GEOLOGICAL SURVEY OF CANADA
BULLETIN 444

CONTRIBUTIONS TO CANADIAN PALEONTOLOGY

Papers by:

M.J. Copeland
T.T. Uyeno and P. Bultynck,
E.W. Bamber and W.J. Sando
R.M. Kalgutkar

1993

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PREFACE

This bulletin, under the general title of *Contributions to Canadian Paleontology*, contains four papers. These papers describe paleontological material such as the enigmatic genus *Anomalocaris* and the possible arthropod *Tuzoia*, from Lower Cambrian strata near Cranbrook, British Columbia, and Lower to Middle Devonian conodonts from the Moose River Basin, Northern Ontario. New information is given about the Viséan rugose coral, *Ankhelasma*, and a detailed account of fungal palynomorphs from the Paleogene of Yukon Territory is presented.

These studies of fauna from different areas of Canada, add valuable insight to the refinement of Canadian stratigraphy, which is necessary for the economic analysis of Canadian sedimentary basins.

Elkanah A. Babcock
Assistant Deputy Minister
Geological Survey of Canada

PRÉFACE

Le présent bulletin de la série intitulée *Contributions to Canadian Paleontology* réunit quatre études. La première décrit des fossiles tels *Anomalocaris*, un genre énigmatique, et *Tuzoia*, qui est peut-être un arthropode; ces fossiles proviennent de strates du Cambrien inférieur près de Cranbrook, en Colombie-Britannique. La seconde traite de conodontes du Dévonien inférieur et moyen en provenance du bassin de la rivière Moose, dans le nord de l'Ontario. La troisième donne de nouveaux renseignements sur le tétracoralliaire viséen *Ankhelasma* et la quatrième, une description détaillée de palynomorphes fongiques du Paléogène qui s'observent au Yukon.

Ces études de faunes provenant de divers endroits au Canada contribuent au perfectionnement de la stratigraphie canadienne, qui est essentiel à l'analyse économique des bassins sédimentaires de notre pays.

Elkanah A. Babcock
Sous-ministre adjoint
Commission géologique du Canada

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ANOMALOCARIS (OF UNKNOWN AFFINITY) AND *TUZOIA* (A POSSIBLE ARTHROPOD) FROM THE LOWER CAMBRIAN EAGER FORMATION NEAR CRANBROOK, BRITISH COLUMBIA

M.J. Copeland[1]

*Copeland, M.J., **Anomalocaris** (of unknown affinity) and **Tuzoia** (a possible arthropod) from the Lower Cambrian Eager Formation near Cranbrook, British Columbia; in Contributions to Canadian Paleontology, Geological Survey of Canada, Bulletin 444, p. 1–5, 1993.*

Abstract

The enigmatic genera *Anomalocaris* and *Tuzoia* are discussed on the basis of additional specimens obtained from strata of the Eager Formation (Lower Cambrian) near Cranbrook, British Columbia that were deposited in shallow water. The exact systematic positions of these genera are still unknown, but much new information on *Anomalocaris* has been obtained by researchers working on the deeper water Middle Cambrian Burgess Shale. The occurrence of these shallow water genera in strata of the Burgess Shale may be ascribed to slumping of a carbonate bank into a deeper water, anaerobic environment.

Résumé

L'auteur examine les genres énigmatiques *Anomalocaris* et *Tuzoia* en se fondant sur d'autres spécimens échantillonnés dans les strates de la Formation d'Eager (Cambrien inférieur), près de Cranbrook en Colombie-Britannique, qui ont été déposées en eau peu profonde. La position systématique exacte de ces genres demeure inconnue, mais des chercheurs qui étudient le Shale de Burgess (Cambrien moyen), une lithologie d'eau plus profonde, ont recueilli de nombreuses nouvelles données sur *Anomalocaris*. La présence, dans les strates du Shale de Burgess, de ces genres d'eau peu profonde peut être attribuable à l'affaissement d'un banc carbonaté vers un milieu anaérobie plus profond.

INTRODUCTION

Two small collections of Lower Cambrian fossils from talus of uncertain stratigraphic position within the Eager Formation about 8.5 km northeast of Cranbrook, British Columbia (lat. 49°30′N; long. 115°46′W) contained specimens of *Anomalocaris* and *Tuzoia*. This is not the first report of these genera from the Eager Formation; Resser (1929, p. 3) recorded that these beds were made known to C.D. Walcott of the United States National Museum by a Colonel H. Pollen. From this locality, Resser described three new species of *Tuzoia* and one new species of *Anomalocaris*. Species of both of these genera also occur in the Middle Cambrian Burgess Shale of British Columbia, a locality made famous by Walcott early this century.

SYSTEMATIC PALEONTOLOGY

Originally, both *Anomalocaris* and *Tuzoia* were assigned to the Arthropoda. In fact, *Anomalocaris*, interpreted as being segmented, with unsegmented appendages and bearing a telson, was considered to be the posterior body part of the carapace *Tuzoia* (see Resser, 1929, p. 6). After much interpretive investigation, Whittington and Briggs (1985) discovered that *Anomalocaris* is one of the two sclerotized oral appendages of a gigantic Cambrian animal of unknown affinity and is synonymous with *Laggania* Walcott and *Peytoia* Walcott. The history of this study is reviewed in a popular publication by Gould (1989, p. 194–206). The genus *Tuzoia* is still considered an arthropod carapace and may, questionably, be placed within the malacostracan subclass Phyllocarida (Rolfe,

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[1] Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario K1A 0E8

1969, p. R328). The presence of both *Anomalocaris* and *Tuzoia* in the Lower Cambrian Eager Formation and the Middle Cambrian Burgess Shale (Fig. 1.1) is unusual in that paleontological "curiosities" are usually of unique occurrence. Other occurrences of isolated appendages of *Anomalocaris canadensis* type are recorded from "Lower and Middle Cambrian rocks of Pennsylvania, California and British Columbia" (Whittington and Briggs, 1985, p. 572) and "*Peytoia*" has been found in the Middle Cambrian of Utah (Conway Morris and Robison, 1982). *Tuzoia* is also recorded from Lower or Middle Cambrian strata from Vermont, Pennsylvania, Utah, and China.

An apparently anomalous situation seems to exist between the occurrence of *Anomalocaris* and *Tuzoia* in the inner detrital belt strata of the Lower Cambrian Eager Formation and the deeper water Middle Cambrian Burgess Shale. However, if Stewart (1991) is correct, the occurrence of these genera in the Burgess Shale resulted from the large scale collapse of inner detrital deposits of the Stephen Formation adjacent to a re-entrant into the Cathedral escarpment and, therefore, some of the Burgess Shale fauna is allochthonous in origin. A similar explanation could apply to the occurrence of *Anomalocaris canadensis* in the Lower Cambrian Latham Shale of California (Briggs and Mount, 1982, p. 1116).

Phylum, Class, Order, Family unknown

Genus *Anomalocaris* Whiteaves, 1892

***Figure 1.1. Anomalocaris canadensis** Whiteaves, 1892, x1.45, Rasetti collection, Université Laval No. F418, Middle Cambrian, Mount Stephen, Field, British Columbia, deposited in the GSC type fossil collection as GSC 102289.*

Type species. Anomalocaris canadensis Whiteaves, 1892

Anomalocaris canadensis Whiteaves, 1892

Plate 1.1, figures 4, 6
(possibly Plate 1.1, figures 2, 3, 5)

Anomalocaris Canadensis Whiteaves, 1892, p. 205, 1 fig. (For complete synonymy see Briggs, 1979, p. 633).

Type material. Hypotypes GSC 101830, a, 101831, 101832, a, 101833, 101834, unfigured hypotype 101836, a.

Remarks. Briggs (1979) was apparently the first to interpret *Anomalocaris canadensis*, on the basis of lectotype GSC 3418, as an ambulatory arthropod appendage. He concluded that both Lower and Middle Cambrian occurrences of the genus in British Columbia belonged within the species *Anomalocaris canadensis* Whiteaves, 1892. Later, Briggs and Mount (1982) also considered anomalocarid remains as arthropod limbs of *A. canadensis*. Subsequently, Whittington and Briggs (1982, 1985) discovered the relationship of *Anomalocaris canadensis* as an oral appendage, and *Peytoia nathorsti* Walcott, 1911 as the circlet of mouth plates, within one taxon, *Anomalocaris canadensis*. We have, therefore, two morphological "species" of *Anomalocaris* in British Columbia, the Lower and Middle Cambrian oral appendage belonging to *A. canadensis* Whiteaves and the Middle Cambrian (i.e., Burgess Shale) circlet of mouth plates belonging to *A. nathorsti* (Walcott). Resser's (1929) species, *Anomalocaris cranbrookensis*, is considered by Briggs (1979) synonymous with *A. canadensis*. Differentiation between *A. canadensis* and *A. cranbrookensis* may be possible only when more complete specimens from the Cranbrook, British Columbia locality become available. Meanwhile the terminology adopted by Whittington and Briggs (1985) is followed in the present report.

From the specimens at hand, the largest representatives from the Eager Formation of the Cranbrook locality have 9 to 11 segments preserved; each segment (except possibly the ultimate) has a distally tapering spine. There is no evidence that each segment had more than one spine (Briggs and Mount, 1982, p. 1113; Whittington and Briggs, 1985, Figure 106) or that the spine bifurcated. This is the most important factor in determining that the appendage did not serve in an ambulatory function.

From the size of these oral appendages and several nearly complete specimens of the entire animal, Briggs (1979) and Whittington and Briggs (1985) have ascertained that the anomalocarid animal attained a length of from 0.5 to 1 m. This indeed indicates that *Anomalocaris* was the largest of all known Cambrian invertebrates.

Phylum Arthropoda?

Class Malacostraca?

Subclass Phyllocarida?

Order and Family unknown

Genus *Tuzoia* Walcott, 1912

Type species. Tuzoia retifera Walcott, 1912

Tuzoia polleni Resser, 1929

Plate 1.1, figure 1

Tuzoia polleni Resser, 1929, p. 9, Pl. 5, figs. 1-3

Type material. Hypotype GSC 101829, a; unfigured specimen GSC 101835, a.

Remarks. Resser (1929, p. 9) described *T. polleni* as having strong reticulations, four posterior spines and five or more spines on the anterior two thirds of the dorsum. He thus distinguished *T. polleni* from other species of the Eager Formation (*T. nodosa* Resser with large and numerous dorsal spines, greater width and short, blunt spines on the mid lateral ridge, and *T. spinosa* Resser with large spines on the mid lateral ridge and marginal spines arranged in "two sets, one a widely and irregularly spaced large set between which a smaller more even set occurs".)

Clearly, the specimen figured here, and possibly a second, imperfect specimen (unfigured specimen GSC 101835) agrees most closely with *T. polleni* in having four dorsal spines in the anterior two thirds of the valve, smaller alar spines at the cardinal angles, three large and two smaller spines on the posterior margin and a mid lateral ridge that is not nodose but is composed of smaller reticulations. Resser did not mention that the anterior and ventral margins anterior of the most ventral posterior spine are minutely crenate. This is evident in the specimen figured by him in Plate 5, figure 1 and is also present in the specimen figured here. The L/H ratios of the specimen figured by Resser are (approximately) 1.34, 1.49, and 1.55, whereas that of the present specimen is 1.36. Compression is undoubtedly a factor in the L/H ratio ranges but either the convexity of the valves of the carapace enclosing the body of the animal was minimal or the carapace material was relatively soft and pliable as the specimen shows no evidence of being cracked, split, or distorted.

ACKNOWLEDGMENTS

The author wishes to acknowledge, with thanks, the collectors of the present material. The larger collection, submitted by Frances Dunne of Spillimacheen, British Columbia, comprises mostly part and counterpart of three specimens of *Anomalocaris*, two specimens with possible anomalocarid affinity, and two specimens of *Tuzoia*. The smaller collection, submitted by David Healing of Castlegar, British Columbia, is a single specimen of *Anomalocaris*. Associated with these specimens are trilobite fragments identified by W.H. Fritz, Geological Survey of Canada, as *Olenellus eagerensis*? Best, 1952 and *Wanneria*? sp. From this general area, Best (1952) listed the trilobites *Olenellus eagerensis, O. gilberti, O. schofieldi*, and *Wanneria walcottana* from the Eager Formation. He concluded that "On the basis of olenellids in the Eager and the gradational lower contact with the Cranbrook, both formations are assigned to the Lower Cambrian" (op. cit., p. 13).

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PLATE 1.1

Anomalocaris and *Tuzoia* from the Lower Cambrian Eager Formation about 8.5 km northeast of Cranbrook, British Columbia

Figure 1. *Tuzoia polleni* Resser, x approx. 1, GSC hypotype 101829. (Partial glabella of *Olenellus eagerensis*? Best at lower right.)

Figure 2. *Anomalocaris*? sp., x1, GSC figured specimen 101830.

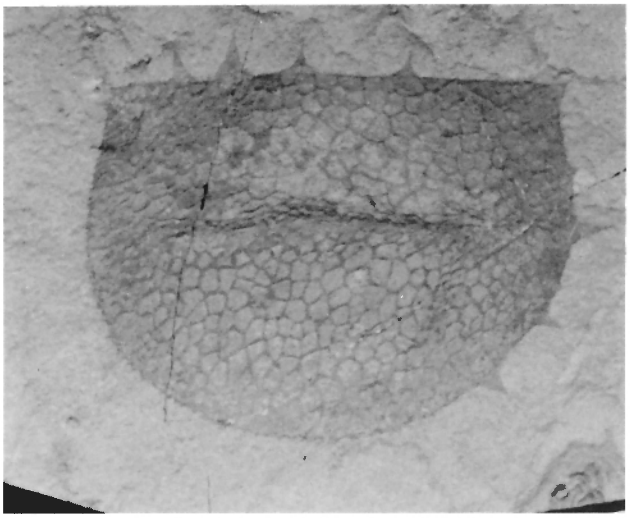
Figure 3. *Anomalocaris* sp., x1, GSC figured specimen 101831.

Figure 4. *Anomalocaris canadensis* Whiteaves, x1, GSC hypotype 101832. Partial olenellid cephalon at upper right.

Figure 5. *Anomalocaris* sp. cf. *A. canadensis* Whiteaves, x1, GSC hypotype 101833.

Figure 6. *Anomalocaris canadensis* Whiteaves, x2, GSC hypotype 101834.

(Figures 1–5 from the collection of Frances Dunne; figure 6 from the collection of David Healing).



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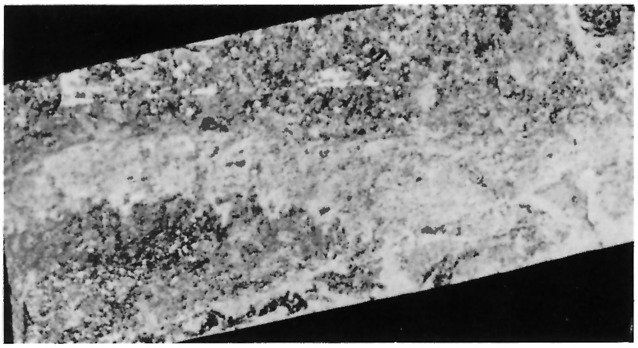

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LOWER TO MIDDLE DEVONIAN CONODONTS OF THE JAAB LAKE WELL, MOOSE RIVER BASIN, NORTHERN ONTARIO

T.T. Uyeno[1] and P. Bultynck[2]

Uyeno, T.T. and Bultynck, P., Lower to Middle Devonian conodonts of the Jaab Lake well, Moose River Basin, Northern Ontario; in Contributions to Canadian Paleontology, Geological Survey of Canada, Bulletin 444, p. 7–35, 1993.

Abstract

Conodonts are described from the Ontario Department of Mines Jaab Lake No. 1 well, located in northern Ontario, and their biostratigraphic, paleoecological, and paleogeographic significance are discussed. The location of the well is close to the depocentre of the Moose River Basin, the more southerly of the two basins that constitute the Hudson Platform.

Conodonts were obtained from (in ascending order) the Stooping River, Kwataboahegan, Murray Island, and Williams Island formations. The faunas, which range in age from late Emsian to (?)earliest Givetian, are dominated by icriodontans, most of which are endemic to North America; only two *Polygnathus* species are present. In the absence of polygnathids, reference to standard conodont zonation is made only indirectly, and a sequence ranging from the *laticostatus* to *ensensis* zones is inferred. Dating is aided by recognizing three regional zones and eleven datum planes. The zones are (in ascending order) the *Latericriodus alces* n. sp., *L. robustus* and *Icriodus angustus* zones; the last two were named earlier by Orr (1971).

The conodont zones are related to zonation based on spores from the same well, as established by McGregor and Camfield (1976) and Richardson and McGregor (1986). Two, and possibly three, T–R eustatic cycles of Johnson et al. (1985) are represented in the Jaab Lake well succession; Ib and Ic in the lower and upper parts, respectively, of the Stooping River Formation, and If at the base of the Murray Island Formation.

During the Eifelian at least, the Jaab Lake conodont faunas had closest affinity to the Eastern Faunal Realm of North America (of Sparling, 1984), with some connection to the northern Michigan Basin.

Résumé

Les auteurs décrivent des conodontes provenant du puits n° 1 du lac Jaab du ministère des Mines de l'Ontario; ils examinent leur importance biostratigraphique, paléoécologique et paléogéographique. Le puits se situe dans le nord de l'Ontario, près du dépocentre du bassin de Moose River, soit le bassin le plus au sud des deux qui constituent la Plate-forme d'Hudson.

Les conodontes proviennent des formations suivantes, données en ordre ascendant : Stooping River, Kwataboahegan, Murray Island et Williams Island. Les faunes, qui s'échelonnent de l'Emsien tardif au tout début (?) du Givétien, comportent principalement des icriodontans, dont la plupart sont endémiques à l'Amérique du Nord; seules deux espèces de *Polygnathus* sont signalées. En l'absence de polygnathides, on ne peut se reporter qu'indirectement aux zones à conodontes établies; on suppose donc l'existence d'une séquence allant de la Zone à *laticostatus* à la Zone à *ensensis*. La présence de 3 zones régionales et de 11 plans de référence facilite la datation. Les zones en question, données en ordre ascendant, sont celles à *Latericriodus alces* n. sp., à *L. robustus* et à *Icriodus angustus*, les deux dernières ayant été nommées par Orr (1971).

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[1] Geological Survey of Canada, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street, N.W., Calgary, Alberta T2L 2A7
[2] Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium

Les zones à conodontes sont liées à la zonation fondée sur les spores dans le même puits, qui a été établie par McGregor et Camfield (1976) ainsi que Richardson et McGregor (1986). Deux, voire trois des cycles eustatiques de T-R décrits par Johnson et al. (1985) sont représentés dans la succession du puits du lac Jaab; il s'agit des cycles **I**b et **I**c dans les parties inférieure et supérieure, respectivement, de la Formation de Stooping River, et du cycle **I**f à la base de la Formation de Murray Island.

C'est au cours de l'Eifélien, à tout le moins, que les faunes de conodontes du lac Jaab se rapprochaient le plus du Royaume faunique oriental de l'Amérique du Nord (décrit par Sparling, 1984), en plus de présenter un certain lien avec la partie nord du bassin du Michigan.

INTRODUCTION

LOCATION AND BRIEF HISTORY OF THE JAAB LAKE WELL

The conodonts described in this report are from cores of the Ontario Department of Mines Jaab Lake No. 1 well, on the north shore of Jaab Lake, about 160 km due west of Moosonee, in northern Ontario (51°11′54″N, 82°56′00″W; GSC loc. C-53085; Figs. 2.1 and 2.2). This location is near the depocentre of the Moose River Basin. The stratigraphic interval covered in this report includes (in ascending order) the Stooping River, Kwataboahegan, Moose River, Murray Island, and Williams Island formations. Of these units, only the Moose River Formation failed to yield any conodonts.

The drilling of the Jaab Lake well was commenced in June 1949, and completed in June of the following year. It reached a depth of 1810 ft. (551.7 m). Since its drilling, the well has been extensively studied. The stratigraphy was initially documented in Hogg et al. (1953, p. 123-125), and subsequently updated and logged by Sanford (*in* Sanford and Norris, 1975, pt. 2, p. 118-138). The megafossils were identified by Alice E. Wilson (*in* Hogg et al., 1953, p. 126-130). More recently, spore assemblages from the well were reported initially by McGregor (*in* McGregor et al., 1970), and subsequently more thoroughly documented by McGregor and Camfield (1976). The acritarchs of the Jaab Lake well were the subject of a thorough study by Playford (1977). The present study complements earlier studies, and an attempt is made to integrate zonal schemes, based on spores and conodonts, and therefore to correlate marine and non-marine zonations.

