of variations of precession is most intense (De Boer and Smith, 1994; Schwarzacher, 1993) and is presumed to dominate the other orbital parameters. But cycle duration is at least partly below the Nyquist frequency and cannot be singled out in our examples. On the other hand, the eccentricity cycles do not show any significant change through time—while others did—and are found frequently dominating all other cyclicities throughout the geological record. The major frequencies of eccentricity are the 0.1 Ma and the 0.413 Ma signals one of which—the 0.1 Ma signal—is well known to be amplified by the albedo-temperature and moisture-ice mass feedback system (Einsele and Ricken, 1991), which itself triggers surface water productivity. Otherwise, the sixteen cycles we were able to extract from our data (Text-fig. 2) amount to a duration of about 6.5 Ma if formed by the 0.413 Ma signal; this corresponds to about two-thirds of total Famennian duration as measured with isotopic data (*e.g.*, Claoué-Long *et al.*, 1992) and is therefore not reasonably considered the dominant frequency. When compared to the results of Tucker *et al.* (1998) who estimated the duration of the Famennian to about 14.5 Ma, a similar unbalanced and improbable ratio in duration has to be assumed. If the above argument proves correct, the cyclicity originates in the 0.1 Ma Milankovitch cycle, and produces a weak signal in our sedimentary sequence that is somehow elevated significantly above depositional background noise (Tucker *et al.*, 1998, fig. 1).

Table 1.—Number of cycles and duration of conodont biozones under consideration.

Conodont zone	Cycles	Duration (ka)
Early *triangularis* zone	0.5	50
Middle *triangularis* zone	1.5	150
Late *triangularis* zone	2.5	250
Early *crepida* zone	5	500
Middle *crepida* zone	6	600

CORRELATION OF CONODONT STRATIGRAPHY AND CYCLOSTRATIGRAPHY

In the stratigraphic interval between the Frasnian/Famennian boundary and the upper limit of the Middle *crepida* Zone 15.5 cycles can be recognized (Text-fig. 2). The distribution of cycles between the individual conodont zones in both sections is equal and allows estimation of zonal duration (Table 1).

The distribution of time between the individual conodont zones is highly unequal, which contrasts to the assumption of Sandberg and Ziegler (1996) of almost equal durations of conodont zones throughout the Famennian. Only the Early and Middle *crepida* Zones conform to the estimates of the above authors concerning their durations, while the complete *triangularis* Zone corresponds in duration to a single subzone. Especially, the duration of the Early *triangularis* Zone (50 ka) is exceptionally short when compared to its presumed duration of 0.5 Ma. This fact can be caused by the presence of a hiatus in the Coumiac section around the Frasnian-Famennian boundary (Schindler, 1990; Schülke, 1995, 1999b) and, consequently, a lack of data which may represent a certain interval of non-deposition. On the other hand, a comparable hiatus has not been observed in the La Serre Trench C section. Therefore, we assume this layer does not represent a considerable amount of time (comp. Klapper, 1997), although this timespan is extraordinarily important to the recovery of conodont fauna.

EVOLUTION AND TIME MEASUREMENT

The main question raised by our results is what influence evolutionary rates exert on the time scale of biostratigraphical units used for the subdivision of rock sequences. In this case study, an extraordinary evolutionary situation with the mass extinction at the Frasnian/Famennian boundary forms the starting point of the re-differentiation of conodonts in the early Famennian. *Palmatolepis*, which nearly became extinct during the Kellwasser event save for a single species (*e.g.*, Sandberg *et al.*, 1988; Ziegler and Sandberg, 1990; Klapper *et al.*, 1993; Schülke, 1995), produced an evolutionary outburst that gave rise to as many as 19 species in the stratigraphical interval under investigation (Schülke, 1999a). Two major phases of species differentiation can be differentiated (Schülke, 1995, 1999b): (1) during Middle and Late *triangularis* Zones, and (2) at the beginning of the Middle *crepida* Zone. Between these phases only gradual change occurs among the species of *Palmatolepis*; this is attributed to subspecific level, because no evident y-branched speciation process can be singled out (Schülke, 1995, 1999a, 2003). The two intervals with increased evolutionary rates correspond to the T/R pairs of the third-order cycles following Johnson *et al.* (1985) (Schülke, 2003). Other early Famennian conodont genera (*Polygnathus*, *Ancyrognathus*, *Icriodus*) do not show a comparable evolutionary outburst, although transformational (intraspecific) morphological changes correspond in timing with the diversification phases in *Palmatolepis* (Schülke, 2003).

On the basis of the facts above several conclusions can be drawn:

(1) Large-scale evolutionary change in conodonts, best shown by an almost complete faunal turnover in *Palmatolepis*, coincides with times of large-scale sea level fluctuations.

(2) During the faunal turnover phases, the rate of development of new morphologies is extremly high due to increased selectional stresses (Schülke, 2003). In addition, new characters do not appear at precisely the same time in different species, but at various levels within a short period. Consequently, this period can be subdivided into a variety of zonal units. On the other hand, the "stasis" phases between faunal turnovers do not provide the stratigrapher with a wide variety of newly developed characters and are therefore less well subdivided, although they may represent longer time intervals. A respective turnover phase, released by the faunal recovery after the Kellwasser mass extinction and the third-order T/R couplet in the basal Famennian, produces as much as three zonal boundaries (Early/Middle *triangularis* Zone, Middle/Late *triangularis* Zone, Late *triangularis*/Early *crepida* Zone).

(3) In contrast, large-scale ecological fluctuation phases and the subsequent evolutionary changes can happen in such a short time interval that several new morphologies appear at or nearly at the same time. It would be unreasonable to use this spectrum of new forms to create extremely short biozones. In most cases, a single zonal boundary produced by such circumstances can be recognized by several species and is consequently very precise. An example of this is the T/R pair at the beginning of the Middle *crepida* Zone, which is marked by a variety of species having their first appearance at or near the zonal boundary between the Early and Middle *crepida* Zones.

In our study, we focused on the recovery of conodonts after the Kellwasser mass extinction, to which our data are able to contribute new estimates about its timing. Several authors (*e.g.*, Morrow and Sandberg, 1996; Schülke, 1998) have focused on this topic and came to nearly identical results. The first recovery of a conodont fauna is presumed by them to be finished in the middle part of the Late *triangularis* Zone. Schülke (1998) subdivided the complete process into two parts following the terms of Harries and Kauffman (1990), Kauffman and Erwin (1995), and Kauffman and Harries (1996). The "survival phase" is restricted to the lower two-thirds of the Early *triangularis* Zone. The "recovery phase," consequently, ranges from the upper part of the Early *triangularis* Zone into the middle of the Late *triangularis* Zone. Based on estimations of average conodont zonal duration, the time elapsed in this process amounts to about 1 Ma (Schülke, 1998) which agrees with the statement of Kauffman and Erwin (1995, p. 16), that "recovery intervals . . . rarely last more than 1–2 Ma." Our sequence stratigraphical results indicate a duration of conodont recovery after mass extinction of about 300–350 ka (compare Table 1) with a survival phase less than 50 ka, which is far more rapid than expected. This fact makes conodonts remarkable when compared to other taxa and their recovery intervals, especially those involved in the Kellwasser mass extinction, whose recoveries were delayed until the beginning of the Middle *crepida* Zone (Schülke, 1997b, 1998, which see for further literature).

In fact, estimates on the duration of recovery intervals after mass extinctions are tested against an independent chronological time scale for the first time in this study. Therefore, nothing can be said as to whether conodonts reveal incomparable high evolutionary rates or not, since ecologically similar organisms throughout the Phanerozoic have not yet been studied like conodonts, and the contemporaneous basal Famennian groups surely exhibit different lifetime strategies.

CONCLUSIONS

Carbonate sedimentation on the drowned Montagne Noire carbonate platform in the basal Famennian was probably triggered by the 0.1 Ma precession cycle. The cyclicity signal retrieved by a time series analysis is relatively weak, but its amplitude rises distinctively above all other waveforms. It is most important that, in both sections under investigation, the same number of cycles is developed in the respective conodont zones; this underpins the assumption of orbital forcing.

The cyclicity forms a true and repetitive chronological signal that allows a test of conodont zonal durations within the interval under consideration. This test shows that zones are not equal in duration, which contrasts with earlier estimations. Immediately after the Kellwasser mass extinction at the Frasnian/Famennian boundary, evolutionary rates were extremely high, so that it is possible to gain high zonal resolution. In contrast, when syn- and autecological conditions are largely stable, evolutionary rates are comparatively low, which results in less biostratigraphical resolution. Further studies are in progress to analyze the Montagne Noire sections throughout the whole Famennian to determine whether the above telescoping of conodont zonal durations demonstrated here is exceptional, due to the faunal recovery after mass extinction, or whether all radiations following minor ecological changes produce similar results.

REFERENCES CITED

Becker, R.T.

1993. Stratigraphische Gliederung und Ammonoideen-Faunen im Nehdenium (Oberdevon II) von Europa und Nordafrika. Courier Forschungsinstitut Senckenberg, vol. 155, pp. 1–405.

Becker, R.T., Feist, R., Flajs, G., House, M.R., and Klapper, G.

1989. Frasnian-Famennian extinction events in the Devonian at Coumiac, southern France. Comptes Rendus de la Académie des Sciences, sér. II, vol. 309, pp. 259–266.

Bergeron, J.

1889. Etude géologique du Massif ancien situé au Sud du Plateau Central. Annales des Sciences Géologique, vol. 22 (1), pp. 1–362.

Böhm, R.

1935. Etudes sur les faunes du Dévonien supérieur et du Carbonifère inférieur de la Montagne Noire. Unpublished Ph.D. dissertation, University of Montpellier, Montpellier, 203 pp.

Buggisch, W.

1991. The global Frasnian-Famennian "Kellwasser Event." Geologische Rundschau, vol. 80, pp. 49–72.

Claoué-Long, J.C., Jones, P.J., Roberts, J., and Maxwell, S.

1992. The numerical age of the Devonian-Carboniferous boundary. Geological Magazine, vol. 129, pp. 281–291.

De Boer, P.L., and Smith, D.G.

1994. Orbital forcing and cyclic sequences. *in* Orbital forcing and cyclic sequences. P.L. De Boer, and D.G Smith, *eds.*, Special Publications of the International Association of Sedimentologists, vol. 19, pp. 1–14.

Derycke, C., Blieck, A., and Turner, S.

1995. Vertebrate microfauna from the Devonian/Carboniferous boundary stratotype at La Serre, Montagne Noire (Hérault, France). Bulletin de la Musée national de l'Histoire naturelle, Paris, 4e sér., vol. 17, pp. 461–485.

Dineley, D.L.

1984. Aspects of a stratigraphic system: the Devonian. MacMillan Publishers, London, 223 pp.

Einsele, G., and Ricken, W.

1991. Limestone-Marl alternation—an overview. *in* Cycles and events in stratigraphy. G. Einsele, W. Ricken, and A. Seilacher, *eds.*, Springer, Berlin-Heidelberg-New York, pp. 23–47.

Engel, W., Feist, R., and Franke, W.

1982. Le Carbonifère anté-stéphanien de la Montagne Noire: rapports entre mise en place des nappes et sédimentation. Bulletin BRGM, vol. 1, pp. 341–389.

Feist, R.

1983. Montagne Noire. IUGS-SDS Guidebook field meeting, Montpellier, 62 pp.

1990. Montagne Noire. IUGS-SDS Guidebook field meeting, Montpellier, 69 pp.

1991. The Late Devonian trilobite crisis. Historical Biology, vol. 5, pp. 197–214.

Feist, R., and Schindler, E.

1994. Trilobites during the Frasnian Kellwasser crisis in European Late Devonian cephalopod limestones. Courier Forschungsinstitut Senckenberg, vol. 169, pp. 195–223.

Flajs, G., and Feist, R.

1988. Index conodonts, trilobites and environment of the Devonian-Carboniferous boundary beds at La Serre (Montagne Noire, France). Courier Forschungsinstitut Senckenberg, vol. 100, pp. 53–107.

Frech, F.

1887. Die Paläozoischen Bildungen von Cabrieres. Zeitschrift der deutschen Geologischen Gesellschaft, vol. 39, pp. 360–487.

Gaertner, H.R. von.

1937. Montagne Noire und Massiv von Mouthumet als Teile des südwest-europäischen Variszikums. Abhandlungen der Gesellschaft der Wissenschaften zu Göttingen, mathematisch-physikalische Klasse, 3. Folge, vol. 17, pp. 1–170.

Girard, C.
1994a. Conodont biofacies and event stratigraphy across the D/C boundary in the stratotype area (Montagne Noire, France). Courier Forschungsinstitut Senckenberg, vol. 168, pp. 299–309.
1994b. Les communautés de conodontes et les crises Kellwasser et Hangenberg de la fin du Dévonien en Montagne Noire (Sud de la France). Unpublished Ph.D. dissertation, University of Montpellier, Montpellier, 111 pp.
1995. Les biofaciès à conodontes à la limite Frasnien/Famennien en Montagne Noire (France). Implications stratigraphiques. Comptes Rendus de la Académie des Sciences, sér II, vol. 321, pp. 689–692.

Girard, C., and Albarède, F.
1996. Trace elements in conodont phosphates from the Frasnian/Famennian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 126, pp. 195–209.

Girard, C., and Feist, R.
1997. Eustatic trends in conodont diversity across the Frasnian-Famennian boundary in the stratotype area, Montagne Noire, Southern France. Lethaia, vol. 29, pp. 329–337.

Grandjean, P., Feist, R., and Albarède, F.
1993. Significance of rare earth elements in old biogenic apatites. Geochimica et Cosmochimica Acta, vol. 57, pp. 2507–2514.

Harries, P.J., and Kauffman, E.G.
1990. Patterns of survival and recovery following the Cenomanian-Turonian (Late Cretaceous) mass extinction in the Western Interior Basin, United States. *in* Extinction events in earth history. E.G. Kauffman and O.H. Walliser, *eds.*, Lecture notes in Earth Sciences, vol. 30, Springer-Verlag, Berlin, pp. 277–298.

Hering, G.
1995. Milankovitch-Zyklen in mitteldevonischen Schelfcarbonaten des Rheinischen Schiefergebirges. Göttinger Arbeiten zur Geologie und Paläontologie, vol. 65, pp. 1–63.

House, M.R., Kirchgasser, W.T., Price, J.D., and Wade, G.
1985. Goniatites from the Frasnian (Upper Devonian) and adjacent strata of the Montagne Noire. Hercynia, vol. 1, pp. 1–19.

Joachimski, M.M., and Buggisch, W.
1993. Anoxic events in the late Frasnian—Causes of the Frasnian-Famennian faunal crisis? Geology, vol. 21, pp. 675–678.

Johnson, J.G., Klapper, G., and Sandberg, C.A.
1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, vol. 96, pp. 567–587.

Kauffman, E.G., and Erwin, D.H.
1995. Surviving mass extinction. Geotimes, vol. 40 (3), pp. 14–17.

Kauffman, E.G., and Harries, P.J.
1996. The importance of crisis progenitors in recovery from mass extinction. Geological Society Special Publication, vol. 102, pp. 15–39.

Klapper, G.
1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. *in* Devonian of the world, vol. III. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir, vol. 14, pp. 171–178.
1997. Graphic correlation of Frasnian (Upper Devonian) sequences in Montagne Noire, France, and western Canada. Geological Society of America Special Paper, vol. 321, pp. 113–129.

Klapper, G., Feist, R., Becker, R.T., and House, M.R.
1993. Definition of the Frasnian/Famennian stage boundary. Episodes, vol. 16, pp. 433–441.

Klapper, G., and Foster, C.T.
1993. Shape analysis of Frasnian species of the Late Devonian conodont genus *Palmatolepis*. Paleontological Society Memoir, vol. 32, pp. 1–35.

Koenen, A. von.
1883a. Sur le Dévonien supérieur et le Carbonifère de l'Herault. Bulletin de la Société géologique de France, 3è sér, vol. 12, pp. 114–115.
1883b. Uber das Oberdevon der Gegend von Montpellier. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, vol. 1883, pp. 170–171.

Lethiers, F., and Feist, R.
1991. Ostracodes, stratigraphie et bathymétrie du passage Dévonien-Carbonifère au Viséen inférieur en Montagne Noire. Géobios, vol. 24 (1), pp. 71–104.

Levy, N.
1999. Mikrofazielle Untersuchungen und Zeitreihen-Analyse einer Kalkstein-Mergel-Wechselfolge des basalen Famenniums (Oberdevon) in "La Serre," Montagne Noire (S-Frankreich). Unpublished Masters Thesis, University of Hannover, 50 pp.

McLaren, D.J.
1970. Presidential address: Time, life, and boundaries. Journal of Paleontology, vol. 44, pp. 801–815.

Morrow, J.R.
2000. Shelf-to-basin lithofacies and conodont paleoecology across Frasnian-Famennian (F-F, mid-Late Devonian) boundary, Central Great Basin (Western U.S.A.). Courier Forschungsinstitut Senckenberg, vol. 219, pp. 1–57.

Morrow, J.R., and Sandberg, C.A.
1996. Conodont faunal turnover and diversity changes through the Frasnian-Famennian (F/F) mass extinction and recovery episodes. *in* North American Paleontological Convention Abstracts, J.E. Repetski, *ed.*, Paleontological Society Special Publications, vol. 8, p. 284.

Morzadec, P., Paris, F., Plusquellec, Y., Racheboeuf, P.R., and Weyant, M.
1988. Devonian stratigraphy and paleogeography of the Armorican Massif (Western France). *in* Devonian of the world, vol. III. N.J. McMillan, A.F. Embry, and D.J. Glass, *eds.*, Canadian Society of Petroleum Geologists Memoir, vol. 14, pp. 401–420.

Müller, G., and Gastner, M.
1971. The "Karbonat-Bombe," a simple device for the termination of the carbonate content in sediments, soils and other material. Neues Jahrbuch für Mineralogie, vol. 1971, pp. 466–469.

Ricken, W.
1986. Diagenetic Bedding. Lecture Notes in Earth Sciences, vol. 6, Springer-Verlag, Berlin, 210 pp.

Rouville, P.G. de.
1887. Monographie géologique de la commune de Cabrieres (Hérualt). Mémoires de l'Académie des Sciences, Lettres de Montpellier, vol. 1887, pp. 1–62.

Sandberg, C.A., and Ziegler, W.
1992. Late Devonian conodont evolution and post-crisis recoveries. Fifth International Conference on Global Bioevents, Göttingen, Abstract Volume, p. 92.
1996. Devonian conodont biochronology in geologic time calibration. Senckenbergiana lethaea, vol. 76, pp. 259–265.

Sandberg, C.A., Ziegler, W., Dreesen, R., and Butler, J.L.

1988. Late Frasnian mass extinction: Conodont event stratigraphy, global changes, and possible causes. Courier Forschungsinstitut Senckenberg, vol. 102, pp. 263–307.

Schindewolf, O.H.

1921. Versuch einer Paläogeographie des europäischen Oberdevonmeeres. Zeitschrift der deutschen Geologischen Gesellschaft, vol. 73, pp. 137–223, 2 pls.

Schindler, E.

1990. Die Kellwasser-Krise (hohe Frasne-Stufe, Ober-Devon). Göttinger Arbeiten zur Geologie und Paläontologie, vol. 46, pp. 1–115.

Schindler, E., Schülke, I., and Ziegler, W.

1998. The Frasnian/Famennian boundary at the Sessacker Trench section near Oberscheld (Dill-Syncline, Rheinisches Schiefergebirge, Germany). Senckenbergiana lethaea, vol. 77, pp. 243–261.

Schülke, I.

1995. Evolutive Prozesse bei *Palmatolepis* in der frühen Famenne-Stufe (Conodonta, Ober-Devon). Göttinger Arbeiten zur Geologie und Paläontologie, vol. 67, pp. 1–108.

1996. Evolution of early Famennian ancyrognathids (Conodonta, Late Devonian). Geologica et Palaeontologica, vol. 30, pp. 33–47.

1997a. Conodont clusters and multielement reconstructions from the Upper Kellwasser horizon at La Serre (Late Frasnian, Montagne Noire, Southern France). Geologica et Palaeontologica, vol. 31, pp. 33–47.

1997b. Der Nehden-Event im Rheinischen Schiefergebirge und im Montagne Noire—ein Vergleich. Terra Nostra, vol. 97/6, p. 112.

1998. Conodont community structure around the "Kellwasser mass extinction event" (Frasnian/Famennian boundary interval). Senckenbergiana lethaea, vol. 77, pp. 87–99.

1999a. Conodont multielement reconstructions from the early Famennian (Late Devonian) of the Montagne Noire (Southern France). Geologica et Palaeontologica, SB 3, pp. 1–124.

1999b. Early Famennian conodont biostratigraphy of the stratotype area (Montagne Noire, Southern France). Bolletino della Società Paleontologica Italiana, vol. 37 (2–3), pp. 375–391.

2003. Famennian conodont biodiversity cycles. Courier Forschungsinstitut Senckenberg, vol. 242, pp. 225–237.

Schwarzacher, W.

1993. Cyclostratigraphy and the Milankovitch theory. Elsevier, Amsterdam, 225 pp.

Scotese, R.C.

1986. Phanerozoic reconstructions: A new look at the assembly of Asia. University of Texas, Institute of Geophysics Technical Report, vol. 66, pp. 1–54.

Smith, D.G.

1994. Cyclicity or chaos? Orbital forcing versus non-linear dynamics. *in* Orbital forcing and cyclic sequences. P.L. De Boer, and D.G. Smith, *eds.*, Special Publications of the International Association of Sedimentologists, vol. 19, Blackwell Scientific Publications, Oxford, pp. 531–544.

Spiehl, M.

1999. Mikrofazielle Untersuchung und Zeitreihenanalyse von Griotte-Kalksteinen des basalen Famenniums (Coumiac, Montagne Noire, Süd-Frankreich, Oberdevon). Unpublished Masters thesis, University of Hannover, 56 pp.

Swan, A.R.H., and Sandilands, M.

1995. Introduction to geological data analysis. Blackwell Scientific Publications, Oxford, 446 pp.

Tucker, R.D., Bradley, D.C., Ver Straeten, C.A., Harris, A.G., Ebert, J.R., and McCutcheon, S.R.

1998. New U-Pb zircon ages and the duration of Devonian time. Earth and Planetary Science Letters, vol. 158, pp. 175–186.

Walliser, O.H.

1980. The geosynclinal development of the Variscides with special regard to the Rhenohercynian zone. *in* Mobile Earth. International Geodynamic Project Final Report FR Germany. H. Closs, K. Gehlen, H. Illies, E. Kuntz, J. Neumann, and E. Seibold, *eds.*, Boppard, pp. 185–195.

1984. Geologic processes and global events. Terra Cognita, vol. 4, pp. 17–20.

Weddige, K.

1997. Die Devon-Korrelationstabelle—eine einheitlich formatierte Korrelationstabelle mit Koordinaten als ein standardisiertes stratigraphische Kommunikationsmittel. Terra Nostra, vol. 97/6, p. 128.

Young, G.C.

1987. Devonian paleontological data and the Armorica problem. Palaeogeography, Palaeoclimatology, Palaeoecology, vol. 60, pp. 283–304.

Ziegler, W., and Lane, H.R.

1987. Cycles in conodont evolution from Devonian to mid-Carboniferous. *in* Palaeobiology of conodonts. R.J. Aldridge, *ed.*, Ellis Howard, Chichester, pp. 147–163.

Ziegler, W., and Sandberg, C.A.

1990. The Late Devonian standard conodont zonation. Courier Forschungsinstitut Senckenberg, vol. 121, pp. 1–115.

1998. Devonian high resolution conodont biochronology. Seventh International Conodont Symposium held in Europe (ECOS VII), Abstract Book, pp. 127–128.

THE TYPE SECTION OF THE OSAGEAN SERIES (MISSISSIPPIAN SUBSYSTEM), WEST-CENTRAL MISSOURI, U. S. A.

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ABSTRACT

The Osagean Series is one of four divisions of the Mississippian Subsystem in North America. Although first described in the latter part of the nineteenth century from truncated outcrops along the Osage River in west-central Missouri, the type Osage has virtually been ignored by stratigraphers, who now define the Osagean on rock and fossil successions exposed in the Mississippi River Valley. This paper revisits the principal reference sections for the type Osage and describes their lithologies, conodonts and calcareous foraminifers and algae. Diagnostic conodonts are limited to the *multistriatus* Zone (Faunal Unit 3B) that correlates to the lower part of the Burlington Limestone and facies-equivalent Fern Glen beds in the Mississippi River Valley. Calcareous microfossils are rare but share elements in common with the type Mississippian, including *Rectogranuliferella godini* that is reported for the first time in North America.

INTRODUCTION

The urgent need for establishing boundary stratotypes within the Carboniferous (*e.g.*, Heckel, 1999, 2001; Sevastopulo *et al.*, 2001; Villa, 2001; Chuvashov, 2002a,b) has led to the reexamination of regional series and stages to find suitable levels for global correlation. In 2001, the Carboniferous Subcommission (SCCS) sponsored a field excursion to the Mississippi River Valley (Heckel, in press) to acquaint the international geologic community with type sections of the Mississippian, including the Osagean Series. Although this series is understood in terms of outcrops in the Mississippi River Valley, its name and original description come from an area in west-central Missouri that has been little studied. This paper describes sections and microfossils from these latter Osagean beds and relates them to the better known Mississippi River Valley and other international standard stratigraphic successions of the same age. Some of these results have been summarized previously in an informal Carboniferous Subcommission guidebook (Lane and Brenckle, 1981) as part of a meeting of a SCCS/SEPM Working Group on the Mississippian of the U. S. A.

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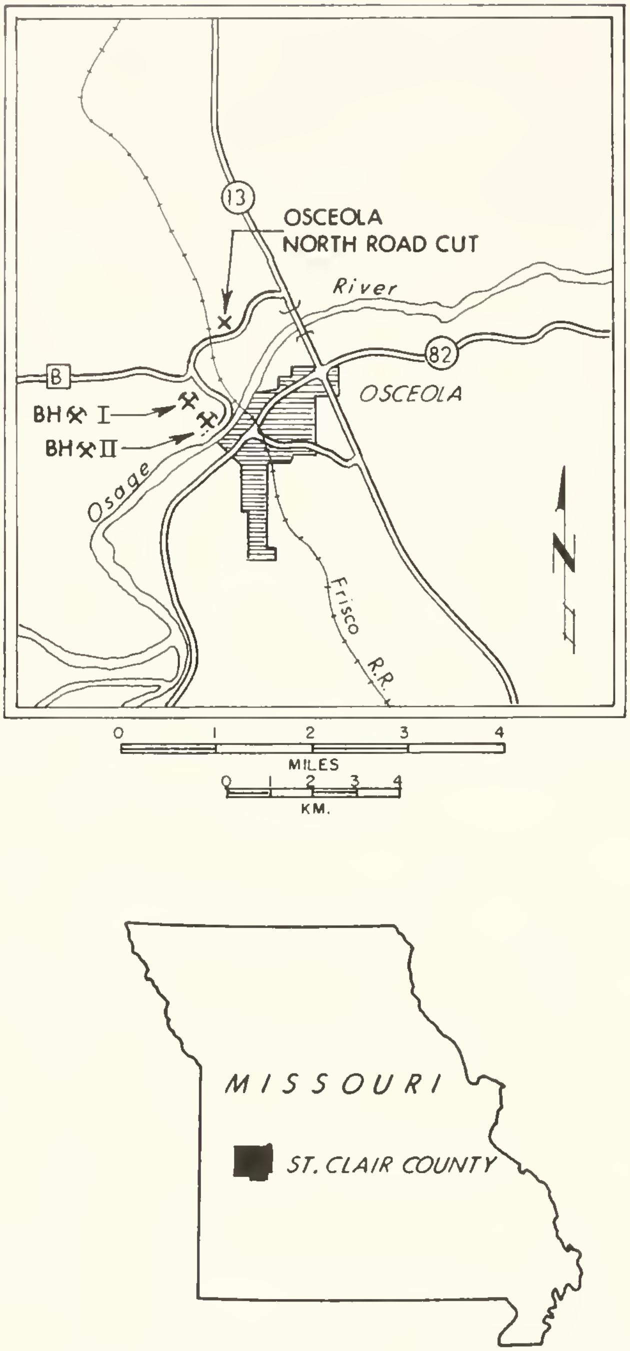


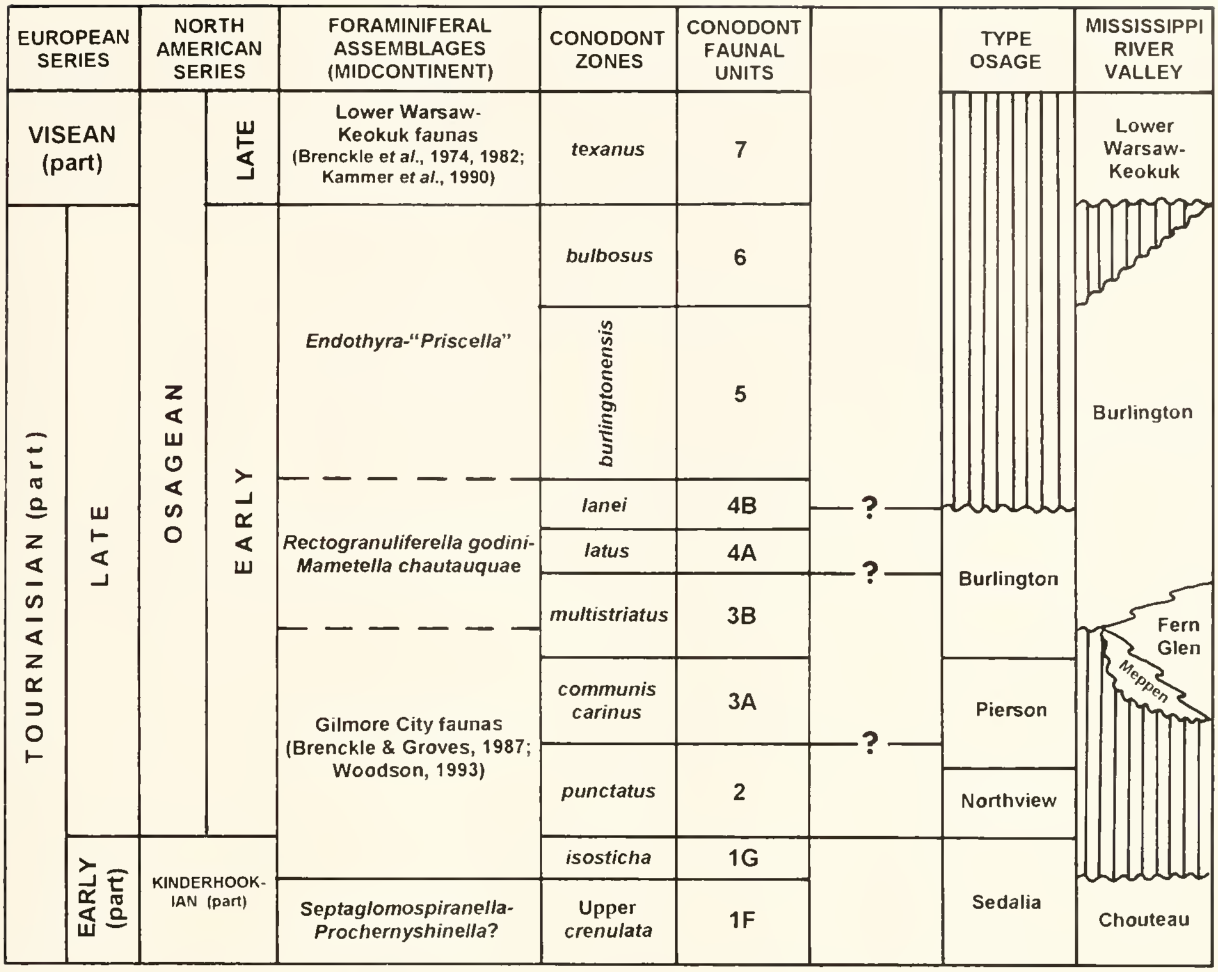
Text-figure 1.—Locality map of the three sections described and sampled for this report. Osceola is located in the center of St. Clair County.

HISTORICAL BACKGROUND

H. S. Williams (1891, p. 169, 172, 265) introduced the term "Osage Group" as one of three divisions of his Mississippian Series and named it for outcrops along the Osage River in west-central Missouri, although no type section was designated (Text-fig. 1). He included the Burlington and Keokuk limestones in the group because he believed faunas from the two formations were present along the river. Keyes (1893, p. 60) noted, however, that the Keokuk was absent along the entire Osage River and proposed (p. 59) the substitute term "Augusta Limestone" [Group] for the Burlington and Keokuk limestones of southeastern Iowa. He (Keyes, 1895) later emended the definition to include the Warsaw Formation at the top of the Augusta. The inadequacies of the type Osage notwithstanding, Weller (1898) and Van Tuyl (1925) promoted use of the term "Osage" because of its priority. The name gained wide acceptance throughout North America and has been used as a serial division (Osagean) of the Mississippian Subsystem since the publication of Ulrich (1911), even though its definition conforms more closely to the concept of the Augusta Group than to the time-stratigraphic interval represented in the type area along the Osage River. Witzke *et al.* (1990, p. 15) reintroduced the term Augusta as a lithostratigraphic grouping for the Burlington-Warsaw interval across Iowa and into Nebraska.

Through the years, the concept of the Osagean has been modified in both west-central Missouri and the Mississippi River Valley (Text-fig. 2). Ulrich (1911) lowered the base of the Osagean in the Mississippi River Valley to include the Fern Glen Formation of Weller (1906), and the dolomitic limestone beds originally included in the lower Fern Glen have been renamed the Meppen Limestone (Willman *et al.*, 1975). Moore (1928) placed his Sedalia Formation of west-central Missouri at the base of the Osagean and mistakenly correlated the lower part of that formation to the lower Fern Glen (=Meppen Limestone). Spreng (1952) and Beveridge and Clark (1952) demonstrated that the upper part of Moore's Sedalia was equivalent to the Northview Shale (Weller, 1906) and Pierson Limestone (Weller, 1906) to the south. They restricted the Sedalia to beds beneath the Northview and placed the Kinderhookian-Osagean boundary at the Northview-Pierson contact. Northview conodonts (Thompson and Fellows, 1970), however, are equivalent to the earliest Osagean conodont *punctatus* Zone (Faunal Unit 2; Text-figs. 2, 3), suggesting that the Kinderhookian-Osagean boundary actually lies at the Northview-Sedalia contact. The dark shales of the Northview probably represent a basal transgressive unit of the Osagean Series.