The reader is referred to Telford (1989) and Norris (in press) for the most recent accounts on the stratigraphy of the Moose River Basin.

GEOLOGICAL SETTING AND GENERAL STRATIGRAPHY

The Moose River Basin, together with the more northerly Hudson Bay Basin, are two erosional remnants of Phanerozoic rocks which constitute the Hudson Platform (Fig. 2.1). The platform, located in the central part of the Canadian Shield, occupies an area of 971 250 square kilometres, about two thirds of which is under the waters of Hudson and James bays (Sanford and Norris, 1973; Norris, 1986, in press). The definition of the platform has been revised to include strata in the more northerly locations by some authors (Sanford, 1987; Telford, 1989). The Moose River Basin is separated from the larger Hudson Bay Basin by a basement structural high referred to as the Cape Henrietta Maria Arch. The Moose River Basin is located principally onshore in northeastern Ontario, with a small extension into the province of Quebec, and occupies an area of about 100 000 square kilometres (Telford, 1989).

Phanerozoic rocks of the Moose River Basin are of Ordovician, Silurian, Devonian, Middle Jurassic, and Early Cretaceous age (Fig. 2.3). In the depocentre of the basin the strata measure about 760 m thick (Norris, in press), of which rocks of Devonian age constitute about 400 m (Telford, 1989). Devonian rocks outcrop near the eastern margin of the basin.

A comprehensive depositional history and an account of the evolution of the Hudson Platform were given by Sanford (1987). Previous investigations of Devonian fossils from the Moose River Basin, aside from those mentioned above, include a listing of conodonts by Uyeno (*in* Sanford and Norris, 1975) and a taxonomic and biostratigraphic study of conodonts from the upper Williams Island and lower Long Rapids formations by Uyeno and Telford (*in* Norris et al., 1992). A sedimentological study of Lower and Middle Devonian strata of the Moose River Basin was conducted by Stoakes (1978).

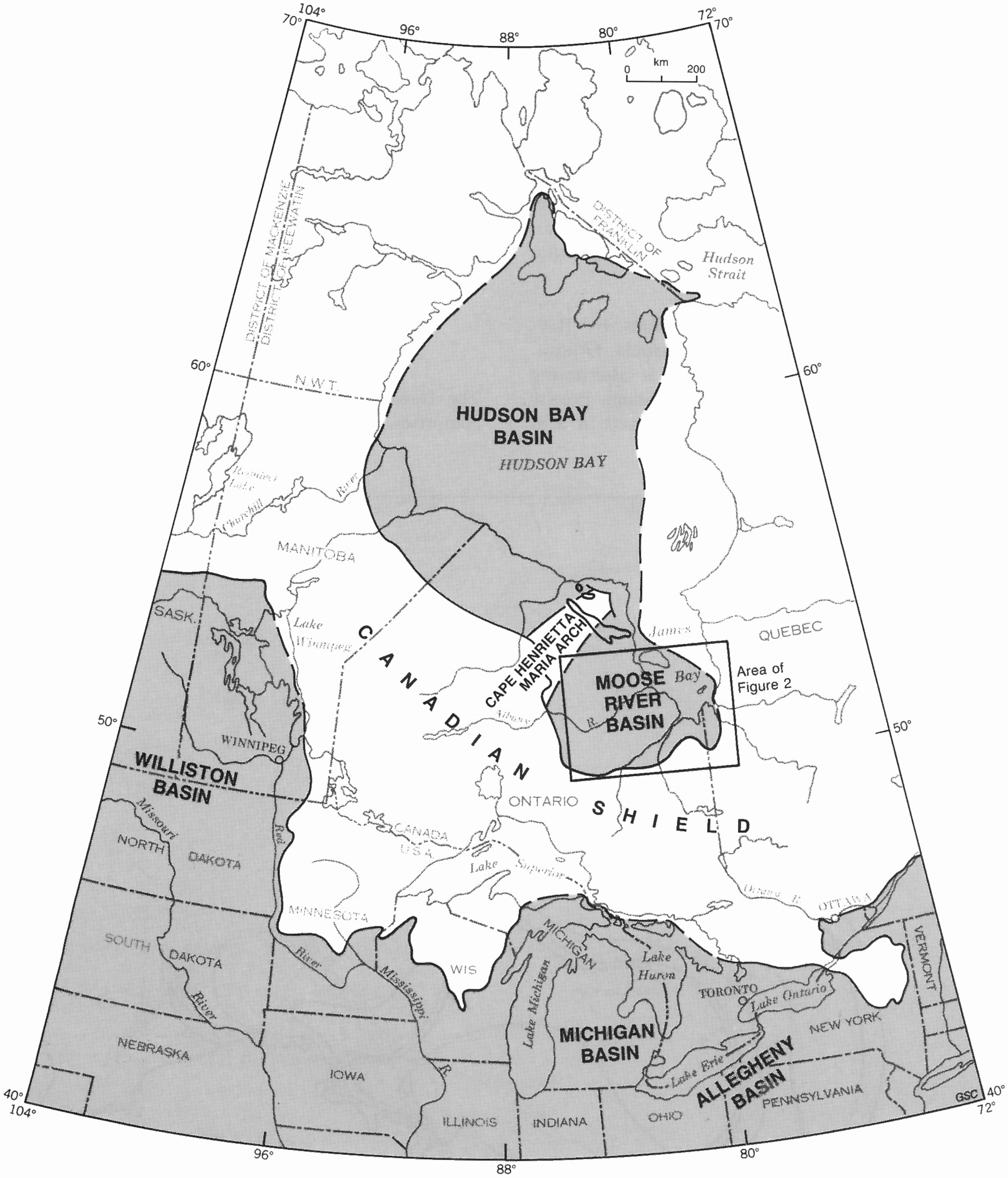

Figure 2.1. *Index map showing the Moose River Basin and adjacent geological provinces. Shaded area indicates area underlain by Phanerozoic rocks. (Modified from Sanford and Norris, 1975).*

PRESENT STUDY

Devonian conodonts of the Jaab Lake well were initially studied by Uyeno in 1967, to aid Operation Winisk, a geological reconnaissance survey of the Hudson Bay Lowlands (see Sanford et al., 1968). The results, presented in an unpublished report, were cited previously by others (e.g., Sanford and Norris, 1975; McGregor and Camfield, 1976). The well was one of the few continuously cored succession then available, and hence critical in elucidating the Devonian stratigraphy of the Moose River Basin and of the entire Hudson Platform.

The well was sampled for conodonts by B.V. Sanford of the Geological Survey of Canada, Ottawa. Most samples were usually collected at alternating 5 foot (1.5 m) intervals (Fig. 2.4). Although precise records of the weights of samples dissolved in acid were not kept, most of the 76 samples weighed about 650 to 700 grams, although extremes ranged from 300 to 1200 grams.

The Jaab Lake conodonts are moderately well preserved and amber in colour, and have a Colour Alteration Index (CAI; Epstein et al., 1977) value of 1 to 1.5. The fauna is dominated by icriodontids with fewer simple cone elements. Only two *Polygnathus* species are present, *P. cooperi* cf. *secus* Klapper, Ziegler and Mashkova, and *P. linguiformis* n. subsp. A.

DEVONIAN STRATIGRAPHY AND SEDIMENTOLOGY

The Devonian succession in the Moose River Basin comprises, in ascending order, the upper member of

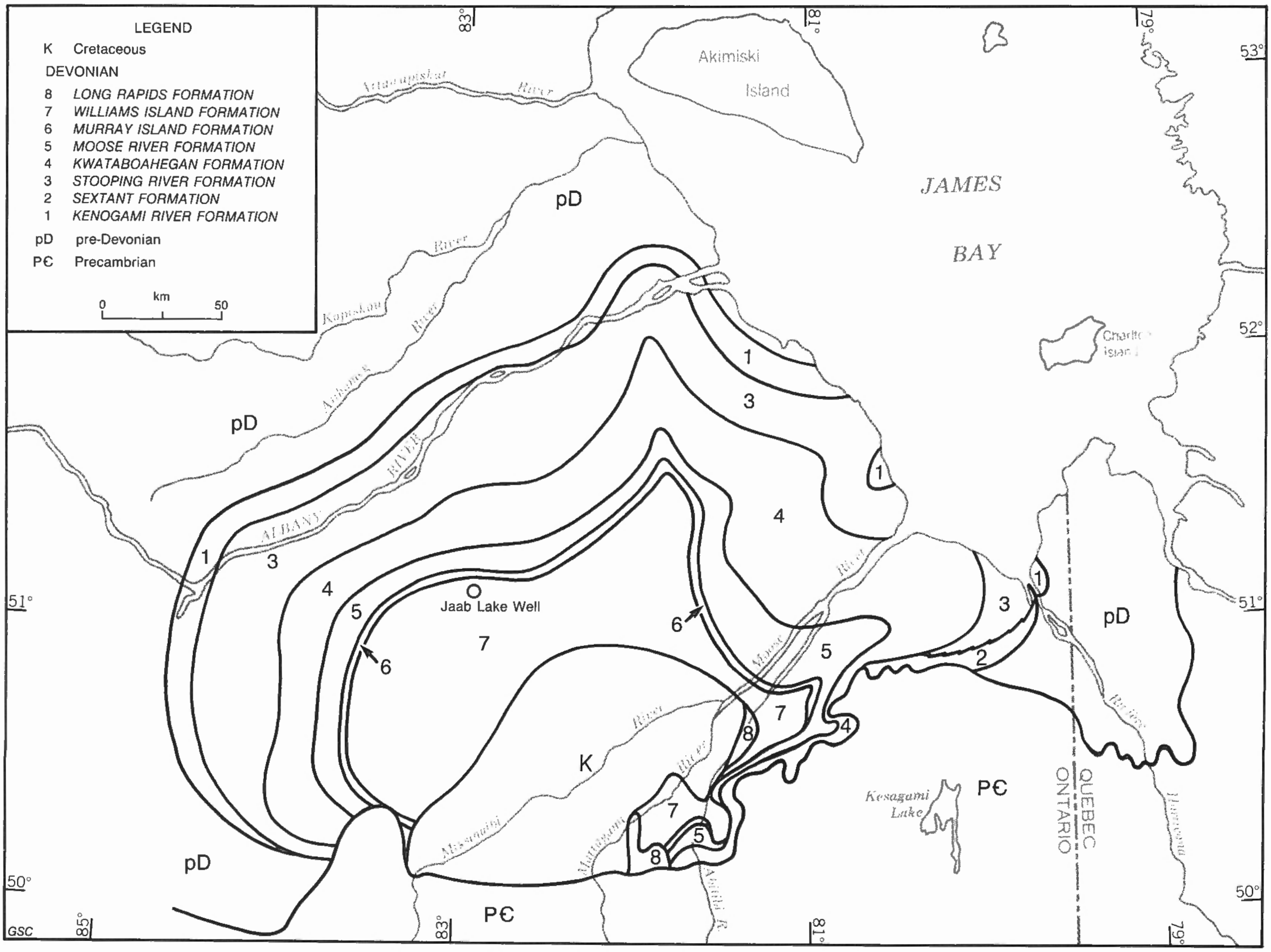

Figure 2.2. Geology of the Moose River Basin. (After Telford, 1989).

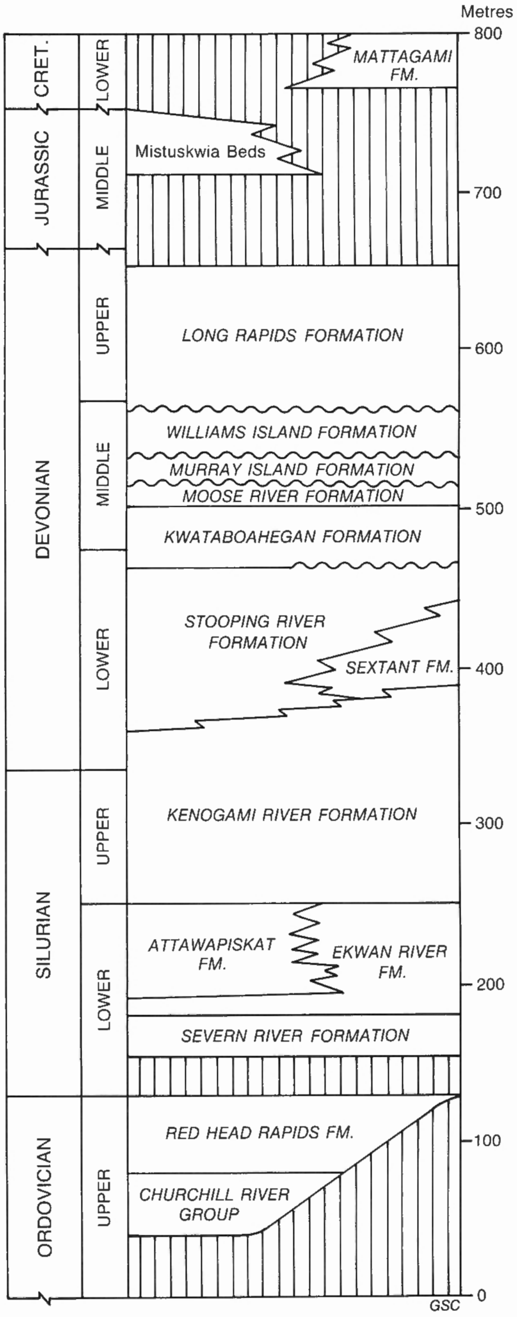

***Figure 2.3.** Paleozoic and Mesozoic stratigraphic units in the Moose River Basin. (After Telford, 1989).*

the Kenogami River Formation, and Sextant, Stooping River, Kwataboahegan, Moose River, Murray Island, Williams Island, and Long Rapids formations (Fig. 2.3). As noted in the introduction, with the exception of the Sextant and Long Rapids formations, the sequence is well represented in the Jaab Lake well.

KENOGAMI RIVER FORMATION, UPPER MEMBER

The upper member is 91 ft. (27.7 m) thick in the Jaab Lake well. It comprises oolitic dolostone, dolostone, and dolomite breccia. In the well, the member consists of a thin interval of calcareous shale at the base, overlain by evaporites and bituminous dolostone, pelletoidal dolostone, and capped by brecciated dolostone. Its lower contact with the middle member of the Kenogami River Formation appears to be transitional and arbitrary (Sanford and Norris, 1975, p. 16, 17). According to Stoakes (1978), the upper member represents a basal transgressive unit, with deposition taking place in supratidal and intertidal flat environments. Although the member was not sampled for conodonts in the Jaab Lake well, outcrop samples did not yield any conodonts. This is to be expected considering the depositional environment.

McGregor and Camfield (1976) reported spores of Gedinnian and Siegenian (Early Devonian) age from the upper member in the Jaab Lake well. It was estimated that the Silurian-Devonian boundary lies within the middle member of the Kenogami River Formation.

STOOPING RIVER FORMATION

The formation conformably overlies the upper member of the Kenogami River Formation throughout most of the Moose River Basin. It comprises limestone, variably dolomitic limestone, and dolostone, with abundant fossils occurring throughout, some of which are silicified (Sanford and Norris, 1975, p. 21). In the Jaab Lake well the formation is 469 ft. (143.0 m) thick. According to Stoakes (1978), the lower part of the formation was deposited in intertidal, and the upper part in open subtidal, environments.

Conodonts abound in the Stooping River Formation, both in outcrops and in the Jaab Lake well. Spores from the formation in the Jaab Lake well were assigned a late Siegenian to late Emsian age by McGregor and Camfield (1976, p. 4).

SEXTANT FORMATION

The formation comprises continental clastic rock, mainly arkosic sandstone, but also includes conglomerates, conglomeratic sandstones, siltstones, shales, and clays (Sanford and Norris, 1975, p. 36). It is overlapped by, and merges northwestward with,

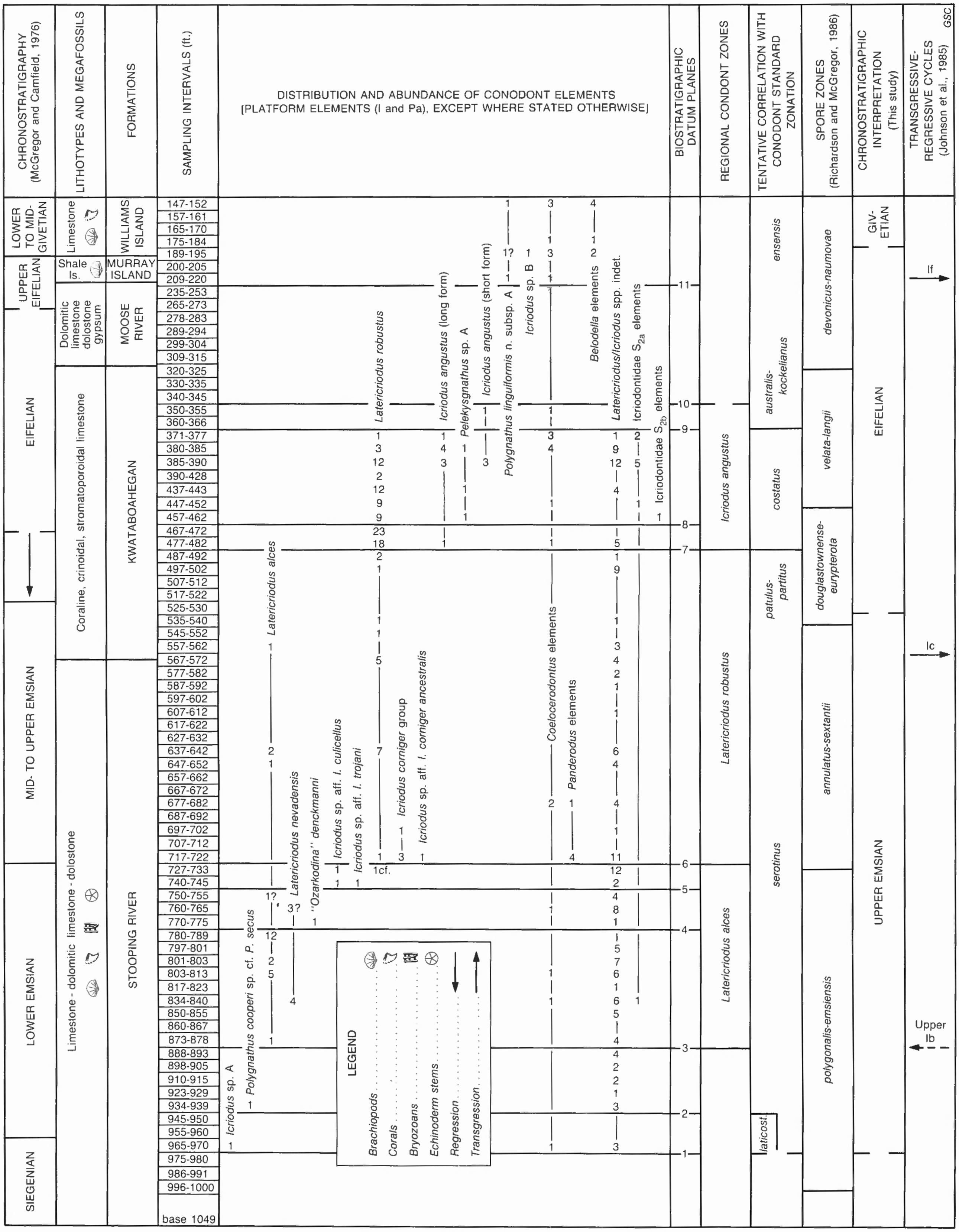

Figure 2.4. Distribution of conodonts in the Jaab Lake well.

marine carbonates of the Stooping River Formation. It may also have a lateral facies relationship with the upper member of the Kenogami River Formation (Stoakes, 1978; Telford, 1989). The depositional environment was continental, but a transgressing sea overlapped the formation and reworked the clastic material seaward (Stoakes, 1978). This conclusion is supported by the recovery of single fragmentary icriodid specimen from an outcrop estimated to be within the upper part of the formation (Uyeno *in* Sanford and Norris, 1975, p. 37). The unit occurs only in the extreme southeastern rim of the Moose River Basin, and is absent in the Jaab Lake well.