Kaiser (1950) in his review of the type Osage of west-central Missouri stated that the most complete section is at the abandoned Bullard-Hunt Quarry (Kaiser's Locality 56), about one mile west of the town of Osceola. This locality now serves as the principal reference section for the Osage Group. Two of our mea-



Text-figure 2.—Osagean microfossil zones/assemblages and their relation to North American Midcontinent formations and western European series. Diagnostic conodonts, belonging to the *multistriatus* Zone, are limited to the lower part of the Burlington Limestone in the type Osage. The upper part of the Burlington in this area is placed within the *lautus* and *lanei* conodont zones (Faunal Units 4A and 4B) by stratigraphic position. The Gilmore City foraminifers are assumed to fit within the hiatus at the Kinderhookian-Osagean boundary in the Mississippi River Valley (Brenckle and Groves, 1987), even though this assemblage cannot be correlated directly to either the Mississippi River Valley or the type Osage because there are no diagnostic foraminifers in common. The *Septaglomospiranella-Prochernyshinella*? foraminiferal assemblage comes from occurrences listed in Lane and Brenckle (in press, fig. 8); the *Rectogranuliferella godini-Mametella chautauquae* assemblage from occurrences discussed in this paper; and the *Endothyra*-"*Priscella*" assemblage is from Witzke *et al.* (1990) and Lane and Brenckle (in press, fig. 8).

sured sections are located within the quarry and a third is nearby (Text-fig. 1).

BIOSTRATIGRAPHY

CONODONTS

Although conodonts are rare and low in diversity in our measured sections, the fauna permits correlation of the type Osage to the Mississippi River Valley conodont succession (Text-fig. 2). At the Osceola North Roadcut (see Text-fig. 4), a late Kinderhookian conodont fauna containing *Siphonodella* sp. and *Elictognathus laceratus* was recovered in the Sedalia. Because of poor preservation, the fauna is assigned questionably to the *isosticha*–Upper *crenulata* Zone of Sandberg *et al.* (1978) [=faunal units 1F and 1G, Text-fig. 2]. Samples from the overlying Northview and Pierson did not yield conodonts. However, in southwestern Missouri, the Northview contains conodonts (Thompson and Fellows, 1970) indicative of the earliest Osagean *punctatus* Zone (Faunal Unit 2) and becomes as young as the *communis carinus* Zone (Faunal Unit 3A). In northeastern Oklahoma, the base of the overlying Pierson is as old as the *punctatus* Zone and the top becomes as young as the *bulbosus* Zone (Faunal Unit 6). At the type Osage, the lower part of the Burlington Limestone contains conodonts belonging to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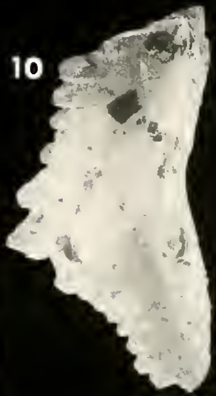
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the *multistriatus* Zone (Faunal Unit 3B) and, thus is equivalent to part of the Pierson to the south. The remainder of the Burlington in the type Osage lacks diagnostic conodonts but is placed tentatively within conodont Faunal Unit 4 (Text-fig. 2) on stratigraphic position. Representative conodonts are illustrated on Plate 1.

CALCAREOUS MICROFOSSILS

Early Osagean foraminifers and algae are sparse in this study as is typical in most of the North American Midcontinent (Brenckle and Groves, 1987). Of a total of 45 samples collected, only five contained calcareous microfossils—all within the Burlington Limestone—and the diversity and total number of specimens are low. The Burlington, although partly dolomitized, retains its primary crinoidal-bryozoan grain-supported texture whereas the subjacent Pierson, Northview and Sedalia formations (see Text-fig. 4) have dolomitic and siliciclastic lithologies that are unfavorable for recovery of calcareous microfossils. Multilocular foraminifers are confined to approximately the same interval represented by samples 17 and 18 at the Osceola North Roadcut (see Text-fig. 4) and samples 8 and 11 at the Bullard-Hunt Quarry Section II (see Text-fig. 6). Foraminifers in this interval include *Rectogranuliferella godini*, questionable *Granuliferella* and indeterminate forms along with the aoujgaliin alga *Stacheoides*? sp. A second microfossiliferous horizon (sample 16, Bullard-Hunt Quarry Section II) contains only the simple, long-ranging foraminifer *Earlandia*.

The Burlington in the Mississippi River Valley has the same primary lithology as its counterpart in the type Osage and, along with the underlying Fern Glen and Meppen formations, also contains few calcareous microfossils. Specimens of *Earlandia* occur throughout the early Osagean there but potentially diagnostic multilocular forms are rare. *Rectogranuliferella godini* has been found only in the Fern Glen at a single locality, Chautauqua West (Brenckle, 1977), along the Mississippi River in association with indeterminate endothyrids *s. l* and aoujgaliin algae (*Mametella chautauquae* Brenckle, 1977; *Stacheoides* sp.), whereas *Endothyra* and "*Priscella*" spp. appear in the upper Burlington (Witzke *et al.*, 1990; Lane and Brenckle, in press). These occurrences are the basis for some of the early Osagean foraminiferal assemblages shown in Text-figure 2. The meager recoveries contrast markedly with the relatively abundant and diverse Early Mississippian North American faunas found in north-central Iowa (Zeller, 1950; Brenckle and Groves, 1987; Woodson, 1993) and west of the Transcontinental Arch (Zeller, 1957; McKay and Green, 1963; Skipp, 1969; Brenckle, 1973; Mamet, 1976; Mamet *et al.*, 1986).

←

PLATE 1

Specimens are reposited at the University of Iowa Paleontology repository (SUI).

Figure

1, 2, 12, 13. *Polygnathus communis communis* Branson and Mehl, P-elements.
1, 2. Upper (×101) and lower (×88) views of SUI-95350, respectively, Burlington Limestone (Bullard-Hunt Quarry II, Sample 11). 12, 13, Lower (×117) and upper (×103) views of SUI-95351, respectively, Burlington Limestone (Osceola North Roadcut, Sample 12).

3. *Ozarkodina* sp. Lateral view (×89) of SUI-95352 (O-element), Burlington Limestone (Bullard-Hunt Quarry I, Sample 8).

4, 5. *Gnathodus typicus* Cooper. Upper (×68) and lower (×62) views respectively of P element SUI-95353, respectively, Burlington Limestone (Osceola North Roadcut, Sample 9).

6. *Siphonodella* sp. Upper view (×89) of P element SUI-95354, Sedalia Formation (Osceola North Roadcut, Sample 2).

7, 11. *Pseudopolygnathus multistriatus* Mehl and Thomas (Morphotype 2) (P element). Upper (×75) and lower (×80) views, respectively, of SUI-95355, Burlington Limestone (Bullard-Hunt Quarry I, Sample 8).

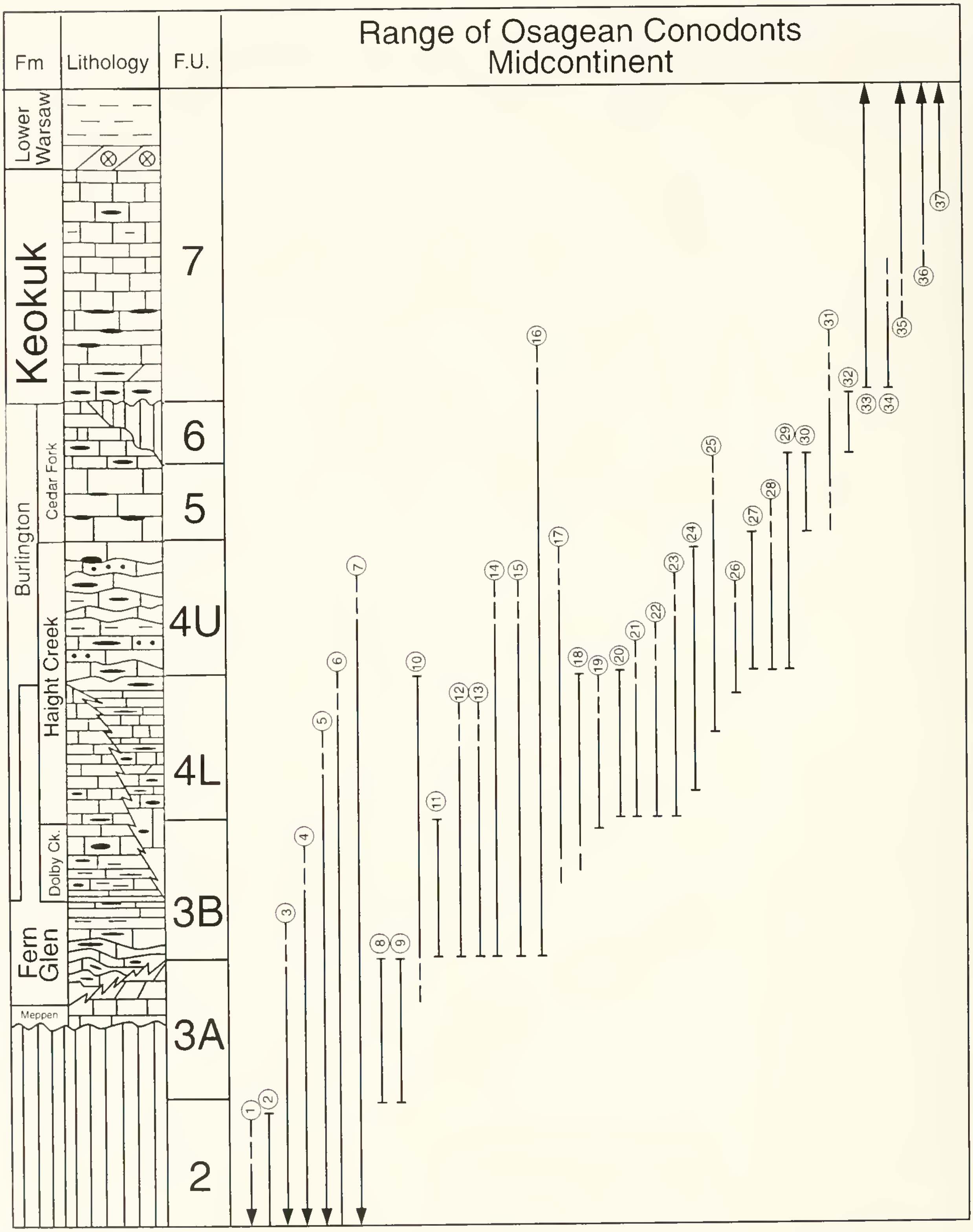
8. *Spathognathodus pulcher* (Branson and Mehl). Lateral view (×86) of P element SUI-95356, Burlington Limestone (Bullard-Hunt Quarry I, Sample 8).

9. *Idioprioniodus furnishi* (Rexroad). Outer lateral view (×46) of O element SUI-95357, Burlington Limestone (Bullard-Hunt Quarry II, Sample 3).

10. *Elictognathus laceratus* (Branson and Mehl). Outer lateral view (×102) of O element SUI-95358, Sedalia Formation (Osceola North Roadcut, Sample 2).

14. Unassigned B—element. Inner lateral view (×64) of SUI-95359, Burlington Limestone (Osceola North Roadcut, Sample 9).

15, 16. *Polygnathus communis* subsp. indet. Lower (×96) and upper (×88) views respectively of P element SUI-95360, Burlington Limestone (Osceola North Roadcut, Sample 15).



Text-figure 3.—Ranges of important conodonts in the Osagean Series of the North American Midcontinent. The formations shown are from the Mississippi River Valley where Faunal Units 2 and lower 3A are missing, but these units are found in the Osagean of southwestern Missouri. Conodonts species are: 1. *Siphonodella isosticha*; 2. *Gnathodus punctatus*; 3. *Gnathodus delicatus*; 4. *Gnathodus praedelicatus*; 5.*Gnathodus semiglaber*; 6. *Gnathodus typicus*; 7. *Polygnathus communis communis*; 8. *Polygnathus communis carinus*; 9. *Staurognathus*

SYSTEMATIC PALEONTOLOGY

Class **FORAMINIFERA** d'Orbigny, 1826

Order **FUSULINIDA** Wedekind, 1937

Superfamily **ENDOTHYRACEA** Brady, 1884

Family **ENDOTHYRIDAE** Brady, 1884

Genus **RECTOGRANULIFERELLA** Conil and Lys *in* Mansy *et al.*, 1989

Type species.—*Palaeospiroplectammina*? *godini* (Conil, 1980).

Rectogranuliferella godini (Conil, 1980)

Plate 2, figures 1–8

Spiroplectamminoides [=*Palaeospiroplectammina*] cf. *S. parva* (Chernysheva). Skipp, 1969, p. 228, pl. 24, figs. 9, 10, 12.

Palaeospiroplectammina? *godini* Conil, 1980, pp. 45–46, pl. 1, figs. 19, 20.

Palaeospiroplectammina aff. *P. parva* (Chernysheva). Lane and Brenckle, 1981, pl. 2, figs. 1–5.

Rectogranuliferella godini (Conil). Conil and Lys *in* Mansy *et al.*, 1989, p. 139, pl. 6, figs. 10–14; Lane and Brenckle, in press, fig. 8.

Measurements (n = 9).—Length: 710–865 μm; width, biserial chambers: 295–355 μm; thickness, biserial chambers: 275–300 μm; diameter, coiled portion: 355–425 μm; diameter, coiled portion/length: 0.41–0.50; number of volutions, coiled portion: about 2; number of chambers in last volution: 7; number of chambers in biserial area: 5–7; interior diameter of proloculus: 55–60 μm; wall thickness of biserial chambers: 20–30 μm.

Description.—Test is composed of a relatively large, slightly skew-coiled immature stage followed by a linearly arranged set of biserial chambers. Volutions in the coiled portion expand slowly and the chambers are slightly to moderately inflated with well developed septation. Biserial chambers inflate very slowly during growth so that the sides of the test appear nearly straight-sided in sagittal section. Their septa that extend about halfway across to the opposite wall are slightly convex and may be thickened along the ends. Wall is coarsely granular-agglutinated. Aperture is a basal slit at the end of the last septum.

Discussion.—*Rectogranuliferella* is a monotypic genus, most of whose specimens have formerly been placed in *Palaeospiroplectammina* because of obvious morphologic similarities. Conil and Lys (*in* Mansy *et al.*, 1989) distinguished *Rectogranuliferella* on the "endothyrin" chamber shape in the coiled portion of the test and on the lighter-colored, coarsely granular-agglutinated wall. They likened the wall structure to that of *Granuliferella* in contrast to the darker, finer-grained test found in typical *Palaeospiroplectammina*. The palaeospiroplectamminin wall, however, is not always homogeneously fine-grained, and the two genera may be confused in specimens where the coiled portion is not well oriented.

The Midcontinent specimens upon which the above description is based were originally thought (Lane and Brenckle, 1981) to be related to *Palaeospiroplectammina parva* (Chernysheva, 1940) in the size of the coiled portion relative to the length of the test and in the number and arrangement of the biserial chambers. They differed in having larger dimensions and more numerous chambers in the last volution of the coiled stage. That assignment is reevaluated in light of the *R. godini* specimens illustrated in Conil (1980) and Mansy *et al.* (1989) that are similar in size, chamber count and wall structure to the Midcontinent specimens. Skipp's (1969) material described as *Spiroplectamminoides* cf. *S. parva* is also herein reassigned to *R. godini* for the same reasons.

Occurrence.—The *R. godini* specimens of Conil (1980) and Mansy *et al.* (1989) are found in early late Tournaisian beds (Belgian foraminiferal zone Cf2) at Avesnois, France. North American examples come from similar age rocks, including the early Osagean Burlington Limestone of west-central Missouri and Fern Glen Limestone of western Illinois in the Midcontinent and the early Osagean upper Whitmore Wash, Thunder Springs and lower Mooney Falls members of the Redwall Limestone in Arizona (Skipp, 1969, foraminiferal zone 2B).

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achorarius; 10. *Pseudopolygnathus multistriatus*; 11. *Gnathodus hamatus*; 12. *Pseudopolygnathus oxypageus*; 13. *Pseudopolygnathus nudus*; 14. *Bactrognathus hamatus*; 15. *Bactrognathus minutus*; 16. *Gnathodus antetexanus*; 17. *Scaliognathus dockali*; 18. *Scaliognathus praeanchoralis*; 19. *Doliognathus dubius*; 20. *Staurognathus cruciformis*; 21. *Doliognathus latus*; 22. *Pseudopolygnathus pinnatus*; 23. *Bactrognathus excavatus*; 24. *Scaliognathus anchoralis europensis*; 25. *Scaliognathus anchoralis anchoralis*; 26. *Bactrognathus distortus*; 27. *Bactrognathus lanei*; 28. *Gnathodus cuneiformis*; 29. *Polygnathus mehli*; 30. *Eotaphrus burlingtonensis*; 31.*Gnathodus pseudosemiglaber*; 32. *Gnathodus bulbosus*; 33. *Gnathodus texanus*; 34. "*Spathognathodus*" *deflexus*; 35. *Taphrognathus varians*; 36. "*Spathognathodus*" *coalescens*; 37. *Apatognathus pinnatus*. The faunal unit scheme is a refinement of those proposed in Lane (1974, 1978) and Lane and Ormiston (1982); it will be published in Lane and Brenckle (in press). Abbreviations: Fm = formation; F.U. = conodont faunal unit. Dolby Ck.(Creek). Haight Creek and Cedar Fork are members of the Burlington Limestone.

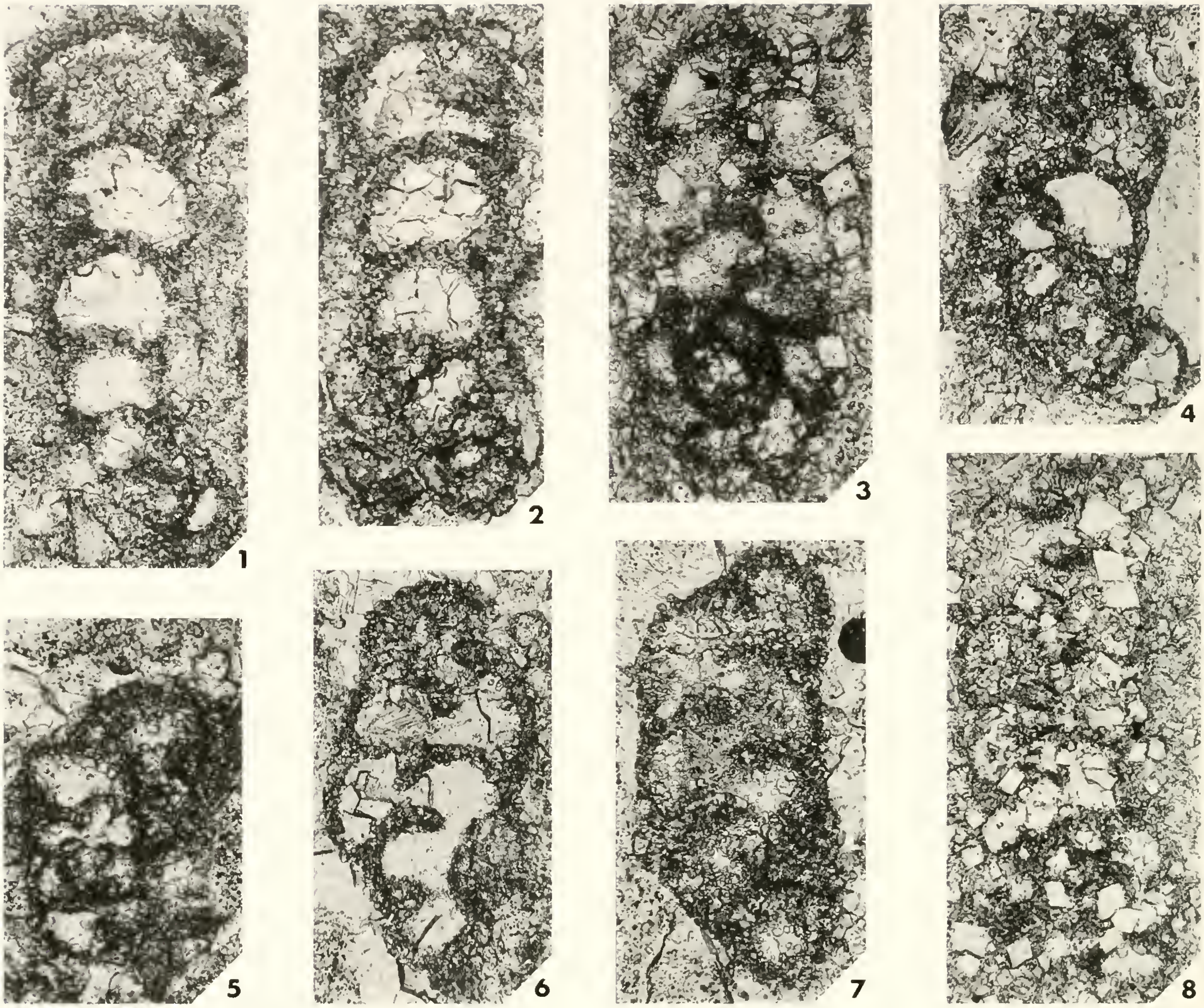


PLATE 2

Rectogranuliferella godini (Conil, 1980), approximately ×95. Specimens 3 and 8 are from the Fern Glen Limestone, Chautauqua West Section, Jersey County, Illinois, described in Brenckle (1977); other specimens are from the Burlington Limestone outcrops described in this paper. Specimens reposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC; repository numbers (USNM) are in parentheses.

Figure
1. (USNM 519336), near-axial section, Bullard-Hunt Quarry II, Sample 9.
2. (USNM 519337), near-axial section, Osceola North Roadcut, Sample 17.
3. (USNM 519338), sagittal section, Chautauqua West, Sample 9.
4. (USNM 519339), oblique-axial section, Bullard-Hunt Quarry II, Sample 9.
5. (USNM 519340), near-axial section of juvenarium, Bullard-Hunt Quarry II, Sample 9.
6. (USNM 519341), tangential-sagittal section, Bullard-Hunt Quarry II, Sample 9.
7. (USNM 519342), tangential-sagittal section, Bullard-Hunt Quarry II, Sample 9.
8. (USNM 519343), sagittal section, Chautauqua West, Sample 10.

REFERENCES CITED

Beveridge, T.R., and Clark, E.L.

1952. A revision of the Early Mississippian nomenclature in western Missouri. Guidebook Sixteenth Regional Field Conference. Kansas Geological Society, pp. 71–79.

Brady, H.B.

1884. Report on the Foraminifera dredged by HMS *Challenger*, during the years 1873–1876. Rept. Scientific Results Explor. Voyage HMS *Challenger*, Zoology, vol. 9, pp. 1–814.

Brenckle, P.L.

1973. Smaller Mississippian and Lower Pennsylvanian calcareous foraminifers from Nevada. Cushman Foundation for Foraminiferal Research, Special Publication No. 11, 82 pp., 10 pls.

1977. *Mametella*, A new genus of calcareous red Algae (?) of Mississippian age in North America. Journal of Paleontology, vol. 51, no. 2, pp. 250–255, 1 pl.

Brenckle, P.L., and Groves, J.R.

1987. Calcareous foraminifers from the Humboldt Oolite of Iowa. Key to early Osagean (Mississippian) correlations between eastern and western North America: Palaios, vol. 1, pp. 561–581, 5 pls. [imprint 1986].

Brenckle, P.L., Lane, H.R., and Collinson, C.

1974. Progress toward reconciliation of Lower Mississippian conodont and foraminiferal zonations. Geology, vol. 2, no. 9, pp. 433–436, 1 pl.

Brenckle, P.L., Marshall, F.C., Waller, S.F., and Wilhelm, M.

1982. Calcareous microfossils from the Keokuk Limestone and adjacent formations, upper Mississippi River Valley: their meaning for North American and intercontinental correlations. Geologica et Palaeontologica, vol. 15, pp. 47–88, 10 pls.

Chernysheva, N.E.

1940. On the stratigraphy of the Lower Carboniferous Foraminifera in the Makorovski district of the south Urals. Society of Moscow Naturalists Bulletin, new series, vol. 48, Geol. Sec. vol. 18, nos. 5–6, pp. 113–135, 2 pl. [in Russian].

Chuvashov, B.I., *ed.*

2002a. Guidebook for Uralian Carboniferous geologic excursions: Part 1—southern Uralian excursion. *In* International symposium on biostratigraphy and boundaries of eastern European Carboniferous stages. Inst. geol. i geokhim. UrO RAN, Ekaterinburg, 72 pp.

2002b. Guidebook for Uralian Carboniferous geologic excursions: Part 2—mid-Uralian excursion. *In* International symposium on biostratigraphy and boundaries of eastern European Carboniferous stages. Inst. geol. i geokhim. UrO RAN, Ekaterinburg, 104 pp.

Conil, R.

1980. Note sur quelques foraminifères du Strunien et du Dinantien d'Europe occidentale. Annales de la Société Géologique de Belgique, vol. 103, pp. 43–53, 2 pls.

Heckel, P.H.

1999. Middle and Upper Pennsylvanian (Upper Carboniferous) cyclothem succession in Midcontinent Basin, U.S.A., Field Trip No. 8, 14th International Congress on the Carboniferous-Permian, Calgary, Canada, August 1999: Kansas Geological Survey Open-file Report 99-27, 236 pp.

2001. Chairman's column. Newsletter on Carboniferous Stratigraphy, vol. 19, pp. 1–3.

In press. Stratigraphy and biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its type region, the Mississippi River Valley of Illinois, Missouri, and Iowa. International Union of Geological Sciences, Subcommission on Carboniferous Stratigraphy Guidebook for Field Conference, September 8–13, 2001. Illinois State Geological Survey Guidebook.

Kammer, T.W., Brenckle, P.L., Carter, J.L., and Ausich, W.I.

1990. Redefinition of the Osagean-Meramecian boundary in the Mississippian stratotype regions. Palaios, vol. 5, pp. 414–431.

Kaiser, C.P.

1950. Stratigraphy of Lower Mississippian rocks in southwestern Missouri. Bulletin of the American Association of Petroleum Geologists, vol. 34, pp. 2133–2172.

Keyes, C.R.

1893. The geological formations of Iowa. Iowa Geological Survey, vol. 1, pp. 13–144.

1895. Geology of Lee County and Geology of Des Moines County. Iowa Geological Survey, Annual Report, vol. 3, pp. 305–492.

Lane, H.R.

1974. Mississippian of southeastern New Mexico and west Texas—a wedge-on-wedge relation. Bulletin of the American Association of Petroleum Geologists, vol. 58, pp. 269–282.

1978. The Burlington Shelf (Mississippian): north-central United States. Geologica et Palaeontologica, vol. 12, pp. 165–176.

Lane, H.R., and Brenckle, P.L.

1981. The type Osage. *In* Mississippian stratotypes. C. Collinson, J.W. Baxter, R.D. Norby, H.R. Lane, and P.L. Brenckle. Illinois State Geological Survey Guidebook, 15th North-Central Geological Society of America Meeting, Ames, Iowa, pp. 1–12, 2 pls.

In press. Type Mississippian subdivisions and biostratigraphic succession. *in* Stratigraphy and biostratigraphy of the Mississippian Subsystem (Carboniferous System) in its type region, the Mississippi River Valley of Illinois, Missouri, and Iowa. P.H. Heckel, *ed.* International Union of Geological Sciences, Subcommission on Carboniferous Stratigraphy Guidebook for Field Conference, September 8–13, 2001. Illinois State Geological Survey Guidebook.

Lane, H.R., and Ormiston, A.O.

1982. Waulsortian facies, Sacramento Mountains, New Mexico. *In* Symposium on the paleoenvironmental setting and distribution of the Waulsortian facies. K. Bolton, H.R. Lane, and D.V. LeMone, *eds.*, El Paso Geological Society and University of Texas at El Paso, International Field Seminar Guide, March 2–6, 1982, pp. 115–182.

Mamet, B.L.

1976. An atlas of microfacies in Carboniferous carbonates of the Canadian Cordillera. Geological Survey of Canada, Bulletin 255, 131 pp., 95 pls.

Mamet, B.L., Bamber, E.W., and Macqueen, R.W.

1986. Microfacies of the Lower Carboniferous Banff Formation and Rundle Group, Monkman Pass map area, northeastern British Columbia. Geological Survey of Canada, Bulletin 353, 93 pp., 18 pls.

Mansy, J.L., Conil, R., Meilliez, F., Khatir, A., Delcambre, B., Groessens, E., Lys, M., Poty, E., Swennen, R., Trentesaux, A., and Weyant, M.

1989. Nouvelles données stratigraphiques et structurales sur le Dinantien dans l'Avesnois. Annales de la Société Géologique du Nord, vol. 108, pp. 125–142, pls. 6–10.

McKay, W., and Green, R.
1963. Mississippian Foraminifera of the southern Canadian Rocky Mountains, Alberta. Research Council of Alberta, Bulletin 10, 77 pp., 12 pls.

Moore, R.C.
1928. Early Mississippian formations in Missouri. Missouri Bureau of Geology and Mines, vol. 21, pp. 1–283.

Orbigny, A.D. d'
1826. Tableau méthodique de la classe des Céphalopodes. Annales des Sciences Naturelles. Paris, ser. 1, vol. 7, pp. 245–314.

Sandberg, C.A., Ziegler, W., Leuterlitz, K., and Brill, S.M.
1978. Phylogeny, speciation, and zonation of *Siphonodella* (Conodonta, Upper Devonian and Lower Carboniferous). Newsletters on Stratigraphy, vol. 7, pp. 102–120.

Sevastopulo, G., Hance, L., Devuyst, F.X., Coen, M., Hou, H., Tian, S., and Wu, X.H.
2001. Progress report of the working group to establish a boundary close to the existing Tournaisian-Visean boundary within the Lower Carboniferous. Newsletter on Carboniferous Stratigraphy, vol. 19, pp. 7–8.

Skipp, B.
1969. Foraminifera. *in* History of the Redwall Limestone of northern Arizona. E.D. McKee and R.C. Gutschick, *eds.*, Geological Society of America, Memoir 114, pp. 173–255, pls. 16–28.

Spreng, A.C.
1952. The lower Pierson fauna of west-central Missouri. Guidebook 16th Regional Field Conference. The Kansas Geological Society, pp. 81–86.

Thompson, T.L., and Fellows, L.D.
1970. Stratigraphy and conodont biostratigraphy of Kinderhookian and Osagean (Lower Mississippian) rocks of southwestern Missouri and adjacent areas. Missouri Geological Survey and Water Resources, Report of Investigations 45, 263 pp.

Ulrich, E.O.
1911. Revision of the Paleozoic Systems. Geological Society of America Bulletin, vol. 22, pp. 281–680.

Van Tuyl, F.M.
1925. The stratigraphy of the Mississippian formations of Iowa. Iowa Geological Survey, Annual Report, vol. 30, pp. 33–359.

Villa, E.
2001. Working group to define a GSSP close to the Moscovian/Kasimovian boundary. Newsletter on Carboniferous Stratigraphy, vol. 19, pp. 8–11.

Wedekind, P.R.
1937. Einführung in die grundlagen der historischen geeologie. Band II. Mikrobiostratigraphie die Korallen- und Foraminiferenzeit. Ferdinand Enke (Stuttgart), 136 pp.

Weller, S.
1898. Osage vs. Augusta. American Geologist, vol. 22, pp. 16–18.
1906. Kinderhook faunal studies—4. Fauna of the Glen Park Limestone. St. Louis Academy of Sciences Transactions, vol. 16, pp. 435–471.

Williams, H.S.
1891. Correlation Papers, Devonian and Carboniferous. United States Geological Survey Bulletin 80, pp. 1–279.

Willman, H.B., *et al.*
1975. Handbook of Illinois Stratigraphy. Illinois State Geological Survey, Bulletin 95, 261 pp.

Witzke, B.J., McKay, R.M., Bunker, B.J., and Woodson, F.J.
1990. Stratigraphy and paleoenvironments of Mississippian strata in Keokuk and Washington counties, southeast Iowa. Iowa Department of Natural Resources, Geological Survey Bureau, Guidebook Series, no. 10, 105 pp.

Woodson, F.J.
1993. Early Mississippian calcareous Foraminifera from the lower part of the Gilmore City Formation, north-central Iowa. Ph.D. thesis, University of Iowa, Iowa City, 83 pp., 6 pls.

Zeller, E.J.
1950. Stratigraphic significance of Mississippian endothyroid Foraminifera. University of Kansas Paleontological Contributions, Article 4, 23 pp., 6 pls.
1957. Mississippian endothyroid Foraminifera from the Cordilleran Geosyncline. Journal of Paleontology, vol. 31, pp. 679–704, 8 pls.