The formation contains fossil plants, including several varieties of the trimerophyte *Psilophyton* and one species of the lycopod *Drepanophycus* (Telford, 1984). Palynological evidence reported by McGregor and Camfield (1976) indicates a middle to late Emsian age for the formation.

KWATABOAHEGAN FORMATION

The formation, comprising massive to thick bedded, cliff-forming limestone, is the most fossiliferous of all Devonian units in the Moose River Basin. It disconformably overlies the Stooping River Formation and is in turn conformably overlain by the Moose River Formation. It is 251 ft. (76.5 m) thick in the Jaab Lake well (Sanford and Norris, 1975, p. 39, 43). According to Stoakes (1978, p. 11), locally developed within the Stooping River Formation are coral-stromatoporoid buildups that can be assigned to the Kwataboahegan Formation. These buildups were deposited in protected subtidal conditions, and generally conform to pre-existing topographic highs. Sanford and Norris (1975, p. 88) believe such highs were produced by relief on the Precambrian basement surface. The buildups developed after a major transgressive phase and are characteristically developed only in the southern portions of the basin (Stoakes, 1978).

The coral and brachiopod faunas have many elements in common with those of the Schoharie, Bois Blanc, and Onondaga formations of the Appalachian Basin, and of the Detroit River Group in the Michigan Basin (Sanford and Norris, 1975). McGregor and Camfield (1976, p. 39) concluded that the lowermost strata of the Kwataboahegan Formation in the Jaab Lake well are upper Emsian.

MOOSE RIVER FORMATION

The formation consists of a sparsely fossiliferous sequence of limestone, dolomitic limestone, dolostone, brecciated carbonate, gypsum, and minor anhydrite. Its upper contact with the Murray Island Formation is sharp, extremely undulating and, in places, appears to be an erosional surface (Sanford and Norris, 1975, p. 53). In the Jaab Lake well, the formation is 104.6 ft. (31.9 m) thick. The depositional environment of the formation, according to Stoakes (1978), was a restricted lagoon, which resulted mainly from restriction of circulation owing to the growth of buildups of the Kwataboahegan Formation.

No conodonts were recovered from the Moose River Formation in the Jaab Lake well. A single polygnathid specimen was recovered from one of the 26 samples collected from the outcropping part of the formation. Other fossils reported by Sanford and Norris (1975, p. 57, 58) include rare ostracodes, bulbous stromatoporoids, tentaculites, and a brachiopod impression. A few spores were reported by McGregor and Camfield (1976, p. 4). The age is considered to be late Eifelian, mainly on the basis of the stratigraphic position of the formation.

MURRAY ISLAND FORMATION

The unit is a relatively thin sequence of fossiliferous limestone, dolomitic limestone and minor shale that is, in some places, overlain abruptly by the shale and limestone of the Williams Island Formation. The upper contact is nowhere well exposed, but is inferred to be disconformable. The formation marks a return to open marine conditions in the basin. In the Jaab Lake well, the lower shale member of the Williams Island Formation is apparently not developed, making the upper boundary of the Murray Island Formation more difficult to pick. The formation in the well is 20 ft. (6.1 m) thick (Sanford and Norris, 1975, p. 58–60).

The megafossils from the formation are not abundant, but include a diverse population of brachiopods that appear to have affinities with the Appalachian, Mid-continent, and Cordilleran faunal provinces (Sanford and Norris, 1975, p. 61). Conodonts were recovered from outcrops of the formation. Accumulated evidence from conodonts, megafossils, and spores (McGregor and Camfield, 1976), indicates a late Eifelian age for the Murray Island Formation.

WILLIAMS ISLAND FORMATION

Within most of the basin the formation was divided by Sanford and Norris (1975) into a lower shale and an upper carbonate member. The lower member consists predominantly of grey shale with soft sandstone, and gypsiferous shale and siltstone; the upper member consists of thin to medium bedded argillaceous limestone and calcareous shale, dolomitic limestone, oolitic limestone, and vuggy limestone and dolostone. The lower and upper member are up to 47 and 45 m thick, respectively (Telford, 1989, p. 128). In the Jaab Lake well, only a part of the upper member is apparently present, and is 42 ft. (12.8 m) thick.

According to Sanford and Norris (1975, p. 89), clastic beds in the lower member suggest intermittent uplift and erosion of highland areas adjacent to the basin. Short periods of supratidal conditions probably alternated with intermittent subtidal intervals, as suggested by the restricted occurrence of marine fossils within both members. Faunal similarities suggest that the basin was connected with eastern North America by a sea.

The brachiopods and corals from the lower member show affinities with those in the Givetian part of the Hamilton Group of southwestern Ontario and New York State, and the corals from the upper member with those from the Traverse Group of Michigan (Norris, 1986, p. 36). A rich brachiopod fauna was described from the uppermost beds in outcrops along Abitibi River by Norris and Sartenaer (*in* Norris et al., 1992). Spores from the lower member were dated as early to middle Givetian in age by McGregor and Camfield (1976). Abundant conodonts were recovered from outcrops of the Williams Island Formation. Conodonts from the 1.3 m thick, green clay shale unit that was assigned to the highest part of the formation, range from the *disparilis* Zone (late Givetian) to within the *asymmetrica* Zone, or Zones 1 and 2 of Klapper (1989), of earliest Frasnian age (Uyeno and Telford, *in* Norris et al., 1992).

LONG RAPIDS FORMATION

The Long Rapids Formation comprises mainly dark bituminous shales, with minor components of mudstone, clay ironstone nodules, and carbonate beds (Sanford and Norris, 1975). According to Bezys and Risk (1978), these beds were deposited in an epicontinental sea. The dark shales were formed under anoxic conditions, and the other facies under oxygenated conditions. The type of sediment deposited was dictated by periodic movements of the pycnocline relative to the sediment-water interface. The formation is absent in the Jaab Lake well.

The carbonate beds have yielded diverse, abundant, well preserved conodont faunas (Uyeno, *in* Sanford and Norris, 1975; Telford, 1985; Uyeno and Telford, *in* Norris et al., 1992). Conodonts from outcrops near the base of the formation along the Abitibi River were assigned to the upper part of Zone 10 and the lower part of Zone 11 of Klapper (1989), of early Frasnian age. About 9 m higher, conodonts of Klapper's (1989) Zone 12, which is equivalent to the Lower *gigas* Zone of Ziegler (1962, 1971), of middle Frasnian age, were recovered. In preliminary observation, the Frasnian–Famennian boundary was estimated to occur about 35–40 m above the base of the formation in the Onakawana B well, near the southeastern edge of the Moose River Basin. A varied brachiopod fauna was reported by Norris and Sartenaer (*in* Norris et al., 1992). The goniatite *Manticoceras* cf. *M. sinuosum* (Hall) is present in the lower parts of the Long Rapids Formation in outcrops along the Abitibi River. The Long Rapids spores may possibly belong to the *ovalis–bulliferus* Assemblage Zone of Frasnian age, and although the spores are locally abundant, they are not well preserved (Richardson and McGregor, 1986, p. 19; McGregor, pers. comm.).

CONODONT BIOSTRATIGRAPHY

The conodont collections from the Jaab Lake well shed new light on the age of this subsurface sequence, especially with regard to the age of the lower and middle parts of the Stooping River Formation. The conodont faunas are generally sparse, however, each sample commonly yielding between two and 15 specimens, and rarely more than 20 specimens. Furthermore, they are not diverse and are dominated by icriodontids. Only four samples produced polygnathids, one from the lower part of the Stooping River Formation, another from the Murray Island Formation, and two from the Williams Island Formation. This makes direct correlation with the Emsian to Givetian conodont standard zonation, based on polygnathids, extremely difficult, if not impossible. Three species of icriodontids, *Icriodus angustus angustus* Stewart and Sweet, *Latericriodus alces* n. sp., and *L. robustus* (Orr), have stratigraphic ranges that are fairly evenly spaced. These species are selected here to subdivide the Jaab Lake well conodont succession into three regional zones, based on the respective lowest occurrences of these species (Fig. 2.4). The *L. alces* Zone is new; the *L. robustus* and *I. angustus* zones were introduced by Orr (1971) and, although reported only from North America, their correlation with the conodont standard zonation is becoming clearer. Klug (1983) modified Orr's (1971) zonation, and suggested the equivalence, in part, of the *L. robustus* Zone (modified) with the *patulus* Zone, and the *I. angustus* Zone (modified) with the *costatus* Zone. These suggested correlations are wholly in agreement with the findings of the present study, as discussed below. In the Jaab Lake well, the occurrence of other *Icriodus* taxa is sporadic.

For reasons cited above, the conodont biostratigraphy of the Jaab Lake well is discussed here in terms of biostratigraphic datum planes (Fig. 2.4; in ascending order, nos. 1 to 11), based on the earliest or latest occurrence of a taxon or taxa. The oldest or youngest possible age for each datum plane is discussed below.

DATUM PLANE 1

(Datum plane 1 is in the lower part of the Stooping River Formation; interval of 965–970 ft., 294.1–295.7 m).

The occurrence of *Icriodus* sp. A marks this datum plane. The oldest known taxa of the genus *Icriodus sensu stricto* (i.e., without a posterior or lateral costa starting from the posterior cusp; see under Systematic Paleontology) are *Icriodus rectus* Weddige, *I. fusiformis* Carls and Gandl, and *I. culicellus* (Bultynck). Based on data from the Guadarrama and Eastern Iberian Chains in Spain (Bultynck, 1979, p. 33, Fig. 3; Carls, 1979), the Armorican Massif in northwestern France (Bultynck and Morzadec, 1979, p. 679), Morocco (Bultynck and Hollard, 1980, p. 26), and from the Rhenish Slate Mountains (Requadt and Weddige, 1978, p. 237, Table 3; Weddige and Requadt, 1985, p. 363–365), these three species have their earliest occurrence in the *laticostatus* Zone. From this we deduce the age of datum plane 1 is probably not older than late Emsian. We are aware of the fact that some icriodontid species assigned to the genus *Icriodus* (e.g., *I. angustoides* Carls and Gandl and *I. trojani* Johnson and Klapper) are older. However, the I elements of these species have a distinct outer posterior or outer lateral costa, which is not present in the species of *Icriodus s.s.* under discussion.

DATUM PLANE 2

(Datum plane 2 is in the lower part of the Stooping River Formation, interval of 934–939 ft., 284.7–286.2 m).

This datum plane is based on the occurrence of *Polygnathus cooperi* cf. *secus*. Data from different authors as summarized in Klapper and Ziegler (1979, p. 204–208) and Klapper and Johnson (1980, Tables 6, 7) indicate that *P. cooperi secus* Klapper, Ziegler and Mashkova is restricted to the *serotinus* and *patulus* zones, and *P. cooperi cooperi* to the *serotinus* through lower *costatus* zones. Considering the age of the datum plane 6 (see below), we suggest that, by virtue of its position, datum plane 2 is within the *serotinus* Zone and is of late Emsian age.

DATUM PLANE 3

(Datum plane 3 is in the middle part of the Stooping River Formation, interval of 873–878 ft., 266.1–267.6 m).

This datum plane is set at the lowest occurrence of *Latericriodus alces* and marks the base of the *alces* Zone. *Latericriodus alces* n. sp. was previously illustrated as *Icriodus latericrescens robustus* by Uyeno (*in* Uyeno et al., 1982) (see Systematic Paleontology), from the lower part of the Bois Blanc Formation in southwestern Ontario, a formation assigned to the *serotinus* Zone. The stratigraphic position of the *alces* Zone, with its base above datum plane 2 and its top coinciding with datum plane 6, lends support to the suggestion that the *alces* Zone may lie entirely within the *serotinus* Zone and is of late Emsian age.

DATUM PLANE 4

(Datum plane 4 is in the middle part of the Stooping River Formation, interval 770–775 ft., 234.7–236.2 m).

This datum plane is of minor importance for the biostratigraphic interpretation of the succession. At this level a single Pb element occurs that is assigned to "*Ozarkodina*" *denckmanni* in form taxonomy. The element was originally described by Ziegler (1956) from the Schönauer Limestone (Emsian, Kellerwald, Germany) where it is associated with *Ozarkodina steinhornensis steinhornensis* (Ziegler), *Polygnathus laticostatus* Klapper and Johnson, and *P. catharinae* Bultynck. Since it has been documented as occurring in other Lower Devonian apparatuses of the genera *Eognathodus* Philip, *Ozarkodina* Branson and Mehl, *Pandorinellina* Müller and Müller, and *Polygnathus* Hinde (among others, Klapper and Philip, 1971; Bultynck, 1971, 1976; Mashkova, 1972; Mawson, 1987; Uyeno, 1990). On the basis of these references, the Pb element under discussion is probably not younger than the *serotinus* Zone, which is of late Emsian age.

DATUM PLANE 5

(Datum plane 5 is in the middle part of the Stooping River Formation, interval of 740–745 ft., 225.6–227.1 m).

Icriodus aff. *I. trojani* and *I.* aff. *I. culcicellus* occur at this level. *Icriodus trojani* ranges in Nevada from the *dehiscens* into the *serotinus* zones (Johnson and Klapper, 1981, p. 1237). *Icriodus culicellus* is best known from the Ardennes (Bultynck, 1972, p. 74, long form), from the Rhenish Slate Mountains (Weddige and Requadt, 1985, p. 358, 364) and from Spain (Bultynck, 1979, p. 33, Fig. 3; Carls, 1979, table). The range of the species extends from the *laticostatus* Zone into the *patulus* Zone. While it is apparent that the "*affinis*" identification (see Systematic Paleontology) of the Jaab Lake specimens does not allow a definite assignment to the *laticostatus* and *serotinus* zones, it does not contradict the late Emsian age proposed for this part of the Stooping River Formation.

DATUM PLANE 6

(Datum plane 6 is in the upper part of the Stooping River Formation, interval of 717–722 ft., 218.5–220.1 m).

This datum plane is characterized by the first occurrence of *Latericriodus robustus* and coincides with the base of the *robustus* Zone. The *robustus* Zone was established by Orr (1971, p. 10–16) in the Devonian succession of the Illinois Basin. The top of the zone is marked by the lowest position of *Polygnathus* "*webbi*" (=*P. costatus costatus* Klapper). *Latericriodus robustus* is endemic to North America and the lowest occurrences are in the Schoharie and Bois Blanc formations of New York (Klapper and Ziegler, 1967), the Bois Blanc Formation of southwestern Ontario (Uyeno et al., 1982), and at the top of the Coils Creek Member, McColley Canyon Formation and the lower part of the Sadler Ranch Formation in Nevada (Kendall et al., 1983, p. 2204, 2205). In the last mentioned area, *L. robustus* co-occurs with *Polygnathus serotinus* Telford. Earlier, Klapper and Johnson (1980, p. 420, Table 6), Uyeno et al. (1982, p. 6, Fig. 5), and Sparling (1983, p. 835, Fig. 9) had correlated the earliest occurrence of *L. robustus*, or the base of the *robustus* Zone in the Schoharie and Bois Blanc formations, with a level within the *serotinus* Zone, but without direct evidence in the presence of *P. serotinus*.

The occurrence of specimens belonging to the *Icriodus corniger* group and particularly of specimens close to *I. rectirostratus* Bultynck, and to *I. corniger ancestralis* at datum plane 6, supports the assignment of this level to the *serotinus* Zone and its correlation with the upper Emsian strata of the type area in the Rhenish Slate Mountains. According to Weddige (1977, p. 390, Table 16) *I. corniger ancestralis* Weddige, *I.* (*corniger*) *rectirostratus* Bultynck, and *P. serotinus* co-occur in the Ballersbach Limestone of the East Rhenish Slate Mountains, and Weddige and Requadt (1985, p. 364, Fig. 7) noted the co-occurrence of *I. corniger ancestralis* and *I.* (*corniger*) *rectirostratus* in the middle part of the upper Emsian at its type area.

A late Emsian age for datum plane 6 can be considered firmly established.

DATUM PLANE 7

(Datum plane 7 is in the middle part of the Kwataboahegan Formation, interval of 477–482 ft., 145.4–146.9 m).

This datum plane is marked by the lowest occurrence of *Icriodus angustus*. It corresponds to the base of the *angustus* Zone and to the top of the *robustus* Zone. The latter is used here in the same sense as Klug (1983), which is different from the original definition given by Orr (1971). Orr recognized a *Polygnathus* "*webbi*" (=*P. costatus costatus*) Zone between the *robustus* and *angustus* zones. *Latericriodus robustus* and *I. angustus* are endemic to North America, whereas *P. costatus costatus* has a mondial geographic distribution and probably belongs to a different biofacies. It seems inadvisable, then, to use the stratigraphic succession of *L. robustus* and *P. costatus costatus* in the same zonal scheme. Consequently, the top of the *robustus* Zone is considered here to coincide with the lowest occurrence of *I. angustus angustus* and the base of the *angustus* Zone.

Icriodus angustus angustus is endemic to an area within North America comprising Kentucky, Indiana, Ohio, Michigan, and southwestern Ontario (Stewart and Sweet, 1956; Klapper and Ziegler, 1967; Orr, 1971; Bultynck, 1976; Klapper and Johnson, 1980; Uyeno et al., 1982; Sparling, 1983). The subspecies ranges from the *costatus* into *kockelianus* zones. Datum plane 7 certainly belongs to the *costatus* Zone (see also datum planes 8 and 9), and it is the first level in the Jaab Lake well succession that can be definitely assigned to the Eifelian. Datum plane 6 is still within the *serotinus* Zone. The temporal equivalents of the *patulus* and *partitus* zones, and hence the Emsian–Eifelian boundary, should be represented between datum planes 6 and 7, as indicated in columns H and J of Figure 2.4. The correlation of the *angustus* Zone with the *costatus* Zone was suggested earlier by Klug (1983), in a study of the Muscatatuck Group of the Illinois Basin.

DATUM PLANE 8

(Datum plane 8 is in the middle part of the Kwataboahegan Formation, interval of 457–462 ft., 139.3–140.8 m).

This level coincides with the first occurrence of *Pelekysgnathus* sp. A, a form that resembles *P.* sp. listed by Bultynck (1976b, p. 123, Fig. 2) from the Dundee Formation and the lowermost part of the Rogers City Formation in northern Michigan. This lithostratigraphic interval belongs to the *costatus* Zone (see also Uyeno et al., 1982, p. 6, Fig. 5).

DATUM PLANE 9

(Datum plane 9 is in the upper part of the Kwataboahegan Formation, interval of 360–366 ft., 109.7–111.6 m).

The highest occurrence of *Latericriodus robustus* marks datum plane 9. On the basis of Uyeno et al. (1982, p. 17–19) and Sparling (1983, p. 835–836), this level is correlated with the top of the *costatus* Zone.

DATUM PLANE 10

(Datum plane 10 is in the upper part of the Kwataboahegan Formation, interval of 340–345 ft., 103.6–105.2 m).

This datum plane is characterized by the highest occurrence of *Icriodus angustus angustus*, or more precisely, the highest occurrence of a short form that may be transitional to *I. calvini* Klapper and Barrick. The latest recorded occurrences of *I. angustus angustus* in Kentucky and Indiana, are correlated by Klapper and Ziegler (1979, Textfig. 4; see also Klapper and Johnson, 1980, p. 422) with a level within the *kockelianus* Zone. It should be stressed, however, that in the Jaab Lake well, the highest sample with *I. angustus angustus* is followed by a 135 ft. (41.1 m) thick interval with stromatoporoidal limestone, dolomitic limestone, dolostone, and gypsum beds from which no conodonts were recovered. According to the conodont standard zonation, datum plane 10 is still certainly of Eifelian age.

DATUM PLANE 11

(Datum plane 11 is in the top of the Moose River Formation–base of the Murray Island Formation, interval 209–220 ft., 63.7–67.1 m).