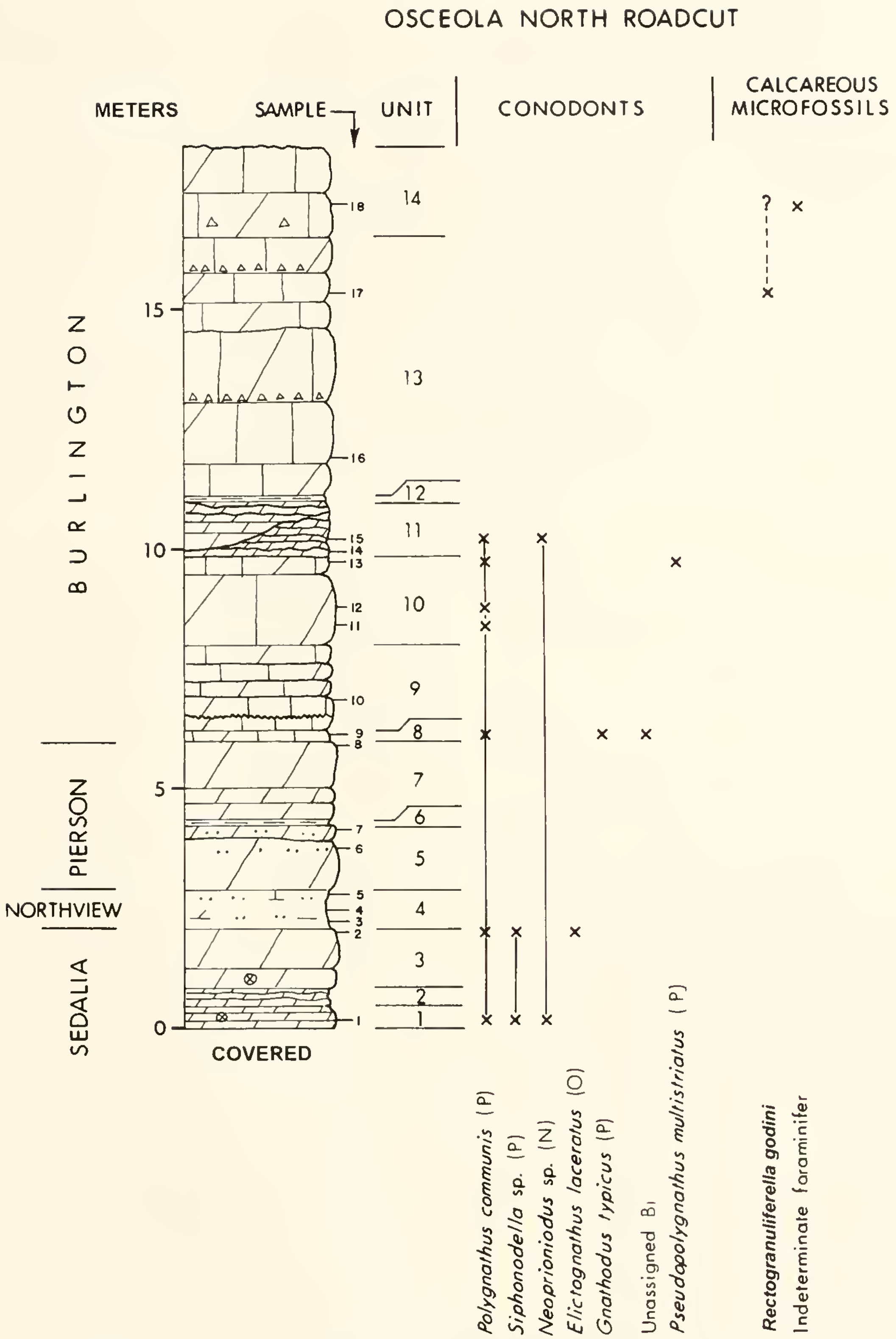
APPENDIX

The following three localities (Text-figs. 4–6) represent the primary reference sections for the Osage Group. They were described and sampled in November 1975 by Gilbert Klapper of The University of Iowa and the authors. Although the Bullard-Hunt Quarry outcrops were well exposed and accessible at that time, the Harry S. Truman Reservoir has since flooded all but the upper part of section II.

The quarry exposes only part of the Burlington Limestone, which is covered at the base and eroded at the top. A nearby section (Osceola North Roadcut, Text-fig. 4), exposes the lower beds of the Burlington and the underlying Pierson, Northview, and Sedalia formations. The Keokuk Limestone and younger Mississippian units are not present in the vicinity of Osceola.

Osceola North Roadcut

This outcrop (Text-fig. 4) is located on the north side of County Route B, 1.45 km west of Missouri Highway 13 and just east of the Frisco Railroad tracks (NW¼, SW¼, NW¼, Sec. 17, T38N, R25W, St. Clair County, Missouri). The section begins within the Sedalia and proceeds through the Northview and Pierson into the Burlington.



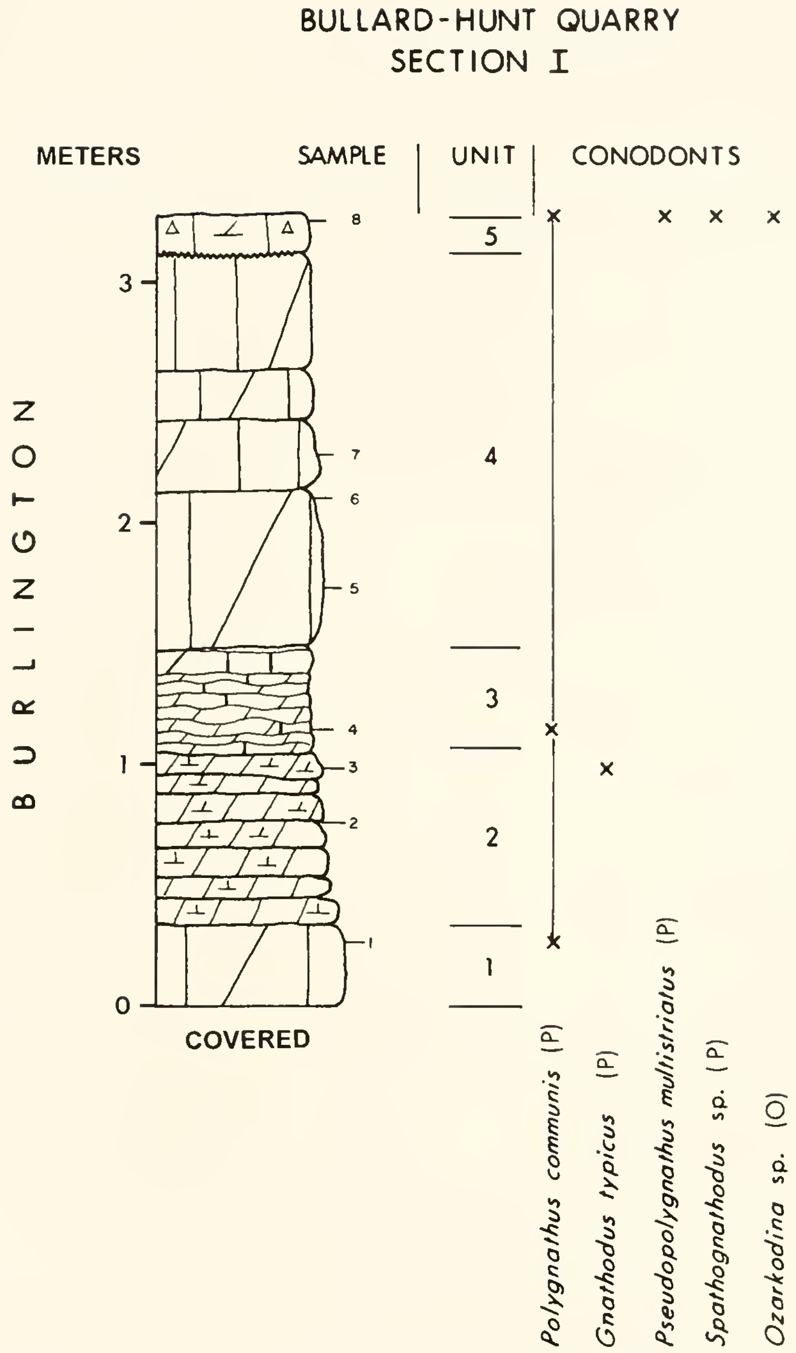
Text-figure 4.—Columnar section and microfossil distribution at Osceola North Roadcut Section. (P) = P element; (N) = N element; (O) = O element; B_1 = B_1 element.

Unit	Lithology	Thickness (meters)
	Sedalia Formation	
1	Buff, argillaceous, fine-grained, vuggy dolomite. Sample 1—whole unit.	0.45
2	Recessive, buff, argillaceous, fine-grained, thin-bedded dolomite.	0.36
3	Buff, argillaceous, fine-grained, vuggy dolomite. Sample 2—1.10 to 1.25 m above base of unit.	1.23
	Total exposed Sedalia Formation	2.04
	Northview Formation	
4	Buff, slightly dolomitic, argillaceous, recessive siltstone. Sample 3—lower 0.15 m; Sample 4—0.30 to 0.45 m above base of unit; Sample 5—upper 0.15 m.	0.75
	Total Northview Formation	0.75
	Pierson Formation	
5	Buff, fine-grained, silty skelmoldic dolomite. Sample 6—0.79 to 1.1 m above base of unit; Sample 7—1.10 to 1.37 m above base of unit.	1.35
6	Brown clay shale	0.09
7	Buff, fine-grained, skelmoldic dolomite, corals. Sample 8—upper 0.19 m.	1.53
	Total Pierson Formation	2.97
	Burlington Limestone	
8	Gray, medium-grained, dolomitic, crinoidal packstone, streaked brown, abundant spirifers. Sample 9—whole unit.	0.24
9	Buff to gray, medium-grained, dolomitic crinoidal-bryozoan wackestone, stylolitic in lower part. Sample 10—0.55 to 0.70 m above base of unit.	1.74
10	Gray, fine- to coarse-grained, massive dolomitized crinoidal wackestone/packstone, abundant stylolites and scattered chert nodules. Sample 11—0.30 to 0.45 m above base of unit; Sample 12—0.61 to 0. 91 m above base of unit; Sample 13—upper 0.12 m.	1.80
11	Gray, vuggy, rubbly, dolomitized crinoidal wackestone/packstone, lenses of less rubbly lithology in lower half. Equivalent to units 3 through 5 at Bullard-Hunt Quarry Section II. Sample 14—lower 0.15 m; Sample 15—from lens at 0.30 m above base of unit.	1.14
12	Buff to gray dolomitic shale.	0.09
13	Gray, medium-grained, dolomitic crinoidal-bryozoan wackestone/packstone, stylolitic, scattered chert bands and nodules. Sample 16—0.67 to 0.82 m above base of unit; Sample 17—4.05 to 4.20 m above base of unit.	5.34
14	Gray, interbedded coarse-grained, dolomitic crinoidal packstone and wackestone. Sample 18—0.67 m above base of unit.	1.89
	Total Burlington Limestone	12.24
	Total Exposed Section	18.00

BULLARD-HUNT QUARRY 1

The section in 1975 exposed the lower part of the Burlington Limestone (Text-fig. 5) above the flooded quarry floor on the east side of the main quarry (SE¼, NW¼, SE¼, Sec. 18, T38N, R25W, St. Clair County, Missouri). The lithology and distribution of microfossils are depicted in Text-figure 5.

Unit	Lithology	Thickness (meters)
	Burlington Limestone	
1	Buff, fine-grained, very dolomitic crinoidal packstone. Sample 1—upper 0.15 m.	0.33
2	Buff, slightly limy dolomitized crinoidal packstone/wackestone. Sample 2—0.37 to 0.52 m above base of unit; Sample 3—upper 0.15 m.	0.66
3	Sucrosic, very limy dolomitized crinoidal-bryozoan packstone. Sample 4—lower 0.15 m.	0.42
4	Buff to gray, fossiliferous, medium to coarse-grained, very dolomitic packstone with finer grained stringers, abundant stylolites, corals, crinoids, brachiopods. Sample 5—0.27 m above base of unit; Sample 6—0.52 to 0.67 m above base of unit; Sample 7—0.67 to 0.82 m above base of unit.	1.68
5	Gray dolomitic crinoidal-bryozoan packstone, rubbly zone at base. Sample 8—whole unit.	0.15
	Total Measured Section:	3.24



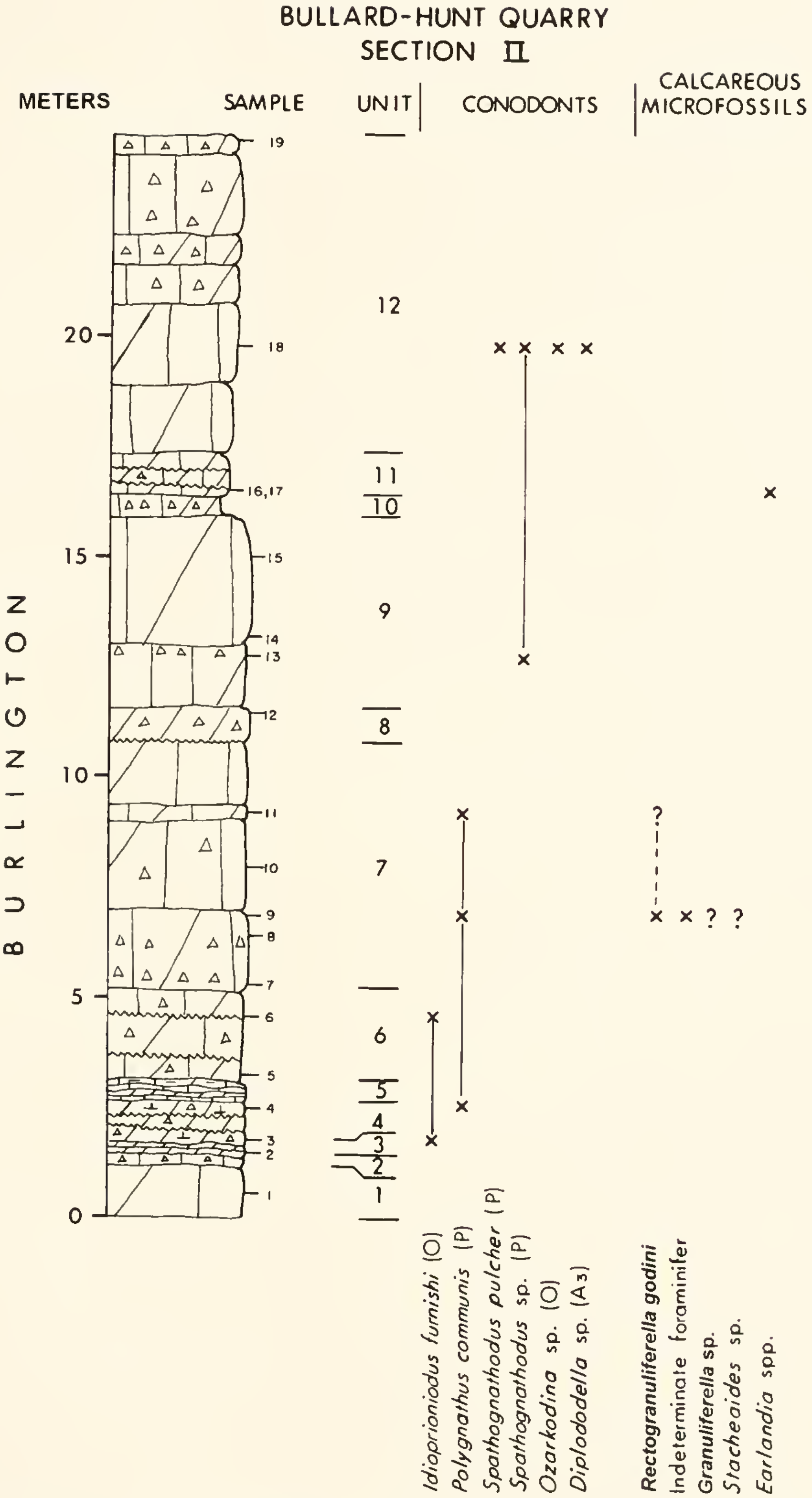
Text-figure 5.—Columnar section and microfossil distribution at Bullard-Hunt Quarry Section I. Conodonts identified as *Spathognathodus* sp. in this section, belong in *Spathognathodus pulcher* (Branson and Mehl). (P) = P element; (O) = O element.

BULLARD-HUNT QUARRY II

This outcrop (Text-fig. 6) exposes the upper part of the Burlington Limestone, the top of which is an erosional surface covered by a regolith. The section (SW¼, NE¼, SE¼, Sec. 18, T38N, R25W, St. Clair County, Missouri) starts near the floor of the quarry facing the Osage River and continues up the steep hillside to the south. The lowest bed correlates to a position 1.22 m below the base of Unit 5 at the Quarry I section.

Burlington Limestone

Unit	*Lithology*	*Thickness (meters)*
1	Gray, medium- to coarse-grained, dolomitic crinoidal-bryozoan packstone with fine-grained dolomitized wackestone stringers. Sample 1—0.30 m above base of unit.	1.20
2	Limestone as below with white chert nodules. Correlates with top of Bullard-Hunt Section I.	0.21
3	Rubbly, gray, argillaceous, dolomitized crinoidal wackestone. Sample 2—0.15 m above base of unit.	0.33
4	Gray, fine- to coarse-grained, dolomitized crinoidal wackestone, stylolitic. Sample 3—lower 0.30 m; Sample 4—upper 0.30 m.	0.84
5	Rubbly, gray, argillaceous, dolomitic, crinoidal wackestone, thickens and thins laterally.	0.45
6	Massive, gray, fine- to coarse-grained, dolomitic crinoidal-bryozoan wackestone, scattered chert nodules, brachiopods, abundant stylolitic surfaces. Sample 5—lower 0.30 m; Sample 6—1.49 m above base of unit.	2.07
7	Fine- to coarse-grained, dolomitic crinoidal-bryozoan packstone/wackestone becoming more crinoidal upward. White fossiliferous chert layer at base and scattered chert nodules above. Sample 7—lower 0.15 m; Sample 8—1.22 m above base of unit; Sample 9—1.60 to 1.75 m above base of unit; Sample 10—2.80 m above base of unit; Sample 11—upper 0.37 m;	5.43
8	Medium- to coarse-grained, dolomitized crinoidal packstone, scattered brown and buff chert. Sample 12—upper 0.30 m.	0.81
9	Gray, medium- to coarse-grained, dolomitic crinoidal-bryozoan packstone/wackestone, fine-grained in places. Buff to white chert layer in top of lower bed. Sample 13— 1.10 m above base of unit; Sample 14—1.37 to 1.67 m above base of unit; Sample 15—3.38 m above base of unit.	4.23
10	Light gray, recessive, dolomitic crinoidal wackestone/packstone. Abundant chert.	0.45
11	Coarse-grained, dolomitic crinoidal-bryozoan packstone, scattered chert and stylolites. Samples 16 and 17—lower 0.30 m.	0.99
12	Pink, medium- to coarse-grained, slightly dolomitic crinoidal packstone, scattered chert clasts, weathers thin-bedded in places. Sample 18—2.44 m above base of unit; Sample 19—upper 0.30 m.	6.99
	Total Measured Section:	24.0



Text-figure 6.—Columnar section and microfossil distribution at Bullard-Hunt Quarry Section II. (O) = O element; (P) = P element; (A_3) = (A_3) element.

FUSULINID WALL STRUCTURE IN THE *PROFUSULINELLA–FUSULINELLA* EVOLUTIONARY TRANSITION

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ABSTRACT

The evolutionary transition from *Profusulinella regia* to *Fusulinella llanoensis* is preserved in a 15-m interval of the Marble Falls Limestone in central Texas. This transition was accomplished by the progressive development of internal epithecal deposits. By definition, the epitheca in *Profusulinella* is secreted only on the floors of chambers and septa. In *Fusulinella*, the epitheca is secreted also on the ceilings of chambers so that it lines the entire chamber cavity. Intermediate populations from the transition interval, assigned to *F. primaeva*, include specimens with profusulinellid walls as well as those in which fusulinellid wall structure is incompletely developed. The *Profusulinella–Fusulinella* evolutionary transition also occurred independently, and at about the same time, in geographically disjunct populations in what are presently Europe (*P.* ex gr. *pseudorhomboides–F.* ex gr. *subpulchra* lineage) and southeast Asia (*P. prisca timanica–Fusulinella* n. sp. lineage). Accordingly, the genus *Fusulinella* is regarded as polyphyletic, with its multiple origins being the result of synchronous parallelism. The stratigraphic appearance of *Fusulinella* characterizes the bases of the informal upper Atokan Series in North America, the upper Kashirian Substage in western Eurasia, the Akiyoshian Series in Japan, and the upper Dalan Stage in South China. If these levels are roughly age equivalent, as is widely accepted, then the rapid global dispersal of early *Fusulinella* spp. from their original loci most likely occurred during an interglacial highstand that allowed interchange among otherwise separate faunal realms.

DEDICATION

This article is dedicated to Gilbert Klapper. Because Gil's name is associated so indelibly with conodonts and Middle Paleozoic stratigraphy, it may surprise some people to learn that he entered the University of Kansas in 1956 with the intention of conducting his Master's thesis research on fusulinids under the supervision of M. L. Thompson. Thompson was the leading North American expert on fusulinids, and it was his policy to require graduate students to prepare at least 1,600 individually oriented thin sections. By his own admission Gil is not particularly dexterous, so the task of orienting and grinding 1,600 fusulinid slides must have seemed not only arbitrary but overwhelming. Gil very much liked and respected Thompson, but he nevertheless decided to drop fusulinids in favor of conodonts. The rest, as they say, is history.

Gil's more than forty years of research on conodonts has greatly advanced the understanding of their taxonomy, evolution, and biostratigraphic utility. In contrast, our knowledge of fusulinid systematics arguably is not much farther along today than in Thompson's era. There is no doubt but that "fusulinidology" would have benefited from Gil's thoughtful work, and I wonder just how differently things might have turned out had Thompson's magic number been, say, 600 instead of 1,600.

INTRODUCTION

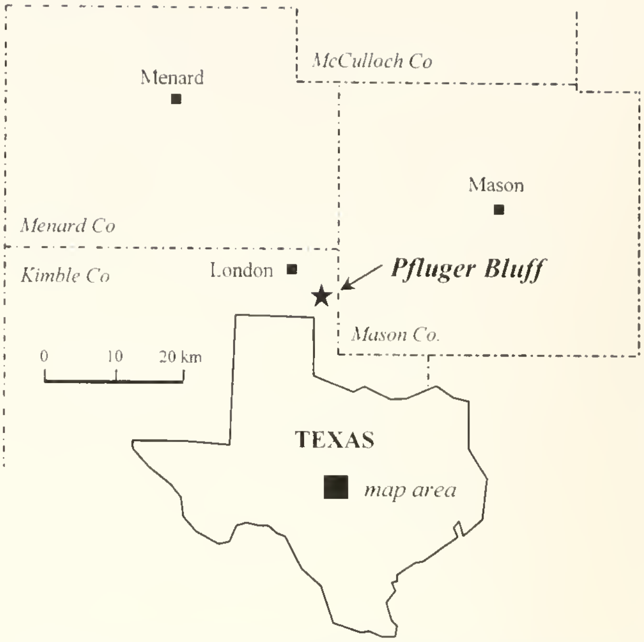
Fusulinacean wall structure has been studied extensively since the late Nineteenth and early Twentieth centuries. Early papers focused almost exclusively on the nature of the keriothecal wall in schwagerinids (Carpenter *et al.*, 1862; Schwager, 1887; Schellwien, 1898; Girty, 1904; Volz, 1904; Douvillé, 1906; Dyhrenfurth, 1909). An understanding of the less advanced fusulinid wall began to emerge somewhat later (Lee, 1923, 1924; Dunbar and Condra, 1928; Lee *et al.*, 1930; Dunbar and Skinner, 1937; Rauser-Chernousova *et al.*, 1951). Detailed descriptions of fusulinid wall structure and its ontogenetic development were published by Dunbar and Henbest (1942), Thompson (1948, 1951; Thompson *in* Loeblich and Tappan, 1964), and Skinner and Wilde (1954a), with those by Dunbar and Henbest (1942) and Skinner and Wilde (1954a) being particularly insightful and accurate. An important feature of those articles was the elucidation of subtle distinctions between profusulinellid- and fusulinellid-type walls (defined below). More recently, Douglass (1977) summarized wall structures within the context of fusulinacean evolution.

Wall structures intermediate between the profusulinellid- and fusulinellid-types were first noted by Thompson (1951). Soon thereafter, Thompson (1953) described two species from Missouri that he considered transitional in development between typical *Pro-*

fusulinella and *Fusulinella.* He remarked on the close similarity of the Missouri specimens to transitional forms known to him from central Texas, west Texas, New Mexico, Wyoming, and Russia and, on the basis of these forms, he correlated the Missouri strata with rock units in the latter areas. The *Profusulinella–Fusulinella* transition in North America occurred in a limited interval spanning the boundary between the informal middle and upper subdivisions of the Atokan Series (Groves, 1986; Douglass, 1987).

Since then, transitional forms have been recognized by other specialists. Solov'eva (1986) erected *Moellerites* to accommodate relatively large and elongate morphotypes with variable wall structure. The genus included two new species along with six species and three subspecies originally described under *Profusulinella* and *Fusulinella.* Species and subspecies assigned to *Moellerites* are restricted on the eastern European Platform and in Tian' Shan' to the Kashirian and lower Podolian substages of the Moscovian Stage. According to E. Villa (pers. commun., 1999, 2000), in the Kashirian Substage of western Eurasia, the lineage from the *Profusulinella pseudorhomboides* species group to the *Fusulinella subpulchra* species group exhibits very gradual development of the fusulinellid-type wall. A similar lineage has been recognized in the Kashirian Substage of northern Thailand where *Profusulinella prisca timanica* gave rise to *Fusulinella* n. sp. (Ueno and Igo, 1997). Thus, the existence of transitional forms is well established; they are widespread geographically and, by virtue of their short geologic range, they have considerable biostratigraphic potential. To my knowledge, however, the progressive modification of wall structure in the *Profusulinella–Fusulinella* transition has not been documented rigorously in a stratigraphically continuous rock sequence.

The purpose of this paper is to record changes in wall structure in the *Profusulinella–Fusulinella* evolutionary transition on the basis of closely spaced samples from an outcrop of the Marble Falls Limestone in the western Llano Uplift region of central Texas (Text-fig. 1). The Marble Falls Limestone on the western flanks of the Llano Uplift formerly was known as the Big Saline Limestone (Cheney, 1940; Plummer, 1950). The Pfluger Bluff locality, from which the present samples were collected, has yielded fusulinaceans that were described and(or) illustrated by Skinner (1931), Thomas (1931), Skinner and Wilde (1954a, 1954b), Thompson (1953), and Groves (1991). Thompson (1947) discussed the age and taxonomic composition of fusulinid assemblages from the Marble Falls Limestone across the eastern, northern, and western flanks of Llano Uplift, but he did not describe or illustrate any specimens from the western area.



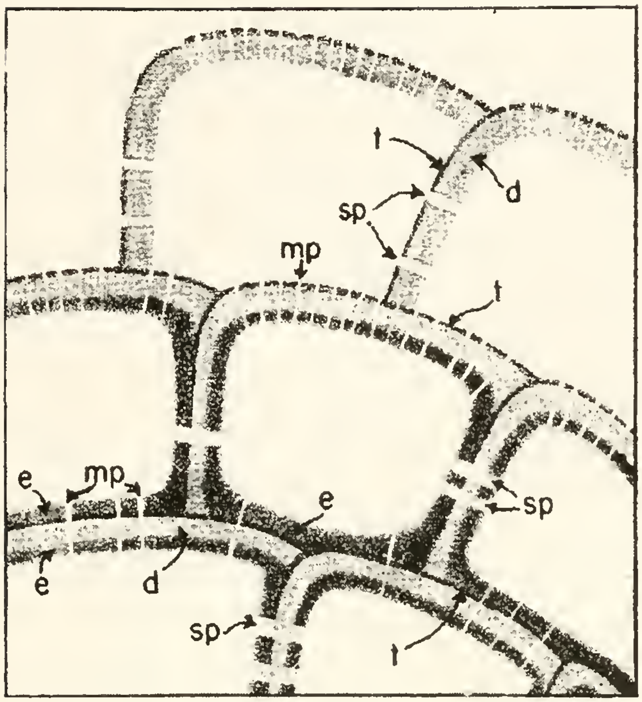
Text-figure 1.—Index map to Pfluger Bluff locality, western Llano Uplift region, central Texas. See Johnson (1983) for locality information.

ACKNOWLEDGMENTS

I am grateful to Gilbert Klapper for his influence on my career in paleontology, and for his continuing friendship. E. Villa, A. Alekseev, and K. Ueno freely shared their knowledge of Moscovian chronostratigraphy and the *Profusulinella–Fusulinella* transition in Eurasia. Stratigraphic sections of the Marble Falls Limestone were measured and described by P. K. Sutherland and W. L. Manger. Samples were collected by Sutherland, Manger, M. K. Nestell, R. C. Grayson, Jr., and their students. Petrographic thin sections were made by Lu Willis, B. J. Harrill, and K. A. Wharton. Wharton expertly prepared an additional 1,200 oriented fusulinid sections (not quite Thompson's magical 1,600). Illustrated specimens are housed at the University of Iowa Paleontology Repository, SUI (Department of Geoscience). The manuscript benefited from critical reviews by P. L. Brenckle and C. A. Ross.

FUSULINID WALL STRUCTURE AND TERMINOLOGY

The fusulinid wall is very finely perforate and consists of three elements (Text-fig. 2). The primary chamber wall is two-layered, being made up of an outer, thin, dark layer—the **tectum**—and an inner, thicker, lighter layer—the **diaphanotheca.** A dark secondary deposit—the **epitheca** (or **tectorium**)—is variably developed as a lining on the floors, septa, and ceilings of the chambers. Because they are primary elements

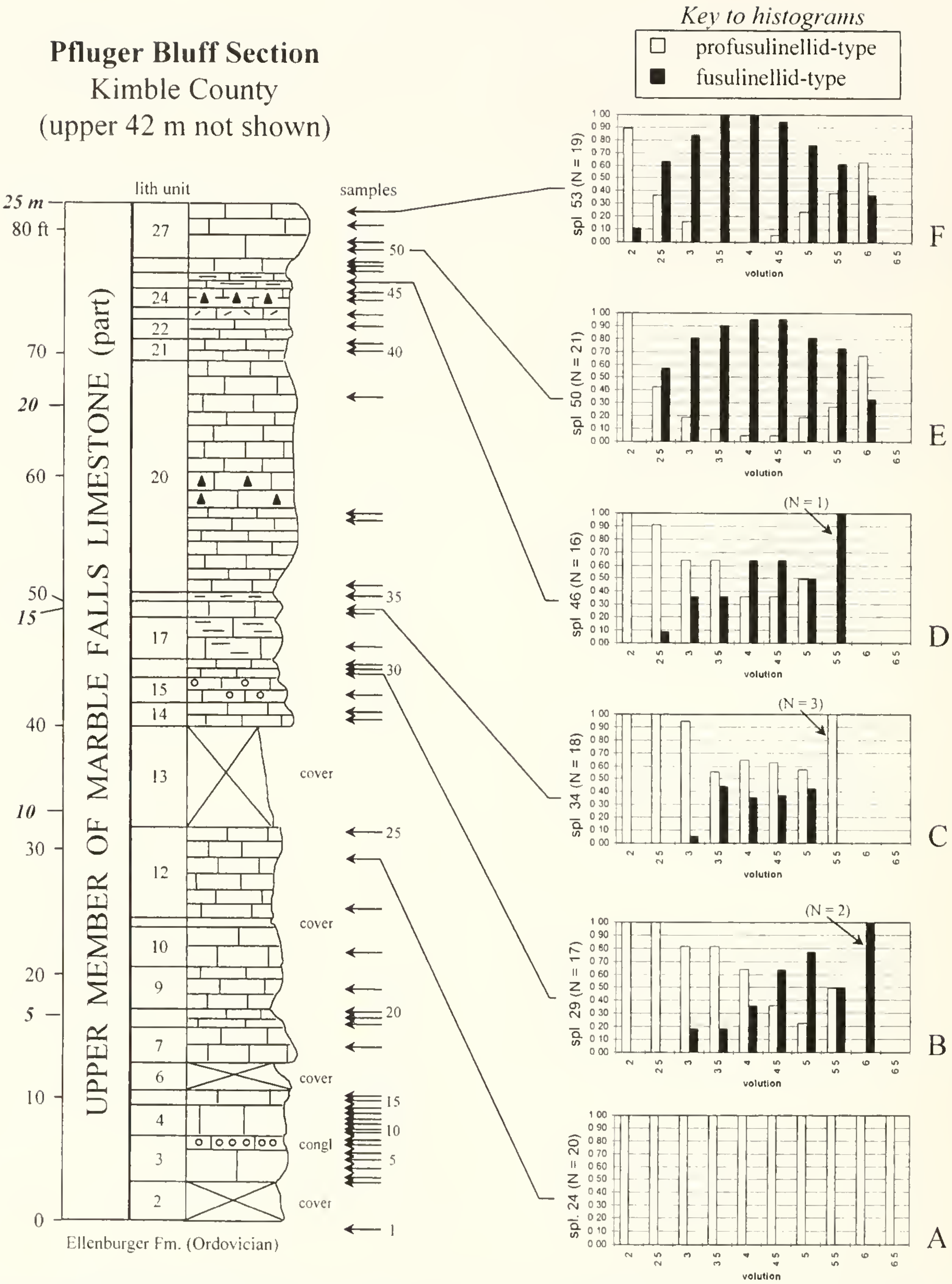


Text-figure 2.—Elements of fusulinid wall structure. Primary two-layered wall, or protheca, consists of the dark tectum (t) and the lighter diaphanotheca (d). The dark epitheca (e) secondarily is secreted as a lining on the chamber floors and septa (as in *Profusulinella*; not shown), or as a lining of the entire chamber cavity, including the chamber ceiling (as in *Fusulinella*; shown here). All wall elements are perforated by fine mural pores (mp) and septal pores (sp), normally seen only in exquisitely preserved material. Note that secretion of the epitheca lags the formation of new chambers, so that at any stage of ontogeny the final several chambers lack secondary deposits. (From Dunbar and Henbest, 1942, fig. 7A; reproduced with permission from the Illinois State Geological Survey.)

and were formed essentially simultaneously, the tectum and diaphanotheca together are known as the **protheca.** The tectum is an organic film that is believed to have served as a template on which calcite crystals of the diaphanotheca were secreted. The presence of organic matter in shell walls was confirmed by Gubler (1934, 1936), who etched fusulinacean thin sections in dilute acid to produce an insoluble residue of the chitin-like substance tectine. Subsequently, on the basis of high voltage transmission electron microscopy of the wall in *Triticites moorei*, Green *et al.* (1980) documented intercrystalline voids and intracrystalline inclusions that are most likely filled with organic matter. The interpretation of the tectum as a substrate for calcification is consistent with observations of chamber formation in certain modern calcareous foraminifers (Myers, 1935; Lutze and Wefer, 1980; Angell, 1980; Hemleben *et al.*, 1986; Wetmore, 1999). Epithecal deposits are calcitic and apparently also contain a fine meshwork of tectine. The difference in darkness between the diaphanotheca and epitheca is mainly a function of crystal size, with the diaphanotheca consisting of relatively large, blocky or columnal crystals and the epitheca consisting of much smaller crystals whose many interfaces cause high internal reflection and refraction of transmitted light.

The epitheca is present in all fusulinids as a continuous layer covering the floors of all but the last few chambers, with the floor covering of a given volution being deposited directly on the outer wall (tectum) of the preceeding volution. The floor covering is thickened in the equatorial region of the test to form a pair of levee-like ridges, or **chomata,** on either side of the sagittal plane. Where the chomata intersect septa, epithecal deposits may be secreted some distance up both the front and back sides of the septa. Fusulinids in which epithecal deposits are limited to the chamber floors, or to the floors and septa, are characterized as having a **profusulinellid-type** wall. In these forms (*e.g.*, *Profusulinella, Eoschubertella, Pseudostaffella*), the inner volutions exhibit a three-layered wall structure consisting of the tectum, diaphanotheca, and the floor deposit of the succeeding volution. Obviously, the wall of the final volution is two-layered, consisting only of the primary layers of the protheca. In the **fusulinellid-type** wall (*e.g.*, *Fusulinella, Beedeina, Wedekindellina*), epithecal deposits are present not only on the chamber floors and septa, but also on the chamber ceilings: *i.e.*, the epitheca completely lines the chamber cavity. In taxa with fusulinellid-type walls, the inner volutions exhibit a four-layered structure consisting of tectum, diaphanotheca, inner epitheca (ceiling deposit), and outer epitheca (floor deposit of succeeding volution). The wall of the final volution is two-layered (protheca only) in the last few chambers, and then three-layered in older chambers that contain the epithecal lining on chamber ceilings.