This datum plane is characterized by the lowest occurrence of *Polygnathus linguiformis* n. subsp. A. Similar forms occur in the Hanonet Formation of the Ardennes (Bultynck, 1970, Pl. 11, Fig. 4). This formation is of the *ensensis* Zone (Bultynck, 1987, p. 151) and immediately underlies the Givet Limestone. The taxon has also been recognized in the uppermost Eifelian conodont collections from the Ou Driss section (Mader area in the pre-Sahara of Morocco) described by Bultynck (1990, p. 98, Fig. 2). It occurs there in the sample interval ODE-8-9 to ODE-8-12 that may belong either to the upper part of the *kockelianus* Zone or the lower part of the *ensensis* Zone. On the basis of these data, datum plane 11 is tentatively assigned to the base of the *ensensis* Zone and to the uppermost Eifelian. The definition of the Eifelian–Givetian boundary is currently being discussed by the International Subcommission on Devonian Stratigraphy; two principal alternatives are the base of the *ensensis* Zone or the earliest occurrence of *Polygnathus hemiansatus* Bultynck, which is within the *ensensis* Zone. Provisional positioning here of the Eifelian–Givetian boundary within the *ensensis* Zone is in agreement with the latter alternative, but it is primarily based on the positioning of this boundary by McGregor and Camfield (1976) on the basis of spores.

PALEOECOLOGICAL AND PALEOGEOGRAPHIC ASPECTS OF THE CONODONT FAUNAS

As noted elsewhere, the upper Emsian to (?)lowest Givetian sequence in the Jaab Lake well was deposited on a shallow nearshore platform, and is represented by supratidal to subtidal, mainly carbonate deposits, with some locally developed coral-stromatoporoid buildups. The generally low conodont frequency and the low species diversity in the samples in this sequence reflect the nearshore environment. The dominance of icriodontids is a common characteristic of shallow water conodont biofacies. The conodonts are most abundant (more than 10 specimens and as many as 35, per sampling interval) at some levels in the middle and upper parts of the Stooping River Formation, and in the middle third of the Kwataboahegan Formation. These relatively greater abundances correspond with the establishment of fully marine conditions over the Moose River Basin as a result of transgressions (Telford, 1989, p. 127).

As noted earlier, the lower part of the Stooping River Formation was deposited in intertidal, and the upper part in open subtidal environments (Stoakes, 1978). The shallower water of the lower Stooping River may reflect a possible regression during the middle part of the *serotinus* Zone (upper part of T-R Cycle Ib of Johnson et al., 1985). In the upper part of the *serotinus* Zone, a widespread transgression occurred (Johnson et al., 1985; start of their T-R Cycle Ic), a level that corresponds approximately with the upper part of the Stooping River Formation (Fig. 2.4). Stoakes (1978) also noted a major transgressive phase about this time. The development of coral-stromatoporoid buildups of the Kwataboahegan Formation subsequently to this transgression was restricted to the southern parts of the Moose River Basin, in protected subtidal conditions, generally conforming to pre-exisiting topographic highs (Stoakes, 1978).

The development of buildups in the Kwataboahegan Formation restricted circulation and resulted in lagoonal facies of the Moose River Formation. The restricted vertical extent of the bioherms and the evaporitic nature of the Moose River Formation suggested to Stoakes (1978) that there was a general lack of subsidence with resultant regressive situation. This assessment is in accord with the finding that the uppermost part of the Kwataboahegan Formation and the Moose River Formation are barren of conodonts.

Conodonts returned with deposition of the Murray Island Formation. This level is at datum plane 11, and coincides with the start of T-R Cycle If (of Johnson et al., 1985), at the base of the *ensensis* Zone.

Latericriodus robustus is the most common conodont species in the upper part of the Stooping River Formation and the lower part of the Kwataboahegan Formation; in the same intervals rare *Coelocerodontus* elements and very rare *Icriodus* specimens occur. There is a similar association in the Bois Blanc and Amerstburg formations in southwestern Ontario (Uyeno et al., 1982, p. 7, Table 1) and also in th Schoharie and Bois Blanc formations of New York State (Klapper and Johnson, 1980, p. 420). *Latericriodus robustus*, ranging from the late Emsian *serotinus* Zone to the middle Eifelian *australis* Zone (see Klapper *in* Klapper and Johnson, 1980, p. 448), was considered endemic to eastern North America, especially during the late Emsian (Telford, 1972, p. 84, Table 1; 1979, p. 207). Subsequently, the species has been reported from Nevada in upper Emsian rocks (Kendall et al., 1983, p. 2205; Johnson and Klapper, 1981, p. 1241). It appears, therefore, that the transcontinental North American Arch had little or no influence on the geographic distribution of *L. robustus*, whereas the eastern and western North American benthic faunas were strongly segregated at this time (Oliver and Pedder, 1989). Sparling (1984, p. 121) suggested the origin of the species in the southwestern part of the North American craton and, through a southern migratory route, establishment in the eastern realm by earliest Eifelian time. The distribution of *L. robustus* suggests that it was either pelagic or nektonic, as suggested for Middle Devonian icriodontids by Sparling (1983, p. 831).

Icriodus angustus angustus, which is present in the middle to upper parts of the Kwataboahegan Formation, does appear to have been endemic to eastern North America during the Eifelian (*costatus* to *kockelianus* zones; see Klapper *in* Klapper and Johnson, 1980, p. 447). Sparling (1984, p. 121, 122) hypothesized its origin in the west or northwest, as a probable descendant of *I. trojani* Johnson and Klapper in Nevada, and migration through a northern path to the Michigan Basin by early Eifelian time. A form similar to *I. trojani* occurs lower in the Jaab Lake well, within the middle Stooping River Formation in an interval considered to be upper Emsian.

Johnson and Klapper (1981, p. 1237) suggested that during the time represented by the upper Lower Devonian *dehiscens* through *serotinus* zones there were no cosmopolitan species of *Icriodus*, and that *I. corniger*, for example, was restricted to Europe and North Africa. In the present study a few specimens from the *serotinus* Zone in the Jaab Lake well are assigned to the *corniger* group. Similarly, Sparling (1983, p. 850, 852) considered the possible presence of the *I. corniger* group in eastern North America in the *patulus* and *costatus* zones.

In the Great Lakes and nearby areas, Sparling (1984) recognized two faunal realms during the *costatus* Zone and younger Eifelian time: the Northwestern, comprising southern Manitoba, Minnesota-Iowa border, southeastern Wisconsin, and northwestern Indiana; and the Eastern, comprising eastern Illinois Basin, north-central Ohio, southwestern Ontario, and New York State. They were separated by the northern Michigan Basin. With the almost total absence of polygnathids, it is difficult to place the Jaab Lake collections in either of these faunal realms. With the preponderance of *L. robustus*, however, it seems most likely that the Moose River Basin was probably most closely associated with the Eastern Faunal Realm. This affinity is also suggested by the associated brachiopods and corals (see under Devonian Stratigraphy and Sedimentology). The presence of a pelekysgnathid similar to that from northern Michigan Basin suggests some affinity with that area as well.

SYSTEMATIC PALEONTOLOGY

The locational notation used in Supplement 2 of Part W of the Treatise on Invertebrate Paleontology (Robison, 1981) is followed herein, with the exception of icriodontid apparatuses. For these, the scheme introduced by Klapper and Philip (1971, 1972), and subsequently expanded by Johnson and Klapper (1981), is used.

The symbol notation used herein were reviewed by Matthews (1973), and are as follows: * = the species is regarded as valid under the terms of Arcticle 11 of the International Code of Zoological Nomenclature (ICZN); and, p = partim.

The type and figured specimens are deposited in the National Type Collection of Plant and Invertebrate Fossils of the Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario.

Phylum CONODONTA Pander, 1856

Class CONODONTATA Pander, 1856

Genus *Icriodus* Branson and Mehl, 1938

Type species. Icriodus expansus Branson and Mehl, 1938.

Remarks. In some intervals of the Jaab Lake well are I elements of *Icriodus* in the restricted sense, which do not have a well differentiated outer-lateral or outer-posterior process. Most of the I elements occur in very small numbers and therefore are mostly treated here in open nomenclature, identified as "affinis" or assigned to a larger group of *Icriodus* species.

Icriodus angustus angustus Stewart and Sweet

Plate 2.4, figures 3-7

*1956 *Icriodus angustus* n. sp. Stewart and Sweet, p. 267, Pl. 33, figs. 4, 5, 11, 15.

1983 *Icriodus angustus* Stewart and Sweet. Sparling, p. 850, Figs. 12AC, AG; 13AD, AE, AV, AW (synonymy to 1982).

1983 *Icriodus angustus angustus* Stewart and Sweet. Klug, p. 84, Figs. 8A-F.

Remarks. Specimens assigned to *I. angustus angustus* include two forms. The long form (Pl. 2.4, figs. 3-5) is characterized by a narrow long spindle with discrete, pointed denticles in the middle and lateral rows. The Jaab Lake specimens lack the development of strong transverse ridges, present in some previously illustrated collections. The denticles of the middle row are smaller than those of the lateral rows and are connected by a low, thin longitudinal ridge. There are five middle-row denticles extending posteriorly of the spindle, two small ones followed by three prominent, high denticles that are inclined posteriorly. The posterior edge of the last denticle has a costa. The basal cavity shows a narrow offset at the outer-posterior extremity.

The short form (Pl. 2.4, figs. 6, 7) has four to five denticles in the lateral rows on the spindle. The straight posterior extension of the middle row beyond the spindle starts with two high denticles, followed by two smaller denticles. The specimens assigned to the short form may be intermediate between *I. angustus angustus sensu stricto* and *I. calvini* Klapper and Barrick (1983). The latter species has a proportionally shorter spindle with only four denticles in the lateral rows and a curved "posterior process". In two samples from the Jaab Lake well (intervals of 371-377 ft. and 385-390 ft.; 113.1-114.9 m and 117.3-118.9 m) the I elements of *I. angustus angustus* are associated with low coniform S_{2a} elements, characterized by distinct anterior and posterior keels and a weak outer-lateral costa. The base of the S_{2a} element is less expanded than in the analogous elements that may belong to *Latericriodus nevadensis* and *L. robustus*.

Material. Nine long I elements; four short I elements; two S_{2a} elements.

Icriodus corniger group

Plate 2.3, figures 8-15

*1966 *Icriodus corniger* n. sp. Wittekindt, p. 629, Pl. 1, figs. 9-12.

1972 *Icriodus corniger* Wittekindt group. Bultynck, p. 73, 74.

1976a Groupe *Icriodus corniger* Wittekindt. Bultynck, p. 52.

1977 *Icriodus corniger* Wittekindt. Weddige, p. 285, 286.

Remarks. The *Icriodus corniger* group includes those I elements in which the posterior margin of the basal cavity is slightly to clearly oblique to the axis of the platform, and forms a fairly pronounced offset or antispur at the outer posterior corner. The posterior two thirds of the spindle exhibits a characteristic *Icriodus*-type denticulation with three well developed longitudinal rows of denticles, as opposed to the anterior third of the spindle, in which such development is obscured. In this part of the spindle, the longitudinal spacing between the denticles or the ridges formed by transversal fusion of denticles, is clearly greater than in the posterior two thirds.

One specimen from the Jaab Lake well (Pl. 2.3, figs. 11, 12; interval of 717–722 ft., 218.5–220.1 m) is similar to *I. corniger ancestralis* Weddige in exhibiting transversally developed median-row denticles posteriorly of the spindle. Two specimens (Pl. 2.3, figs. 8, 9, 13–15) are close to *I. corniger corniger* (compare with specimens figured by Bultynck, 1985, Pl. 6, figs. 6, 10) and one specimen (Pl. 2.3, fig. 10) is similar to *I. rectirostratus* Bultynck.

Material. Five I elements.

Icriodus aff. *I. culicellus* (Bultynck)

Plate 2.3, figures 5–7

aff. *1976a *Caudicriodus culicellus* n. sp. Bultynck, p. 37–40, Pl. 10, figs. 5, 7–14.

Remark. The spindle is narrow and long with numerous pointed, discrete denticles in the middle and lateral rows. The extension of the middle-row denticles posterior of the spindle is relatively long with a high, laterally compressed posterior cusp, the posterior margin of which has a costa. The basal cavity is very narrow anteriorly and slightly expanded posteriorly with an approximate rectangular outline on the outer side. By these characteristics the specimens are similar to *Icriodus culicellus*. In most specimens of *I. culicellus* from the type area in the Ardennes, however, the denticles are more closely space, whereas the present specimens show greater spacing, especially in the anterior two thirds of the spindle.

Material. Two I elements.

Icriodus aff. *I. trojani* Johnson and Klapper

Plate 2.3, figures 3, 4

aff. p. *1981 *Icriodus trojani* n. sp. Johnson and Klapper, p. 1242, 1243, Pl. 2, figs. 19, 22–24, 27–29 (only).

Remarks. The specimen identified here as *I.* aff. *I. trojani* is similar to the costate morphotype of *I. trojani*, the morphotype that includes the holotype. The similarities include the distinct costa on the outer side posteriorly that descends from the tip of the relatively high posterior cusp over the upper surface of the narrowly expanded basal cavity. *Icriodus* aff. *I. trojani* is also similar to *I.* aff. *I. culcicellus* from the present study, but in the latter, there is no costa on the upper surface of the posteriorly expanded basal cavity.

Material. One I element.

Icriodus sp. A

Plate 2.3, figures 1, 2

Remarks. The lowest productive interval in the Stooping River Formation and in the Jaab Lake well produced a single typical *Icriodus* I element. The denticles on the spindle are round, discrete and of nearly equal size. Three median-row denticles extend posteriorly of the spindle. The posterior cusp is round, slightly higher than other denticles and does not have a posterior or lateral costa. The preservation of the cavity margins is too poor to allow specific identification. Since it is, however, relevant for biostratigraphic interpretation the specimen is figured herein.

Icriodus sp. B

Plate 2.4, figures 16, 17

Remarks. One *Icriodus* I element from a sample at the boundary between the Murray Island and Williams Island formations (interval of 189–195 ft.; 57.6–59.4 m) is characterized by a short spindle with a triangular outline, with four round to slightly oval shaped lateral-row denticles and five round medial-row denticles. The medial-row denticles alternate with those of the lateral rows. The posterior extension of the middle row posteriorly of the spindle has three denticles not markedly higher than others. The specimen is similar in general outline to one of the figured specimens from the Harrogate Formation in southeastern British Columbia, which was assigned to *Icriodus expansus* Branson and Mehl by Chatterton (1974, Pl. 1, figs. 6, 7). The same author (1979, p. 202,

203) suggested that some of these specimens are close in several respects to *Icriodus norfordi* Chatterton and he correlated the Harrogate conodont faunas with the (*Parapolygnathus angusticostatus*)-*Polygnathus curtigladius* Faunal Unit (op. cit., 1979, p. 171) of Uyeno (1979, p. 236, 238) which is of late Eifelian age (approximate equivalent to the *kockelianus* Zone, according to Klapper and Johnson, 1980, Table 8, p. 445).

Material. One I element.

Genus *Latericriodus* Müller, 1962

Type species. Icriodus latericrescens Branson and Mehl, 1938.

Remarks. The I elements of *Latericriodus* have an outer lateral denticulated process that joins the main platform at the position of the posterior cusp, or anteriorly of it, and which is clearly differentiated from the platform. See also Bultynck (1976a, p. 47, 48) and Weddige (1985, p. 361).

In some of the samples from the Jaab Lake well, the I elements of *Latericriodus* are associated with S_{2a} elements, low-triangular coniforms with anterior and posterior keels and an outer lateral costa. One of these samples also yielded an S_{2b} element, a coniform with a high cusp and an elliptical base that may belong either to *Latericriodus* or *Pelekysgnathus*.

Latericriodus alces n. sp.

Plate 2.1, figures 7-18

p. 1982 *Icriodus latericrescens robustus* Orr. Uyeno *in* Uyeno et al., Pl. 4, figs. 1-6 (only).

Diagnosis. In representative I elements of *Latericriodus alces* the spindle is slender with a moderately long denticulated outer lateral process that joins the posterior cusp in its middle part at an angle of 90° or slightly greater. An inner spur, commonly rounded and smooth, joins the spindle at about the posteriormost denticle of the inner lateral row. Between the last middle-row denticle on the spindle and the posterior cusp, there is a gap with a low ridge or a small denticle. The spindle narrows anteriorly and posteriorly. The lateral rows have up to ten rounded denticles. The denticles of the middle row are smaller and lie in a slight depression in the posterior part of the spindle. In lateral view of the upper surface is arched. The posterior cusp is well developed but is not higher than the denticles on the spindle. The cavity is narrowly expanded anteriorly and moderately in its posterior third. The posterior margin is curved from the outer-distal tip of the outer lateral process to the posterior cusp and then continues approximately in a straight line. The small posteriorly and laterally directed projection extends only slightly beyond the line formed by the outer lateral process and the inner spur.

Remarks. Latericriodus alces appears to fill the morphological gap between the slender, stratigraphically later forms of *L. nevadensis* and *L. robustus*. Johnson and Klapper (1981, p. 1241) suggested a phylogenetic relationship between the two species. The new species differs from the late form of *L. nevadensis* by exhibiting a gap, with a low ridge, between the posteriormost middle-row denticle of the spindle and posterior cusp, and by the arched upper surface as laterally viewed. The outline of the basal cavity is similar in the two species. *Latericriodus alces* can be readily distinguished from the stratigraphically early forms of *L. nevadensis* by the depression with small middle-row denticles in the posterior part of the spindle. In *L. robustus* the junction between the outer lateral process and the spindle is located more anteriorly and the depression with the middle-row denticles in the posterior part of the spindle is more accentuated. Moreover, the I elements of *L. robustus* have a well developed posteriorly and laterally directed projection extending well beyond the line formed by the outer lateral process and the inner spur, a characteristic best displayed in lower view. Some of the specimens assigned to *L. robustus* by Uyeno *in* Uyeno et al. (1982, Pl. 4, figs. 1-6) do not show this characteristic offset and therefore are included here in *L. alces.*

No S_{2a} or S_{2b} elements were recovered in the samples with the I elements of *L. alces.*

Material. 25 I elements (one intermediate between *L. alces* and *L. robustus*).

Etymology. From the Latin *alces*, for moose, in reference to the type locality in the Moose River Basin.

Type series. Holotype, the specimen illustrated in Plate 2.1, figures 10-12, GSC 100040. Paratypes, the four specimens illustrated in Plate 2.1, figures 7-9, 13-18, GSC 100039, 100041-100043.

Type locality and type strata. Jaab Lake well, GSC loc. C-53085, interval between 801 and 803 ft. (244.1-244.8 m), Stooping River Formation.

Latericriodus nevadensis (Johnson and Klapper)

Plate 2.1, figures 1-4, (?)5, (?)6

*1981 *Icriodus nevadensis* n. sp. Johnson and Klapper, p. 1239, 1241, 1242, Pl. 1, figs. 1-6, 8-12, 17, 20, 21; Pl. 2, figs. 1-4, 13, 14; Textfig. 2F, G, I, J.

Remarks. In the I elements assigned herein to *L. nevadensis*, the spindle is relatively narrow and the middle-row denticles are substanially smaller than those of the lateral rows, particularly in the posterior part of spindle. This is characteristic of the late forms of *L. nevadensis* according to the original description of Johnson and Klapper (1981, p. 1239). Between the posteriormost denticle of the middle row on the spindle and the posterior cusp, there are one or two denticles of equal height as the cusp; this contrasts with *L. alces* in which there is a gap, with a low ridge or a small denticle, in this position. Most of the specimens have a narrowly to moderately expanded basal cavity posteriorly, although one specimen has a broadly expanded basal cavity. (See also *L. alces*.)

In the interval of 834-840 ft. (254.2-256.0 m), the S_{2a} element that is associated with the I elements is figured here in Plate 2.1, figure 4.

Material. Four large I elements; three small I elements questionably assigned to this species; one S_{2a} element.

Latericriodus robustus (Orr)

Plate 2.2, figures 4-19; Plate 2.4, figures 1, 2

1967 *Icriodus latericrescens* n. subsp. A. Klapper and Ziegler, p. 75, Pl. 8, figs. 7, 9; Pl. 9, figs. 1-7.

*1971 *Icriodus latericrescens robustus* n. subsp. Orr, p. 37, 38, Pl. 2, figs. 14-17.

1980 *Icriodus latericrescens robustus* Orr. Klapper and Johnson, p. 448, Pl. 3, fig. 16 (synonymy up to 1977).

p. 1982 *Icriodus latericrescens robustus* Orr. Uyeno *in* Uyeno et al., p. 32, Pl. 4, figs. 25, 26, 31-38, (?)figs. 8-24 [*non* figs. 1-6 = *L. alces*].

1983 *Icriodus latericrescens robustus* Orr. Sparling, p. 850, 851, Figs. 10A, Z; 11C, D.