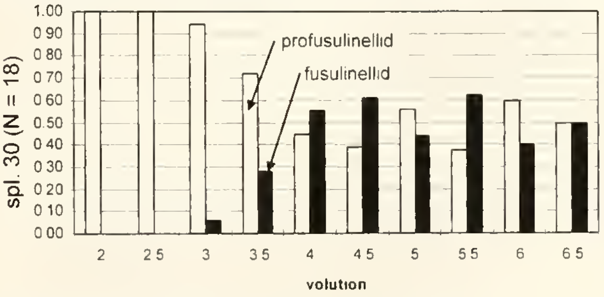
For historical completeness, it must be noted that M. L. Thompson, otherwise an authority, consistently misinterpreted the development of the fusulinid wall and ignored other, more correct views. Thompson (1948, 1951; Thompson *in* Loeblich and Tappan, 1964) believed that the fusulinid primary wall is single-layered, consisting only of the tectum. In the profusulinellid-type wall, he correctly regarded the floor covering as a secondary deposit, the "outer tectorium," but erroneously considered the diaphanotheca also to be a secondary deposit that he termed the "inner tectorium." In the fusulinellid-type wall, he correctly identified the inner and outer tectoria, but thinking that the inner tectorium was homologous with the incorrectly identified corresponding term in the profusulinellid-type wall, was then compelled to regard the fusulinellid diaphanotheca as a novel element that



Text-figure 3.—Stratigraphic columnar section for the Pfluger Bluff locality showing positions of samples and selected sample histograms. Histograms depict at half-volution increments the percentage of specimens with profusulinellid-type walls (white bars) and the remaining percentage with fusulinellid-type walls (black bars). See Johnson (1983) for locality information and detailed stratigraphic descriptions.

Sample 30	volution no.										
specimen	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
1	p	p	p	p	f	p	p				
2	p	p	p	p	p	f	f	f	f		
3	p	p	p	p	p	p					
4	p	p	p	p	p	p	f	f	f	p	
5	p	p	p	p	f	f	f	f	f	f	p
6	p	p	p	f	f	p					
7	p	p	p	p	p	f	f	f	p		
8	p	p	p	p	f	f	f	p	p	p	p
9	p	p	p	p	p	f	p	p	p	p	
10	p	p	p	f	f	f	p				
11	p	p	p	p	p	p	p				
12	p	p	p	p	f	f	p				
13	p	p	p	f	f	f	f	p			
14	p	p	p	p	p	p	p	f	p	p	
15	p	p	p	p	p	f	f	f	p		
16	p	p	f	f	f	f	p				
17	p	p	p	p	f	f	p				
18	p	p	p	f	f	p	p				

summary statistics											
profusulinellid	18/18	18/18	17/18	13/18	8/18	7/18	9/16	3/8	3/5	1/2	n/a
fusulinellid	0/18	0/18	1/18	5/18	10/18	11/18	7/16	5/8	2/5	1/2	n/a



Text-figure 4.—Example data sheet for recording wall structure observations at half-volution increments (sample 30, N = 18 specimens). Abbreviations: p, profusulinellid-type wall; f, fusulinellid-type wall. Note that summary statistics and corresponding histogram do not include observations from the final ½ volution of unabraded specimens (*e.g.*, specimens 5, 8). The population represented in this sample includes specimens with exclusively profusulinellid-type walls (*e.g.*, specimens 3, 11), some with extremely limited development of fusulinellid-type walls (*e.g.*, specimens 1, 9), and the remainder with moderate development of fusulinellid-type walls. This population is assigned to *Fusulinella primaeva* (Skinner, 1931).

is somehow inserted between the tectum and inner tectorium. Clearly this interpretation cannot be supported by observations, nor does it make sense developmentally. I believe a source of confusion for Thompson was the fact that the diaphanotheca in the fusulinellid-type wall appears lighter than in the profusulinellid-type wall. This is probably because in the fusulinellid-type wall the diaphanotheca is sandwiched between two darker layers (tectum and ceiling epitheca), whereas in the profusulinellid-type wall it is adjacent to the tectum only and is not underlain by another wall layer. In fact, in the profusulinellid-type wall, the inner surface of the diaphanotheca commonly is in contact with clear, chamber-filling calcite cements. There is also evidence that crystal size within the diaphanotheca increased with evolutionary grade, resulting in a progressively lighter appearing diaphanotheca through time. In typical *Profusulinella*, the diaphanotheca is relatively finely crystalline and does not differ much in optical density from the epitheca (*e.g.*, Skinner and Wilde, 1954a, pl. 46, figs. 6–9, pl. 47, figs. 3, 4, 7, 8). In advanced *Profusulinella*, such as *P. kentuckyensis* Thompson and Riggs *in* Thompson *et al.*, 1959, the diaphanotheca is more coarsely crystalline and locally transparent (*e.g.*, Douglass, 1987, pl. 1, figs. 2, 3, 12). Among the present collections there are highly advanced *Profusulinella* with light, coarsely crystalline or fibrous diaphanothecae (see Pl. 2, figs. 1, 3, 5, 6). The wall in these specimens is identical to that in primitive *Fusulinella*, the only difference being the presence in *Fusulinella* of an epithecal layer internal to the diaphanotheca.

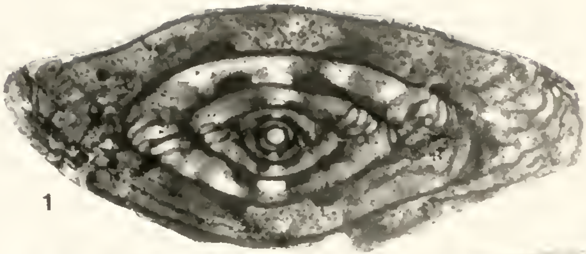
PROFUSULINELLA–FUSULINELLA EVOLUTIONARY TRANSITION

MATERIAL AND METHODS

Samples for this study were collected at the well-known Pfluger Bluff locality in northeastern Kimble County, Texas, where the Marble Falls Limestone is 54 m thick (Text-figs. 1, 3; Johnson, 1983; Groves, 1991). The Marble Falls Limestone at this locality is medial to late Atokan in age (Groves, 1991), although regionally its age ranges from early Morrowan to late Atokan (Thompson, 1947; Manger and Sutherland, 1984). Locally, it rests unconformably on the Ordovician Ellenburger Formation and is overlain unconformably by the Desmoinesian Strawn Group. The late Atokan Smithwick Formation, which overlies the Marble Falls Limestone across much of the Llano Uplift region, is missing at Pfluger Bluff as a consequence of non-deposition or pre-Strawn erosion. A total of 115 samples was collected at an average spacing of 0.47 m. The *Profusulinella–Fusulinella* transition here occurs within an interval roughly 10–25 m above the base of the exposure.

Approximately 3,000 fusulinacean and non-fusulinacean foraminifers from Pfluger Bluff were photographed and identified in order to establish the stratigraphic distribution of taxa and the precise age of the sampled interval (Groves, 1991, 1992). Detailed examination of fusulinid wall structure then was performed on specimens below and immediately above the stratigraphically lowest occurrence of unquestionable fusulinellid-type walls. The examination involved noting the development of epithecal deposits at every half-volution throughout the spiral growth of the shells (Text-fig. 4).

Unlike other taxonomically important characters,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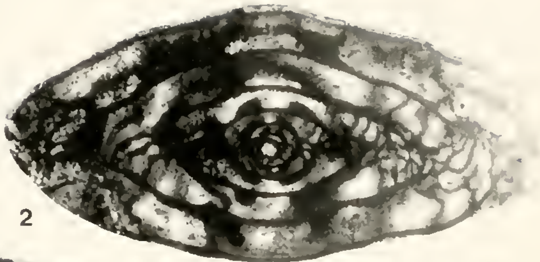
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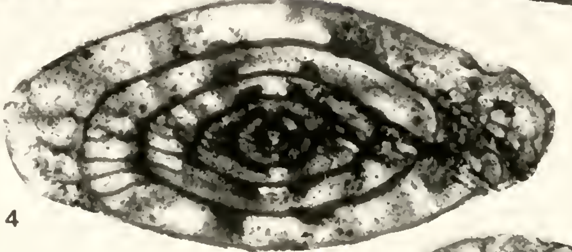
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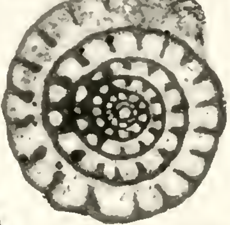
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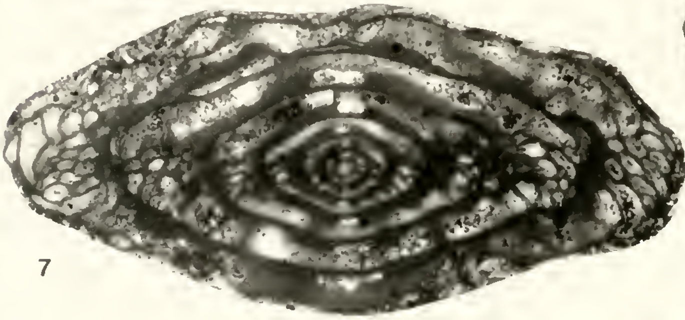
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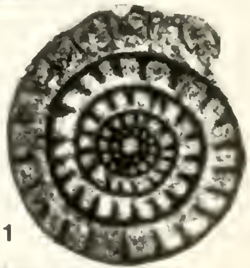
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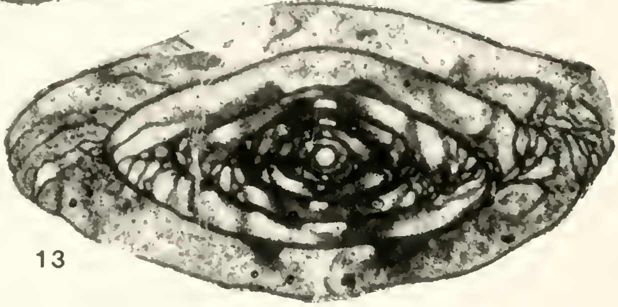
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wall structure can be studied in all conceivable orientations. Sagittal sections are generally most useful as they allow for the observation of wall structure continuously throughout spiral growth, but the area of observation is limited to the equatorial plane. Axial sections allow for the observation of wall structure longitudinally, from pole to pole, but the observations can be made only at half-volution increments. Oblique sections allow for observation continuously throughout spiral growth, and they particularly reveal the nature of epithecal deposits where the septa intersect chomata. Tangential sagittal and tangential axial sections allow the same kinds of observations as sagittal and axial sections, respectively, but they do not pass through the proloculus and therefore preclude examination of the earliest ontogenetic stages.

OBSERVATIONS

The transition from profusulinellid- to fusulinellid-type wall structure in sampled populations at Pfluger Bluff is shown graphically in Text-figure 3. Histograms in this figure depict at half-volution increments the percentage of specimens from a given sample exhibiting profusulinellid-type walls and the remaining percentage with fusulinellid-type walls (see also Text-fig. 4). Observations are not reported for the initial 1.5 volutions because confident determination of wall structure in the juvenarium generally is not possible. Neither are observations reported for the final half volution of complete, unabraded specimens because the wall in the last several chambers of such specimens consists of the protheca only. Observations for the final half volution of abraded specimens are reported, however, because these specimens likely possessed one or more additional volutions during the life of the individual.

Wall structure was examined only in specimens with 4.5 or more volutions. Accordingly, for a given sample, statistics for volution 3.5 may include observations from the penultimate volution of some individuals, the antepenultimate volution of others, and so on. This undoubtedly skews the statistics because, in all but the earliest few volutions, secondary deposits tend to be better developed with increasing spiral distance from the last chamber. The effect is probably minor, though, because the majority of examined specimens possess 5 to 6 volutions and there is therefore a high degree of developmental uniformity among specimens. Moreover, the effect should be roughly equal among samples, so that when considered stratigraphically, the emerging evolutionary pattern is valid.

At the Pfluger Bluff section, lithologic units 2–14 yielded specimens with exclusively profusulinellid-type walls (Text-fig. 3, histogram A). Representative specimens are illustrated on Plates 1 and 2. Of special importance, certain of the specimens from the lower part of the Pfluger Bluff section exhibit the rudiments of a transparent, relatively coarsely crystalline diaphanotheca (Pl. 2, figs. 1, 3, 5, 6). In other, more typical profusulinellids, the diaphanotheca is finely crystalline and darker (Pl. 2, figs. 2, 4).

The stratigraphically lowest occurrence of fusulinellid-type wall structure was noted in unit 15 (sample 28), which contains only rare specimens. Specimens occur very abundantly in unit 16 (samples 29–31) (Pls. 3 and 4). Most of these exhibit fusulinellid-type wall structure in at least one volution, although specimens with only profusulinellid-type walls were observed in both samples 29 and 30 (Text-fig. 3, histogram B; Text-fig. 4). The histograms for these samples are representative of populations from the unit as a whole. Among the specimens in samples 29 and 30, those with fusulinellid-type walls in volutions 4.5 and higher slightly outnumber those with profusulinellid-type

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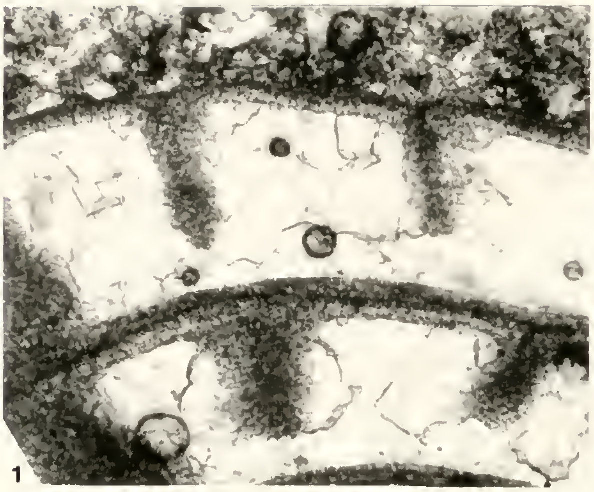
←

PLATE 1

1–13. *Profusulinella regia* Thompson, 1948, all ×30.
  1. SUI 94747: axial section, spl. 16.
  2. SUI 94748: axial section, spl. 24.
  3. SUI 94749: sagittal section, spl. 18.
  4. SUI 94750: axial section, spl. 16.
  5. SUI 94751: sagittal section, spl. 16.
  6. SUI 94752: sagittal section, spl. 18.
  7. SUI 94753: axial section, spl. 24.
  8. SUI 94754: axial section, spl. 16.
  9. SUI 94755: sagittal section, spl. 16.
  10. SUI 94756: axial section, spl. 18.
  11. SUI 94757: sagittal section, spl. 16.
  12. SUI 94758: axial section, spl. 16.
  13. SUI 94759: axial section, spl. 18.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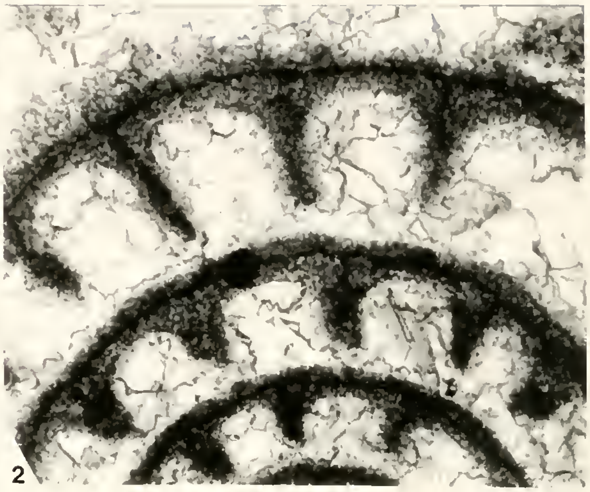
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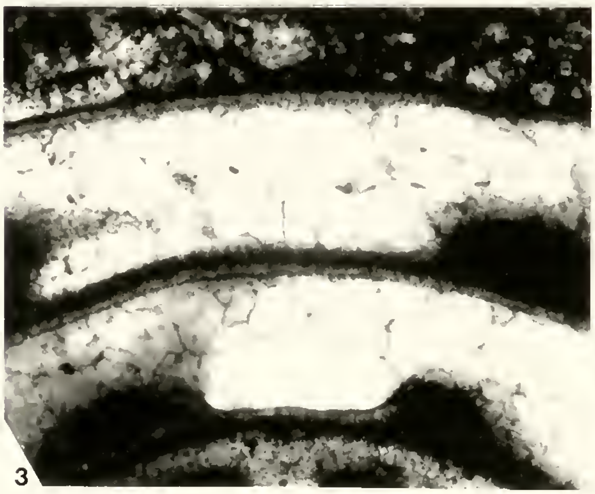
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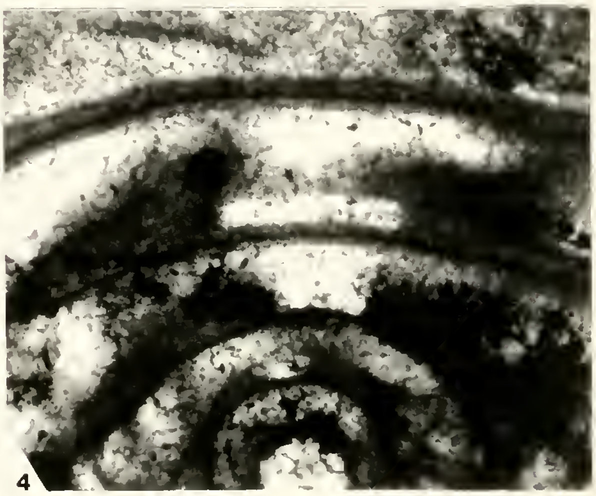
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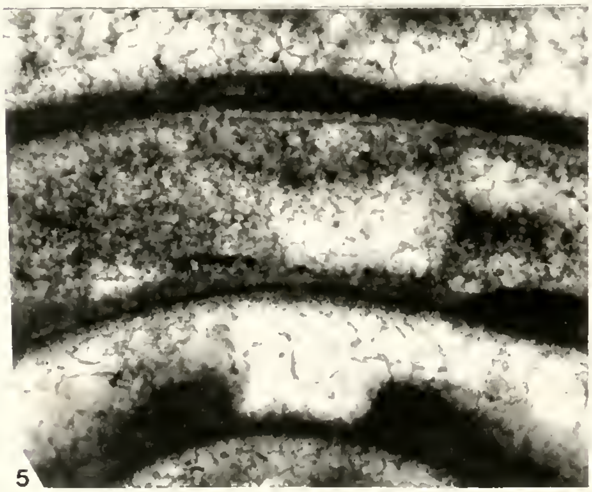
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6

walls. Profusulinellid-type walls are more prevalent in volution 4, even more so in volutions 3.5 and 3. Wall structure in volutions 2.5 and 2 is exclusively profusulinellid. Although the appearance of fusulinellid-type walls in units 15 and 16 seems abrupt (especially when comparing histograms A and B in Text-fig. 3), it is important to note that in most specimens the four-layered structure is weakly developed. In some cases the ceiling epitheca is quite thin (Pl. 4, figs. 5, 6). In others it is both thin and discontinuous, being patchily distributed longitudinally within a given chamber (Pl. 4, fig. 1).

Units 17 through 25 contain populations with generally thicker and more continuously developed ceiling epithecal deposits. In unit 18, however, there still occur rare specimens with profusulinellid-type wall structure throughout growth and several specimens with fusulinellid-type wall structure limited to a single volution. As high as unit 25, most samples contain at least a few specimens with profusulinellid-type walls in the mid-volutions, but other specimens from these samples exhibit fusulinellid-type wall structure as early as volution 2.5 (Text-fig. 3, histogram D).

Unit 27 is the stratigraphically lowest interval in which fusulinellid-type walls are well developed in most volutions of most specimens (Text-fig. 3, histograms E and F) (Pls. 5 and 6). Fusulinellid-type wall structure was observed as early as volution 2 in some specimens, and it is prevalent by volution 2.5. The seeming increase in the relative frequency of profusulinellid-type walls in volutions 5 through 6 in samples 50 and 53 is real but somewhat misleading. In these samples, the profusulinellid-type walls were observed among unabraded specimens in which deposition of the epithecal ceiling deposit lagged formation of the final chamber by a full volution or more. The ceiling epitheca in these specimens is well developed in the antepenultimate and earlier volutions.

Fusulinids from units 28 and higher were not examined for this study. Previous work indicated that specimens with fully developed fusulinellid-type wall structure continue throughout the remainder of the section (Groves, 1991). The only exception is sample 84 (unit 35, 40.6 m above the base of the exposure), which yielded specimens with less well developed fusulinellid-type walls similar to those in units 15–25.

INTERPRETATIONS

TAXONOMY AND NOMENCLATURE

In a previous study of fusulinaceans from the Marble Falls Limestone (Groves, 1991), I assigned Pfluger Bluff specimens with typical profusulinellid-type walls to *Profusulinella regia* Thompson, 1948 and those with well developed fusulinellid-type walls to *F. llanoensis* (Thomas, 1931). Specimens from the transition interval were less easily accommodated by the admittedly typological approach, and this led to the identification of unnamed species in both *Profusulinella* and *Fusulinella* within certain samples (*e.g.*, 28, 31, 33). In contrast, in the present study all of the fusiform fusulinids from a given sample are treated as belonging to a single population. This is justifiable because, although characters other than wall structure may vary among specimens both within and among samples, generally within a given sample there is not clear-cut evidence for discrete morphologic clusters. Populations with exclusively profusulinellid-type walls still fit neatly within the concept of *P. regia* (samples 2–27), and those with well-developed fusulinellid-type walls still fit neatly within *F. llanoensis* (samples 50 and higher). Intervening populations in which some specimens are profusulinellid and others are variably fusulinellid now are assigned to *Fusulinella primaeva* (Skinner, 1931), but with the proviso that the concept of *F. primaeva* must accommodate even greater variation in wall structure than is exhibited by the holotype and single paratype (cf. Groves and Sanderson, 1990). When considered in isolation, the present taxonomy of fusulinids at Pfluger Bluff suggests anagenesis without overlapping stratigraphic ranges of the constituent species.

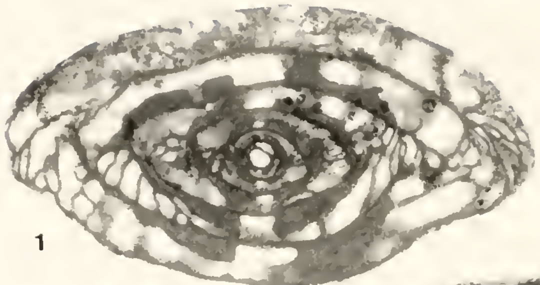
The typological approach resulted in the pigeonholing of specimens into two genera without allowances

←

PLATE 2

1–6. *Profusulinella regia* Thompson, 1948, all ×150.

1. SUI 94760: sagittal section showing light colored, blocky or columnar crystals of "advanced" diaphanotheca, spl. 24.
2. SUI 94751: sagittal section with darker, microgranular diaphanotheca (more typical of profusulinellid-type wall structure), spl. 16.
3. SUI 94761: axial section showing light colored, blocky or columnar crystals of diaphanotheca, spl. 24.
4. SUI 94762: axial section showing typically profusulinellid diaphanotheca, spl. 16.
5. SUI 94763: axial section showing very slightly blocky crystalline structure in diaphanotheca of outermost volution, spl. 16.
6. SUI 94764: axial section showing light colored, blocky or columnar crystals of diaphanotheca in outermost volution, spl. 24.



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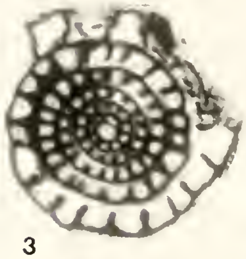

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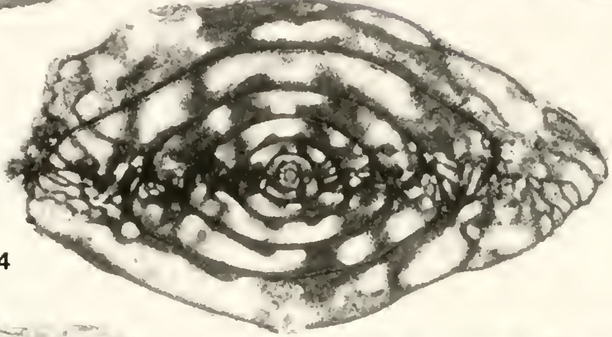

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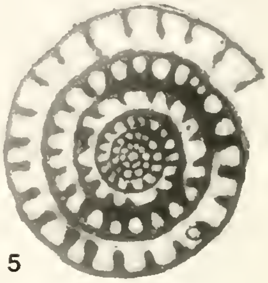

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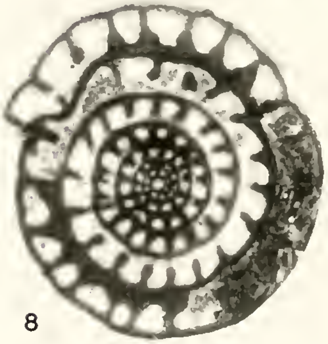

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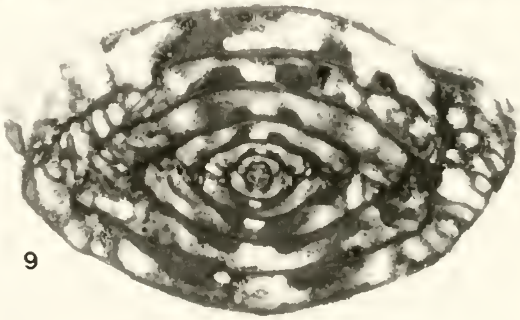

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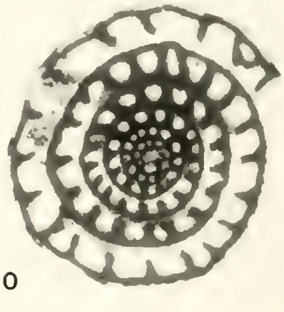

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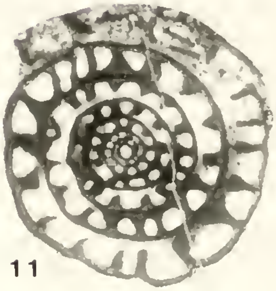

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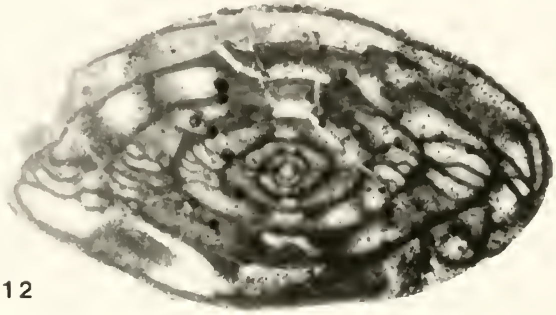

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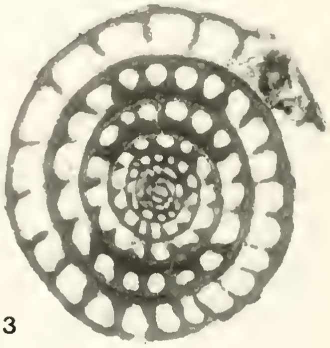

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for intra-population variation in a genus-delimiting character. The population approach, in contrast, allows for the inclusion within a single variable species (*F. primaeva*) of specimens that previously had been assigned to separate genera. The population approach more accurately reflects reality and enables a more meaningful analysis of the course of evolution.

The foregoing paragraphs illustrate the nomenclatural and taxonomic difficulties of parsing an evolutionary continuum. The difficulties arise largely because paleontologic taxa, especially paleontologic genera, are mental constructs with fixed boundaries whose purpose is to assist in organization and classification. The constructs function perfectly well in most cases, but they do not readily accommodate variation among individuals in transitional populations. Conveniently, in this case there existed already a named species (*F. primaeva*) to which the transitional forms can be referred. On the basis of fusulinellid-type wall structure in at least some individuals, I prefer to assign the *primaeva* populations to *Fusulinella*, but the generic designation is immaterial and these transitional populations could just as easily be retained in *Profusulinella*. Certainly, there is no need to erect a new genus for the intermediate morphotypes.

The creation of new genera for transitional forms is a troubling habit among some fusulinacean specialists (*e.g.*, Rauser-Chernousova *et al.*, 1996, in which 14 such genera were established!). Such genera are not only unnecessary, but they actually promote uncertainty insofar as they themselves are subject to the same taxonomic limitations as the end-members on either side of the transition. Specifically, the genus *Moellerites* Solov'eva 1986 is not a useful receptacle for specimens intermediate between *Profusulinella* and *Fusulinella* because it presents the taxonomist with two new dilemmas where previously there was only one: *i.e.*, how does one define and apply the taxonomic limits separating *Profusulinella* from *Moellerites* and those separating *Moellerites* from *Fusulinella*?

HETEROCHRONY (ACCELERATION)

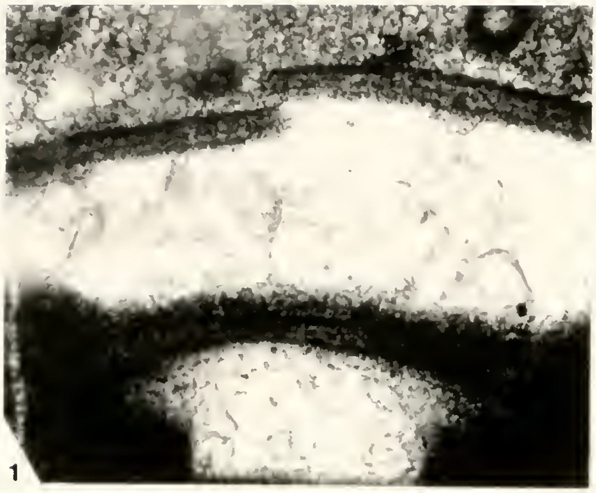
The progressive development of fusulinellid-type wall structure in populations at Pfluger Bluff not only is an example of anagenesis, but also of the category of heterochrony termed "acceleration" (de Beer, 1940; see discussion in Gould, 1977, p. 221–234). In the stratigraphically oldest populations exhibiting fusulinellid-type wall structure, the ceiling epitheca is not present before volution 3.0 (Text-fig. 3, histograms B and C). In these populations, the ceiling epitheca is present in only a small percentage of specimens in volution 3.0, and in less than half of the specimens in volutions 3.5 and 4.0. The earliest ontogenetic appearance of the ceiling epitheca in successively younger populations is in volution 2.5 (Text-fig. 3, histograms D and E) and, eventually, in volution 2.0 (Text-fig. 3, histogram F). In unit 27, a majority of specimens exhibit fusulinellid-type wall structure as early as volution 2.5. Thus, the ontogenetic appearance of fusulinellid-type wall structure was accelerated through time, occurring in progressively earlier developmental stages in stratigraphically younger populations.

The adaptive significance of the ceiling epitheca is unclear, but presumably its presence would have increased shell strength and ballast, both of which would have been advantageous to organisms living in high energy environments where mechanical abrasion might result in injury or death. Developmental acceleration is thought to occur when an advantageous adaptation that first appears late in ontogeny subsequently augments its selective value by appearing earlier (Stebbins, 1974).

←

PLATE 3

1–13. *Fusulinella primaeva* (Skinner, 1931), all ×30.
  1. SUI 94765: axial section, spl. 34.
  2. SUI 94766: axial section, spl. 30.
  3. SUI 94767: sagittal section, spl. 34.
  4. SUI 94768: axial section, spl. 34.
  5. SUI 94769: sagittal section, spl. 29.
  6. SUI 94770: axial section, spl. 34.
  7. SUI 94771: axial section, spl. 34.
  8. SUI 94772: sagittal section, spl. 30.
  9. SUI 94773: axial section, spl. 30.
  10. SUI 94774: sagittal section, spl. 29.
  11. SUI 94775: sagittal section, spl. 30.
  12. SUI 94776: axial section, spl. 29.
  13. SUI 94777: sagittal section, spl. 30.