1983 *Icriodus latericrescens robustus* Orr. Klug, p. 86, Figs. 8M-U.

1988 *I. latericrescens robustus* Orr. Sparling, Fig. 10-4.

Remarks. The I elements of *L. robustus* from the Jaab Lake well have a well developed to large outer-lateral process with a straight to strongly recurved axis, which joins the main platform at the anterior margin of the posterior cusp or immediately anteriorly of it, at an angle of 90° or slightly greater. The upper surface of the process is well to strongly denticulated with one to three rows of denticles, which are usually connected by cross ridges. The lateral-row denticles on the spindle are robust and round. The median-row denticles are round but smaller than those of the lateral rows, particularly in the posterior part of the spindle where they lie in a shallow depression. In large specimens the median-row denticles are minute and are connected by a longitudinal ridge. The posterior tip of the main platform forms a pronounced, almost rounded offset, which is well displayed in lower view. On the inner side is a moderately to strongly developed spur, which may be smooth or ornamented with a thin ridge. The basal cavity is narrowly to broadly expanded. All the specimens belong to the intermediate or advanced morphotypes of *L. robustus* described by Uyeno, *in* Uyeno et al. (1982, p. 32). Some of the simple morphotype of *L. robustus* described by that author are assigned herein to *L. alces* (see also under species).

In three of the seventeen samples from the Jaab Lake well, the I elements are associated with low-triangular S_{2a} elements that have an expanded base (Pl. 2, fig. 15). An S_{2b} element was recovered from the interval of 457-462 ft. (139.3-140.8 m), associated with the I elements of *L. robustus* and of *Pelekysgnathus* sp. A, and is illustrated in Plate 2.4, figure 12.

Material. 108 I elements (1 cf.); six S_{2a} elements; (?)one S_{2b} element.

Genus *Pelekysgnathus* Thomas, 1949

Type species. *Pelekysgnathus inclinatus* Thomas, 1949.

Pelekysgnathus sp. A

Plate 2.4, figures 9-13

Remarks. Three *Pelekysgnathus* I elements were recovered from the middle to upper parts of the Kwataboahegan Formation in the Jaab Lake well. The elements are short and high in lateral view. The main axis is straight to slightly curved. The upper surface bears five to six triangular denticles with free, pointed tips. Two partially fused cusps occur at the posterior end. In lateral view the upper margin of the unit is straight to slightly arched, the highest point being at the posterior or anterior cusp. The basal cavity is narrow with an inconspicuous expansion beneath the two cusps.

Pelekysgnathus sp. A resembles *P.* sp. listed by Bultynck (1976b, Table 1) from the Dundee Limestone and the basal part of the Rogers City Limestone in northern Michigan (figured herein in Pl. 2.4, fig. 9). In the Michigan specimens the upper surface bears up to eight denticles.

In both the Jaab Lake and Michigan collections, the I elements are associated with S_{2b} elements.

Material. Three I elements; one S_{2b} element (which may belong to *Latericriodus robustus*).

Genus *Polygnathus* Hinde, 1879

Type species. Polygnathus dubius Hinde, 1879.

Polygnathus cooperi cf. *secus* Klapper, Ziegler and Mashkova

Plate 2.3, figures 16–18

cf. *1978 *Polygnathus cooperi secus* subsp. nov. Klapper, Ziegler and Mashkova, p. 108, 109, Pl. 2, figs. 18, 23, 24, 26–28.

Remarks. One Pa element from the lower part of the Stooping River Formation (interval of 934-939 ft.; 284.7-286.2 m) is assigned to *P. cooperi* Klapper on the basis of the platform outline and the presence of a node and a short transverse ridge on a small tongue. The carina is located closer to the inner margin than to the outer margin in the posterior half of the platform. On the inner side, the anterior platform margin joins the free blade in a convex curve and is serrate. A closer comparison can therefore be made with *P. cooperi secus* than with the nominate subspecies.

Material. One Pa element; one M element.

Polygnathus linguiformis n. subsp. A

Plate 2.4, figures 14, 15

p. 1970 *Polygnathus linguiformis linguiformis* Hinde, gamma forma nova. Bultynck, Pl. 11, fig. 4 (only).

Remarks. That part of the platform anterior to the tongue is relatively short in comparison to *P. linguiformis linguiformis*, especially the inner platform which, in the nominate subspecies, is about the same length as the tongue. The inner and outer platform halves are separated from the carina by an adcarinal trough and the outer platform margin is much higher than the inner margin. The tongue is relatively long, with strong transversal ridges and is sharply deflected downward.

Similar specimens occur in the Hanonet Formation ("Co2d") in the Ardennes, and are assigned to the *ensensis* Zone.

Material. Three Pa elements (one questionably assigned).

"*Ozarkodina*" *denckmanni* Ziegler

Plate 2.3, figure 19

1956 *Ozarkodina denckmanni* n. sp. Ziegler, p. 103, Pl. 6, figs. 30, 31; Pl. 7, figs. 1, 2.

Remarks. A sample from the middle part of the Stooping River Formation (interval of 770–775 ft.; 234.7-236.2 m) contained a single Pb element corresponding to the form-species "*Ozarkodina*" *denckmanni*. Pb elements of this type have been assigned to Lower Devonian multielement species belonging to the genera *Eognathodus* Philip, *Ozarkodina* Branson and Mehl, *Pandorinellina* Müller and Müller, and *Polygnathus* Hinde (Klapper and Philip, 1971, p. 440; Mashkova, 1972; Uyeno, 1990).

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PLATE 2.1

Figures 5, 6, 13–18, x80; all others x48. All specimens are from the Jaab Lake well, GSC loc. C-53085; all are from the Stooping River Formation

Figures 1–4. *Latericriodus nevadensis* (Johnson and Klapper)

(From interval 834–840 ft., 254.2–256.0 m).

1, 2. GSC 100034, lower an upper views of I element.

3. GSC 100035, upper view of I element.

4. GSC 100036, outer lateral view of S_{2a} element.

Figures 5, 6. ?*Latericriodus nevadensis* (Johnson and Klapper)

(From interval 760–765 ft., 231.6–233.2 m).

5. GSC 100037, upper view of I element.

6. GSC 100038, upper view of I element.

Figures 7–18. *Latericriodus alces* n. sp.

7–9. GSC 100039, oblique inner lateral, upper, and lower views of paratype I element. (From interval 803–813 ft., 244.8–247.8 m).

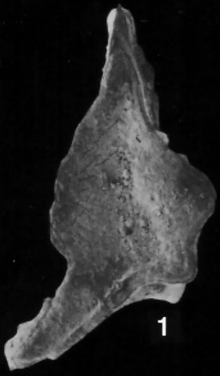
10–12. GSC 100040, oblique outer lateral, upper, and outer lateral views of holotype Pa element. (From interval 801–803 ft., 244.1–244.8 m).

13, 14. GSC 100041, outer lateral and upper views of paratype I element, outer lateral process incomplete. (From interval 801–803 ft., 244.1–244.8 m).

15, 16. GSC 100042, lower and outer lateral views of paratype I element. (From interval 873–878 ft., 266.1–267.6 m).

17, 18. GSC 100043, upper and lower views of paratype I element. (From interval 647–652 ft., 197.2–198.7 m).

PLATE 2.1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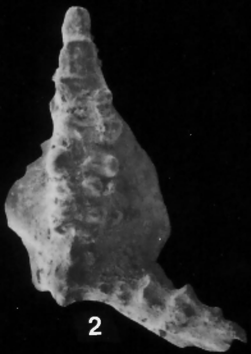
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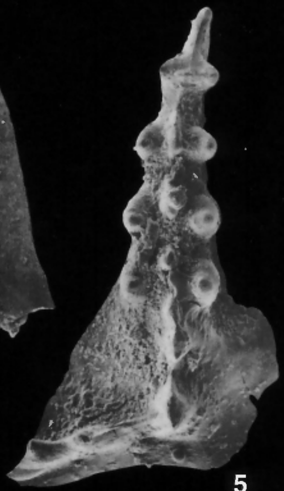
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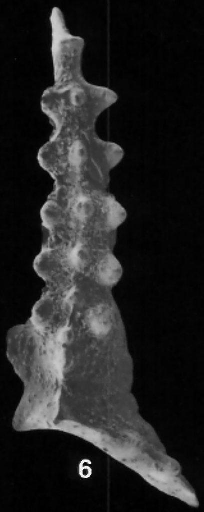
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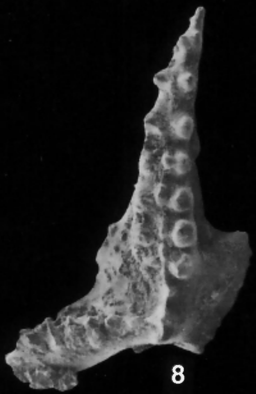
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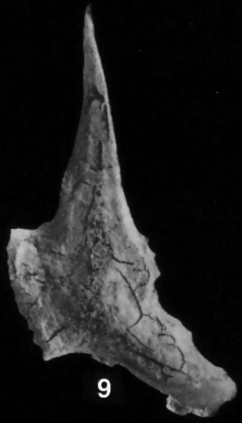
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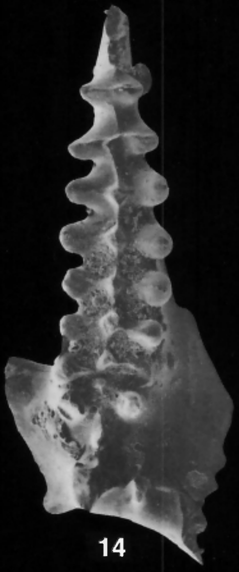
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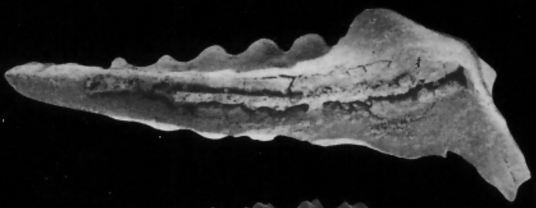
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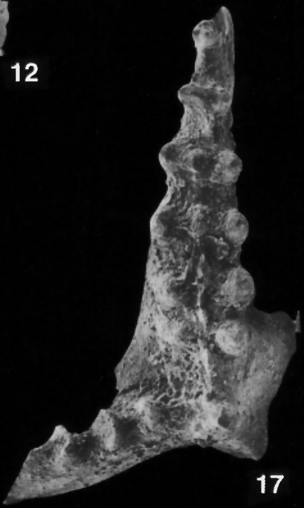
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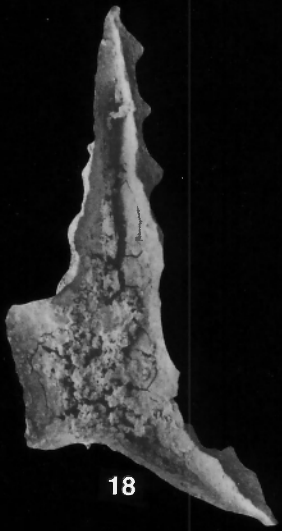
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PLATE 2.2

Figures 4, 8, 13–16, x80; all others x48. All specimens are from the Jaab Lake well, GSC loc. C-53085; figures 1–10 are from the Stooping River Formation; figures 11–19 are from the Kwataboahegan Formation

Figures 1, 2. *Latericriodus alces* n. sp. transitional to *L. robustus* (Orr)

GSC 100044, lower and upper views of I element. (From interval 637–642 ft., 194.2–195.7 m).

Figure 3. *Latericriodus* cf. *L. robustus* (Orr)

GSC 100045, upper view of I element, outer lateral process broken. (From interval 727–733 ft., 221.6–223.4 m).

Figures 4–19. *Latericriodus robustus* (Orr)

(Figs. 4–7 from interval 637–642 ft., 194.2–195.7 m).

4. GSC 100046, upper view of I element.

5. GSC 100047, upper view of I element.

6, 7. GSC 100048, lower and oblique outer lateral views of I element.

(Figs. 8–10 from interval 567–572 ft., 172.8–174.3 m).

8. GSC 100049, upper view of small I element.

9. GSC 100050, upper view of I element.

10. GSC 100051, upper view of I element.

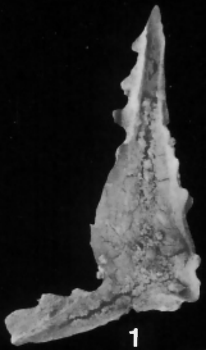
11, 12. GSC 100052, upper and lower views of I element. (From interval 487–492 ft., 148.4–150.0 m).

13, 14. GSC 100053, upper and lower views of I element. (From interval 467–472 ft., 142.3–143.9 m).

15. GSC 100054, oblique upper view of S_{2a} element. (From interval of 447–452 ft., 136.2–137.8 m).

16–19. GSC 100055, 100056, 100057, and 100058, respectively, upper view of four I elements. (From interval 477–482 ft., 145.4–146.9 m).

PLATE 2.2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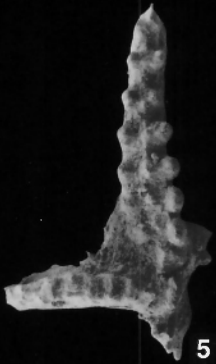
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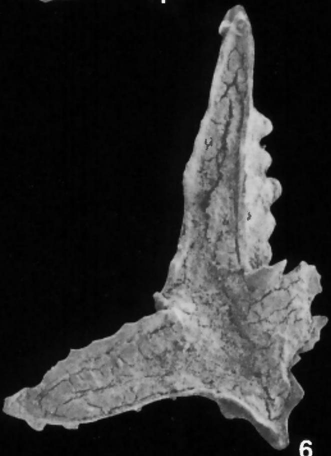
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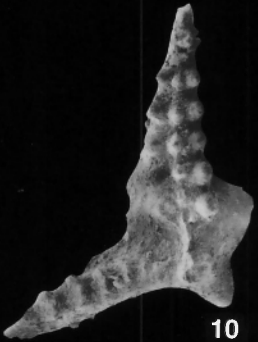
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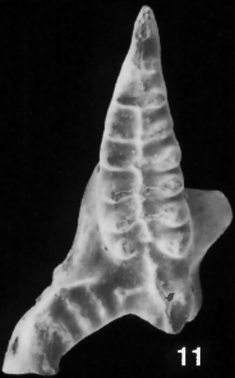
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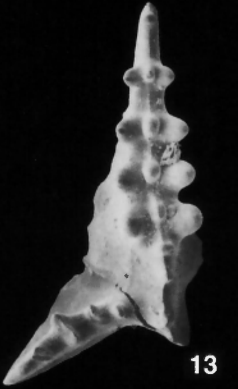
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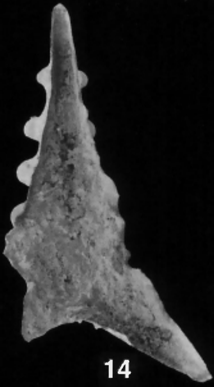
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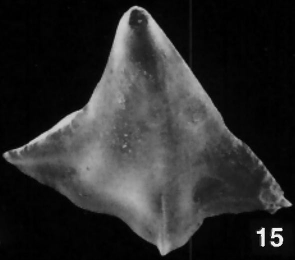
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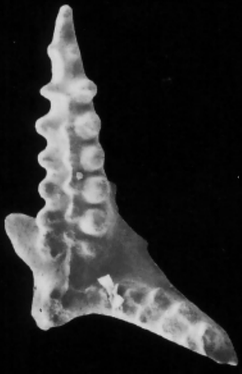
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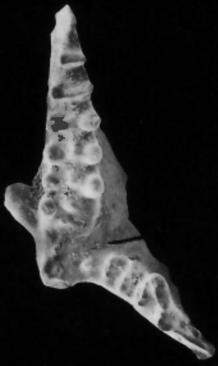
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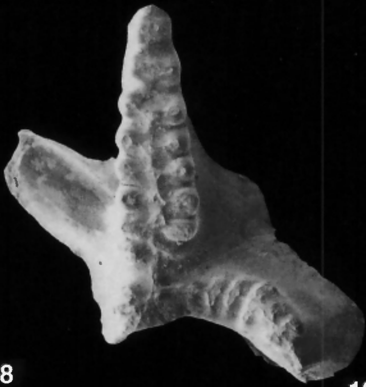
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PLATE 2.3

All figures x80. All specimens are from the Jaab Lake well, GSC loc. C-53085; all are from the Stooping River Formation

Figures 1, 2. *Icriodus* sp. A

GSC 100059, upper and lower views of I element. (From interval 965–970 ft., 294.1–295.7 m).

Figures 3, 4. *Icriodus* aff. *I. trojani* Johnson and Klapper

GSC 100060, upper and outer lateral views of I element. (From interval 740–745 ft., 225.6–227.1 m).

Figures 5–7. *Icriodus* aff. *I. culicellus* (Bultynck)

5, 6. GSC 100061, upper and outer lateral views of I element. (From interval 740–745 ft., 225.6–227.1 m).

7. GSC 100062, oblique upper view of I element. (From interval 727–733 ft., 221.6–223.4 m).

Figures 8–15. *Icriodus corniger* group

(Figs. 8–12 from interval 717–722 ft., 218.5–220.1 m).

8, 9. GSC 100063, upper and lower views of I element, close to *I. corniger corniger* Wittekindt.

10. GSC 100064, upper view of I element similar to *I. rectirostratus* Bultynck.

11, 12. GSC 100065, outer lateral and upper views of I element close to *I. corniger ancestralis* Weddige.

13–15. GSC 100066, lower, upper, and oblique outer lateral views of I element close to *I. corniger corniger* Wittekindt. (From interval 697–702 ft., 212.4–214.0 m).

Figures 16–18. *Polygnathus cooperi* cf. *secus* Klapper, Ziegler and Mashkova

GSC 100067, oblique upper, upper, and lower views of Pa element. (From interval 934–939 ft., 284.7–286.2 m).

Figure 19. "*Ozarkodina*" *denckmanni* Ziegler

GSC 100068, outer lateral view of Pb element. (From interval 770–775 ft., 234.7–236.2 m).

PLATE 2.3


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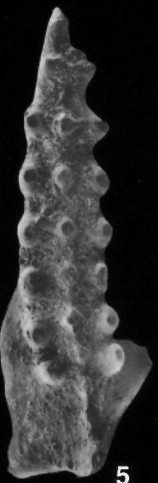
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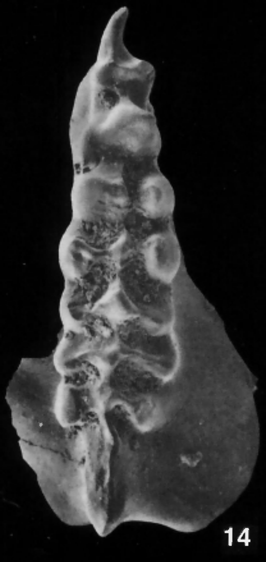
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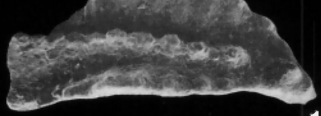
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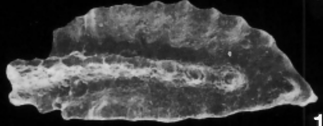
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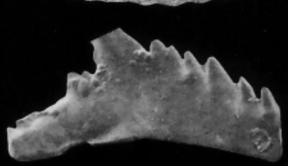
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PLATE 2.4

Figures 9, 14, 15, x48; all others x80. All specimens are from the Jaab Lake well, GSC loc. C-53085, except figure 9 (see below)

(Figures 1–8, 10–13 are from the Kwataboahegan Formation.)

Figures 1, 2. *Latericriodus robustus* (Orr)

GSC 100069, lower and upper views of I element. (From interval 487–492 ft., 148.4–150.0 m).

Figures 3–8. *Icriodus angustus angustus* Stewart and Sweet

3–5. GSC 100070, upper, oblique outer lateral, and lower views of I elements, long form. (From interval 477–482 ft., 145.4–146.9 m).

6, 7. GSC 100071, upper and outer lateral view of I element, short form. (From interval 350–355 ft., 106.7–108.2 m).

Figure 8. S_{2a} element; may belong either to *Latericriodus robustus* (Orr) or to *Icriodus angustus angustus* Stewart and Sweet

GSC 100072, outer lateral view. (From interval 371–377 ft., 113.1–114.9 m).