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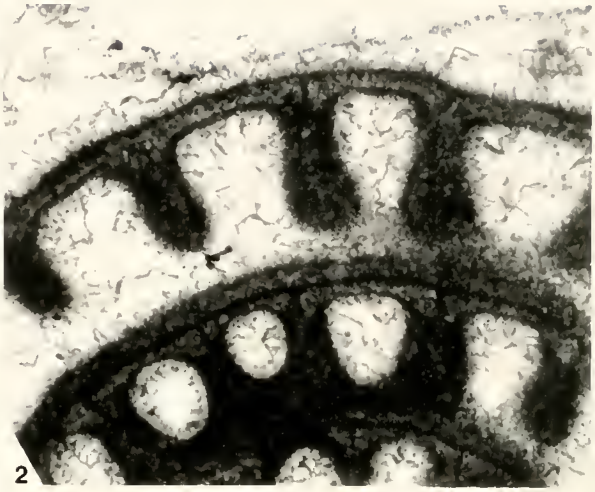

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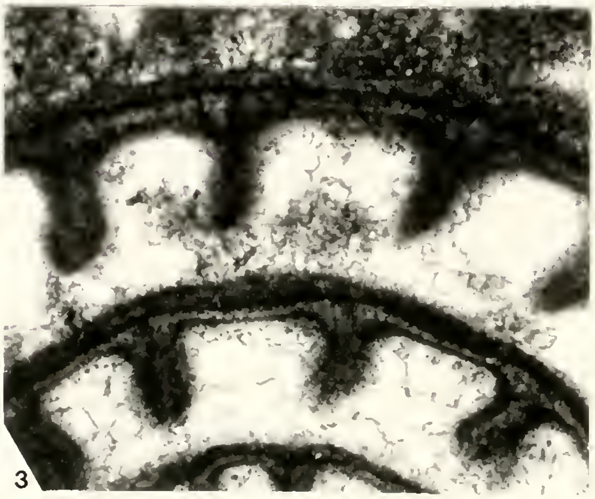

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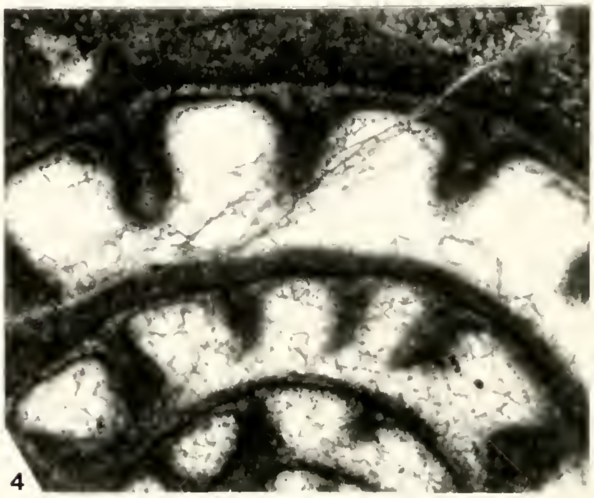

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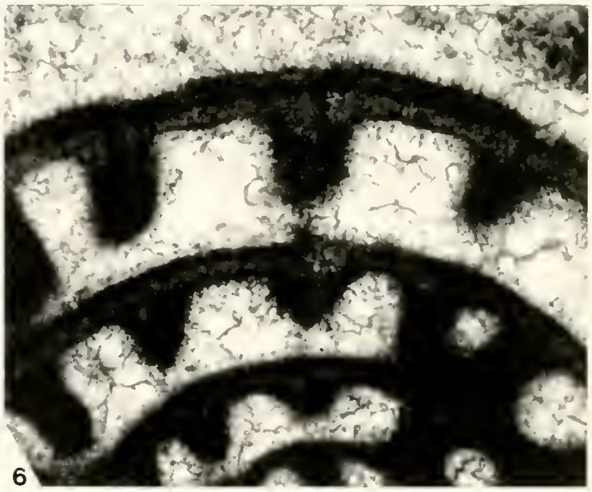

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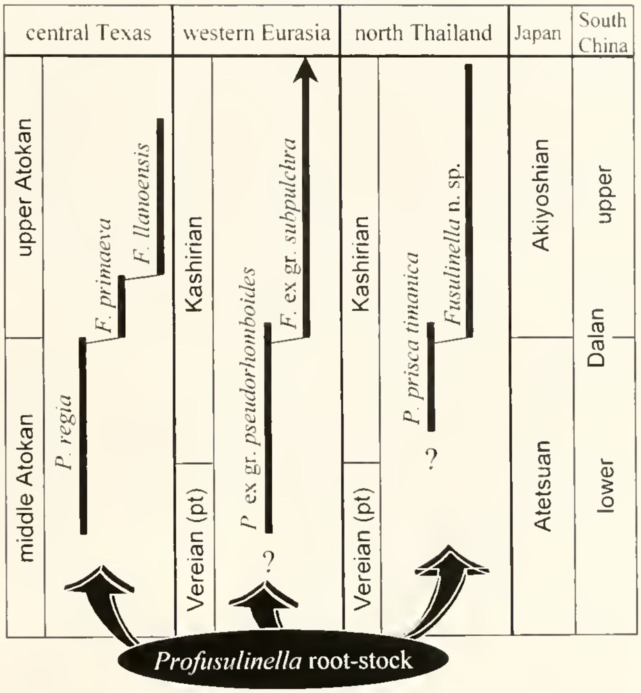
SYNCHRONOUS PARALLELISM VS. COLLATERAL EVOLUTION

As noted earlier, specimens transitional between *Profusulinella* and *Fusulinella* are known from numerous localities in the United States, Europe, Tian' Shan', and northern Thailand, and still others undoubtedly remain to be discovered. Did the *Profusulinella–Fusulinella* evolutionary transition occur independently in these widely separated areas, or did it occur only once in a panmictic, global population?

The overwhelming bulk of evidence argues against a global population. Fusulinids were benthonic inhabitants of shallow marine, tropical to subtropical paleoenvironments, and they are found most commonly in carbonate or mixed carbonate-siliciclastic lithologies. Because of their mode of life and paleoenvironmental preferences, Pennsylvanian paleoclimate and paleogeography conspired to isolate fusulinid faunas. By late Atokan/late Kashirian time, most major land areas had assembled to form Pangaea, resulting in the closure of the former circumequatorial seaway and the fragmentation of formerly contiguous shallow marine biotopes (Rowley *et al.*, 1985; Ross and Ross, 1985). High latitude land areas were glaciated periodically (Crowell, 1978), presumably with a concomitant cooling of adjacent marine shallow waters. Consequently, Pennsylvanian fusulinids were highly provincial. Marine communication between the Midcontinent-Andean and Eurasian-Arctic faunal realms probably was infrequent and channeled primarily through the mid-paleolatitude Franklinian Geosyncline (Ross, 1967; Ross and Ross, 1985). Given these circumstances, it is remarkable that geographically disjunct populations of advanced profusulinellids apparently underwent identical modifications in wall structure at about the same time. The *Profusulinella–Fusulinella* evolutionary transition seems to have occurred independently in at least three areas (Text-fig. 5): in the central United States (*P. regia–F. primaeva–F. llanoensis*); separately in the *Profusulinella prisca timanica–Fusulinella* n. sp. lineage in northern Thailand (Ueno and Igo, 1997); and separately in the *P.* ex gr. *pseudorhomboides–F.*



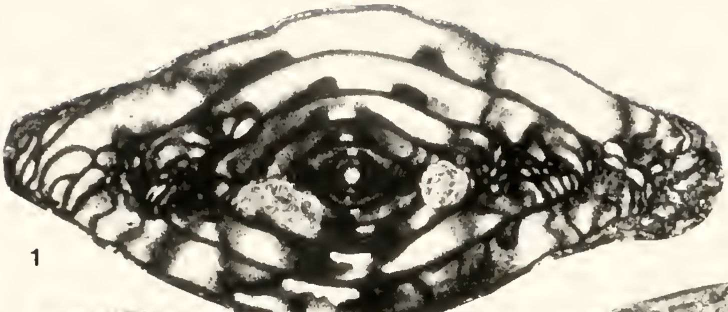
Text-figure 5.—Independent, synchronous origins of *Fusulinella* spp. from *Profusulinella* spp. in central Texas (this study), western Eurasia (E. Villa, pers. commun., 1999, 2000), and northern Thailand (Ueno and Igo, 1997). Stratigraphic appearance of *Fusulinella* characterizes the bases of the informal upper Atokan Series in North America (Groves, 1986), Akiyoshian Stage in Japan (Toriyama, 1967), and upper Dalan Series in South China (Gao *et al.*, 1983). This level falls within the Kashirian Substage of the Moscovian Stage of the standard chronostratigraphic scale for the East European Platform (Ivanova *et al.*, 1979). Vertical scale is non-linear.

←

PLATE 4

1–6. *Fusulinella primaeva* (Skinner, 1931), all ×150.

1. SUI 94766: axial section showing very faint development of epitheca on chamber ceiling of ultimate and penultimate volutions, spl. 30.
2. SUI 94769: sagittal section showing faint development of epitheca on septa and chamber ceiling of ultimate, penultimate, and antepenultimate volutions; septa of penultimate volution have merged with epithecal floor deposits (chomata); note light diaphanotheca in ultimate volution, spl. 29.
3. SUI 94772: sagittal section showing faint development of epitheca on septa and chamber ceiling of ultimate, penultimate, and antepenultimate volutions; note light diaphanotheca in ultimate and penultimate volutions, spl. 30.
4. SUI 94778: sagittal section showing faint development of epitheca on septa and chamber ceiling of ultimate volution and part of penultimate volution; note light diaphanotheca in ultimate volution, spl. 30.
5. SUI 94778: sagittal section showing very faint development of epitheca on septa of ultimate volution and on septa and chamber ceiling of antepenultimate volution, spl. 30.
6. SUI 94769: sagittal section showing very faint development of epitheca on septa and chamber ceiling of ultimate, penultimate, and antepenultimate volutions, spl. 29.



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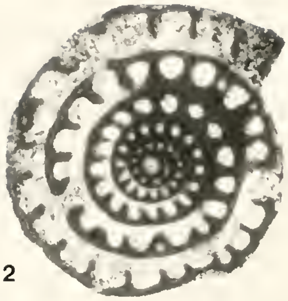

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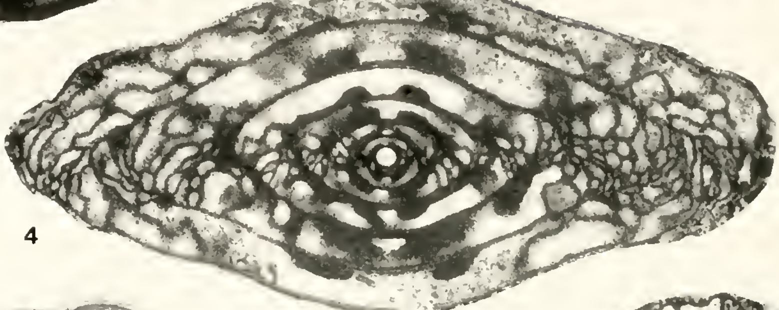

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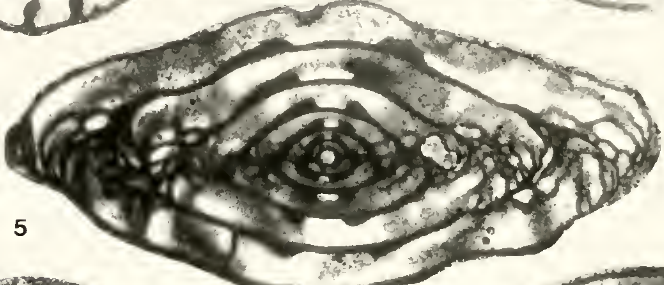

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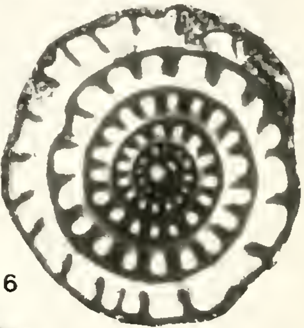

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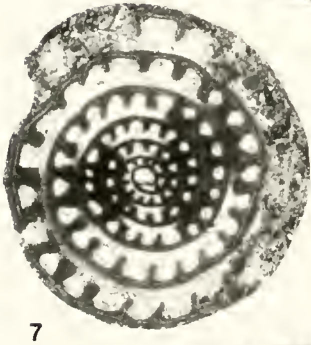

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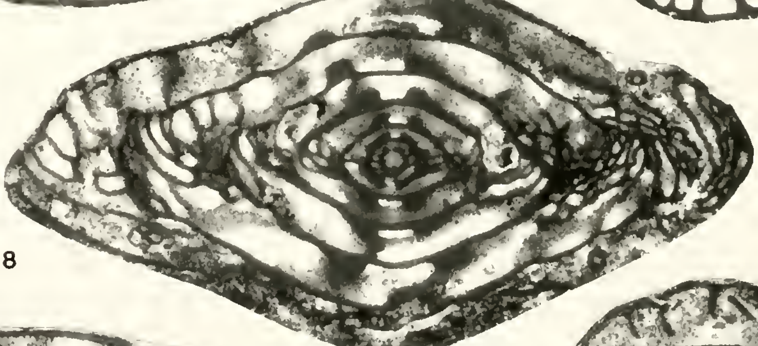

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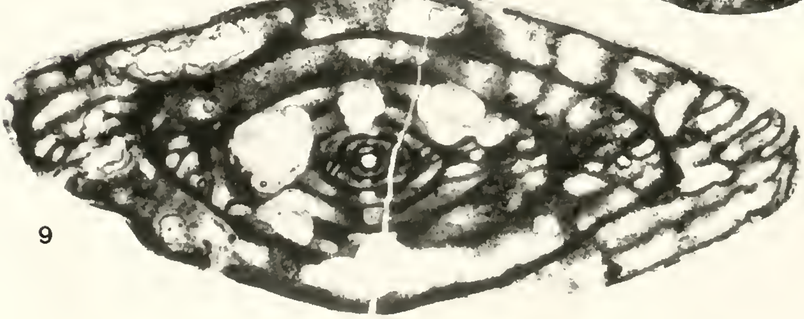

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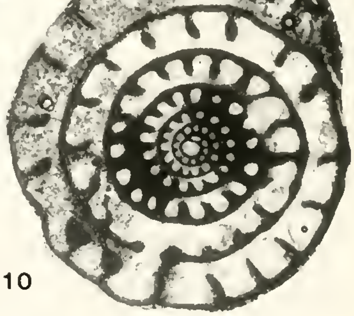

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ex gr. *subpulchra* lineage of Europe (E. Villa, personal communication, 1999, 2000). This interpretation suggests that *Fusulinella* is a polyphyletic genus and that its multiple origins are the result of synchronous or nearly synchronous parallelism. Parallelism of this type apparently is common, having been documented in Cretaceous ammonites (Kennedy and Cobban, 1976; Kennedy, 1977), angiosperms (Wolfe *et al.*, 1975; Doyle, 1977), and other groups of fusulinaceans (Ginkel and Villa, 1999), to cite just a few examples. According to Mayr (1963), parallelism occurs when closely related species (*i.e.*, organisms with a common heritage) respond similarly to similar selection pressure.

A related concept—collateral evolution—requires discussion, but less adequately describes the *Profusulinella–Fusulinella* transition. As conceived by Shaw (1969), collateral evolution occurs when a geographically widely distributed ancestral character responds to selection pressure to produce identical transition series leading to identical descendant characters. Shaw considered that a given mutation could arise simultaneously in multiple places and then be incorporated in all areas that are subject to a given change in selection pressure. In this sense, collateral evolution does not differ substantially from synchronous parallelism. It is clear from Shaw's discussion, however, that he envisioned collateral evolution as operating in a globally distributed (mondial) taxon or lineage (see also Springer and Murphy, 1994), as opposed to closely related but genetically distinct populations. As discussed above, it is difficult to accept that a global population of *Profusulinella* could exist while other fusulinids were so markedly provincial. For example, the contemporaneous genera *Neostaffella*, *Verella*, and *Eofusulina* occur widely throughout Eurasia, but no occurrences have been documented in the Midcontinent-Andean realm. More troubling, if advanced profusulinellids worldwide did in fact constitute a mondial taxon, then a wholesale rethinking of traditional species concepts is required. On morphologic criteria, most specialists would agree that *P. regia* is distinct from *P.* ex gr. *pseudorhomboides* and from *P. prisca timanica*.

Finally, it is interesting to note that the transition from profusulinellid-type to fusulinellid-type wall structure also occurred in an entirely separate clade of fusulinids, the Pseudostaffellinae, in connection with the origin of *Neostaffella* from *Pseudostaffella*. The independent acquisition of a ceiling epitheca in the Fusulininae and Pseudostaffellinae was cited by Groves (1997) as an example of convergence and one of many patterns of repetitive evolution among Late Paleozoic foraminifers. This event in the Pseudostaffellinae occurred in the Early Bashkirian Substage (Askynbashian), significantly earlier than in the Fusulininae.

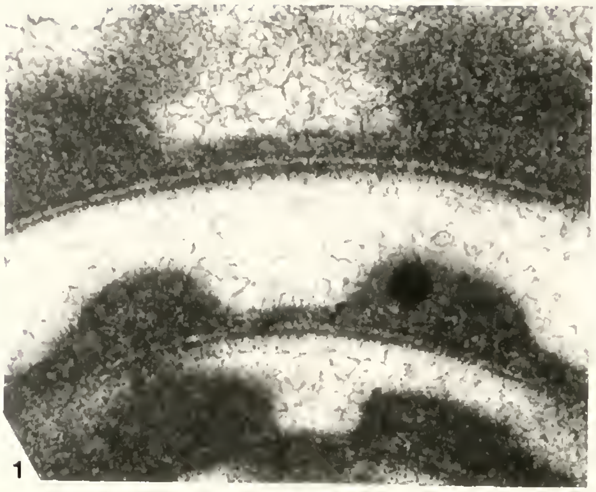
Biostratigraphy

The stratigraphic appearance of *Fusulinella* has been utilized since the 1940's for correlating upper Atokan rocks in North America (Dunbar and Henbest, 1942; Thompson, 1945, 1948), and more recently, in South America (Altiner and Savini, 1995). In western Eurasia, this event characterizes the base of the upper division of the Kashirian Substage of the Moscovian Stage (Solov'eva, 1963, 1977; Ginkel, 1965; Ivanova *et al.*, 1979). [Solov'eva (1985, 1986) and Solov'eva *et al.* (1985) proposed a revision of the Moscovian Stage in which the "Tsninsky Horizon" was recognized between the Vereisky and Kashirsky horizons. Subsequent work has shown that the "Tsninsky" interval is equivalent to the lower Kashirsky, and thus redundant (A. Alekseev, pers. commun., 1999). If one employs "Tsninsky" as a discrete chronostratigraphic unit, however, then the appearance of *Fusulinella* would fall at the base of the upwardly revised Kashirian Substage.] The base of the Zone of *Fusulinella* defines both the base of the Akiyoshian Stage in Japan (Toriyama, 1967) and the base of the upper substage of the Dalan Stage in South China (Gao *et al.*, 1983).

←

Plate 5

1–10. *Fusulinella llanoensis* (Thomas, 1931), all ×30.
  1. SUI 94779: axial section, spl. 53.
  2. SUI 94780: sagittal section, spl. 52.
  3. SUI 94781: sagittal section, spl. 52.
  4. SUI 94782: axial section, spl. 52.
  5. SUI 94783: axial section, spl. 50.
  6. SUI 94784: sagittal section, spl. 50.
  7. SUI 94785: sagittal section, spl. 53.
  8. SUI 94786: axial section, spl. 50.
  9. SUI 94787: axial section, spl. 50.
  10. SUI 94788: sagittal section, spl. 52.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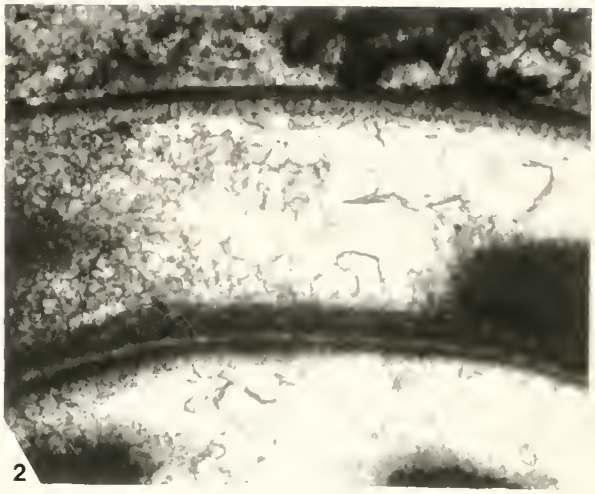
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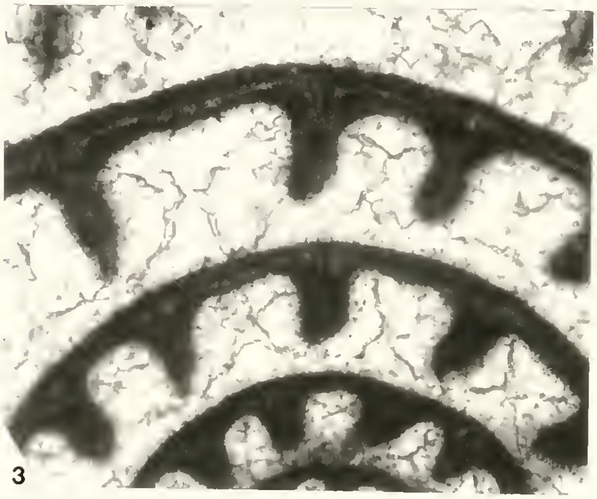
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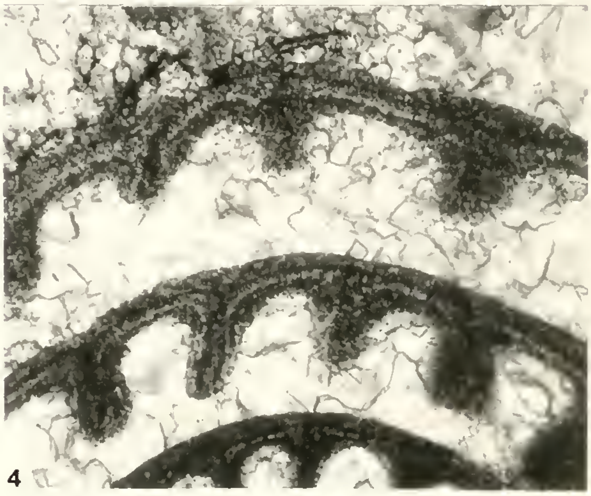
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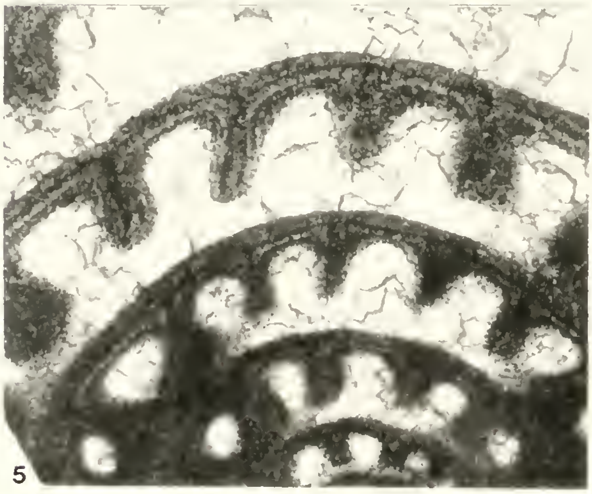
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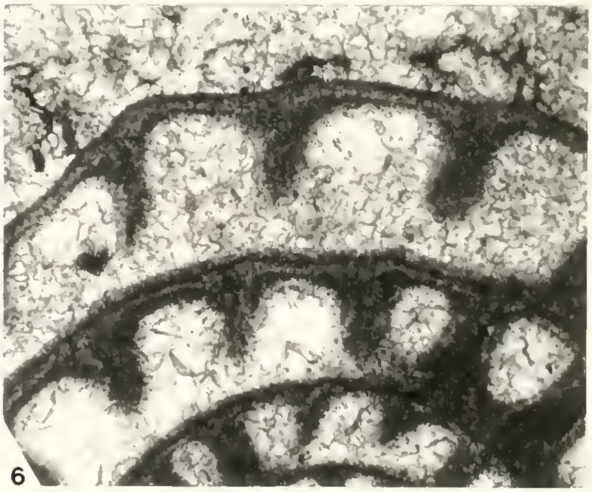
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Historically, specialists have accepted that the bases of the upper Atokan, upper Kashirian, Akiyoshian, and upper Dalan are approximately equivalent in age (Text-fig. 5; Toriyama, 1967; Ivanova *et al.*, 1979; see Aisenverg *et al.*, 1979 for an alternate interpretation). The appearance of *Fusulinella*, therefore, implicitly was bestowed significant weight in intercontinental correlations, but the actual worldwide timing of this event needs to be evaluated independently of axiomatic fusulinid-based correlations.

If one accepts that earliest *Fusulinella* arose independently and synchronously (by whatever means) in at least three widely separated areas, and that the migratory appearance of *Fusulinella* throughout the remainder of the paleo-tropics and subtropics followed soon thereafter, then some mechanism must be invoked for the rapid dispersal outward from the original loci. Given the paleogeographic and paleoclimatic constraints cited above, such dispersal most likely occurred during an interglacial highstand that would have flooded low land areas and warmed the shallow seas in the mid-paleolatitudes. Published coastal onlap curves for the Pennsylvanian depict glacio-eustatic cyclicity, but there are conflicting interpretations regarding the amplitude and frequency of highstands during late Atokan/late Kashirian time. According to the curve in Ross and Ross (1987, fig. 3), the appearance of *Fusulinella* coincided approximately with a minor rise in sea level, but in terms of overall second-order eustacy, this span of Atokan time was characterized by relatively low sea levels. By comparision, the curve derived by Alekseev *et al.* (1996, fig. 10) for the Moscow Syneclise shows higher frequency cycles during Kashirian time and a relatively more pronounced late Kashirian flooding event. It is unclear whether or not the late Kashirian transgression was of a sufficient magnitude to assist the distribution of *Fusulinella*. This, too, must be evaluated in greater detail by integrating sequence stratigraphy with multidisciplinary, high resolution biostratigraphy.

CONCLUSIONS

1. The evolutionary transition from *Profusulinella* to *Fusulinella* does not involve the acquisition of new characters, but rather the progressive development of secondary wall deposits. In the profusulinellid-type wall the epitheca is restricted to septa and the floors of chambers. In the fusulinellid-type wall it is secreted also on the ceilings of chambers so that it forms a lining of the entire chamber cavity. In primitive *Fusulinella*, the ceiling epitheca is thin and discontinuous, whereas in more advanced forms it is thicker and more continuously developed.
2. The diaphanotheca in *Fusulinella* typically appears lighter and more transparent than in *Profusulinella*. This may be partly illusory: in *Fusulinella* the diaphanotheca appears light because it is underlain by the darker ceiling epitheca; in *Profusulinella* it appears dark because it is in direct contact with clear, chamber-filling cement. Additionally, the diaphanotheca in typical *Profusulinella* is finely crystalline, resulting in relatively high internal refraction and reflection of transmitted light. Crystal size within the diaphanotheca apparently increased with evolutionary grade, so that advanced *Profusulinella* and *Fusulinella* possess more coarsely crystalline diaphanothecae that allow greater transmittance of light.
3. An anagenetic transition from profusulinellid-type to fully fusulinellid-type wall structure has been documented in a thin (15 m) interval of the Marble Falls Limestone at the Pfluger Bluff locality in central Texas. Advanced profusulinellids are assignable to *P. regia*. Well developed fusulinellids are assignable to *F. llanoensis*. Transitional populations assigned to *F. primaeva* include specimens with both profusulinellid- and variably developed fusulinellid-type walls. Fusulinellid-type wall structure at Pfluger Bluff occurs in progressively earlier on-

←

PLATE 6

1–6. *Fusulinella llanoensis* (Thomas, 1931), all ×150.
1. SUI 94782: axial section, spl. 52.
2. SUI 94789: axial section showing block or columnar crystals of diaphanotheca in ultimate volution (without epitheca on chamber ceiling) and well-developed epitheca on chamber ceiling of penultimate volution, spl. 50.
3. SUI 94790: sagittal section showing well-developed epitheca on septa and chamber ceiling of outer three volutions, spl. 50.
4. SUI 94785: sagittal section showing very thick epitheca on septa and chamber ceiling of outer three volutions, spl. 53.
5. SUI 94785: sagittal section showing very thick epitheca on septa and chamber ceiling of outer three volutions, spl. 53.
6. SUI 94791: sagittal section showing faint epitheca on septa and chamber ceiling of ultimate volution; and thicker epithecal deposits in penultimate volution, spl. 50.

togenetic stages in successively younger populations, representing a type of heterochrony known as acceleration. Available evidence suggests that similar transitions, involving the *P.* ex gr. *pseudorhomboides–F.* ex gr. *subpulchra* lineage and the *P. prisca timanica–Fusulinella.* n. sp. lineage, occurred independently in Europe and southeast Asia, respectively. Thus, *Fusulinella* is a polyphyletic genus and its nearly synchronous, multiple origins represent a striking example of parallelism.

4. The stratigraphic appearance of *Fusulinella* characterizes the base of the informal upper part of the Atokan Series in North and northern South America, the upper part of the Kashirian Substage of the Moscovian Stage in western Eurasia, the base of the Akiyoshian Series in Japan, and the base of the upper part of the Dalan Stage in South China. These horizons are considered roughly age equivalent by most authors, implying rapid and widespread dispersal of *Fusulinella* spp. from their original populations. The appearance of *Fusulinella* may prove highly useful in intercontinental biostratigraphy, but this datum first must be evaluated independently through multidisciplinary investigations that integrate biostratigraphy with sequence stratigraphy.

REFERENCES CITED

Aisenverg, D.E., Brazhnikova, N.E., Vassilyuk, N.P., Vdovenko, M.V., Gorak, S.V., Dunaeva, N.N., Zernetskaya, N.V., Poletaev, V.I., Potievskaya, P.D., Rotai, A.P., and Sergeeva, M.T.

1979. The Carboniferous sequence of the Donetz Basin: a standard section for the Carboniferous System. *in* The Carboniferous of the USSR. R.H. Wagner, A.C. Higgins, and S.V. Meyen, *eds.*, Yorkshire Geological Society Occasional Publication 4, pp. 197–224.

Alekseev, A.S., Kononova, L.I., and Nikishin, A.M.

1996. The Devonian and Carboniferous of the Moscow Syneclise (Russian Platform): stratigraphy and sea-level changes. Tectonophysics, vol. 268, pp. 149–168.

Altiner, D., and Savini, R.

1995. Pennsylvanian foraminifera and biostratigraphy of the Amazonas and Solimõs basins (north Brazil). Revue de Paléobiologie, vol. 14, pp. 417–453.

Angell, R.W.

1980. Test morphogenesis (chamber formation) in the foraminifer *Spiroloculina hyalina* Schultze. Journal of Foraminiferal Research, vol. 10, pp. 89–101.

Carpenter, W.B., Parker, W.K., and Jones, T.R.

1862. Introduction to the study of the foraminifera. Ray Society Publications, London. 319 pp.

Cheney, M.G.

1940. Geology of north-central Texas. American Association of Petroleum Geologists Bulletin, vol. 24, pp. 65–118.

Crowell, J.C.

1978. Gondwanan glaciation, cyclothems, continental positioning, and climate change. American Journal of Science, vol. 278, pp. 1345–1372.

de Beer, G.R.

1940. Embryos and ancestors. Clarendon Press, Oxford, 197 pp.

Douglass, R.C.

1977. The development of fusulinid biostratigraphy. *in* Concepts and Methods of Biostratigraphy, E.G. Kauffman and J.E. Hazel, *eds.*, Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, pp. 463–481.

1987. Fusulinid biostratigraphy and correlations between the Appalachian and Eastern Interior basins. U. S. Geological Survey Professional Paper 1451, 95 pp.

Douvillé, H.

1906 Sur la structure du test dans les fusulines. Académie des Sciences de Paris, Comptes Rendus, Mémoires, vol. 143, pp. 258–261.

Doyle, J.A.

1977. Patterns of evolution in early angiosperms. *in* Patterns of evolution, as illustrated by the fossil record. A. Hallam, *ed.*, Developments in Palaeontology and Stratigraphy, 5. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, pp. 501–546.

Dunbar, C.O., and Condra, G.E.

1928. The Fusulinidae of the Pennsylvanian System in Nebraska. Nebraska Geological Survey Bulletin II, Second Series, 135 pp. [imprint 1927].

Dunbar, C.O., and Henbest, L.G.

1942. Pennsylvanian Fusulinidae of Illinois. Illinois State Geological Survey Bulletin 67, 218 pp.

Dunbar, C.O., and Skinner, J.W.

1937. Permian Fusulinidae of Texas. The University of Texas Bulletin No. 3701, pp. 517–825.

Dyhrenfurth, G.

1909. Die Fusulinen von Darwas. *in* Monographie der Fusulinen, Pt. II, E. Schellwien, Palaeontographica, vol. 56, pp. 137–176.

Gao Lianda, Wang Zengji, and Wu Xianghe

1983. The Middle Carboniferous of China. *in* The Carboniferous of the world. Part I, China, Korea, Japan, and S.E. Asia., R.H. Wagner, C.F. Winkler Prins, and L.F. Granados, *eds.*, Instituto Geologico y Minero de España, and Empressa Nacional Adaro de Investigaciones Mineras, S. A., IUGS Publication No. 16, pp. 56–86.

Ginkel, A.C. van

1965. Carboniferous fusulinids from the Cantabrian Mountains (Spain). Leidse Geologische Mededelingen, Deel 34, 225 pp.

Ginkel, A.C. van, and Villa, E.

1999. Late fusulinellid and early schwagerinid foraminifera: relationships and occurrences in the Las Llacerias section (Moscovian/Kasimovian), Cantabrian Mountains, Spain. Journal of Foraminiferal Research, vol. 29, pp. 263–290.

Girty, G.H.

1904. *Triticites*, a new genus of Carboniferous foraminifera. American Journal of Science, vol. 17, pp. 234–240.

Gould, S.J.

1977. Ontogeny and phylogeny. Belknap Press (Harvard), Cambridge, Massachusetts and London, England, 501 pp.

Green, H.W., II, Lipps, J.H., and Showers, W.J.

1980. Test ultrastructure of fusulinid foraminifera. Nature, vol. 283, pp. 853–855.

Groves, J.R.

1986. Foraminiferal characterization of the Morrowan-Atokan (lower Middle Pennsylvanian) boundary. Geological Society of America Bulletin, vol. 97, pp. 346–353.

1991. Fusulinacean biostratigraphy of the Marble Falls Limestone (Pennsylvanian), western Llano region, central Texas. Journal of Foraminiferal Research, vol. 21, pp. 67–95.

1992. Stratigraphic distribution of non-fusulinacean foraminifers in the Marble Falls Limestone (Lower-Middle Pennsylvanian), western Llano region, central Texas. *in* Recent advances in Middle Carboniferous biostratigraphy—a symposium, P.K. Sutherland and W.L. Manger, *eds.*, Oklahoma Geological Survey Circular 94, pp. 145–161.

1997. Repetitive patterns of evolution in Late Paleozoic foraminifers. *in* Late Paleozoic foraminifera—their biostratigraphy, evolution, and paleoecology and the mid-Carboniferous boundary, C.A. Ross, J.R.P. Ross, and P.L. Brenckle, *eds.*, Cushman Foundation for Foraminiferal Research Special Publication No. 36, pp. 51–54.

Groves, J.R., and Sanderson, G.A.

1990. Systematics of the North American species of *Profusulinella* (Middle Pennsylvanian Fusulinidae). Micropaleontology, vol. 36, pp. 105–140.

Gubler, J.

1934. Structure et sécrétion du test des Fusulinidés. Annales de Protistologie, vol. 4, pp. 1–24.

1936. Les Fusulinidés du Permien de l'Indochine, leur structure et leur classification. Société Géologique de France, Mémoires, n. s., vol. 11, no. 4, pp. 1–173 [imprint 1935].

Hemleben, C., Anderson, O.R., Berthold, W.U., and Spindler, M.

1986. Calcification and chamber formation in foraminifera—a brief overview. *in* Biomineralization in lower plants and animals, B.S.C. Leadbeater and R. Riding, *eds.*, The Systematics Association, Special Volume No. 30, Clarendon Press, Oxford, pp. 237–249.

Ivanova, E.A., Solov'eva, M.N., and Shik, E.M.

1979. The Moscovian Stage in the USSR and throughout the world. *in* The Carboniferous of the USSR, R.H. Wagner, A.C. Higgins, and S.V. Meyen, *eds.*, Yorkshire Geological Society Occasional Publication 4, pp. 117–146.

Johnson, D.W.

1983. Carbonate petrography, microfacies, and depositional history of the Marble Falls Formation (Pennsylvanian), Llano region, central Texas. unpublished Master's thesis, University of Oklahoma, Norman, 258 pp.

Kennedy, W.J.

1977. Ammonite evolution. *in* Patterns of evolution, as illustrated by the fossil record, A. Hallam, *ed.*, Developments in Palaeontology and Stratigraphy, 5. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, pp. 251–304.

Kennedy, W.J., and Cobban, W.A.

1976. Aspects of ammonite biology, biostratigraphy and biogeography. The Palaeontological Association (London), Special Papers in Palaeontology, vol. 17, 94 pp.

Lee, J.S.

1923. A graphic method to aid specific determination of fusulinoids and some results of its application to the Fusulinae from North China. Geological Society of China Bulletin, vol. 2, pp. 51–86.

1924. New terms in the description of the Fusulinidae. Geological Society of China Bulletin, vol. 3, pp. 13–14.

Lee, J.S., Chen, S., and Chu, S.

1930. The Huanglung Limestone and its fauna. Academica Sinica, Memoirs of the National Research Institute of Geology, vol. 9, pp. 85–143.

Loeblich, A.R., Jr., and Tappan, H.

1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida. *in* Treatise on Invertebrate Paleontology, R.C. Moore, *ed.*, Geological Society of America and University of Kansas Press, Part C, Protista (2), 2 vols., 900 pp.

Lutze, G.H., and Wefer, G.

1980. Habitat and asexual reproduction of *Cyclorbiculina compressa* (Orbigny), Soritidae. Journal of Foraminiferal Research, vol. 10, pp. 251–260.

Manger, W.L., and Sutherland, P.K.

1984. Preliminary conodont biostratigraphy of the Morrowan-Atokan boundary (Pennsylvanian), eastern Llano Uplift, central Texas. *in* The Atokan Series (Pennsylvanian) and its boundaries—a symposium, P.K. Sutherland and W.L. Manger, *eds.*, Oklahoma Geological Survey Bulletin 136, pp. 115–122.

Mayr, E.

1963. Populations, species, and evolution. Harvard University Press, Cambridge, Massachusetts and London, England, 453 pp.

Myers, E.H.

1935. The life history of *Patellina corrugata* Williamson, a foraminifer. University of California, Scripps Institute of Oceanography, Technical Series, vol. 3, pp. 355–392.

Plummer, F.B.

1950. The Carboniferous rocks of the Llano region of central Texas. The University of Texas Publication No. 4329, 170 pp.

Rauser-Chernousova, D.M., Bensh, F.R., Vdovenko, M.V., Gibshman, N.B., Leven, E. Ya., Lipina, O.A., Reitlinger, E.A., Solov'eva, M.N., and Chediya, I.O.

1996. Reference book on the systematics of Paleozoic foraminifera (Endothyroida, Fusulinoida). Rossiiskaya Akademiya Nauk, Geologicheskii Institut. Moskva "Nauka," 204 pp. [in Russian].

Rauser-Chernousova, D.M., Gryslova, N.D., Kireeva, G.D., Leontovich, G.E., Safonova, T.P., and Chernova, E.I.

1951. Middle Carboniferous fusulinids of the Russian Platform and adjacent regions. Akademiya Nauk SSSR, Institut Geologicheskii Nauk, Ministerstvo Neftiyanoi Promyshlennosti SSSR, Trudy, 380 pp. [in Russian].

Ross, C.A.

1967. Development of fusulinid (Foraminiferida) faunal realms. Journal of Paleontology, vol. 41, pp. 1341–1354.

Ross, C.A., and Ross, J.R.P.

1985. Carboniferous and Permian biogeography. Geology, vol. 13, pp. 27–30.

1987. Late Paleozoic sea levels and depositional sequences. *in* Timing and depositional history of eustatic sequences: constraints on seismic stratigraphy. C.A. Ross and D. Haman, *eds.*, Cushman Foundation for Foraminiferal Research, Special Publication 24, pp. 137–168.

Rowley, D.B., Raymond, A., Parrish, J.T., and Lottes, A.L.

1985. Carboniferous paleogeographic, phytogeographic, and paleoclimatic reconstructions. International Journal of Coal Geology, vol. 5, pp. 7–42.

Schellwien, E.

1898. Die Fauna des karnischen Fusulinenkalks, Pt. II. Palaeontographica, vol. 44, pp. 237–282.

Schwager, C.

1887. Protozoa. *in* Salt Range fossils. W. Waagen and J. Wentzel, India Geological Survey Memoir, Palaeontologica Indica, Series 13, vol. 1, pp. 983–990.

Shaw, A.B.

1969. Adam and Eve, paleontology, and the non-objective arts. Journal of Paleontology, vol. 43, pp. 1085–1098.

Skinner, J.W.

1931. Primitive fusulinids of the mid-continent region. Journal of Paleontology, vol. 5, pp. 253–259.

Skinner, J.W., and Wilde, G.L.

1954a. Fusulinid wall structure. Journal of Paleontology, vol. 28, pp. 445–451.

1954b. New Early Pennsylvanian fusulinids from Texas. Journal of Paleontology, vol. 28, pp. 796–803.

Solov'eva, M.N.

1963. Stratigraphy and fusulinid zones of the Middle Carboniferous deposits of central Asia. Akademiya Nauk SSSR, Trudy Geologicheskogo Instituta, Izdatel'stvo Akademiya Nauk SSSR, Vypusk 76, 133 pp. [in Russian].

1977. Zonal stratigraphy of the Middle Carboniferous deposits of the USSR on fusulinid faunas. Akademiya Nauk SSSR, Ordena Trudovogo Krasnogo Znameni Geologicheskii Institut, Voprosy Mikropaleontologii, vol. 19, pp. 43–67 [in Russian with English summary].

1985. Correction of the USSR general Carboniferous scale in connection with restudying the Moscovian Stage stratotype and a new model for the correlation of the lower Moscovian Substage. Dixième Congrés International de Stratigraphie et de Géologie du Carbonifère, Madrid, 12–17 September 1983, Compte Rendu, vol. 1, pp. 21–26.

1986. Fusulinid zonal scale of the Moscovian Stage based on restudy of stratotypes of intrastadial subdivisions. Akademiya Nauk SSSR, Ordena Trudovogo Krasnogo Znameni Geologicheskii Institut, Voprosy Mikropaleontologii, vol. 28, pp. 3–23 [in Russian].

Solov'eva, M.N., Fisunenko, O.P., Goreva, N.V., Barskov, I.S., Gubareva, V.S., Dzhenchuraeva, A.V., Dalmatskaya, I.I., Ivanova, E.A., Poletaev, V.I., Popov, A.V., Rumyantseva, Z.S., Teteryuk, V.K., and Shik, E.M.

1985. New data on stratigraphy of the Moscovian Stage. Dixième Congrés International de Stratigraphie et de Géologie du Carbonifère, Madrid, 12–17 September 1983, Compte Rendu, vol. 1, pp. 11–20.

Springer, K.B., and Murphy, M.A.

1994. Punctuated stasis and collateral evolution in the Devonian lineage of *Monograptus hercynicus*. Lethaia, vol. 27, pp. 119–128.

Stebbins, G.L.

1974. Flowering plants: evolution above the species level. Harvard University Press, Cambridge, 399 pp.

Thomas, N.L.

1931. New early fusulinids from Texas. The University of Texas Bulletin No. 3101, pp. 27–33.

Thompson, M.L.

1945. Pennsylvanian rocks and fusulinids of east Utah and northwest Colorado correlated with Kansas section. State Geological Survey of Kansas Bulletin, vol. 60, no. 2, pp. 17–84.

1947. Stratigraphy and fusulinids of pre-Desmoinesian Pennsylvanian rocks, Llano Uplift, Texas. Journal of Paleontology, vol. 21, pp. 147–164.

1948. Studies of American fusulinids. University of Kansas Paleontological Contributions, Protozoa, Article 1, 184 pp.

1951. Wall structures of fusulinid foraminifera. Contributions from the Cushman Foundation for Foraminiferal Research, vol. 2, pp. 86–91.

1953. Primitive *Fusulinella* from southern Missouri. Journal of Paleontology, vol. 27, pp. 321–327.

Thompson, M.L., Shaver, R.H., and Riggs, E.A.

1959. Early Pennsylvanian fusulinids and ostracods of the Illinois Basin. Journal of Paleontology, vol. 33, pp. 770–792.

Toriyama, R.

1967. The fusulinacean zones of Japan. Memoirs of the Faculty of Science, Kyushu University, Series D, Geology, vol. 18, pp. 35–260.

Ueno, K., and Igo, H.

1997. Late Paleozoic foraminifers from the Chiang Dao area, northern Thailand. *in* Proceedings of the XII International Congress on the Carboniferous and Permian, Part 1. M. Podemski, S. Dybova-Jachowicz, K. Jaworowski, J. Jureczka, and R. Wagner, *eds.*, Prace Państwowego Instytutu Geologicznego, pp. 339–358.

Volz, W.

1904. Zur Geologie von Sumatra, Anhang II, Einige neue Foraminiferen und Korallen sowie Hydrokorallen aus dem Oberkarbon Sumatras. Geologie und Paläontologie, Abhandlungen, Koken (Jena), vol. 10, pp. 177–194.

Wetmore, K.L.

1999. Chamber formation in *Archaias angulatus*. Journal of Foraminiferal Research, vol. 29, pp. 69–74.

Wolfe, J.A., Doyle, J.A., and Page, V.M.

1975. The bases of angiosperm phylogeny: paleobotany. Annals of the Missouri Botanical Garden, vol. 62, pp. 801–824.

SHAPE MODELS AS A BASIS FOR MORPHOLOGICAL ANALYSIS IN PALEOBIOLOGICAL SYSTEMATICS: DICOTYLEDONOUS LEAF PHYSIOGRAPHY

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ABSTRACT

A primary goal of contemporary biological systematics is to document patterns of covariation between morphological characters and a host of physiochemical variables. These investigations are necessary in order to understand (1) the origins and maintenance of discontinuities in the morphological plexus (which form the basis for the "species" concept) and (2) the effect of environmental variation on species. In paleontology, these two research programs also can serve as the empirical basis through which morphological data can be used as proxies to estimate a wide range of physiochemical variables for which direct measurement is impossible. Application of this research program has been especially successful in paleobotany where it has, up to now, rested on a traditional qualitative approach to morphological analysis. However, by making use of the tools of geometric morphometrics—especially those that pertain to construction of shape models—the power of this approach to systematic investigation can be extended and enhanced. Morphometric modeling analysis of five leaf-shape characters drawn from the work of Jack Wolfe (1993) illustrates the techniques involved in this approach to systematic studies and the sorts of improvements in the characterization of morphological data that can be expected. In each of the cases examined here, the model-based results represented character concepts more fully and more accurately than text-based character-state definitions and exemplar illustrations drawn from real leaves alone. By placing the analysis of morphological variation on a firm quantitative footing, improvements can also be realized in documenting the nature of the relation between morphological and physiochemical variables.

INTRODUCTION

While biological systematics (the study of the kinds and diversity of organisms, Simpson, 1961) is both important and interesting in its own right, its continued relevance to the larger scientific enterprise is based on the value of systematic data as proxies for a wide variety of other natural phenomena. Indeed, it is so commonplace to learn that measurements of environmental quality or relative degrees of environmental perturbation are based on observations of plants and animals living in particular locations or habitats, that we often fail to appreciate—or in many cases even to recognize—this link. Nowhere is the importance of proxy-based analyses more evident than in the earth sciences where paleontological data are used to estimate a host of physiochemical variables that would be impossible to obtain otherwise (*e.g.*, temperature, salinity, humidity, rainfall, productivity). These proxy-level relations between biotic information and environmental parameters represent value-added adjuncts to the traditional role of paleontological data in chronostratigraphical analysis.

Given our increasing dependence on the accuracy of proxy-based quasi-measurements for understanding our planet's past, present, and future, it is surprising that its basis has not come under closer scrutiny. In drawing attention to this issue I am, of course, excepting the excellent work that has gone into documenting, analyzing, and understand the nature of relations between biochemical data and physical variables. Reaching, perhaps, its acme in the area of isotopic paleontology (*e.g.*, MacFadden and Bryant, 1992), the study of the chemical composition of organic materials—and how these compositions vary with a wide variety of local and global environmental changes—has engendered revolutions in fields such as paleoceanography, paleoclimatology, and paleoecology.

The chemical analysis of organismal structures, however, does not constitute the basic data of systematics. Those data are morphological. Sadly, efforts to document relations between morphological variation and variations in virtually all physical, chemical, temporal, geographical, ecological, spatial, and evolutionary variables remain almost entirely relegated to qualitative, almost anecdotal forms of analysis.

There are many explanations for the relative lack of attention that has been paid to investigating the nature of these relations. For the most part, these fall into two categories: the complexity of inferring cause and effect from historical data, and the complexity of morphological analysis. With respect to the former, although it is true that morphological data can be influenced by multiple external and internal forcing factors (many of which have strongly random component of variation that also differs between habitats and species), this problem is also present in biochemical data, albeit often to a somewhat lesser degree. Strategies to deal with this sort of complexity have been developed throughout biology (*e.g.*, Falconer, 1981; Sokal and Rohlf, 1995), as they have in other branches of science. Consequently, there seems no *a priori* reason to believe that the quantitative evaluation of cause-and-effect hypotheses cannot be handled successfully in systematics. Rather, I suspect that the more significant obstacle to progress in this area lies in the data-analysis challenges presented by morphological data.

The quantification of morphology has long been a "holy grail" of sorts in systematics. Attempts to test hypotheses by appealing to morphological measurements are as old as biology itself (Mayr, 1982; Mayr and Ashlock, 1991). The quantitative study of biological proportions informed art as well as anatomy in the Renaissance (Bookstein, 1993) and modern, statistical biometry can trace its heritage back over a century to the founding works of Francis Galton and Karl Pearson (Steigler, 1986). In this historical context the work of D'Arcy Wentworth Thompson (*e.g.*, Thompson, 1917) deserves special mention as being the first to propose an elegant graphic—though, until recently, mathematically intractable—form of morphological analysis that explicitly embodied the notion of shape transformation and the implicit idea of shape modeling.

More recently, the work of Kendall (1984), Bookstein (1986, 1991, 1996a,b,c, 1997) Bookstein and Green (1993), Goodall (1991), MacLeod (1999), as well as contributions to compendium volumes edited by Rohlf and Bookstein (1990), Marcus *et al.* (1993), Marcus *et al.* (1996), and MacLeod and Forey (2002), have extended, combined, and synthesized the various strands of modern biological shape analysis into a cohesive framework. Within this framework virtually any structural character used in the systematic description or diagnosis of any organism (modern or fossil) can be represented, compared, and contrasted with corresponding structures in other organisms. Using these methods, the resulting morphological ordinations can then be compared with ordinations of other non-morphological and/or non-biological variables in order to test and refine hypotheses of causal relation. Once this relation is understood, use of the morphological variable as a proxy for the causal environmental variable is relatively straightforward.

This ability to analyze patterns of covariation between geometrically complex morphological and non-morphological variables, along with a realization of the almost infinite geometrical complexity of biological objects (see Bookstein, 1994; MacLeod, 1999), has forced a refocusing of the entire field of morphometrics. The classical idea that morphometrics is about the "quantitative study of biological shape" (Hughes, 2001), in the holistic sense of attempting to represent all available shape information contained within a organism's body, has now been abandoned (Bookstein, 1991, 1994; MacLeod, 1999). Since shape variation is found at all measurement scales, it is impossible to summarize holistic shape variation with simple sets of measurements. (Note: this problem has important implications for the study of "shape disparity" between different organismal groups (*e.g.*, Foote, 1991, 1996, 1997); see Wills (2001) for a discussion.) Moreover, as demonstrated by MacLeod (1999), even seemingly minor changes in the way the same set of structures are measured (*e.g.*, two-dimensional versus three-dimensional representations of landmark data) can result in dramatic changes in shape-similarity assessments. Accordingly, morphometric theory has now concentrated on the more tractable goal of studying quantitatively patterns of covariation with (and only with) those aspects of organismal morphology deemed relevant to the problem at hand (see Bookstein, 1993; MacLeod, 1999). Although this localization of the realized targets of morphometric analysis may strike some as a semantic difference without practical distinction, the morphometric literature is replete with examples where practitioners have mistaken patterns of localized shape variation in a particular structure (*e.g.*, the relatively location of an eye or fin, the two-dimensional outline of a shell) with the holistic "shape" of the entire organism. Whereas the former is a legitimate target of morphometric investigation, the latter is an abstract philosophical concept that cannot be assessed empirically even for relatively simple organisms. This paradigm shift remains to be fully implemented in many research programs. Nevertheless, its deep connection with the idea of using character-based morphological data as quantitative proxies for the environmental covariates seems both obvious and natural.

In the development of this new, geometrically focused approach to morphometric analysis, one aspect that has received comparatively little attention is the extent to which these new methods support direct shape modeling procedures and the utility of such procedures in systematic contexts. Following from Thompson's (1917) conceptual work on transformational morphometrics, the ability to create shape models that can be related to ordinations of measured shapes in linear "shape spaces" is implicit in all modern morphometric methods (see MacLeod, 1999, 2001a for examples). MacLeod (2002b) has explored the use of shape models to create need-specific qualitative shape classification systems for use in several earth-science contexts. The present contribution applies a refined methodology for creating eigenshape-based shape models to a series of five leaf-shape characteristics in order to illustrate: (1) new strategies for shape-model construction and comparison of unknown objects with constructed shape models, and (2) the use and utility of these modeling procedures in an explicitly systematic context.

ACKNOWLEDGMENTS

This contribution had its genesis in two events that both occurred some time ago. At a research meeting sponsored by AMOCO in Tulsa in the early 1990s, Gilbert Klapper asked me to demonstrate the operation of an early version of my eigenshape-based modeling program. It was during the running of a simple dataset through the program and explaining the results that I first realized the systematic implications of the shape models. The other event involved Scott Wing who, at about the same time, asked me to write a small utility program for him in order to allow a student who was working on a "morphometric analysis of Jack Wolfe's leaf data" to change the format of some outline data the student had collected. I've been intrigued with the morphometrics of leaves every since. For their unintentional contributions to this study, it is hereby dedicated to Gil (on the occasion of his retirement) and to Scott. The extended eigenshape software set used in this investigation is available for free download from the PaleoNet Pages FTP sites: http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html (PaleoNet East); http://www.ucmp.berkeley.edu/Paleonet/ftp/ftp.html (PaleoNet West). A previous draft of this article was read by Jim Barrick, Tim Carr, and an anonymous reviewer. The comments of all three spurred me to modify and, I hope, to improve the final product. However, these individuals bear no responsibility for any mistakes or misconceptions that might remain.

DICOTYLEDONOUS LEAF PHYSIOGRAPHICAL CHARACTERS

In order to standardize paleobotanical observations for use in a proxy-based system of environmental inferences, Wolfe (1993, 1995) established a series of seven leaf-shape characters and 29 associated character states. These characters were similar to standard, modern-leaf, descriptive characters (*e.g.*, Hickey, 1973; Stearn, 1992). Based on analyses of modern floras, Wolfe (1993, 1995) demonstrated that leaf-shape compositional analysis could be employed as a morphological proxy for mean annual temperature and water stress.

Text-figure 1.—Outlines for Wolfe's (1993, 1995) leaf lobateness exemplars (redrawn from Wolfe, 1993). See text for discussion.

Wolfe's motivation for undertaking these studies was to standardize the descriptive leaf-shape nomenclature to achieve a better understanding of the quantitative relation between variations in leaf physiognomy and variation in local environmental factors. In adopting this approach, Wolfe (1995) followed the strategy of Imbrie and Kipp (1971), who used a factor-analytic approach to inferring sea-surface temperatures from planktonic foraminiferal assemblages. Although Wolfe (1993, 1995) substituted correspondence analysis (Nishisato, 1980; Greenacre, 1984) and canonical correspondence analysis (ter Braak and Prentice, 1988) for Imbrie and Kipp's (1971) factor-analysis procedure (in order to circumvent the latter's restriction to portraying linear relationships among variables), the basic concept was identical: to estimate a series of equations that could be used to calculate indices of environmental state from a morphology-based data set.

Wolfe's empiricism and commitment to quantitative analysis are to be commended. His efforts were rewarded with interpretations that were in reasonable agreement with previous studies and consistent among the modern localities included in his datasets (Wolfe, 1995). Nonetheless, it is somewhat ironic to realize in hindsight that his desire to standardize the identification of his character-state morphologies went largely unfulfilled. For example, Wolfe's "lobed" leaf-shape character (Text-fig. 1) was defined as follows:

> A species receives a score of 0 if no leaves are lobed, a score of 0.5 if some leaves are lobed and some are unlobed, and a score of 1.0 if all leaves are lobed. Lobing can be either pinnately lobed (for example, many *Quercus*) or palmately lobed (for example, many *Acer*). Both pinnately and palmately lobed [leaves] were scored separately but were later combined because separate scoring appeared to produce no refinement. In order to be pinnately lobed, a lamina must be incised so that a line connecting the sinuses between the lobes is approximately parallel to the midrib. . . . In palmately-lobed leaves, the

lobes are entered by a primary vein that originates near the base of the leaf. (Wolfe, 1993, p. 21).

On first reading, this seems like a reasonable and objective subdivision of the possible lobate variation types. Closer inspection shows that it focuses on the distinction between pinnate and palmate lobe types—a distinction that is not used in scoring the character for environmental analysis. In the context of this definition, the critical class boundary between "lobed" and "unlobed" states remained undefined. Moreover, the definition is both highly technical in the sense of using many terms that would be understood only by experienced paleobotanists, and arbitrary in the sense of failing to demonstrate that the shape-class boundary definitions represent natural discontinuities in the structure of leaf-shape variation. For actual users of Wolfe's scheme—many of whom might not be experienced paleobotanists, specifically trained in its use—the most practical identification aid would be a graphical summary illustrating the range of acceptable intraclass variational types, perhaps augmented by a written description of the class-boundary criteria.

The morphometric modeling tools Wolfe needed to realize his goal of providing more rigorous definitions of his character states have been available from the late 1980s, though few understood their potential at that time. Lohmann and Schweitzer (1990) made a brief mention of a modeling extension to Lohmann's (1983) eigenshape technique. This method focused on the representation of shape as a deformation of the object's outline in a manner generally suitable for leaf-shape data. MacLeod and Rose (1993) reformulated Lohmann and Schweitzer's (1990) method and applied it to a problem in the inference of functional morphology (see MacLeod, 2001b, for an extension of that study). Still, owing to the fact that Wolfe's leaf characters combine outline and landmark-based observations to capture the complex morphologies paleobotanists have traditionally used to describe leaves, a method of morphometric analysis was needed that combined both observation types in a way that approximated the sorts of comparisons made by real paleobotanists on real leaves. MacLeod (1999) developed such an extension for eigenshape analysis. Shape-modeling procedures based exclusively on landmarks have also been available since 1990 (see Bookstein, 1990, 1991) and could, in principle, be used to analyze and construct models from data such as Wolfe's. The use of landmark-based models derived from these procedures in applied systematic contexts, however, still remains to be fully explored (but see MacLeod, 2001a, 2002a; Rohlf, 2002).

METHODS

The shape modeling method employed in this investigation is derived from eigenshape analysis (Lohmann, 1983; Lohmann and Schweitzer, 1990; MacLeod, 1999). In its current formulation (MacLeod, 1999) eigenshape analysis can be viewed as a special case of relative warp analysis (Bookstein, 1991) that is defined over an extraordinary variety of data types (*e.g.*, landmarks, boundary coordinates, mixtures of both).

Standard eigenshape analysis begins—as do all geometric morphometric procedures—with the reduction of a complex shape to a set of simple measurements via collection of two-dimensional or three-dimensional coordinate positions at corresponding semilandmark locations on all specimens within a sample (see Bookstein, 1996b, 1996c or MacLeod, 1999, 2001a for discussions of semilandmarks). These coordinate positions are assumed to correspond across the sample, though the nature of this correspondence may vary (*e.g.*, phylogenetic correspondence or homology, functional correspondence, topological correspondence).

Once the target shapes in a sample have been abstracted via coordinate-point digitization, the coordinate values are transformed into sets of object-specific shape functions (*e.g.*, the ϕ or ϕ^* functions of Zahn and Roskies, 1972; the tangent angle function of Bookstein, 1978; a column vector of raw coordinate values as in MacLeod, 2001a; see Text-fig. 2A) and assembled into a data matrix. After these shape functions have been obtained, similarities and differences among the shapes they represent can be summarized by comparing their terms.

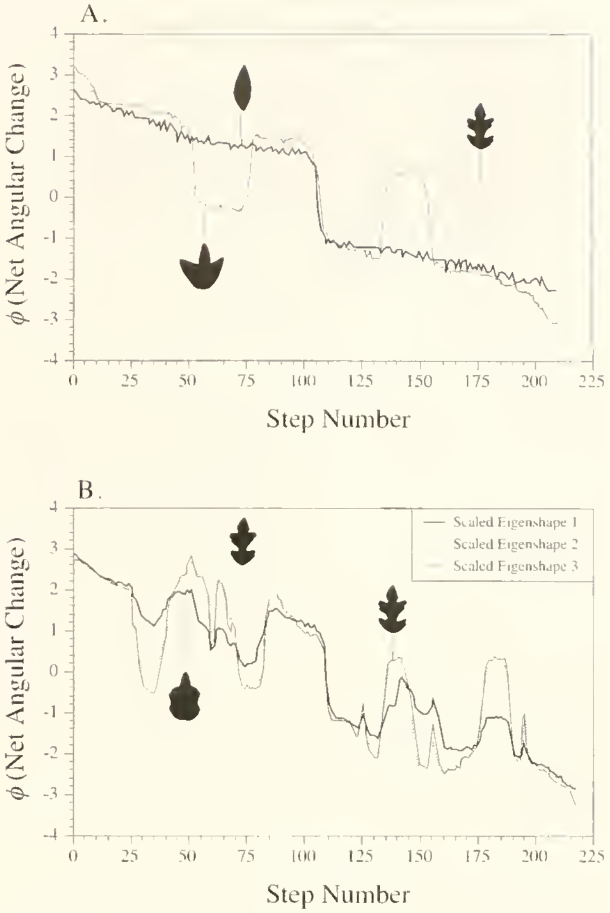
These comparisons can be made in a number of ways. For exploratory purposes, it is often convenient to calculate the R-mode covariance matrix between the terms of each shape function within the sample. Submitting this shape-covariance matrix to a multivariate vector-based analysis procedure—usually singular-value decomposition—can help identify major trends of shape covariation existing among the measured specimens. This procedure employs eigenanalysis to align a series of multivariate vectors parallel to the predominant shape-variation trends and at right angles to one another. The alignment is organized such that the longest vector corresponds to the trend that accounts for the greatest proportion of shape covariation within the sample, the second longest vector corresponds to the trend that accounts for the second greatest proportion of shape covariation, and so on. The resulting vector array summarizes contrasting patterns of shape variation in a generalized, sample-specific, linear, geometrical space.

One interesting by-product of this analytic strategy is that the resultant vectors are themselves shape functions. These shape functions represent sample-based theoretical shapes in that they do not correspond to any known object. Using the conventions of multivariate analysis, these latent-shape vectors are typically used to form the axes of a mutually orthogonal coordinate system within which the shape-similarity relations may be portrayed. This is possible because each vector joins the shape function (which is a single point in the shape subspace) to the origin of the coordinate system in such as way that intermediate positions along the vector represent linear approaches to the unitary (but hypothetical) morphological state represented by the vector. A shape's position along any singular vector can be represented by the covariance between a specimen's shape function and the latent shape function represented by the vector axis. By inverting this logic, however, it becomes obvious that, in a system of orthogonal shape vectors so defined, any position within the shape hyperspace also corresponds to a unique shape, either realized *or* theoretical.

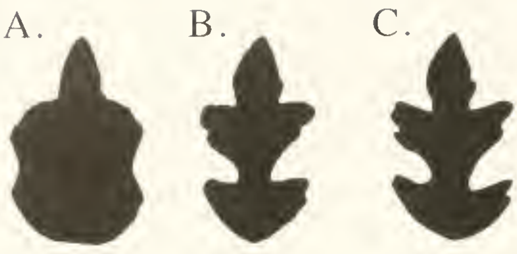
Using the same logic, it can be appreciated that the representation of the set of shape vectors as continuous axes, along which intermediate positions are possible, means that the chord between the coordinate system's origin and any of the sample-defined latent shape vectors defines a linear shape-transformation series. One way this series can be modeled is by altering the amplitude of the latent-shape function via multiplication of each term by a constant value (Text-fig. 2B). MacLeod (1999) shows that this constant can be related directly to the coordinate location (covariance value) of actual or theoretical objects within the multivariate shape space.

Consequently, specific models of shape states consistent with any location within the shape space can be calculated by appropriately scaling the various singular shape vectors by specific covariance values (representing coordinate positions within the shape space) and then summing these scaled values as variables across all vectors involved in model construction (Text-fig. 3). This procedure is analogous to the manner in which radial Fourier harmonic series (amplitude and phase-angle spectra) can be combined to reconstruct closed-form shapes (see Christopher and Waters, 1974; Kaesler, 1997).

The procedure outlined above defines a family of shape functions that can be used, for example, to graphically represent the shape contrasts specified by each latent shape vector. Of course, if an incomplete coordinate location is specified (*e.g.*, a model is constructed using only first few latent shape vectors), the resultant model will only represent one of a number of alternative shapes that might exist at that location. Nevertheless, this modeling procedure can be used to compute the shape of an infinite series of theoretical, modeled shapes in a highly controlled and geometrically rigorous manner. Such modeled shape series can



Text-figure 2.—Zahn and Roskies (1972) shape functions for Wolfe's (1993) leaf lobateness exemplar shapes. The "step number" variable locates the sequence of short line segments used to represent each leaf's shape (210 steps overall). The ϕ value represents the orientation of the line segments in terms of the net angular change from the previous segment's orientation (expressed in radians). The Zahn and Roskies (1972) shape function is capable of expressing any shape (open or closed) as a linear mathematical function irrespective of the shape's complexity. A. Three shape functions corresponding to Wolfe's (1993) exemplar shapes. Note the relation of shape function complexity to the complexity of the leaf icon outline. B. Decomposition of the pinnately lobate exemplar (see Text-fig. 1) into three shape vectors via eigenshape analysis. These vectors represent the latent shape functions calculated (via eigenanalysis) from the pairwise shape covariance matrix for all three exemplar shapes. Once obtained, these hypothetical shapes (which quantify patterns of shape similarity and dissimilarity within the exemplar set) can be amplitude-scaled by the covariance between any observed shape (in this case the pinnately lobate exemplar shape) and each of the three latent shapes (or "eigenshapes"). As can be seen from B., this amplitude-scaling operation can be used to reconstruct (or model) any original shape from the eigenshape decompositions.



Eigenshape 1 ($\lambda = 88.76\%$)

Eigenshape 1 + Eigenshape 2 ($\lambda = 96.99\%$)

Eigenshape 1 + Eigenshape 2 + Eigenshape 3 ($\lambda = 100.00\%$)

Text-figure 3.—Details of Cartesian shape models corresponding to each of the reconstructed shape vectors shown in Text-figure 2B. A. Cartesian shape model corresponding to the scaled eigenshape 1 vector. B. Cartesian shape model corresponding to the scaled eigenshape 1 plus eigenshape 2 vectors. C. Cartesian shape model corresponding to the scaled eigenshape 1 plus eigenshape 2 plus eigenshape 3 vectors. Note that each scaled eigenshape vector adds a unique component of shape variation to the reconstruction. The progressive increase in the observed shape variance represented on the successive models means that, even in more complex cases (*e.g.*, analyses based on samples containing more than three objects), the reconstructed shape can almost always be made to converge on a reasonably accurate approximation of the original object's morphology by concatenating only the first few scaled shape vectors. This dimensionality reduction is one of the primary purposes of eigenshape analysis.

be quite useful in interpreting morphological data and testing systematic hypotheses.

EXAMPLES AND RESULTS

Wolfe (1993) illustrated six morphological characters (other than size) that served as the basis of his physiographical system: leaf lobateness, marginal-tooth spacing, marginal-tooth shape, apex shape, base shape, and leaf shape. Of these, marginal-tooth spacing was excluded from consideration in this study because it is not a shape-based characteristic. Eigenshape-based shape models were calculated for the five remaining characters using Wolfe's (1993) drawings (Text-fig. 4) as the reference exemplars for each modeling procedure.

In order to take advantage of as much relevant geometrical information as possible, the extended eigenshape method (MacLeod, 1999) was employed in the creation of each shape model sequence. Extended eigenshape analysis takes advantage of landmark point locations along the boundary outline to subdivide the overall outline into corresponding outline segments (Text-fig. 5). Once these segments have been recognized, the spatial resolution of each outline segment is adjusted such that all corresponding segments in the sample meet a common representational quality criterion. This procedure has the added advantage of weighting the subsequent analysis by the complexity of each segment's shape.