Figures 9–13. *Pelekysgnathus* sp. A

9. GSC 100073, inner lateral view of I element. (Sample 01, Bultynck, 1976, p. 137, Table 1; top of Dundee Limestone, Rogers City, Michigan).

10, 11. GSC 100074, oblique outer lateral and upper views of I element. (From interval 437–443 ft., 133.2–135.0 m).

12. GSC 100075, inner lateral views of S_{2b} element. (From interval 457–462 ft., 139.3–140.8 m).

13. GSC 100076, inner lateral view of I element. (From interval 457–462 ft., 139.3–140.8 m).

Figures 14, 15. *Polygnathus linguiformis* n. subsp. A

GSC 100077, lower and upper views of Pa element. (From interval 147–152 ft., 44.8–46.3 m; Williams Island Formation).

Figures 16, 17. *Icriodus* sp. B

GSC 100078, upper and lower views of I element. (From interval 189–195 ft., 57.6–59.4 m; Murray Island Formation).

PLATE 2.4


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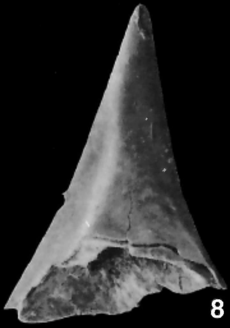
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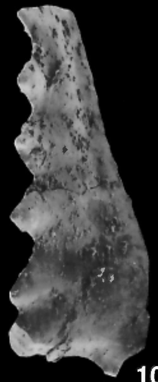
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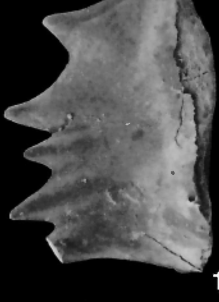
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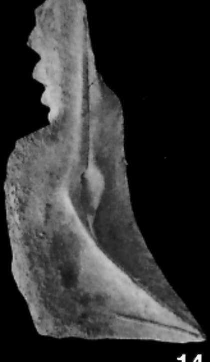
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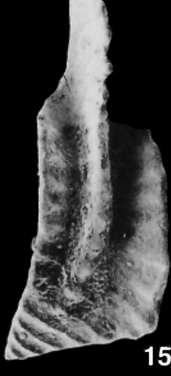
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NEW INFORMATION ON THE SKELETAL STRUCTURE AND SYSTEMATICS OF THE VISÉAN RUGOSE CORAL *ANKHELASMA*

E.W. Bamber[1] and W.J. Sando[2]

*Bamber, E.W. and Sando, W.J., New information on the skeletal structure and systematics of the Viséan rugose coral **Ankhelasma**; in Contributions to Canadian Paleontology; Geological Survey of Canada, Bulletin 444, p. 37–49, 1993.*

Abstract

Carinae and tabulae, previously unknown in *Ankhelasma*, have been discovered in *A. circulare* sp. nov., from east-central British Columbia, and occur in numerous representatives of the type species, *A. typicum*, from nearby Canadian localities and the western U.S.A. Ontogenetic study of silicified and calcareous specimens has shown that their prominent, axially fused counter and alar protosepta and pericardinal septal plates extend without interruption throughout the corallum. Intervening, weakly rhopaloid metasepta withdraw abaxially soon after insertion and are attached to the counter sides of the stationary alar protosepta and to the pericardinal septal plates. A new family, the Ankhelasmatidae, is proposed for these corals.

Résumé

Des carènes et des cloisons transversales, auparavant inconnues dans le genre *Ankhelasma*, ont été reconnues dans des échantillons de l'espèce *A. circulare* sp. nov. du centre est de la Colombie-Britannique et dans de nombreux spécimens de l'espèce type *A. typicum* provenant d'endroits voisins du Canada et de l'ouest des États-Unis. L'étude ontogénique de spécimens silicifiés et calcaires montre qu'il y a prolongation sans interruption, dans tout le corallum, des protoseptes antipodes et alaires de même que des plaques septales péricardinales, toutes ces structures étant proéminentes et rattachées à l'axe. Des métaseptes intercalaires, faiblement rhopalodes, se sont éloignés de l'axe peu après leur insertion; ils sont fixés aux contre-parois des protoseptes alaires stationnaires et des plaques septales péricardinales. On propose une nouvelle famille, les Ankhelasmatidés, pour ces coraux.

INTRODUCTION

The genus *Ankhelasma* was named by Sando (1961) for small, ceratoid or trochoid, solitary rugose corals first discovered in lower Viséan rocks in the Crawford Mountains of northeastern Utah. These corals are distinguished by an unusually strong development of five axially fused septal elements (Pl. 3.1, figs. 1, 17; Pl. 3.2, figs. 1, 12, 13, 15, 16), referred to as septal plates by Sando (1961). As discussed below, three of these plates are the counter and alar protosepta, and will be referred to as such throughout this paper. Use of the term pericardinal septal plates will be confined to the remaining two plates, which border the well developed cardinal fossula on the convex side of the corallum. The fossula contains a short cardinal septum. Dissepiments are absent. Subcalicular features of mature coralla are very poorly preserved in the type specimens from Utah and Montana (Sando, 1961, p. 67). As a result, no evidence of tabulae was found in these specimens.

Since the establishment of the genus, regional coral studies by the writers in the U.S.A. and Canada have shown that *Ankhelasma* is restricted to lower and lower middle Viséan strata in a narrow belt near the Viséan shelf margin in the Western Interior region of North America (Sando and Bamber, 1985; Sando

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[1] Geological Survey of Canada, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street N.W., Calgary, Alberta T2L 2A7
[2] United States Geological Survey, Washington, D.C., U.S.A.

et al., 1991). During these studies, Bamber discovered well preserved specimens from numerous localities in east-central British Columbia that revealed clear evidence of tabulae and carinae — features not previously noted in the type material of *Ankhelasma*. Moreover, the Canadian specimens suggest a different morphogenesis for some skeletal elements than that originally proposed for the genus. Restudy of the original type material and other specimens from the U.S.A. by Sando confirmed the presence of the skeletal features discovered in the Canadian material. A previously unstudied collection from Utah (USGS loc. 27074-PC) contains numerous recrystallized, calcareous specimens in which tabulae and carinae are well preserved.

The purpose of this paper is to illustrate and describe the new skeletal features and redescribe the ontogenetic development of *Ankhelasma*. A new species is described from Canadian specimens, and a new family, the Ankhelasmatidae, is established for the genus. Detailed geographic and geological data for the collections that form the basis of the paper (see locality register) are given in Sando et al. (1991, Appendix A and C). Type material is in the type collections of the Geological Survey of Canada, Ottawa, and the United States National Museum, Washington, D.C.

DESCRIPTION OF SKELETAL STRUCTURES

CARINAE

In most of our collections of *Ankhelasma*, carinae have been destroyed by dolomitization, recrystallization, or imperfect silicification. They were found in etched silicified specimens from only a few localities in Canada and the U.S.A. and are present in thin sections from the recrystallized, calcareous specimens from Utah (USGS loc. 27074-PC). Carinae occur in the calices of mature and immature coralla (Pl. 3.1, figs. 1, 3–7). They have been observed in specimens with cardinal-counter diameters as small as 2.8 mm. (Pl. 3.1, fig. 7; this corresponds to growth stage 4 of Sando, 1961, p. 73). Poorly expressed carinae are present near the top of the calice in the holotype of *Ankhelasma typicum* (Pl. 3.2, fig. 16; Sando, 1961, Pl. 18, fig. 7; Sando et al., 1991, Fig. 2A) from USGS loc. 17722-PC in Utah, and are well expressed in the upper part of calices in specimens of *A. typicum* from USGS loc. 27968-PC in Nevada (Sando et al., 1991, Fig. 2C). Well preserved carinae were first found in specimens of *Ankhelasma circulare* sp. nov. from GSC locs. C-4562 and C-110910 in east-central British Columbia. Elsewhere in this area, poorly preserved carinae occur in specimens of *A. typicum* from GSC loc. C-79699.

The external features of carinae in *Ankhelasma* are best shown by the well preserved, silicified Canadian specimens (Pl. 3.1, figs. 1, 3–7). In the following description of these features, the terminology of Hill (1981, p. F18) is used. Carinae in this genus occur in all quadrants as opposite and subopposite ridges on the sides of all major and minor septa. On the thickened protosepta and pericardinal septal plates, they are evident only in the thinner peripheral parts, high in the calice (Pl. 3.1, figs. 3, 5, 6, 13). They generally are almost perpendicular to the corallum wall and extend almost horizontally across the sides of the septa, or are slightly elevated toward the axis (Pl. 3.1, fig. 15). In a few of the specimens studied, the carinae slope gently downward from the wall into the calice. At the wall, those on adjacent septa join to form narrow platforms connecting the septa. All carinae reach the axial edges of the septa, where they protrude slightly to produce a low serration. The ridges formed by the carinae may be perpendicular to, or inclined downward toward, the sides of the septa (Pl. 3.1, figs. 14, 16). The carinae are arranged in regular rows, with vertical spacing between rows of approximately 0.4 mm. Spacing between rows is surprisingly consistent through all growth stages studied (Pl. 3.1, figs. 3–7). Rare extra carinae or pairs of carinae occur between rows. Throughout the entire range of mature and immature specimens in which they occur, carinae are most strongly expressed near the top of the calice, become less prominent downward, and disappear near the calice floor, where the septa show noticeable rhopaloid thickening (Pl. 3.1, figs. 1, 4, 6). From thin section study it appears that this downward disappearance of carinae at successive growth stages is the result of coating and thickening of the septa by deposition of stereoplasm during growth of the corallum (Pl. 3.1, figs. 13, 14).

In thin sections of calcareous specimens (USGS loc. 27074-PC), carinae are clearly visible as projections from the lateral surfaces of septa, or are represented internally by extensions of the dark median lines in thickened septa (Pl. 3.1, figs. 13, 14, 16). Other aspects of septal microstructure have been almost entirely destroyed by recystallization. A thin section cut obliquely near the wall, across the fossula (Pl. 3.1, fig. 13), shows the cardinal septum, flanked by the pericardinal septal plates and pinnately arranged metasepta and minor septa, all of which are clearly carinate high in the calice but lose their carinae as they become thicker downward. In other tangential sections perpendicular to the thickened parts of septa (Pl. 3.1, fig. 14), dark lateral projections marking former carinae are covered by stereoplasm and the septa are entirely joined laterally. A longitudinal thin section cut obliquely through the median planes of several septa (Pl. 3.1, fig. 15) shows contiguous rows of calcite crystals, which may represent recrystallized, coarse trabeculae, sloping gently upward toward the axis, approximately perpendicular to the corallum wall and parallel to carinae observed in silicified specimens. Indistinct dark lines bisecting these rows have the same vertical spacing as carinae observed in other specimens.

TABULAE

In east-central British Columbia, tabulae were found in more than 60 specimens from nine localities (GSC locs. C-4562, C-7398, C-7399, C-7421, C-7422, C-79699, C-110910, C-110911, C-110912). Tabulae in etched, silicified specimens and longitudinal thin sections from four Canadian localities are illustrated in Plate 3.1, figures 1, 8–12. Many etched silicified specimens from Nevada (USGS loc. 27968-PC) and Utah (USGS locs. 27065-PC, 17722- PC) show tabulae forming floors of mature calices and some broken, inclined tabulae adjacent to the thickened protosepta and pericardinal septal plates in the calices. Transverse sections of specimens from Nevada (USGS loc. 27974-PC) have intercepts of tabulae in the fossula and elsewhere in the central part of the corallum. The subcalicular part of the interior of the mature corallum is not silicified in most silicified specimens, so that acid etching ordinarily removes any record of the tabulae below the calice. The best records of tabulae are in longitudinal and transverse thin sections of well preserved specimens that have not been etched with acid. Such specimens were not available when *Ankhelasma* was originally described. Details of subcalicular tabulae (Pl. 3.1, figs. 10–12, 15; Fig. 3.1) and other skeletal elements can be seen in thin sections from a more recent collection of unsilicified, calcite specimens of *A. typicum*? from Utah (USGS 27074-PC). The following description is based mainly on these specimens and on silicified specimens from Canada.

Tabulae forming the floors of calices are well preserved in numerous mature and immature, silicified specimens from GSC locs. C-4562 and C-110910. The upper surfaces of these tabulae are irregular and undulose (Pl. 3.1, figs. 8, 9). Near the wall, they may be approximately horizontal, and in the central part of the tabularium most are moderately to steeply inclined upward toward the corallum axis (Pl. 3.1, figs. 1, 8–11, 15; Fig. 3.1). Their angle of slope is greatest where the protosepta and pericardinal septal plates are strongly elevated above the calice floor (Pl. 3.1, figs. 1, 8, 10, 12, 15; Fig. 3.1). In some mature coralla in which these septal structures are not strongly elevated (Pl. 3.1, fig. 9), the tabulae are only slightly inclined.

Thin sections from calcite specimens (USGS loc. 27074-PC) and partly silicified specimens (GSC locs. C-4562, C-7399 and C-110912) show tabulae strongly thickened by stereoplasm at several levels in the corallum. The intervals between thickened tabulae are occupied by one to three thin tabulae showing considerable variation in shape and orientation (Pl. 3.1, figs. 11, 15; Fig. 3.1). Nine to eleven tabulae occur in a vertical distance of 10 mm.

In longitudinal thin sections that pass through both the cardinal and counter quadrants and intersect the left or right alar septum, the tabulae are gently curved to subplanar and have a general slope downward from the cardinal to the counter side of the corallum (Pl. 3.1, fig. 11). In both quadrants, tabulae range from concave upward through subplanar to convex upward and commonly are inclined from the corallum wall downward toward the alar septum.

In longitudinal thin sections cut across the cardinal-counter plane (Pl. 3.1, figs. 10, 12, 15; Fig. 3.1), the thickened tabulae are generally concave upward, although a few are slightly convex. They are attached to the corallum wall at angles near 90°, slope upward toward the counter-cardinal plane at fairly low angles over most of the tabularium, and most rise steeply to join the counter septum and septal plates. The thin, irregularly shaped tabulae may be strongly concave upward, subplanar, or slightly to strongly convex upward. Some slope downward from the wall to join septal plates or underlying tabulae. There are also small, thin, highly convex, steeply sloping tabellae(?) adjacent to the pericardinal septal plates. Rarely, the peripheral part of a thin tabula extends upward along the corallum wall past one or two other tabulae.

In the cardinal fossula, thick and thin tabulae alternate as in the remainder of the tabularium (Pl. 3.1, figs. 12, 15; Fig. 3.1). Most are strongly concave upward, but some of the thin tabulae are subhorizontal and almost flat or convex upward. Tabulae within the fossula are also visible on broken surfaces of silicified specimens. In transverse thin sections of specimens at mature growth stages (Pl. 3.1, fig. 17; Pl. 3.2, fig. 1) the tabulae are expressed as curved intercepts between the protosepta and septal plates.

MORPHOGENESIS OF SEPTA AND TABULAE

Sando's (1961) original conception of the morphogenesis of the internal skeletal features of *Ankhelasma* was based on specimens that did not reveal the presence of tabulae. Hence, he thought that the open space within the corallum was filled by deposition of stereoplasm in order to elevate the calice floor as the polyp grew larger and moved upward into progressively higher parts of the expanding corallum. Sando thought that all septa were vertically continuous, except in the axial region of the mature corallum. The discovery of tabulae in *Ankhelasma* requires a somewhat different interpretation of skeletal morphogenesis. The new evidence shows that tabulae formed successive calice floors upon which the polyp rested, and that only the protosepta and pericardinal septal plates reached the axial area at all growth stages.

Longitudinal sections through the tabularium (Pl. 3.1, figs. 10–12, 15; Fig. 3.1; Pl. 3.2, fig. 2) show the protosepta and pericardinal septal plates to be continuous through tabulae in the axial area. In addition, on the exterior of abraded specimens lacking walls, these five septal structures (Pl. 3.2, figs. 3–5) can be traced without interruption throughout the length of the corallum. The metasepta approach the axial area only in early growth stages (Pl. 3.1, fig. 7; Pl. 3.2, figs. 10, 11), after which they withdraw abaxially and are restricted to the outer tabularium (Pl. 3.1, figs. 1, 6, 8, 9, 17; Pl. 3.2, figs. 12, 13). Protosepta, pericardinal septal plates and metasepta show much vertical variation in thickness. In longitudinal section, they are strongly thickened immediately above thickened tabulae and taper upward toward the next thick tabula (Pl. 3.1, fig. 11; Pl. 3.2, fig. 2). They do not change thickness at intervening thin tabulae. Repeated thickening of the metasepta, coupled with abaxial retreat and thinning toward the top of the calice, gives them a slightly rhopaloid aspect (Pl. 3.1, figs. 3–6, 8, 9, 13; Pl. 3.2, figs. 15, 16). In some mature specimens, one or more protosepta or pericardinal septal plates withdraw from the axis, leaving a low, open area in the central part of the tabularium (Pl. 3.1, figs. 9, 15; Fig. 3.1).

Tracing of septa on the exteriors of abraded, silicified specimens shows that the counter and alar protosepta, developed at a very early growth stage (Pl. 3.2, figs. 6–8), are identical with the strongly developed counter and alar septa that fuse axially with the pericardinal septal plates to distinguish the genus in later growth stages. The nature and origin of the pericardinal septal plates forming the sides of the fossula are not fully understood. They appear with the counter and alar protosepta at an early growth stage (Pl. 3.2, figs. 3, 5–9) and continue without interruption into maturity. Throughout most of the corallum they show a median dark line in thin section (Pl. 3.2, figs. 12, 13) and continue to develop in the axial area after withdrawal of the metasepta adjacent to the cardinal fossula (Pl. 3.1, figs. 1, 3–9; Pl. 3.2, figs. 1, 10–16). Thus, they are independent septal structures similar to the counter and alar protosepta. On the surfaces of abraded specimens, however, the pericardinal septal plates show no median dark lines along their peripheral margins (Pl. 3.2, fig. 5). This suggests that they may not have originated as independent septa and may have formed initially by fusion of metasepta. Serial thin sections that might reveal structural relationships of the pericardinal septal plates to the protosepta and metasepta in earliest growth stages have so far not been obtained in the study of the material available.

Throughout the growth of the coral, the alar protosepta and pericardinal septal plates maintain their positions and do not migrate laterally within the corallum. No counter lateral protosepta are developed. The septa designated as counter laterals by Sando (1961) are regarded here as metasepta of the counter quadrants. The cardinal protoseptum does not appear within the cardinal fossula until after the insertion of the third series of metasepta (Pl. 3.2, figs. 6–9, 10, 11, 14), but it may be developed earlier within the corallum wall. Metasepta are inserted at four positions in the corallum (Pl. 3.1, figs. 1, 3, 4–6; Pl. 3.2, fig. 9, 11, 14–16). Those in the counter quadrants arise in the usual position, adjacent to the alar protosepta. Metasepta in the cardinal quadrants, which are pinnately arranged with respect to the fossula, are inserted at the corallum wall, where they are initially fused with the peripheral parts of the pericardinal septal plates. The metasepta remain attached to the pericardinal septal plates for a short time, (Pl. 3.2, figs. 6, 7, 9–11), but later withdraw toward the corallum wall (Pl. 3.1, figs. 1, 4, 6, 9; Pl. 3.2, figs. 1, 12, 13, 15, 16). In the counter quadrants, the axial margins of newly inserted metasepta are attached to the alar protosepta (Pl. 3.1, figs. 3, 5, 6. Pl. 3.2, figs. 6–16), rather than to previously inserted metasepta as in most rugose corals (Hill, 1981, p. F19). After insertion, all metasepta migrate toward the counter protoseptum and withdraw from the axial part of the corallum (Pl. 3.1, figs. 1, 4, 6; Pl. 3.2, figs. 15, 16).

The system of septal notation used in Plates 3.1 and 3.2 is a simplified version of that used by Sando (1961, p. 66, Pl. 17, 18), adjusted to show the pattern of septal development described above. The protosepta and pericardinal septal plates are designated by upper case letters (counter — K, alar — A, pericardinal septal plates — SP) and the metasepta (Pl. 3.2, figs. 14–16) are numbered in order of their appearance in each quadrant. The pattern and sequence for the insertion of minor septa in *Ankhelasma* were described by Sando (1961, p. 68, 69).

SYSTEMATIC PALEONTOLOGY

The names of institutions mentioned in the text and plate explanations are abbreviated as follows:

GSC — Geological Survey of Canada, Ottawa.
USGS — United States Geological Survey, Washington, D.C.
USNM — United States National Museum of Natural History, Washington, D.C.