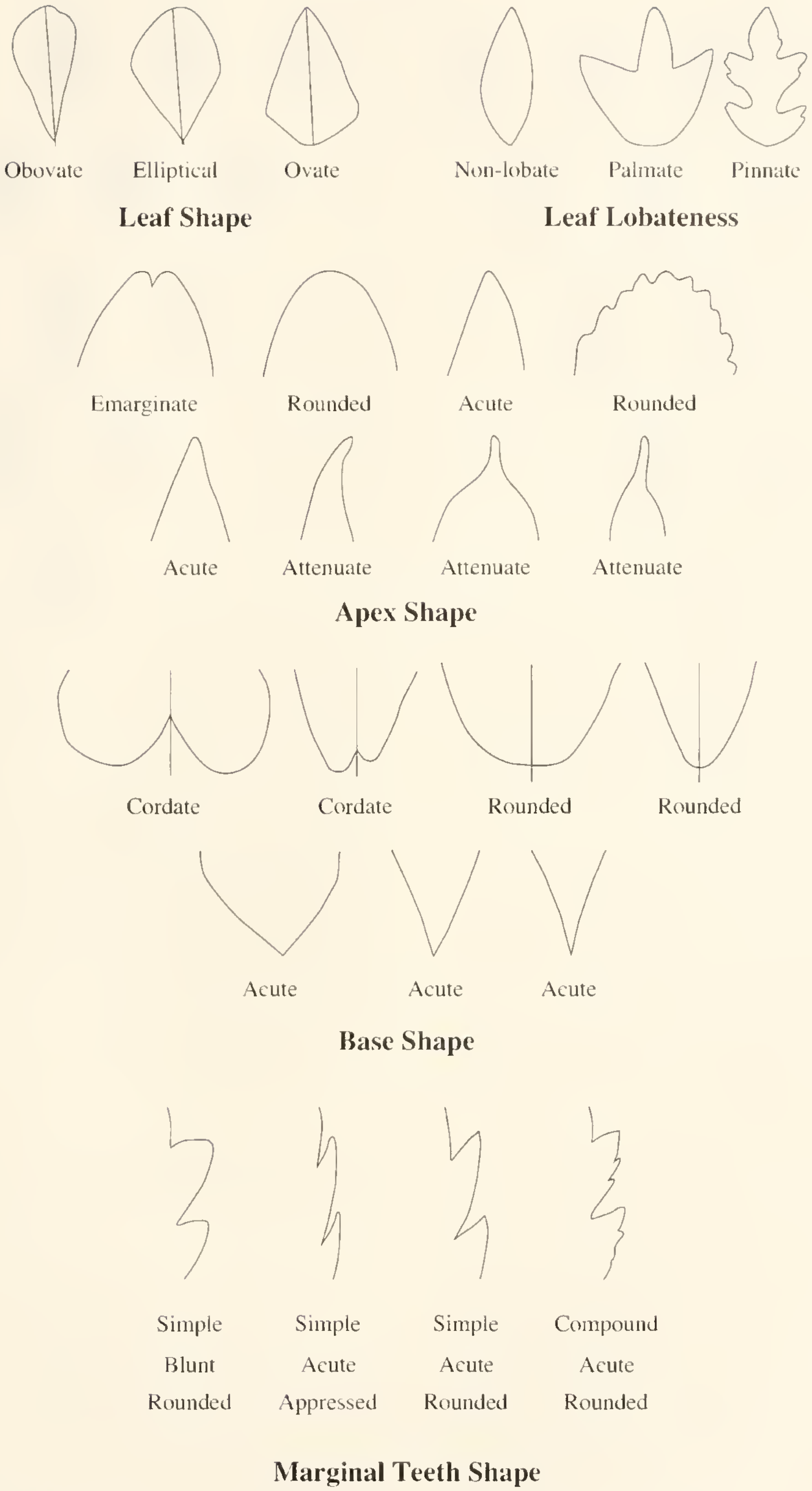
Each shape was originally sampled at a resolution of 250 equally spaced points, and then back interpolated such that each landmark-defined segment was represented by a set of equally spaced boundary coordinate points. This interpolation procedure proceeded iteratively until the interpolated perimeter of each segment on each object was at least 99.0 percent the length of the original (digitized) perimeter. Text-figure 5 also shows the boundary coordinate point counts for each shape segment on a representation of the mean shape of each analyzed character.

LEAF SHAPE

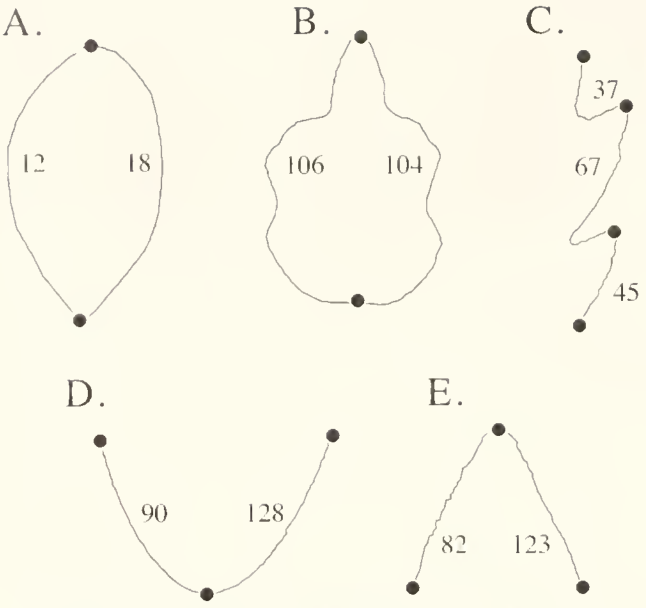
Leaf shape is the simplest of the five analyzed characters. Wolfe (1993) illustrates three exemplar shapes (Text-fig. 4) representing the obovate (widest chord perpendicular to the central axis located in apical third of leaf), elliptical (widest chord located in median third of leaf), and ovate (widest chord located in basal third of leaf) conditions. The three vector axes of the eigenshape decomposition of these data (Text-fig. 6) show that these exemplar shapes are not evenly distributed in the shape subspace. Rather, the obovate and elliptical exemplars are more similar to each other than either is to the ovate exemplar. The reason for this somewhat counterintuitive result is readily apparent from detailed inspection of the elliptical exemplar (see Text-fig. 4) whose asymmetries give it a slightly obovate character.

Modeling the shapes that exist on the plane joining Wolfe's three leaf-shape exemplars, and slightly deforming the implied triangle of shape intermediacy to conform to a ternary diagram (Text-fig. 7), shape models can be reconstructed at convenient nodal positions. Comparison of these intermediate shapes to Wolfe's leaf-shape character-state definitions suggests that models 1–4, 6, 7, and possibly 8 of Text-figure 7 all exhibit the obovate condition. In contrast, shape models 13–15 are ovate. The remaining shape models (5, 9–12 of Text-fig. 7) all match the qualitative elliptical leaf-shape definition.

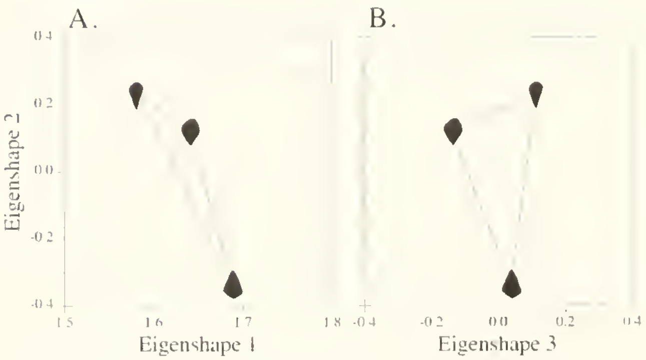
This simple exploration of the leaf-shape subspace constructed via reference to Wolfe's leaf-shape exemplars, in turn, allows a pattern of chords to be drawn within an intermediacy plane (Text-fig. 8). Geometrical exploration of this shape-intermediacy plane enables the approximate boundaries of Wolfe's leaf shape character-state classes to be recognized and mapped. These boundaries represent results of a continuously variable, quantitative assessment of morphological variation that eliminates the need for rhetorical descriptions-definitions in an analytical context. Such



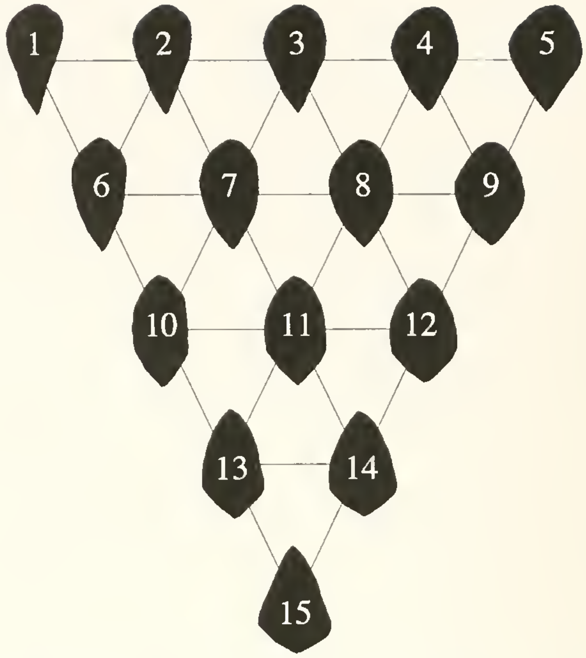
Text-figure 4.—Characters and character-state exemplars used to model dicotyledonous leaf physiography in this investigation. Redrawn from Wolfe (1993).



Text-figure 5.—Cartesian representations of mean shape models) for each of the five character-state sets shown in Text-figure 4: A. leaf shape. B. leaf lobateness, C. marginal tooth shape, D. leaf-base shape, E. leaf-apex shape. In addition to the mean forms these diagrams illustrate the positions of boundary landmarks used to subdivide the outline into corresponding segments (and so ensure segment correspondence) and the number of outline points necessary to represent each outline segment to at least the 99% tolerance criterion. See text for discussion.



Text-figure 6.—Ordination of the three leaf shape exemplars in the space of the three eigenshape axes; $\lambda_1 = 97.54\%$, $\lambda_2 = 2.06\%$; $\lambda_3 = 0.40\%$). In order to visualize the ordination in three-dimensional space imagine that, relative to plot A, plot B is rotated 90°. Note that this ordination delimits a triangular space within a plane that is inclined at an angle to the three eigenshape vectors. This space contains the coordinate positions for all shapes that can be considered intermediate to the exemplar shapes. Regions of shape variation whose boundaries represent the boundaries of shape variation characteristic of each character state will be found within this triangular space.

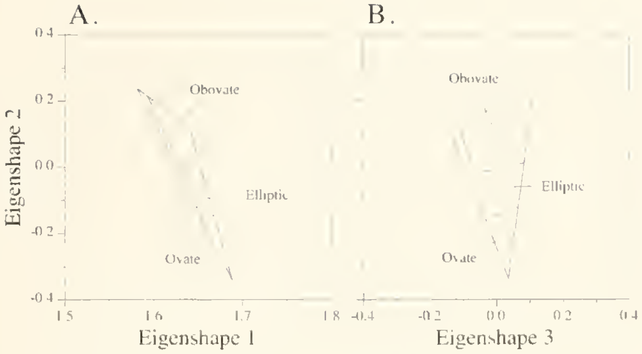


Text-figure 7.—Shape models for a regular grid of positions within the leaf-shape character intermediacy plane. These models were obtained by scaling the three eigenshape vectors resulting from the analysis of the exemplar shape functions by the coordinate positions of locations within the intermediacy plane (Text-fig. 6) and then summing the scaled vectors together in the manner shown in Text-figure 2B. Coordinate positions for each model as follows. (1) 1.583, 0.230, 0.112; (2) 1.597, 0.200, 0.049; (3) 1.611, 0.171, −0.014; (4) 1.625, 0.141, −0.077; (5) 1.639, 0.111, −0.140; (6) 1.609, 0.092, 0.092; (7) 1.623, 0.062, 0.029; (8) 1.637, 0.032, −0.034; (9) 1.651, 0.002, −0.097; (10) 1.636, −0.047, 0.071; (11) 1.650, −0.077, 0.008; (12) 1.664, −0.107, −0.055; (13) 1.662, 0.186, 0.051; (14) 1.676, −0.215, −0.012; (15) 1.688, −0.324, 0.031. See text for a discussion of the shape models relative to the definitions of the exemplar states. Shape model series such as these can be used to explore the geometric spaces within which these forms exist and map the limits of morphological character-state variation.

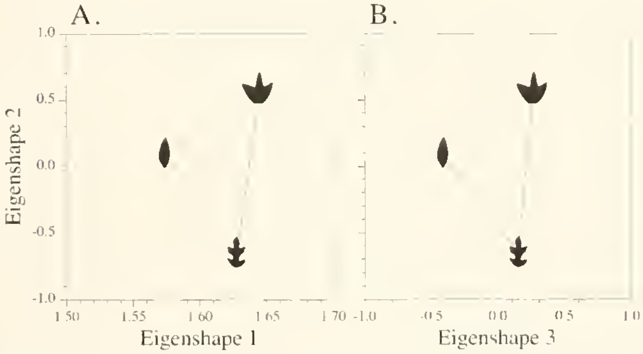
models can usefully supplement textual descriptions of the character-state class boundaries, as well as becoming the subjects of further analysis in their own right.

LEAF LOBATENESS

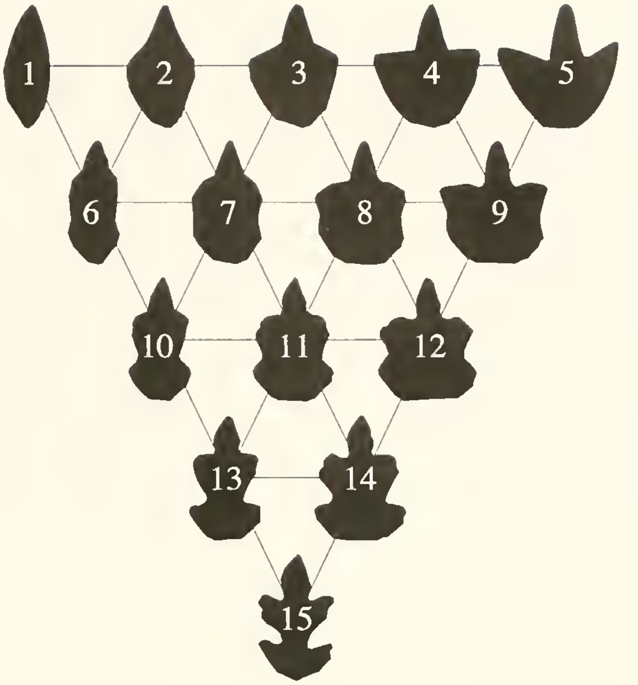
Application of extended eigenshape analysis to Wolfe's (1993) three leaf-lobateness character exemplars (Text-fig. 4) shows that non-lobate, pinnately lobate, and palmately lobate leaves form an approximately equilateral triangular distribution in the shape subspace formed by the first three multivariate shape vectors (Text-fig. 9). This arrangement suggests that pinnately lobate and palmately lobate leaves are as distinct from one another as either are from non-lobate leaves. Note also that the ordination of these end-members shapes in the subspace is such that neither the distinction between non-lobate and pinnately lobate



Text-figure 8.—Subregions of the leaf-shape intermediacy plane that correspond to the character states described by Wolfe (1993). Once these regions have been defined and extended into the higher dimension so that they represent hypervolumes rather than planar regions, they can be used to understand the geometry of character-state variation. Even more importantly, shapes within the geometric range of the exemplar shapes can be projected into this space and compared to both the space-defining exemplars and the set of intermediacy models. Such exercises can be used to more objectively assign morphologies to character-state concepts and (via the ordinations) test the relationship between shape change and variation in a host of other causal or derivative variables.



Text-figure 9.—Ordination of the three leaf-lobateness exemplars in the space of the three eigenshape vectors; $\lambda_1 = 88.76\%$, $\lambda_2 = 8.23\%$; $\lambda_3 = 3.01\%$). In order to visualize the ordination in three-dimensional space imagine that, relative to plot A, plot B is rotated 90°. Note that is ordination delimits a triangular space within a plane that is inclined at an angle to the three eigenshape axes. This space contains the coordinate positions for all shapes that can be considered intermediate to the exemplar shapes. Regions of shape variation whose boundaries represent the boundaries of shape variation characteristic of each character state will be found within this triangular space.



Text-figure 10.—Shape models for a regular grid of positions within the leaf-lobateness character intermediacy plane. These models were obtained by scaling the three eigenshape vectors resulting from the analysis of the exemplar shape functions by the coordinate positions of locations within the intermediacy plane (Text-fig. 9) and then summing the scaled vectors together in the manner shown in Text-figure 2B. Coordinate positions for each model as follows. (1) 1.575, 0.100, −0.422; (2) 1.593, 0.211, −0.253; (3) 1.610, 0.323, −0.084; (4) 1.628, 0.434, 0.086; (5) 1.645, 0.545, 0.255; (6) 1.589, −0.087, −0.279; (7) 1.606, 0.024, −0.110; (8) 1.624, 0.136, 0.060; (9) 1.641, 0.247, 0.229; (10) 1.602, −0.274, −0.136; (11) 1.620, −0.163, 0.033; (12) 1.637, −0.052, 0.203; (13) 1.616, −0.461, 0.007; (14) 1.633, −0.350, 0.176; (15) 1.629, −0.648, 0.150. See text for a discussion of the shape models relative to the definitions of the exemplar states. Shape model series such as these can be used to explore the geometric spaces within which these forms exist and better define the limits of morphological character-state variation.

leaves, nor the distinction between non-lobate and palmately lobate leaves, is captured completely by any single vector.

Using these three eigenshape vector functions as a starting point, a series of intermediate shapes can be modeled for a series of regularly spaced positions within the shape-intermediacy plane. Any transition between non-lobate, pinnately lobate, or palmately lobate leaves can be represented as a linear shape-transformation series via reference to these models. By explicitly illustrating intermediate forms in this manner, a lobateness shape scale, consistent with the Wolfe's lobateness concepts, can be devised. Such a scale is of arguably greater utility than end-member exemplars and written descriptions. Text-figure 10 shows the results of this modeling exercise.

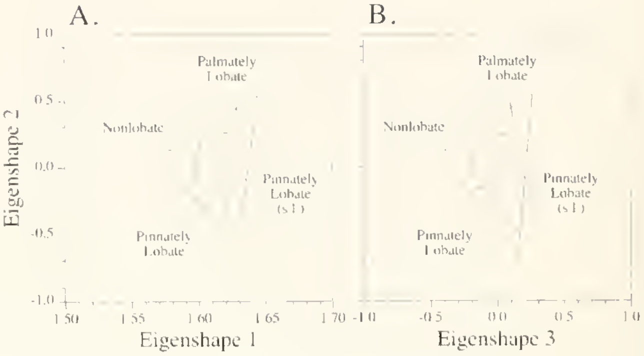
Over the range of linear models illustrated in Text-figure 10, Wolfe's (1993) non-lobate concept can be seen as being restricted to a relatively small area of the shape subspace. Wolfe (1993) did not provide a definition of a non-lobed leaf, but a provisional definition might be based on the absence of pronounced protuberances or sulci arising along the median region of the leaf margin. Hickey (1973) provides an arbitrary definition of a marginal indentation > 0.25 of the distance between leaf margin and the leaf's long axis as the criterion for lobe-recognition. Under Hickey's (1973) definition, models 1, 2, 6, and possibly 7 of Text-figure 10 would described as non-lobed leaves. This would imply that the remaining shape models all exhibit some aspect of the lobate condition (see also Stearn, 1992).

Within this larger group, Wolfe's (1993) definition of pinnate lobation (a line joining the sulci lies approximately parallel to the midrib, or central axis) is similarly restrictive. Only models 10, 13, and 15 of Text-figure 10 are strictly consistent with this definition of the pinnate condition. If Wolfe's (1993) definition is broadened slightly to admit leaves whose intersulcus lines lie at angles between 0° and 30° of the central axis, however, models 11 and 14 might be added to this group.

As mentioned above, the definition of palmate lobation (lobes supported by radial midribs that meet at a common basal point, see Stearn, 1992; Wolfe, 1993) suffers from being based on a different criterion than pinnate lobation. It is therefore possible, in principle, for a leaf to be both palmate and pinnate simultaneously. The resultant ambiguity might be remedied by focusing on the radially directed character of the lobes themselves rather than the nature of their support. Regardless, any reasonably specific geometric definition of the palmate character state imposes another set of highly restrictive conditions on the realizable shape range. Results presented in Text-figure 10 suggest that only shapes 4, 5, and 9 meet the palmate criteria. The remaining models (3, 8, 9, and 12) specify a broad boundary area between pinnate and palmate lobation that, at least under Wolfe's (1993) classification, would be correctly assigned to an undifferentiated lobate *sensu lato* category.

Taking these results into consideration, an estimate of the boundaries between Wolfe's (1993) leaf lobateness shape classes—including the pinnate-palmate distinction—can be quantitatively related to the modeled shape plane (Text-fig. 11). By combining text-figures 10 and 11, a table of leaf lobateness can be constructed to guide those wishing to consistently score leaves according to Wolfe's (1993) leaf-lobateness classes. In addition, the data derived from such an exercise could be used to further develop and refine the relation between leaf lobateness and environmental state.

There are at least two general points worth noting about this example. First, without the geometric formalism and ability to explore shape transitions that underlies the modeling approach, it seems unlikely that shape-class boundary definitions could be sharpened as quickly as they were in this analysis. The character of the lobate (undifferentiated) region is particularly instructive. In the absence of such shape models, it is doubtful that the character of shapes that did not fit into any of Wolfe's (1993) three canonical categories could have been recognized as easily.

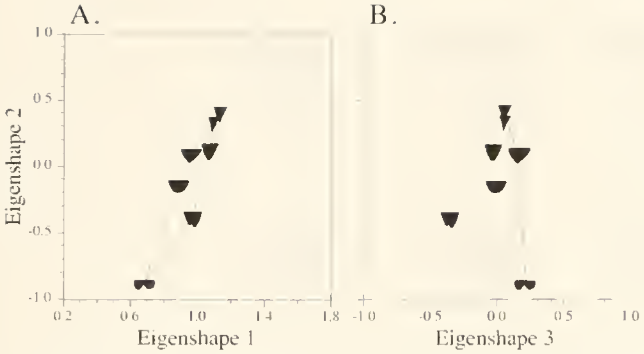


Text-figure 11.—Subregions of the leaf-lobateness intermediacy plane that correspond to the character states described by Wolfe (1993). Once these regions have been defined and extended into higher dimensions so that they represent hypervolumes rather than planar regions they can be used to understand the geometry of character-state variation.

Second, these models make plain the contingent nature of many character-state assignments. For example, even though the leaf apex in end-member shapes 1 (unlobed exemplar) and 5 (palmate exemplar) is similar—and would be described as acute in both instances (see below)—the transitional model 2 exhibits an attenuated apex. The apparent reversal occurs not because the nature of the tip has changed substantially, but because the nature of other aspects of the shape (in this case the median and basal regions) are changing and forcing a concomitant change in the apical region. This coincidence is primarily due to the limited number and morphological character of Wolfe's three lobateness exemplar shapes.

LEAF BASES

Wolfe's (1993) leaf-base character is complicated by the number of similar exemplars he includes in his illustration (Text-fig. 4). Yet, a scattering of the seven exemplar shapes in the subspace of the first three eigenshape vectors (representing 99.26% of total shape variance, Text-fig. 12) shows them to be arranged on or close to a plane inclined to the three vector axes. This plane joins the most acute (base characterized by straight sides denoting an angle of less than 90° and coming to a definite point) and cordate (rounded basal lobes extending [basally] below the central axis termination) forms. The first vector axis expresses the relative width of the basal region, the second captures the acute-cordate distinction mentioned above, and the third represents the relative depth of the basal region.



Text-figure 12.—Ordination of the three leaf-base shape exemplars in the space of the three eigenshape vectors; λ_1 = 81.76%, λ_2 = 15.07%; λ_3 = 2.43%). In order to visualize the ordination in three-dimensional space imagine that, relative to plot A, plot B is rotated 90°. Note that this ordination delimits a roughly quadrilateral space within a plane that is inclined at an angle to the three eigenshape vectors. This space contains the coordinate positions for all shapes that can be considered intermediate to the exemplar shapes. Regions of shape variation whose boundaries represent the boundaries of shape variation characteristic of each character state will be found within this quadrate space.

[Note: for this analysis Wolfe's (1993) figures were assumed to represent the entire basal region.] Within this space most of the non-extreme exemplars are arrayed along, and slightly above, the line that joints the narrowest and deepest acute and cordate shapes.

Using this inclined plane joining the extreme shapes as the most representative shape modeling surface, and deforming that plane slightly into a rectilinear grid, the character of shapes representing linear intermediates between those extremes at known locations within the space of the first three eigenshape vectors can be determined. These are shown in Text-figure 13.

The interpretation of the modeled shape-transformation plane is both natural and relatively obvious—much more so than the somewhat abstract shape-subspace scattergrams of Text-figure 12. The most striking shape-related results revealed by these models are differences in the spatial scope of Wolfe's (1993) three basal-shape character states. Shape models 1–10 of Text-figure 13 correspond to his definition of acute leaf base morphologies. Hickey's (1973) classification would distinguish three states within this complex: decurrent bases (concave sides, models 1–5 of Text-fig. 13), cuneate bases (straight sides, presumably corresponding to models intermediate between rows 1–5 and 6–10 of Text-fig. 13), and acute bases (convex sides, models 6–10).

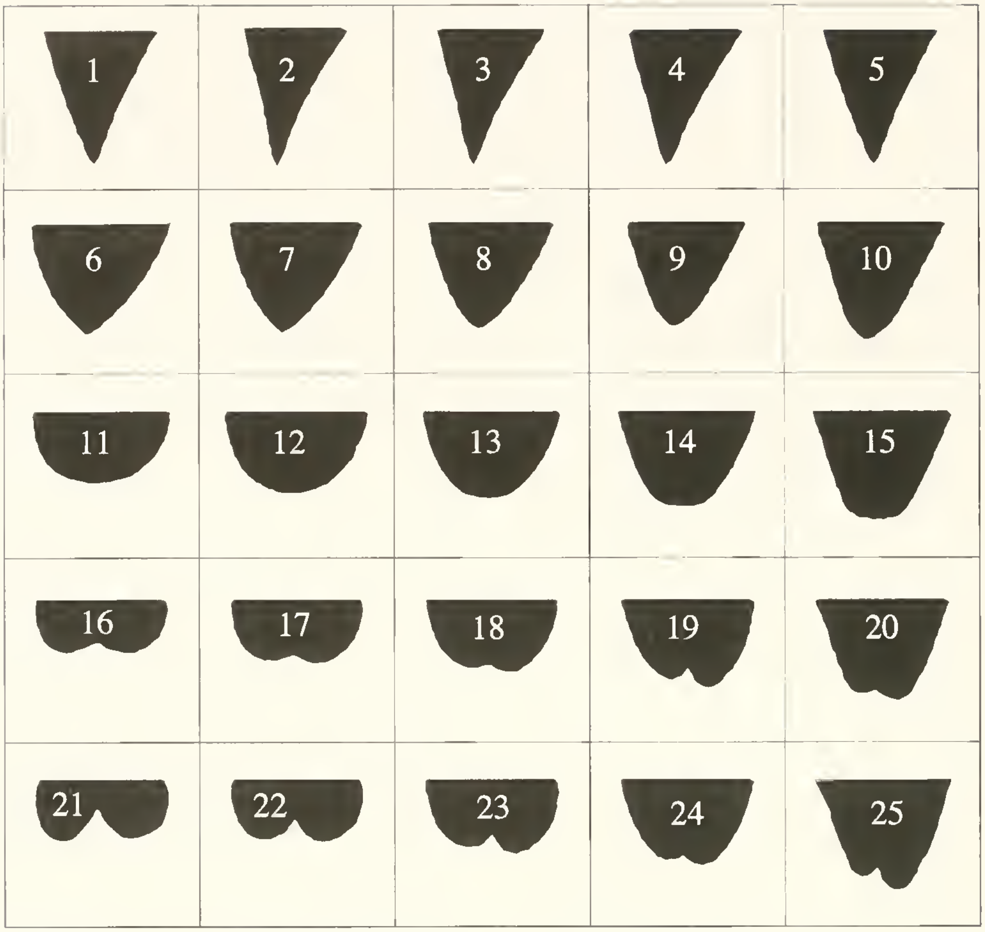
In a similar vein, Hickey's (1973) and Wolfe's (1993) cordate state is consistent with shape models 16–25 of Text-figure 13. Hickey's (1973) additional cordate-type basal character states (lobate, sagittate) could easily be represented on a similar shape decomposition diagram.

The broad regions of shape variation that characterize the acute and cordate leaf-base morphologies in Text-figure 13 stand in marked contrast to the rounded-base state (angle formed by tangents to the basal margin, joined at the midrib base are < 180°, but > 90°) that, in this analysis, is restricted to models 11–15. [Note: the "squared off" nature of model 15 is such that it could possibly be allied with Hickey's (1973) truncate basal state.] This distinction may be more apparent than real, however. Certainly Hickey's (1973) leaf-character classification would recognize a greater number of states in this model set than Wolfe's (1993). Of perhaps more importance from a systematic point of view though, is the observation that the difference between the acute (model sets 1–5 and 6–7, Text-fig. 13) and the rounded states (model set 11–15) appears qualitatively greater than the difference between the two cordate states (model sets 16–20 and 21–25), despite the fact that, in terms of measured shape difference, the intervals these model sets represent are equivalent. Based on these interpretations the modeled shape subspace can be subdivided geometrically in such as way as to render the boundaries of Wolfe's (1993) character-state definitions much less ambiguous (Text-fig. 14).

LEAF APICES

Like Wolfe's leaf-base exemplars, his leaf-apex exemplars (Text-fig. 4) represent a family of alternative shapes. In the subspace of the first three eigenshape vectors (representing 98.47% of total shape variance), these define a twisted, trapezoidal plane formed by four outlying shapes (Text-fig. 15). These outliers represent the most attenuate and rounded morphologies. Interpretation of this shape space also mirrors that of the leaf-base analysis. The first eigenshape vector expresses differences in the relative width of the apex region, the second expresses the contrast between expansion and contraction of the leaf tip, and the third represents differences in the smoothness of the apex margin.

As before, the inclined plane delimited by the shape outliers can serve to define a surface on which to reconstruct a series of shape-deformation models useful for understanding the nature of shape transitions within this character (Text-fig. 16). After correcting for different orientations, the range of leaf-apex shape models is seen to be virtually identical to those of the leaf-base shape subspace (compare Text-figures 13 and 16). In both cases the upper model range is occupied by forms with either straight or concave sides converging to a tip. These forms are consistent with the acute con-



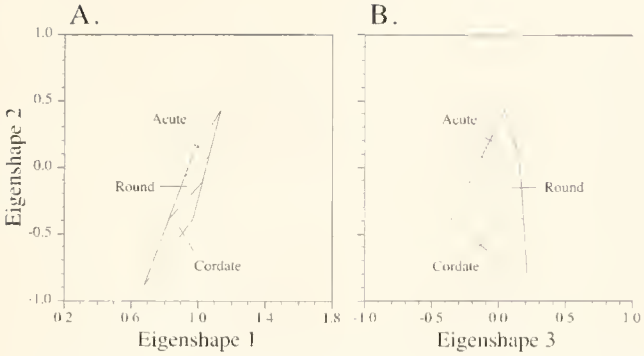
Text-figure 13.—Shape models for a regular grid of positions within the leaf-base shape character intermediacy plane. These models were obtained by scaling the first three eigenshape vectors resulting from the analysis of the exemplar shape functions by the coordinate positions of locations within the intermediacy plane (Text-fig. 12) and then summing the scaled vectors together in the manner shown in Text-figure 2B. Coordinate positions for each model as follows. (1) 1.132, 0.426, 0.040; (2) 1.123, 0.406, 0.044; (3) 1.114, 0.386, 0.048; (4) 1.105, 0.366, 0.052; (5) 1.096, 0.346, 0.056; (6) 1.019, 0.101, 0.083; (7) 1.030, 0.117, 0.051; (8) 1.041, 0.132, 0.018; (9) 1.052, 0.148, −0.015; (10) 1.063, 0.164, −0.048; (11) 0.907, −0.224, 0.127; (12) 0.937, −0.173, 0.057; (13) 0.968, −0.122, −0.013; (14) 0.999, −0.070, −0.082; (15) 1.030, −0.019, −0.152; (16) 0.794, −0.549, 0.170; (17) 0.844, −0.462, 0.064; (18) 0.895, −0.375, −0.043; (19) 0.946, −0.288, −0.149; (20) 0.996, −0.202, −0.255; (21) 0.681, −0.874, 0.213; (22) 0.752, −0.752, 0.070; (23) 0.822, −0.629, −0.073; (24) 0.893, −0.507, −0.216; (25) 0.963, −0.384, −0.359. See text for a discussion of the shape models relative to the definitions of the exemplar states. Shape model series such as these can be used to explore the geometric spaces within which these forms exist and better define the limits of character-state variation.

dition, though for this character Wolfe (1993) distinguished between the attenuate or "drip tip" (concave sides) and acute *sensu stricto* (straight sided) conditions. Similarly, the lower part of the model range is occupied by broadly rounded forms that exhibit a smooth boundary (models 11–12 of Text-fig. 16), a single, medially located indentation (models 16, 17, 21, and 22) or multiple and dispersed indentations (models 14, 15, 18–20, and 23–25). The primary difference between the two model sets stems from Wolfe's (1993) inclusion of a rounded exemplar with a crenulated margin.

Hickey's (1973) qualitative classification also reflects this overall similarity between the geometries of character states assigned to based and apical complexes. Curiously though, in both Hickey's (1973) and Wolfe's (1993) classifications, identical shapes are given different names when they appear in the basal and apical regions (*e.g.*, attenuate, apical vs. decurrent, basal). No doubt this counterintuitive nomenclature has a historical origin along with an obvious practical utility. Nonetheless, it can be a source of confusion that is simply not present in the shape-modeling approach to morphological analysis. Mappings of the leaf-apex character-state boundaries are shown in Text-figure 17.

MARGINAL TOOTH SHAPE

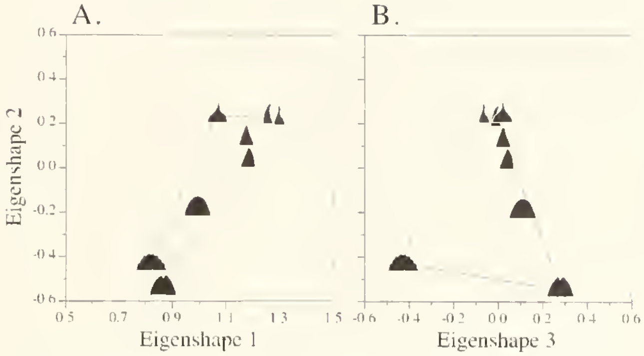
The most complex system of shape models in the Wolfe (1993) dataset is represented by the marginal



Text-figure 14.—Subregions of the leaf-base shape intermediacy space that correspond to the character states described by Wolfe (1993). Once these regions have been defined and extended into higher dimensions so that they represent hypervolumes rather than planar regions, they can be used to understand the geometry of shape character-state variation.

tooth shape exemplars (Text-fig 18). Wolfe's four exemplar shapes can be scattered in an empirical shape subspace formed by the first three eigenshape vectors (representing 98.44% of the total shape variance). The first marginal tooth eigenshape vector embodies the contrast between appressed (apical flank concave, basal flank convex) and rounded (apical and basal flanks convex) forms that comes about via rotation of the tooth tips forward and down. The second vector presents a contrast between a different aspect to tooth appression, in this instance via lateral translation of the angular sinuses upward. The third vector encodes the contrast between simple and compound marginal teeth. Within this space, Wolfe's four shape exemplars define a triangular plane that exhibits a distinct bend in the region of the mean shape. This complex, bent plane presents a convenient surface on which to base this character's shape-model analysis.

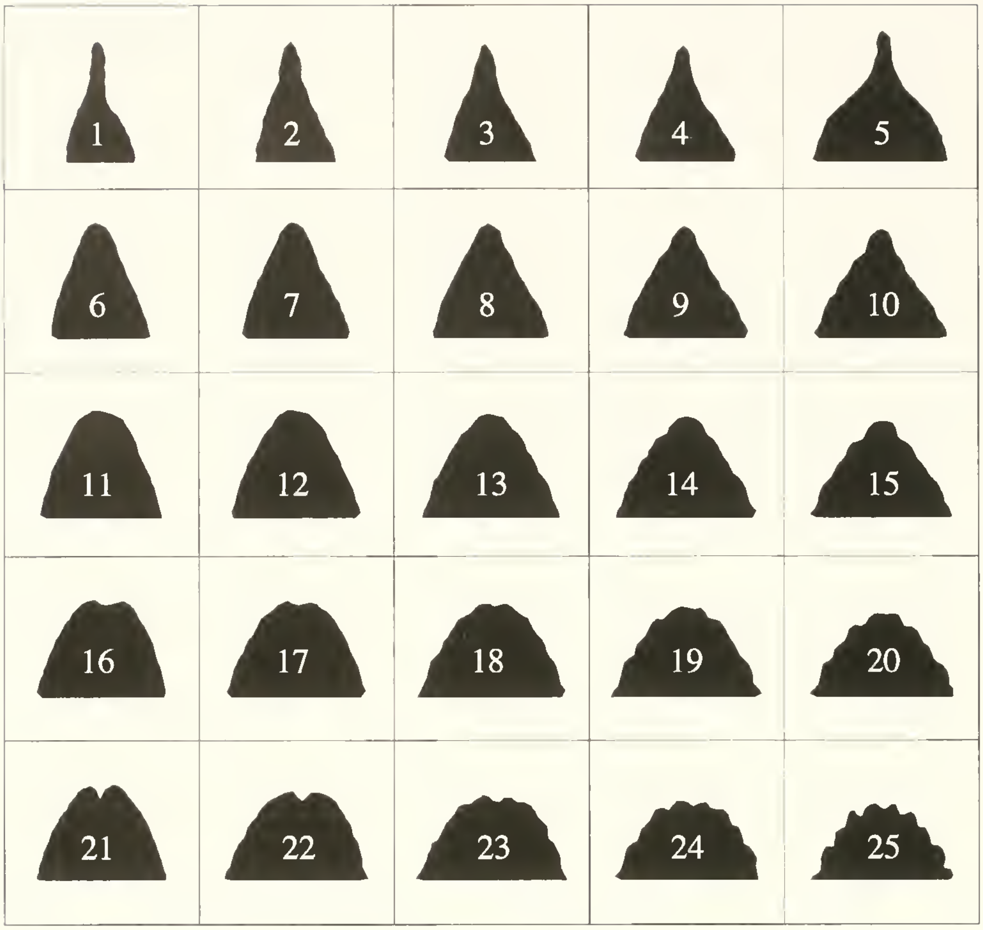
Inspection of the marginal tooth shape models existing on this character's exemplar plane (Text-fig. 19) shows the tooth-shape "character" to actually represent a character complex, with several different and overlapping marginal tooth-shape character states revealing themselves. Both eigenshape analysis and the eigenshape-based model series represent all of these morphological complexities in a logically formulated, linear deformational system. For example, models 1–9 of Text-figure 19 conform to Wolfe's (1993) "rounded" state (apical and basal flanks convex). This morphology corresponds to Hickey's (1973) convex-convex serration type. Models 10–15 conform to Wolfe's (1993) "appressed" state (apical flank concave, basal flank convex) and to Hickey's (1973) concave-convex serration type. A different character-state distribution is present for the tooth tips which, in Wolfe's model space, may be acute (apical and basal flanks form a sharp point) or blunt (no definition provided in either Hickey, 1973, or Wolfe, 1993). The former condition is represented by models 1–2, 7–8, 10–11, 13, and 15 of Text-figure 19, while the latter corresponds to models 3–5, 8–9, 12, and 14. Finally, models 1–4, 6–8, 10–12, and 13 exhibit pronounced compound morphologies (teeth exhibit smaller, subsidiary teeth, typically on their basal flanks; no corresponding character state given in Hickey 1973), whereas models 4–5, 9, 12, 14, and 15 exhibit plain margins throughout. Text-figure 20 maps the positions of the overlapping character-state fields present in this character's model set.



Text-figure 15.—Ordination of the three leaf-apex shape exemplars in the space of the three eigenshape vectors: $\lambda_1 = 89.34\%$, $\lambda_2 = 6.36\%$; $\lambda_3 = 2.74\%$). In order to visualize the ordination in three-dimensional space imagine that, relative to plot A, plot B is rotated 90°. Note that this ordination delimits a roughly quadrilateral space within a plane that is inclined at an angle to the three eigenshape vectors. This space contains the coordinate positions for all shapes that can be considered intermediate to the exemplar shapes. Regions of shape variation whose boundaries represent the boundaries of shape variation characteristic of each character state will be found within this quadrate space.

DISCUSSION

The dicotyledonous leaf model sets presented above are not intended to represent the last word (or graph) in systematic morphometrics for dicotyledonous plants. Obviously, Wolfe's leaf-character exemplar sets are far too restricted to be used as a basis for quantitative descriptions of generalized leaf physiography. This is not a criticism of Wolfe's work because he did not set out to create a generalized classification system for the description of leaf morphology. As his 1995 study shows, the physiographical characters he employed were sufficient to make detailed and consistent inferences about the climates of Tertiary localities. Nevertheless, the foregoing exercise in quantitative leaf-shape modeling has value in what it reveals about: (1) the subtle complexities of this simple, two-dimensional, shape system, (2) the needs of taxonomists, (3) the capabilities of modern imaging technology and numerical data analytic approaches to address those

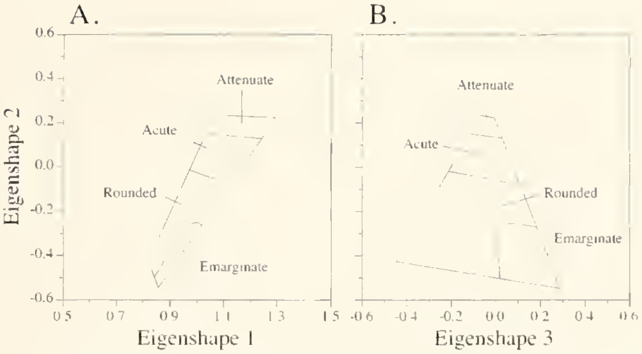


Text-figure 16.—Shape models for a regular grid of positions within the leaf-apex shape character intermediacy plane. These models were obtained by scaling the first three eigenshape vectors resulting from the analysis of the exemplar shape functions by the coordinate positions of locations within the intermediacy plane (Text-fig. 15) and then summing the scaled vectors together in the manner shown in Text-figure 2B Coordinate positions for each model as follows. (1) 1.263, 0.228, 0.196; (2) 1.215, 0.229, 0.132; (3) 1.167, 0.230, 0.068; (4) 1.118, 0.230, 0.004; (5) 1.070, 0.231, −0.060; (6) 1.161, 0.034, 0.075; (7) 1.123, 0.042, 0.017; (8) 1.085, 0.051, −0.040; (9) 1.047, 0.059, −0.098; (10) 1.009, 0.067, −0.155; (11) 1.060, −0.160, 0.146; (12) ; 1.032, −0.144, 0.047 (13) 1.004, −0.129, −0.053; (14) 0.976, −0.113, −0.152; (15) 0.948, −0.098, −0.251; (16) 0.958, −0.353, 0.216; (17) 0.940, −0.330, 0.076; (18) 0.922, −0.307, −0.065; (19) 0.905, −0.285, −0.205; (20) 0.887, −0.262, 0.346; (21) 0.856, −0.547, 0.287; (22) 0.849, −0.517, 0 105; (23) 0.841, −0.487, −0.077; (24) 0.834, −0.456, −0.259; (25) 0.826, −0.426, −0.441. See text for a discussion of the shape models relative to the definitions of the exemplar states. Shape model series such as these can be used to explore the geometric spaces within which these forms exist and better define the limits of morphological character-state variation.

needs directly, and (4) the role of geometric morphometrics in systematics.

Owing primarily to the relative lack of attention paid to leaves as character complexes (Hickey, 1973) and botanical descriptive traditions (see Linnaeus, 1751; Lindley, 1835; Bentham, 1861; Gray, 1879; Lee, 1948), the systematics of leaf shape in dicotyledonous plants—like the comparative morphology of most groups—has developed in an *ad hoc* manner, heavily dependent on the availability of adequate exemplars. This approach is both justifiable and efficient when exploring the morphological *terra incognita* of a relatively unstudied clade. Unnecessary problems arise when different terms are applied to the same morphological feature and when the same term is applied to different morphologies, of course, but these are largely matters of communication. As the morphology and taxonomy of a group becomes better known, however, the opportunity arises to achieve a true systematization of morphological concepts that have been observed in the group.

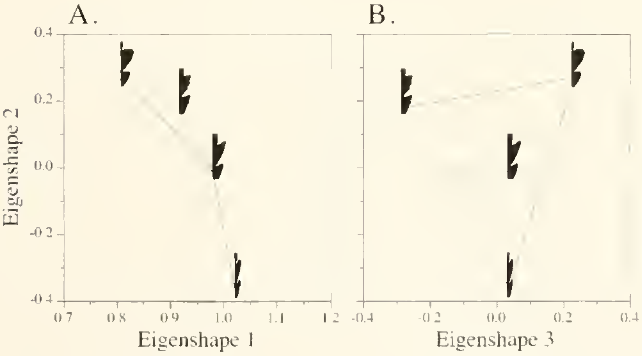
Stearn (1956, 1992) and Hickey (1973) attempted to devise such a system for dicotyledonous leaves as a whole. Wolfe (1993, 1995) applied the same concept to those aspects of leaf morphology that he identified as being correlated with different climatic regimes. But, because these studies were based on the qualitative analysis of leaf exemplars, the systematic leaf-



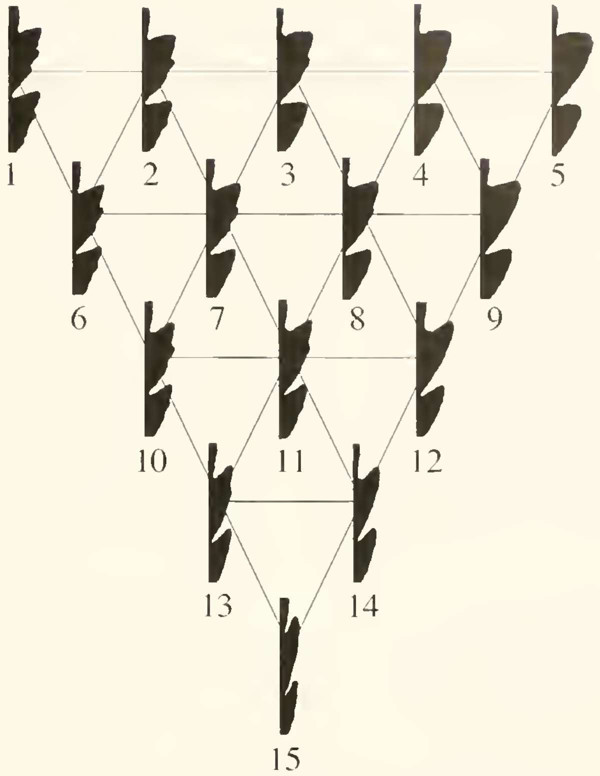
Text-figure 17.—Subregions of the leaf-apex shape intermediacy space that correspond to the character states described by Wolfe (1993). Once these regions have been defined and extended into higher dimensions so that the represent hypervolumes rather than planar regions, they can be used to understand the geometry of shape character-state variation.

character classifications advocated by these (and other) authors remained illusive. All possible shape alternatives were not systematically considered, much less illustrated. Indeed, by relying on traditional definitions of leaf characters—and concepts as to what constitutes a nameable morphological feature—all three classifications became hostages to ambiguity in several senses. This ambiguity manifests itself in: (1) different types of morphological relationships being used to recognize alternative states of the same character (*e.g.*, Wolfe's "lobateness" character discussed above), (2) different descriptive terms and definitions being applied to the same morphological feature (*e.g.*, see Hickey's, 1973 "lobate margin" and "crenulate margin" character states), and (3) quantitative ranges of non-shape-specific parameters (*e.g.*, aspect ratios) being used to establish an apparently discrete, discontinuous morphological classification for aspects of shape that were known to vary continuously and broadly within, as well as between, species (*e.g.*, see Hickey's, 1973 leaf-form characters that were modified from Stearn's, 1956 original form classification).

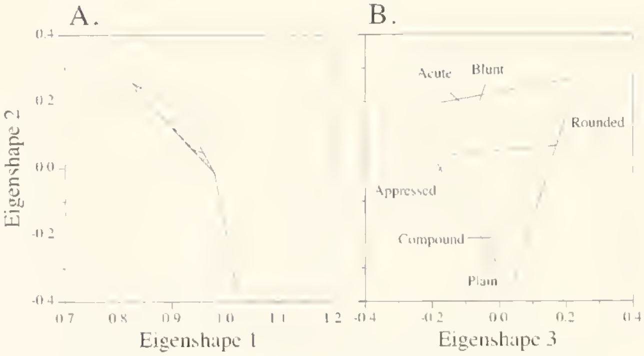
The shape modeling approach described and illustrated herein represents an alternative to the more idiosyncratic and qualitative approaches employed in these previous attempts to describe, illustrate, and systematize dicotyledonous leaf-shape observations. Even



Text-figure 18.—Ordination of the three marginal tooth-shape exemplars in the space of the three eigenshape vectors; λ_1 = 88.93%, λ_2 = 5.96%; λ_3 = 3.55%). In order to visualize the ordination in three-dimensional space imagine that, relative to plot A, plot B is rotated 90°. Note that this ordination delimits a bent triangular space both limbs of which are inclined to the three eigenshape axes. This space contains the coordinate positions for all shapes that can be considered intermediate to the exemplar shapes. Regions of shape variation whose boundaries represent the boundaries of shape variation characteristic of each character state will be found within this bent triangular space.



Text-figure 19.—Shape models for a regular grid of positions within the leaf marginal tooth-shape character intermediacy plane. These models were obtained by scaling the first three eigenshape vectors resulting from the analysis of the exemplar shape functions by the coordinate positions of locations within the intermediacy plane (Text-fig. 18) and then summing the scaled vectors together in the manner shown in Text-figure 2B. Coordinate positions for each model as follows. (1) 0.913, 0.176, −0.286; (2) 0.888, 0.199, −0.156; (3) 0.863, 0.223, −0.027; (4) 0.837, 0.246, 0.103; (5) 0.812, 0.269, 0.233; (6) 0.946, 0.082, −0.230; (7) 0.929, 0.097, −0.090; (8) 0.912, 0.113, 0.049; (9) 0.896, 0.128, 0.188; (10) 0.979, −0.013, −0.174; (11) 0.979, −0.013, −0.015; (12) 0.979, −0.013, 0.143; (13) 0.998, −0.187, −0.070; (14) 0.998, −0.187, 0.088; (15) 1.017, −0.360, 0.033. See text for a discussion of the shape models relative to the definitions of the exemplar states. Shape model series such as these can be used to explore the geometric spaces within which these forms exist and better define the limits of morphological character-state variation.



Text-figure 20.—Subregions of the leaf marginal tooth-shape intermediacy space corresponding to the character states described by Wolfe (1993). Once these regions have been defined and extended into higher dimensions so that the represent hypervolumes rather than planar regions, they can be used to understand the geometry of shape character-state variation.

more importantly, this approach preserves and extends the levels of complexity, accuracy, and flexibility required for taxonomic and ecological investigations. Specifically, the shape-modeling tools of geometric morphometrics make it an easy matter to (1) locate the shapes of interest within the hypermanifold of all possible shapes (see Kendall, 1984; Goodall, 1991; Bookstein, 1991), (2) ensure that corresponding regions are consistently matched across all shapes, both actual and theoretical (see Bookstein, 1991; MacLeod, 1999), (3) accurately represent ordinations of shapes within the sample based on consistent linear measures of similarity, (4) use these ordinations to define points, trajectories, planes and volumes within this shape space that are of interest to taxonomists, and (5) construct linear shape-deformation models at points, along trajectories, and within planes or volumes to represent any aspect of shape state or variational mode. Once such models are constructed they can be displayed as additional exemplars, compared qualitatively to real leaves, or compared to prior textual definitions of characters and character states. Because these shape models are referenced to sets of quantitatively defined shape vectors, each is unique and uniquely specifiable (thus avoiding the problems of inadvertent ambiguity in definition or usage), each exists over a complete and continuously variable range of possibilities (thus avoiding problems involving the arbitrary subdivision of shape change continua), and each can be used—along with ordination analyses—to understand the characteristics of shape variation in the group and experiment with the full range of species or structure-specific shape-related phenomena (*e.g.*, morphological integration *sensu* Olson and Miller, 1958; developmental constraints *sensu* Smith *et al.*, 1985; ecophenotypy *sensu* Wolfe, 1995).

In addition, the fact that the methods used to analyze the shape and construct the shape models are fully generalized means that complex organic bodies can be subdivided into their traditional taxonomic characters and analyzed in isolation from other such parts (see MacLeod, 2002b, for additional examples). This means that the standard procedures of qualitative taxonomic good practice can be wholly transferred into the morphometric realm by altering the level of the analysis such that complex morphologies are disassembled, analyzed, and then those results compared to results obtained by corresponding analyses of either partially-reconstructed or intact complexes. Moreover, the roles of variation in specific morphological components relative to those exhibited by the entire morphological complex can be explored and used to refine both intrinsic (*e.g.*, developmental) or extrinsic (*e.g.*, ecophenotypic) control.

Feeding back the more formal into the biological side of morphological analysis, the ability to obtain accurate models of morphological structures quickly, easily, and with great flexibility has substantial implications for the entire field of systematics in general, and paleontological systematics in particular, owing to the latter's dependence on morphological data. As shown above, sets of shape models can be used to examine the appropriateness of character-state definitions by showing whether they provide adequate coverage for the theoretical or the realized range of shape-based morphological variation within specific organismal groups. If gaps in this coverage are evident, shape models can aid in the development of new definitions—or the modification of old—to address the problem.

Even more importantly, though, shape models can be used to explore the boundaries that divide the realized morphological space within which organic forms exist and through which operational taxonomic groups are identified. In this sense, the shape-modeling approach to morphological analysis can be used to reconnect morphology-based taxonomic analysis with its main purpose, which is not the search for new and better exemplars of morphological characters or groups, but rather the continuing exploration of the discontinuities of morphological variation between species that serve to distinguish one from another. It is the origin, maintenance, and patterns of covariation responsible for such discontinuities, seen against the background of the theoretically continuous pattern of morphological variation, that give systematic data meaning. In the absence of an ability to access this continuous groundmass of possible morphologies—which can only be gained via modeling—the systematic assessment of discontinuities in patterns of morphological variation becomes much more difficult than it otherwise need be.

Finally, a word about technology. Even though the mathematical methods necessary for the construction of generalized geometrical shape models from eigenvector data have been available for several decades now, part of the reason why these methods have not been better integrated into contemporary systematic practice is technological. The easy, quick, efficient, and flexible quantitative analysis of morphological variation in systematics presupposes ready access to computers powerful enough to collect, process, and manage high-resolution digital images, in addition to the software necessary to access, segment, and extract spatial data from these images. Fortunately, recent developments in the consumer photography and computer markets have brought sophisticated digital imaging and image processing-measurement within the budgets of virtually all serious systematists. Currently available digital cameras with circa three-million-pixel resolutions produce images of morphological structures at a level of detail well above that needed for routine shape analysis. For example, the data used in this study were collected from images whose basal resolutions were 262,144 pixels. Even these relatively low-resolution images (by photographic standards) contained more data points than were needed to constrain the outline segments of all the analyzed characters.

More limiting is the range and user-friendliness of the software used by morphometricians to segment these images and extract quantitative information from outlines and landmarks. Whereas up until the last few years it could be argued that such technological thresholds prevented most systematists from taking advantage of morphometric methods in general, and shape modeling methods in particular, those issues have now been addressed. Commercial products have long been available to fulfill this need. In the last few years, however, a number of public-domain software packages have appeared—some programmed by systematists for systematists—that fulfill the basic needs of morphometric data collection as well as the available commercial software. In this context, Wayne Rasband's NIH Image Package for Apple Macintosh™ computers (http://rsb.info.nih.gov/nih-image/, the equivalent Scion Image package for Window's PCs (http://www.scioncorp.com/), and Jim Rohlf's collection of morphometrics software (http://life.bio.sunysb.edu/morph/) deserve special mention. These applications are all available via free download from publicly accessible web sites. When combined with a digital camera and the eigenshape data analysis-modeling routines used herein (the latter also freely available via public website, see Acknowledgments), these systems effectively remove the technological impediment from those interested in pursuing shape-model analyses.

SUMMARY

In order to realize its potential as an indispensable source of information about the natural environment—past, present, and possibly future—systematics must improve its capacity to summarize patterns in morphological data and relate those patterns to a wide range of other variables. At present, morphological analyses are largely undertaken in the same way they have been undertaken for centuries, via visual inspection by trained taxonomists whose conclusions are influenced by the number and quality of morphological exemplars (or representations thereof) they have seen during the course of their careers. The problems arising from this approach are manifested in the breathtakingly low observed reproducibilities of systematic studies (*e.g.*, Zachariasse *et al.*, 1978; Lipps, 1997; MacLeod, 1998). While efforts are continually undertaken to better define and systematize the state of morphological knowledge for virtually all organismal groups, these efforts are hampered by the enormous scope of the task which grows larger with each passing year (see Kaesler, 1993).

Recent developments in the field of morphometrics may provide aspects of a solution to this problem. With the adoption of a more geometrically focused paradigm, refinement in practitioners' appreciation of appropriate analytic targets, and the development of new analytic and graphical tools, morphometrics has reached the level of sophistication necessary to make positive contributions to routine morphological analysis in systematics. In particular, the ability of geometric morphometrics to express its results in terms of shape models that can be interpreted in a manner natural to qualitatively trained systematists suggests that these devices can be of use in providing the range of shape exemplars needed by systematists to improve their diagnoses. Exemplar datasets assembled with the aid of these shape models can help refocus the systematics community on a structured exploration of the morphological discontinuities that can be used to unambiguously define taxa instead of the endless search for more or better morphological exemplars that merely represent them.

In order to make a preliminary evaluation of the potential of shape models to improve morphological analyses, a morphometric investigation of five dicotyledonous leaf characters used by Wolfe (1993, 1995) to infer Tertiary climatic parameters was undertaken. In each case, the range of exemplars used by Wolfe (1993) to illustrate his character states was analyzed using the extended eigenshape method. The shape spaces thus created were used to define shape-intermediacy surfaces that quantitatively represented the limits of exemplar-based shape variation for major aspects of the character's variational modes. Shape modeling procedures (described herein) were then used to explore these shape intermediacy subspaces within each character. The goals of these explorations were to identify and illustrate the boundaries between character states. Once the character-state system had been geometrically defined, the morphometric representation of each shape system was then compared to equivalent graphic and definitional representations taken from the paleobotanical literature. In each case the morphometric models represented the character concepts accurately and provided a range of alternative morphologies that was a least as great—in some instances greater—than was immediately obvious using the textual character-state definitions and exemplar illustrations drawn from real leaves alone. In those cases where apparent discrepancies between the morphometric results went beyond the descriptive-exemplar formulations, improvements were indicated in both the formulation of definitions and the recognition of additional character states.

As a consequence of these results, and owing to the widespread availability of hardware-software systems that can be obtained at very moderate cost, the following recommends are made: (1) additional explorations of the potential of geometric morphometrics to contribute to systematic analyses in all contexts be undertaken; (2) students receive increased exposure to and training in morphometric methods of data analysis and representation; (3) efforts continue to improve the quality and user-friendliness of the morphometrics software, especially the provision of web-based data analysis tools; (4) attempts be made to rehabilitate the image of morphometric analyses in the systematics community and better integrate morphometrics into the corpus of systematic theory (see Macleod, 2001a, 2002a,b; MacLeod and Forey, 2002, for examples). Since the basic data of systematics is morphology, and the language of morphology is geometry, it is necessary that systematics becomes more geometric in theory and in practice.

REFERENCES CITED

Bentham, G.

1861. Flora Hongkongensis, Lovell Reeve, London, 482 pp.

Bookstein, F.L.

1978. The measurement of biological shape and shape change. Springer, Berlin, 191 pp.

1986. Size and shape spaces for landmark data in two dimensions. Statistical Science, vol. 1, pp. 181–242.

1990. Higher-order features of shape change for landmark data. *in* Proceedings of the Michigan Morphometrics Workshop. F.L. Bookstein and F.J. Rohlf, *eds.*, The University of Michigan Museum of Zoology, Special Publication No. 2, Ann Arbor, MI, pp. 237–250.

1991. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge, 435 pp.

1993. A brief history of the morphometric synthesis. *in* Contributions to Morphometrics. L.F. Marcus, E. Bello, and A García-Valdecasas, *eds.*, Museo Nacional de Ciencias Naturales 8, Madrid, pp. 18–40.

1994. Can biometrical shape be a homologous character? *in* Homology: The Hierarchical Basis of Comparative Biology. B.K. Hall, *ed.*, Academic Press, San Diego, CA, pp. 197–227.

1996a. Combining the tools of geometric morphometrics. *in* Advances in morphometrics. L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor, and D.E. Slice, *eds.*, Plenum Press, New York, pp. 131–151.

1996b. Landmark methods for forms without landmarks: Localizing group differences in outline shape. *in* Proceedings of the Workshop on Mathematical Methods in Biomedical Image Analysis. A. Amini, F.L. Bookstein, and D. Wilson, *eds.*, IEEE Computer Society Press, San Francisco, pp. 279–289.

1996c. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. Medical Image Analysis, vol. 1, pp. 1–20.

1997. Landmark methods for forms without landmarks: Localizing group differences in outline shape. Medical Image Analysis, vol. 1, pp. 225–243.

Bookstein, F.L., and Green, W.D.K.

1993. A feature space for edgels in images with landmarks. Journal of Mathematical Imaging and Vision, vol. 3, pp. 213–261.

Christopher, R.A., and Waters, J.A.

1974. Fourier analysis as a quantitative descriptor of miosphere shape. Journal of Paleontology, vol. 48, pp. 697–709.

Falconer, D.S.

1981. Introduction to quantitative genetics. Longman, London, 340 pp.

Foote, M.

1991. Analysis of morphological data. *in* Analytical Paleobiology. N.L. Gilinsky and P.W. Signor, *eds.*, University of Tennessee, Knoxville, TN, pp. 59–86.

1996. Models of morphological diversification. *in* Evolutionary Paleobiology. D. Jablonski, D.H. Erwin, and J. Lipps, *eds.*, University of Chicago Press, Chicago, IL, pp. 63–86.

1997. Sampling, taxonomic description, and our evolving knowledge of morphological disparity. Paleobiology, vol. 23, pp. 181–206.

Goodall, C.R.

1991. Procrustes methods in the statistical analysis of shape. Journal of the Royal Statistical Society, Series B, vol. 53, pp. 285–339.

Gray, A.

1879. The botanical textbook, New York, 442 pp.

Greenacre, M.J.

1984. Theory and applications of correspondence analysis. Academic Press, London, 364 pp.

Hickey, L.J.

1973. Classification of the architecture of dicotyledonous leaves. American Journal of Botany, vol. 60, pp. 17–33.

Hughes, N.C.

2001. Morphometrics and intraspecific variation. *in* Palaeobiology II. D.E.K. Briggs and P.R. Crowther, *eds.*, Blackwell Science Ltd, Oxford, pp. 492–494.

Imbrie, J., and Kipp, N.G.

1971. A new micropaleontological method for quantitative paleoclimatology: Application to a Pleistocene Caribbean core. *in* The Late Cenozoic Glacial Ages. K.K. Turekian, *ed.*, Yale University Press, New Haven, CT, pp. 72–181.

Kaesler, R.L.

1993. A window of opportunity: peering into a new century of paleontology. Journal of Paleontology, vol. 67, pp. 329–333.

1997. Phase angles, harmonic distance, and the analysis of form. *in* Fourier descriptors and their applications in biology. P.E. Lestrel, *ed.*, Cambridge University Press, Cambridge, pp. 106–125.

Kendall, D.G.

1984. Shape manifolds, procrustean metrics and complex projective spaces. Bulletin of the London Mathematical Society, vol. 16, pp. 81–121.

Lee, A.T.

1948. The genus *Swainsona*. Contributions to the New South Wales Herbarium, vol. 1, pp. 131–271.

Lindley, J.

1835. Introduction to botany. London, 508 pp.

Linnaeus, C.

1751. Philosophia botanica novae seu Institutionum phytographicarum Podromus. Göttingen, 451 pp.

Lipps, J.

1997. The Cretaceous-Tertiary boundary: the El Kef blind test. Marine Micropaleontology, vol. 29, pp. 65–66.

Lohmann, G.P.

1983. Eigenshape analysis of microfossils: A general morphometric method for describing changes in shape. Mathematical Geology, vol. 15, pp. 659–672.

Lohmann, G.P., and Schweitzer, P.N.

1990. On eigenshape analysis. *in* Proceedings of the Michigan morphometrics workshop. F.J. Rohlf and F.L. Bookstein, *eds.*, The University of Michigan Museum of Zoology, Special Publication No. 2, Ann Arbor, MI, pp. 145–166.

MacFadden, B.J., and Bryant, J.D.

1992. Stable isotope and trace element geochemistry of vertebrate fossils: interpreting diets and climates. Palaeogeography, Palaeoecology, Palaeoclimatology, vol. 107, pp. 197–328.

MacLeod, N.

1998. Impacts and marine invertebrate extinctions. *in* Meteorites: flux with time and impact effects. M.M. Grady, R. Hutchinson, G.J.H. McCall, and D.A. Rotherby, *eds.*, The Geological Society of London, London, pp. 217–246.

1999. Generalizing and extending the eigenshape method of shape visualization and analysis. Paleobiology, vol. 25, pp. 107–138.

2001a. Landmarks, localization, and the use of morphometrics in phylogenetic analysis. *in* Fossils, phylogeny, and form: an analytical approach. G. Edgecombe, J. Adrain, and B. Lieberman, *eds.*, Kluwer Academic/Plenum, New York, pp. 197–273.

2001b. The role of phylogeny in quantitative paleobiological analysis. Paleobiology, vol. 27, pp. 226–241.

2002a. Phylogenetic signals in morphometric data. *in* Morphometrics, shape, and phylogenetics. N. MacLeod and P. Forey, *eds.*, Taylor and Francis, London, pp. 100–138.

2002b. Geometric morphometrics and geological form-classification systems. Earth Science Reviews, vol. 59 (2002), pp. 27–47.

MacLeod, N., and Forey, P.

2002. Morphometrics, shape, and phylogenetics. Taylor and Francis, London, 308 pp.

MacLeod, N., and Rose, K.D.

1993. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. American Journal of Science, vol. 293-A, pp. 300–355.

Marcus, L.F., Bello, E., and García-Valdecasas, A.

1993. Contributions to morphometrics. Museo Nacional de Ciencias Naturales 8, Madrid, 264 pp.

Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P., and Slice, D.E.

1996. Advances in morphometrics. Plenum Press, New York, 587 pp.

Mayr, E.

1982. The growth of biological thought: diversity, evolution, and inheritance. Harvard University Press, Cambridge, 974 pp.

Mayr, E., and Ashlock, P.D.

1991. Principles of systematic zoology. McGraw-Hill, New York, 475 pp.

Nishisato, S.

1980. Analysis of categorical data: dual scaling and its applications. Toronto University Press, Toronto, 300 pp.

Olson, E., and Miller, R.

1958. Morphological integration. University of Chicago Press, Chicago, 317 pp.

Rohlf, F.J.

2002. Geometric morphometrics and phylogeny. *in* Morphometrics, Shape, and Phylogeny. N. MacLeod and P. Forey, *eds.*, Taylor and Francis, London, pp. 175–193.

Rohlf, F.J. and Bookstein, F.L.

1990. Proceedings of the Michigan morphometrics workshop. The University of Michigan Museum of Zoology Special Publication 2, Ann Arbor, MI, 380 pp.

Simpson, G.G.

1961. Principles of animal taxonomy. Columbia University Press, New York, 247 pp.

Smith, J.M., Burian, R., Kauffman, S., Albrech, P., Campbell, J., Goodwin, B., Lande, R., Raup, D., and Wolpert, L.

1985. Developmental constraints and evolution. Quarterly Review of Biology, vol. 60, pp. 265–287.

Sokal, R.R., and Rohlf, F.J.

1995. Biometry: the principles and practice of statistics in biological research (third edition). W. H. Freeman, New York, 887 pp.

Stearn, W.T.

1956. Shapes of leaves. Journal of the Royal Horticultural Society, vol. 165, pp. 158–164.

1992. Botanical Latin: history, grammar, syntax, terminology and vocabulary. David & Charles, Newton Abbot, Devon, 546 pp.

Steigler, S.M.

1986. The history of statistics: the measurement of uncertainty before 1900. Harvard University Press, Cambridge, MA, 410 pp.

ter Braak, C.F., and Prentice, I.C.

1988. A theory of gradient analysis. Advances in Ecological Research, vol. 18, pp. 271–317.

Thompson, D.W.

1917. On growth and form. Cambridge University Press, Cambridge, 793 pp.

Wills, M.A.

2001. Morphological disparity: a primer. *in* Fossils, phylogeny and form: an analytical approach. J.M. Adrain, G.D. Edgecombe, and B.S. Lieberman, *eds.*, Kluwer Academic/Plenum, New York, 55–144 pp.

Wolfe, J.A.

1993. A method of obtaining climatic parameters from leaf assemblages. United States Geological Survey Bulletin 2040, pp. 1–71.

1995. Paleoclimatic estimates from Tertiary leaf assemblages. Annual Review of Earth and Planetary Science, vol. 23, pp. 119–142.

Zachariasse, W.J., Riedel, W.R., Sanfilippo, A., Schmidt, R.R., Brolsma, M.J., Schrader, H.J., Gersonde, R., Drooger, M.M., and Brokeman, J.A.

1978. Micropaleontological counting methods and techniques—an exercise on an eight meters section of the Lower Pliocene of Capo Rossello, Sicily. Utrecht Micropaleontological Bulletins, vol. 17, pp. 1–265.

Zahn, C.T., and Roskies, R.Z.

1972. Fourier descriptors for plane closed curves. IEEE Transactions, Computers, vol. C-21, pp. 269–281.

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