Phylum COELENTERATA Frey and Leuckart, 1847

Class ANTHOZOA Ehrenberg, 1834

Subclass RUGOSA Milne-Edwards and Haime, 1850

Order STAURIIDA Verrill, 1865

Family ANKHELASMATIDAE n. fam.

Type genus. Ankhelasma Sando, 1961.

Distribution. Lower and middle Viséan of the Western Interior region of Canada and U.S.A.

Diagnosis. Small, solitary, ceratoid or trochoid coralla, weakly to strongly flattened on cardinal side in intermediate growth stages. Well developed cardinal fossula on convex side of corallum. Fossula bounded laterally by pericardinal septal plates and axially by fused axial edges of counter and alar protosepta. Metasepta withdrawn from axial area in mature growth stages, weakly rhopaloid; minor septa short; all septa bear opposite to subopposite carinae, occurring as horizontal to gently sloping ridges in upper part of calice. Septal pattern pinnate, characterized by five prominent, vertically continuous, axially joined septal structures (counter and alar protosepta and pericardinal septal plates); pericardinal septal plates and alar protosepta maintain original position throughout ontogeny; metasepta migrate toward counter septum from four loculi of insertion adjacent to cardinal fossula and alar protosepta; insertion of short cardinal septum in fossula retarded. Tabulae undulose, ranging in orientation from approximately horizontal to steeply elevated adaxially; thick tabulae alternating with one or more thin tabulae. Septa strongly thickened by stereoplasm below calice. Dissepiments absent. Microstructure poorly known, probably trabecular.

Discussion. Ankhelasma, the only genus here assigned to the new family Ankhelasmatidae, does not appear to be closely related to any other group of rugose corals. It has been placed in the Hapsiphyllidae (Sando, 1961), the Polycoeliidae (Ivanovsky, 1973) and the Zaphrentoididae (Hill, 1981). From these and all other families, it is distinguished by its continuous, stationary, axially fused pericardinal septal plates and protosepta.

Genus *Ankhelasma* Sando, 1961

Ankhelasma Sando, 1961, p. 66, 67.
Ankhelasma Sando, 1961. Hill, 1981, p. F318; Sando and Bamber, 1985, p. 17, 18; Sando et al., 1991, Fig. 2.

Type species. Ankhelasma typicum Sando, 1961.

Diagnosis. As for Ankhelasmatidae.

Distribution. As for Ankhelasmatidae.

Discussion. Ankhelasma comprises two species (described below), distinguished by slight but consistent differences in corallum shape and in the ratio of septal number to diameter. The ancestry of the genus is not definitely known. Sando (1961, p. 67) suggested that it may have developed from *Homalophyllites* Easton (now considered synonymous with *Sychnoelasma* Lang, Smith and Thomas), but the skeletal structure in *Sychnoelasma* is typical for the Zaphrentoididae, without carinae and without the long counter and alar protosepta and pericardinal septal plates that characterize *Ankhelasma*.

Ankhelasma typicum Sando, 1961

?Plate 3.1, figures 13–17; Plate 3.2, figures (?)1, (?)2, 3–9, (?)10–13, 14–16; (?)Figure 3.1

Ankhelasma typicum Sando, 1961, p. 67–70, Pl. 17, figs. 5–30, Pl. 18, figs. 1–10.
Ankhelasma sp. cf. *A. typicum* Sando, 1961, p. 70–72, Pl. 17, figs. 1–4, Pl. 18, fig. 11.

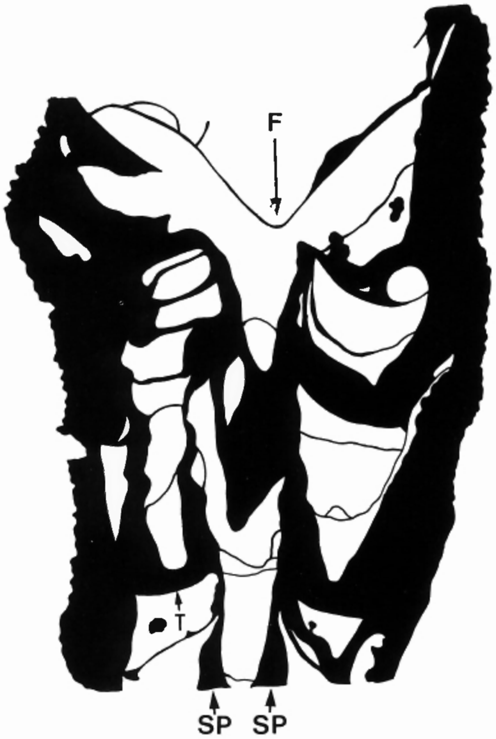

Figure 3.1. ***Ankhelasma typicum*** *Sando(?), hypotype USNM 456318. Ink drawing of longitudinal section, perpendicular to fossula, near axis (see Pl. 3.1, fig. 15; x6). SP, pericardinal septal plates; F, fossula; T, thick tabula. Note alternation of thick and thin tabulae, and continuity of pericardinal septal plates. Recrystallized parts of skeletal elements restored. Pericardinal septal plates withdrawn from axis at maturity.*

Ankhelasma typicum Sando. Hill, 1981, Fig. 208 (2a, b); Sando and Bamber, 1985, Pl. 1, fig. 9; Sando et al., 1991, Figs. 2a-d.
non *A. typicum* Sando. Sando et al., 1991, Figs. 2g, h.

Material. Type series listed by Sando (1961) for *A. typicum*—holotype: USNM 120201; figured paratypes: USNM 120202-120217; unfigured paratypes: USNM 120218-120227. Hypotypes: USNM 424262 (Sando et al., 1991); USNM 120228 (*Ankhelasma* sp. cf. *A. typicum* of Sando, 1961); USNM 456316-456325 (figured), USNM 456326-456335 (unfigured) (*A. typicum* Sando(?)); GSC 100103-100105, 100147 (figured), GSC 100139-100146, 100148 (unfigured).

Occurrence and age. Ankhelasma typicum is by far the more widespread and abundant of the two species of *Ankhelasma*. It occurs at numerous localities in lower and lower middle Viséan strata in the Western Interior region of Canada and the U.S.A., from east-central British Columbia to Nevada. It is known exclusively from shallow marine carbonates deposited in a narrow belt on the landward side of the Viséan shelf margin. Detailed information on stratigraphy, location, age and abundance is listed for each occurrence by Sando et al. (1991, Appendix A, C). Information for samples used in the present study is given in the locality register. Evidence for the early and early middle Viséan ages for this species was derived from its association with foraminifers, conodonts, and other corals (Sando et al., 1991).

Diagnosis (emended). *Ankhelasma* having 34 to 45 major septa at maturity (diameter 12-13 mm), moderate to pronounced flattening on cardinal side of corallum in intermediate growth stages.

Description and discussion. The general features of the septa and tabulae in *Ankhelasma typicum* are described above in the sections dealing with skeletal structure and morphogenesis. In his original description, Sando (1961, p. 67-69) provided detailed information on ontogenetic changes in corallum shape and size of the species, and on morphological features that are well preserved in the silicified type specimens. A revision of his proposed septal insertion plan (Sando, 1961, Pl. 18, figs. 2-7), arising from our new interpretation of the morphogenesis of *Ankhelasma* discussed above, is shown for three of the type specimens, re-illustrated in Plate 3.2, figs. 14-16. Poorly preserved carinae and the remnants of a broken tabula can be seen in the calice of the holotype (Sando, 1961, p. 7).

Ankhelasma typicum has more septa at corresponding diameters (Fig. 3.2) and more pronounced flattening of the corallum than does *A. circulare* sp. nov. Specimens from USGS loc. 27074-PC (Pl. 3.1, figs. 13-17; Pl. 3.2, figs. 1, 2, 10-13), tentatively assigned to *A. typicum*, have a septal number/diameter ratio comparable to that of this species, but the flattening of the corallum is less pronounced than normal.

Ankhelasma circulare sp. nov.

Plate 3.1, figures 1-9, 12

A. n. sp., Sando et al., 1991, figs. 2E, F.

Material. Type series—holotype: GSC 89984 (illustrated by Sando et al., 1991); figured paratypes: GSC 100094-100099, 100102; unfigured paratypes: GSC 100106-100138. Unstudied specimens: 10 silicified specimens from type locality (GSC loc. C-110910);

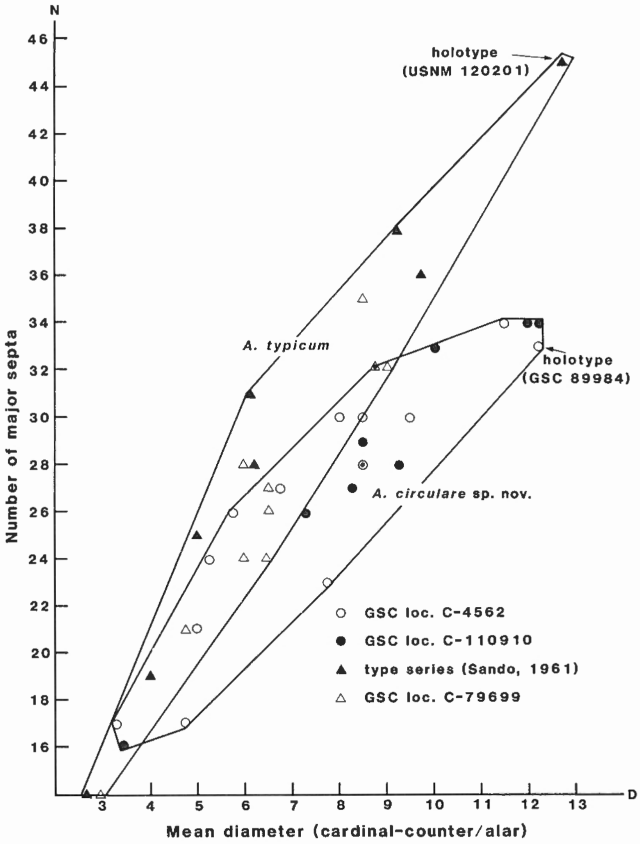

Figure 3.2. Relationship between mean diameter (mean of counter-cardinal and alar dimensions) and number of major septa in ***Ankhelasma typicum*** *Sando (triangles) and* ***A. circulare*** *sp. nov. (circles)*

more than 200 incomplete specimens etched from limestone, and numerous other specimens still enclosed in limestone matrix from GSC loc. C-4562.

Occurrence and age. Ankhelasma circulare has been found only in east-central British Columbia (Sando et al., 1991, p. B11-B15, B24, B25). It occurs at two localities (GSC locs. C-4462, C-110910) in middle-slope carbonates of the Prophet Formation, deposited on the seaward side of the Viséan shelf margin. The species is early middle Viséan in age, based on its association with microfossils of Foraminifer Zone 12 (Mamet and Skipp, 1970).

Diagnosis. Ankhelasma having approximately circular outline in transverse section, corallum slightly flattened on cardinal side in intermediate growth stages of some specimens; 30–34 major septa at maturity (diameter 8-12.5 mm).

Etymology. Latin adjective *circularis*, meaning circular.

Description. Corallum strongly curved, broadly ceratoid, rarely trochoid; transverse section approximately circular at all growth stages, some specimens slightly flattened on convex side in intermediate growth stages (Pl. 3.1, fig. 2). Main features of septa and tabulae are those characteristic for genus (described above in sections on skeletal structure and morphogensis; Pl. 3.1, figs. 1-9, 12); septal number and corallum diameter are shown in Figure 3.2).

Holotype. GSC 89984, an incomplete, silicified, ceratoid specimen (Pl. 3.1, figs. 1-3); length 17.7 mm, youngest growth stages not preserved; 34 major septa at cardinal-counter and alar diameter of 12.5 mm; cardinal septum present in fossula in uppermost part of calice, difficult to distinguish because fossula narrowed by slight crushing of specimen near wall; carinae well expressed on most major and minor septa in upper calice; well developed tabula visible at base of calice; subcalicular structure destroyed by acid etching during removal of specimen from matrix.

Discussion. All known specimens of this species are partly or completely silicified and in many, the skeletal structures below the calice are poorly preserved. Transverse and longitudinal sections through four paratypes (GSC 100102, 100121, 100122, 100132) show alternation of thick and thin tabulae (Pl. 3.1, fig. 12) in which the orientation, shape, and spacing are closely similar to those in *Ankhelasma typicum*; in some mature specimens, one or more of the protosepta and septal plates are withdrawn from the axial area and are reduced to low ridges on the calice floor in the peripheral part of the tabularium (Pl. 3.1, fig. 9). As previously noted, *A. circulare* is distinguished from *A. typicum* Sando by a nearly circular transverse outline and relatively low septal number (Fig. 3.2).

LOCALITY REGISTER

GSC loc. C-4562. Mountain Creek, British Columbia; lat. 55°23′30″N, long. 122°26′00″W; 149.3–150 m below top of Prophet Formation; *Ankhelasma circulare* sp. nov.; early middle Viséan.

GSC loc. C-7398. Belcourt Creek, British Columbia; lat. 54°21′30″N, long. 120°29′40″W; 15 m above base of Baril(?) Member, Mount Head Formation; *Ankhelasma typicum* Sando; early Viséan.

GSC loc. C-7399. Same location as C-7398; 31.1 m above base of Wileman(?) Member, Mount Head Formation; *Ankhelasma* sp. indet.; early Viséan.

GSC loc. C-7421. Jarvis Lakes, British Columbia; lat. 54°06′45″N, long. 120°13′15″W; 40.8–43.6 m above base of Mount Head Formation; *Ankhelasma typicum* Sando; early to (?)early middle Viséan.

GSC loc. C-7422. Same location as C-7421; 35.4–36.9 m above base of Mount Head Formation; *Ankhelasma* sp. indet.; early Viséan.

GSC loc. C-79699. Same location as C-7398; 38.4 m above base of Wileman(?) Member, Mount Head Formation; *Ankhelasma typicum* Sando; early Viséan.

GSC loc. C-110910. South Mountain Creek, British Columbia; lat. 55°22′00″N, long. 122°23′15″W; 134.1 m below top of Prophet Formation; *Ankhelasma circulare* sp. nov.; early middle Viséan.

GSC loc. C-110911. Narraway River, British Columbia; lat. 54°10′35″N, long. 120°15′20″W; upper part of Mount Head Formation; *Ankhelasma typicum* Sando; early(?) Viséan.

GSC loc. C-110912. Wapiti River, British Columbia; lat. 54°29′05″N, long. 120°43′08″W; lower part of Baril Member, 85.3 m below top of Mount Head Formation; *Ankhelasma* sp. indet.; early to (?)early middle Viséan.

USGS loc. 17722-PC. Rex Peak, Crawford Mountains, Utah; N 1/2 sec. 31, Tp. 11 N, Rge. 8 E; Brazer Dolomite, 37.5–40.5 m above base of upper member; *Ankhelasma typicum* Sando; early Viséan.

USGS loc. 27065-PC. Samak, Utah; S 1/2 NE 1/4 sec. 25, Tp. 2 S, Rge. 6 E; Brazer Dolomite, 1.5 m below top of member 2; *Ankhelasma* sp. cf. *A. typicum* Sando; early Viséan.

USGS loc. 27074-PC. Trail Hollow, Utah; NW 1/4 sec. 33, Tp. 3 S, Rge. 9 W; Brazer Dolomite, 1.5–7.6 m below top of member 2; *Ankhelasma typicum* Sando(?); early Viséan.

USGS loc. 27968-PC. Potosi Mine, Nevada; CN 1/2 SW 1/4 NE 1/2 sec. 12, Tp. 23 S, Rge. 57 E; Yellowpine Member, Monte Cristo Limestone, 0–1.2 m above base; *Ankhelasma typicum* Sando; early Viséan.

USGS loc. 27974-PC. Tungsten Gap, Nevada; CN 1/2 sec. 10; tp. 15 S, Rge. 64 E; Yellowpine Member, Monte Cristo Limestone, 1.5–7.6 m above base; *Ankhelasma typicum* Sando; early middle Viséan.

ACKNOWLEDGMENTS

We are grateful to A.E.H. Pedder, W.A. Oliver, Jr., and J.T. Dutro, Jr. for their useful comments on the manuscript. J. Fedorowski and D. Weyer gave helpful advice on the skeletal structure of *Ankhelasma*, particularly concerning its septal development. Several collections of *Ankhelasma* used for this study were made by B.C. Richards. Excellent technical help was provided by: R.D. Michie (thin section preparation); B.C. Rutley, W.B. Sharman, and C.C. Ryley (photography), and D.R. Then (drafting).

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PLATES 3.1 and 3.2

PLATE 3.1

(Figures x4 unless otherwise stated.)

Figures 1–9, 12. *Ankhelasma circulare* sp. nov.

1–3. Holotype, GSC 89984, from GSC loc. C-110910. 1, view of calice, showing protosepta (C, K, A), pericardinal septal plates (SP), carinate, rhopaloid septa, inclined tabula, and cardinal fossula (narrowed near wall by slight crushing of specimen). 2, alar view of corallum, showing slight flattening in immature stage on cardinal (right) side. 3, oblique view of calice, showing relationship between alar septum (A) and adjacent metasepta of right cardinal and counter quadrants.

4–6. Views of calices showing carinate, rhopaloid septa and relationships between protosepta, pericardinal septal plates and metasepta.

4. Paratype, GSC 100094, from GSC loc. C-4562, note pericardinal septal plates (SP) bordering fossula and pinnately arranged metasepta in cardinal quadrants.

5. Paratype, GSC 100095, from GSC loc. 110910, note left alar septum (A) with attached metasepta of counter quadrants and parallel metasepta of cardinal quadrants.

6. Paratype, GSC 100096, from GSC loc. C-4562, showing older metasepta withdrawn from axial area.

7. Paratype, GSC 100097, exterior view of calice of immature corallum from GSC loc. C-4562, showing earliest growth stage in which carinae have been observed, at counter-cardinal diameter of 2.8 mm.

8, 9. Paratypes, GSC 100098, 100099, respectively, from GSC loc. C-110910, showing undulose tabulae and metasepta withdrawn from axial area. 9, right alar protoseptum (A) also withdrawn, other protosepta and pericardinal septal plates form low ridges on calice floor.

12. Paratype, GSC 100102, from GSC loc. C-4562, longitudinal thin section through cardinal quadrants cut perpendicular to cardinal fossula in inner tabularium, showing alternating thick and thin tabulae and continuous pericardinal septal plates (SP), x6.

Figures 10, 11. *Ankhelasma* sp. indet.

10. Hypotype, GSC 100100, from GSC loc. C-110912, longitudinal thin section through counter quadrants, cut perpendicular to counter- cardinal plane in inner tabularium, showing continuous counter septum (K).

11. Hypotype, GSC 100101, from GSC loc. C-7399, longitudinal thin section through left cardinal and counter quadrants, cut slightly oblique to cardinal-counter plane through inner tabularium, showing continuous alar septum (A) and tabulae with general slope downward from cardinal (left) to counter side of corallum.

Figures 13–17, *Ankhelasma typicum* Sando(?), from USGS loc. 27074-PC

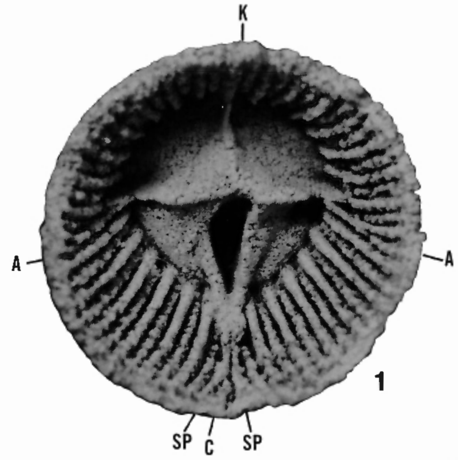
13. Hypotype, USNM 456316, tangential longitudinal thin section cut near wall, across cardinal fossula, showing rhopaloid septa bearing carinae in upper part of calice.

14. Hypotype, USNM 456317, tangential thin section cut near wall, showing dark median lines in septa and lateral projections extending into carinae; angles variable between median lines and projections, carinae covered by stereoplasm in lower part of section where septa laterally contiguous; x15.

15. Hypotype, USNM 456318, slightly oblique longitudinal thin section near axis, cut through cardinal quadrants across fossula, showing pericardinal septal plates (SP) withdrawn at maturity, alternating thick and thin tabulae, and short metasepta (see Fig. 3.1 for ink drawing of section); recrystallized (?)trabeculae in septa on right probably mark positions of ridges (carinae), corallum wall not preserved.

16. Hypotype, USNM 456319, oblique thin section through counter quadrants, showing carinae on septa in upper part of calice, x6.

17. Hypotype, USNM 456320a, slightly oblique, transverse thin section of mature specimen, cut near base of calice, showing thick metasepta and axially fused protosepta and septal plates joined by intercepts of thick and thin tabulae; protosepta and pericardinal septal plates partly recrystallized in axial area and near periphery adjacent to fossula; x6.



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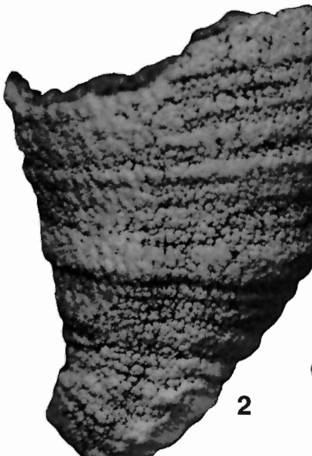

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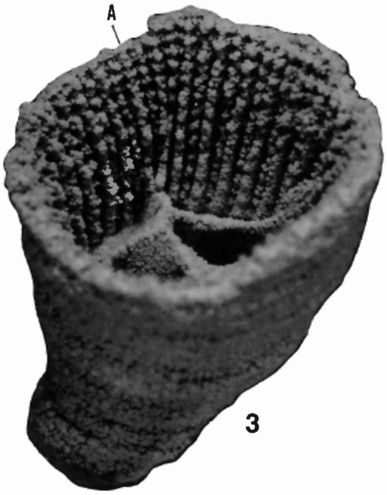

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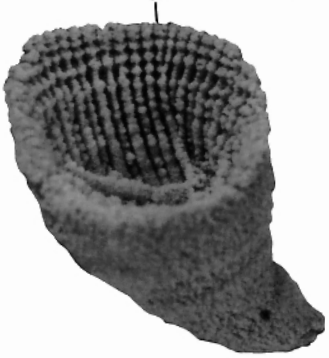

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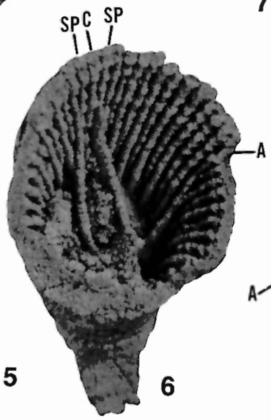

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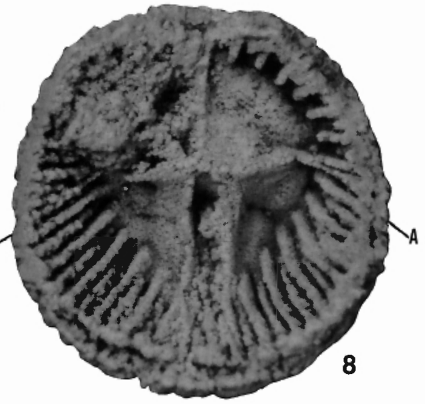

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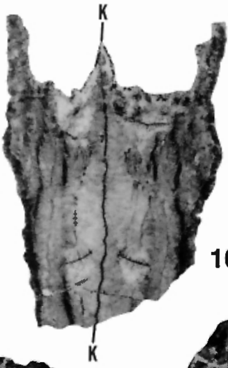

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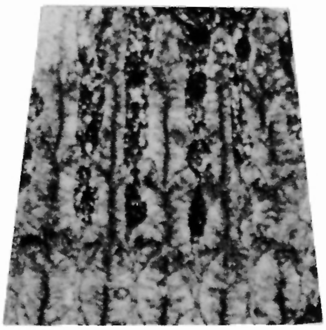

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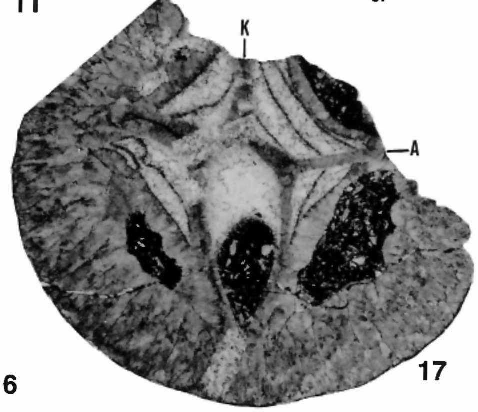

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PLATE 3.2

Figures 1, 2, 10–13, *Ankhelasma typicum* Sando(?), from USGS loc. 27074-PC.

1. Hypotype, USNM 456320b, transverse thin section cut approximately 2 mm below thin section illustrated in Plate 3.1, figure 17; x4.

2. Hypotype, USNM 456321, longitudinal thin section cut near corallum wall, showing continuous alar septum (A); x4.

10. Hypotype, USNM 456322, transverse thin section of immature growth stage (approximately stage 7 of Sando, 1961), showing stereoplasmic thickening of septa and relationship between metasepta and protosepta, x10.

11. Holotype, USNM 456323, oblique transverse thin section of immature specimen, approximately at growth stage 5 of Sando (1961), showing metasepta attached to pericardinal septal plates (SP) and alar protosepta (A), x15.

12, 13. Hypotypes, USNM 456324, 456325, respectively, transverse thin sections cut near base of calice of mature specimen,showing axially fused protosepta (K, A, C) and pericardinal septal plates (SP) and abaxial withdrawal of all but most recently inserted metasepta, x8.

Figures 3–9. *Ankhelasma typicum* Sando, from GSC loc. C-79699.

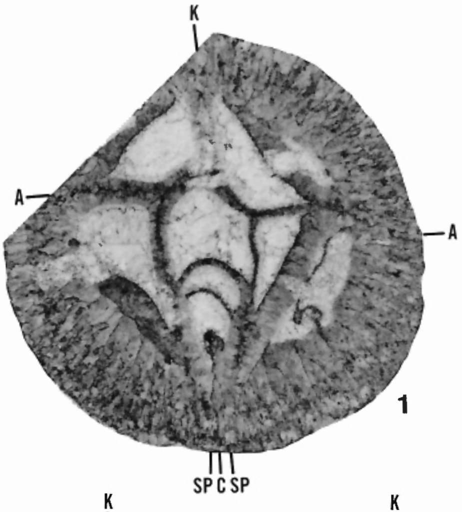
3, 4. Hypotype, GSC 100103, lateral views of abraded specimen showing continuity of pericardinal septal plates and counter protoseptum from early growth stage to maturity. 3, cardinal quadrants showing pericardinal septal plates (SP) and pinnately attached metasepta; 4, counter side showing counter septum (K) and parallel metasepta; x4.

5. Hypotype, GSC 100147, lateral view of cardinal quadrants in early growth stages, showing pericardinal septal plates (SP) and pinnately attached metasepta; x8.

6–9. Scanning electron micrograph of acid-etched, silicified fragments of coralla, showing counter (K) and alar (A) protosepta, and pericardinal septal plates (SP) with attached metasepta in earliest growth stages, x6. 6–8, hypotype, GSC 100104, view of proximal end, specimen inverted. 6, oblique view of cardinal quadrants; 7, cardinal and counter quadrants, viewed approximately along axis; 8, oblique view of left cardinal and counter quadrants; 9, hypotype, GSC 100105, view of distal end.

Figures 14–16. Type specimens of *Ankhelasma typicum* Sando.

Paratypes, USNM 120206, 120208 and holotype 120201, respectively, from USGS loc. 17722-PC; figures reproduced from Sando (1961, Pl. 18, figs. 4, 5, 7) to show revised septal notation from growth stage 4 (fig. 14; x8) to maturity (fig. 16; x4); note remnants of broken tabula and poorly expressed carinae in holotype (fig. 16); magnification of fig. 15 = x6.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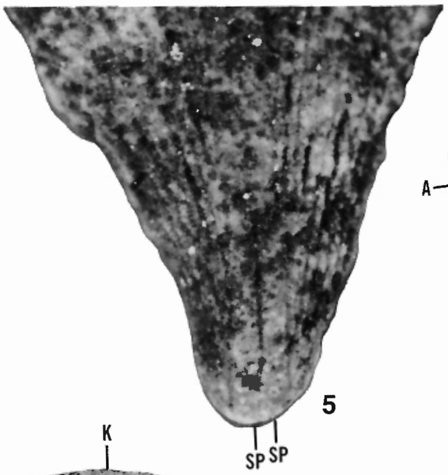
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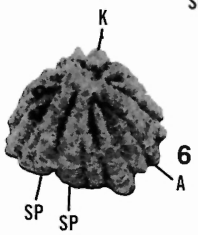
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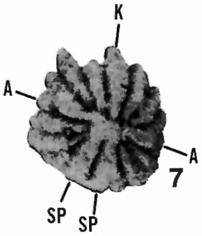
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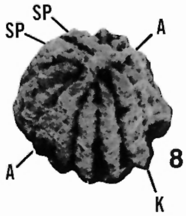
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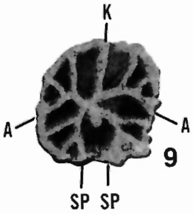
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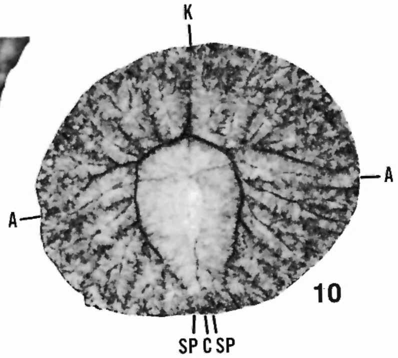
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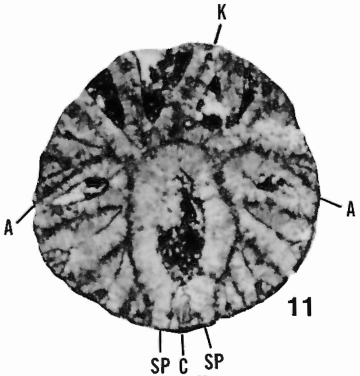
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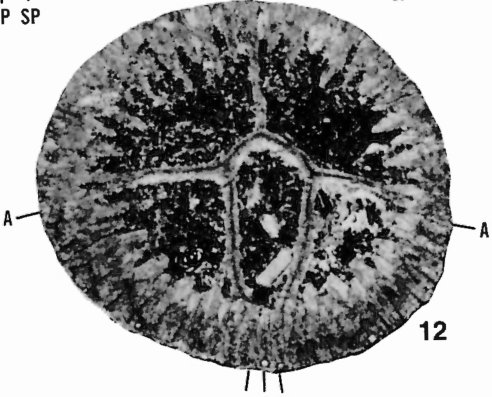
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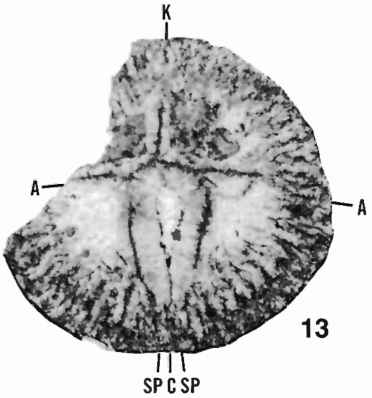
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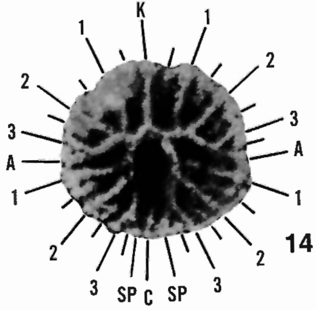
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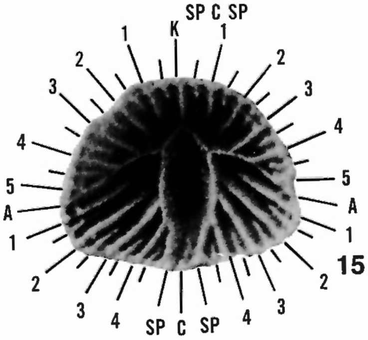
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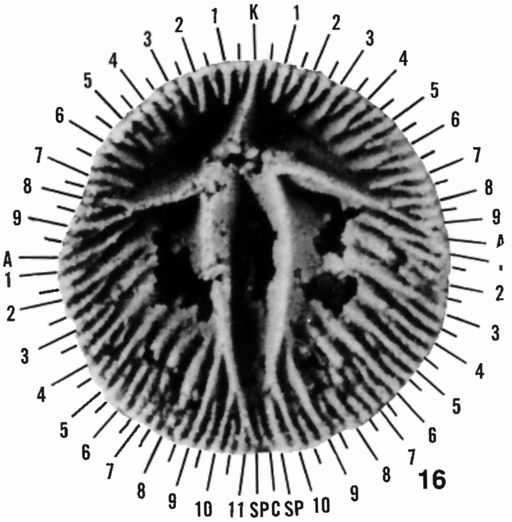
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PALEOGENE FUNGAL PALYNOMORPHS FROM BONNET PLUME FORMATION, YUKON TERRITORY[1]

R.M. Kalgutkar[2]

Kalgutkar, R.M., Paleogene fungal palynomorphs from Bonnet Plume Formation, Yukon Territory; in Contributions to Canadian Paleontology, Geological Survey of Canada, Bulletin 444, p. 51-105, 1993.

Abstract

Samples from the Bonnet Plume Formation of the Yukon Territory yielded a rich assemblage of fungal spores. Most are referable to Ascomycetes and Deuteromycetes. The fungal spores were well preserved. The importance of controlled oxidation and the effect of ammonium hydroxide in the disintegration of the palynomorphs during laboratory processing is discussed.

A total of 25 genera and 73 species of fungal spores were investigated. Twenty-six new species were described. The spore assemblages are characterized by *Chaetosphaerites*, *Ctenosporites*, *Desmidiospora*, *Dictyosporites*, *Exesisporites*, *Fusiformisporites*, *Involutisporonites*, *Pesavis*, *Psilodiporites*, *Reduviasporonites*, *Staphlosporonites* and *Striadiporites*. The dominant fungal spore species in the total assemblage are *Brachysporisporites pyriformis*, *Diporicellaesporites mediocoloratus* sp. nov., *D. pluricellus*, *D. aequabilis* sp. nov., *D. anklesvarensis*, *Monoporisporites singularis*, and *Psilodiporites krempii*. Some fungal spores appear morphologically similar to their probable modern equivalents.

The presence of microthyriaceous and *Meliola*-like fructifications (Kalgutkar, 1985) in these samples suggest that the climate during the deposition of the Bonnet Plume Formation was mesothermal and humid. The common occurrence of many saprophytic fungal spores is indicative of a marshy habitat with a warm, moist microclimate, which was ideal for fungal spore growth.

The whole fungal population is characterized by the presence of species specific to each sample. This is a reflection of the floral diversity in the distribution of fungal species in the Bonnet Plume Formation. The coefficient of floristic similarity (K values) suggests that samples C-68305 and C-68329 are more closely related to each other in their species distribution than they are to sample C-68304.

The samples range in age between Late Paleocene and Early Eocene, based on angiosperm pollen and fungal spores. The presence of *Momipites triradiatus*, *Caryapollenites imparalis*, *C. wodehousei*, *Pterocarya stellatus*, and the occurrence of *Caryapollenites inelegans* and *Tilia vescipites* in samples C-68304 and C-68305 is supportive of a Late Paleocene age. An observation of a single specimen of *Juglans* sp. within the same stratigraphic interval of another section, however, is suggestive of an Early Eocene age. The presence of *Ctenosporites eskerensis*, *Diporicellaesporites pluricellus* and *Diporisporites anklesvarensis*, which are mainly restricted to the Eocene of the Arctic, also favour an Eocene age for the samples.

Résumé

Des échantillons de la Formation de Bonnet Plume, au Yukon, contiennent un riche assemblage de spores fongiques bien conservés, dont la plupart proviennent d'ascomycètes et de

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[1] Dedicated to the memory of the late Professor Birbal Sahni

[2] Geological Survey of Canada, Institute of Sedimentary and Petroleum Geology, 3303-33rd St. N.W., Calgary, Alberta T2L 2A7

deutéromycètes. Une analyse de l'importance de l'oxydation contrôlée et de l'effet de l'ammoniac sur la désagrégation des palynomorphes au cours du traitement en laboratoire est présentée dans le texte.

Ont été étudiés 25 genres et 73 espèces de spores fongiques, mais aussi décrites 26 nouvelles espèces. Les assemblages de spores se caractérisent par la présence de *Chaetosphaerites*, *Ctenosporites*, *Desmidiospora*, *Dictyosporites*, *Exesisporites*, *Fusiformisporites*, *Involutisporonites*, *Pesavis*, *Psilodisporites*, *Reduviasporonites*, *Staphlosporonites* et *Striadiporites*. Quant aux espèces de spores fongiques *Brachysporisporites pyriformis*, *Diporicellaesporites mediocoloratus* sp. nov., *D. pluricellus*, *D. aequabilis* sp. nov., *D. anklesvarensis*, *Monoporisporites singularis* et *Psilodiporites krempii*, elles sont dominantes dans l'ensemble de l'assemblage. Certains spores fongiques ressemblent morphologiquement à ce qui est considéré comme leur équivalent actuel.

La présence de fructifications tant microthyriacées que du du type *Meliola* (Kalgutkar, 1985) dans ces échantillons porte à croire que le climat était mésothermique et humide pendant l'accumulation de la Formation de Bonnet Plume. La présence fréquente de nombreux spores fongiques saprophytes témoigne d'un milieu marécageux au microclimat chaud et humide, idéal pour la croissance de ces éléments.

L'ensemble de la population de champignons se caractérise par la présence d'espèces particulières à chaque échantillon, ce qui reflète la diversité florale dans la distribution des espèces fongiques de la Formation de Bonnet Plume. En ce qui concerne la distribution des espèces, le coefficient de similarité floristique (valeurs K) suggère que les échantillons C-68305 et C-68329 sont plus étroitement reliés l'un à l'autre qu'à l'échantillon C-68304.

Les pollens d'angiospermes et les spores fongiques indiquent que les échantillons s'échelonnent du Paléocène tardif à l'Éocène précoce. La présence de *Momipites triradiatus*, de *Caryapollenites imparalis*, de *C. wodehousei*, de *Pterocarya stellatus*, de *Caryapollenites inelegans* et de *Tilia vescipites* dans les échantillons C-68304 et C-68305 atteste qu'ils remontent au Paléocène tardif. Cependant, un spécimen unique de *Juglans* sp. échantillonné dans le même intervalle stratigraphique d'une autre coupe est plutôt associé à l'Éocène précoce. La présence de *Ctenosporites eskerensis*, de *Diporicellaesporites pluricellus* et de *Diporisporites anklevarensis*, qui se limite principalement à l'Éocène dans l'Arctique, indique aussi que les échantillons remontent à l'Éocène.

INTRODUCTION

During the palynological study of continental Cretaceous–Tertiary miospore floras of the Bonnet Plume Formation, well preserved and noteworthy fossil fungal remains were encountered. This study adds to the earlier work of the author (Kalgutkar, 1985) on the fungal fructifications from the Bonnet Plume Formation. The fungal assemblages were found to be particularly abundant in the uppermost sediments of the formation, which ranges between Late Paleocene and Eocene in age, based on palynological interpretations (Kalgutkar, 1985).

This paper illustrates and presents an account of fungal forms, notably the sporomorphs, and describes their morphology, taxonomy, distribution, and affinities. The primary objectives are to reveal the morphological variety and differentiation of fossil fungal propagules, to provide the nomenclature necessary for further documentation, and to determine possible affinities to modern descendants from distinctive fossil characteristics. These objectives are intended to further elucidate significance of fossil fungi in biostratigraphic, taxonomic, and paleoenvironmental studies.

This study is based on rich fungal material present in these samples from Section 77-LBA-W4 of the Bonnet Plume Formation, as measured and sampled by D.G.F. Long in 1977. Section 77-LBA-W4 is of the uppermost part of the Bonnet Plume Formation, and is located on Peel River, 65°54′N, 135°04′W. Three samples, C-68304, C-68305 and C-68329 (Fig. 4.1), out

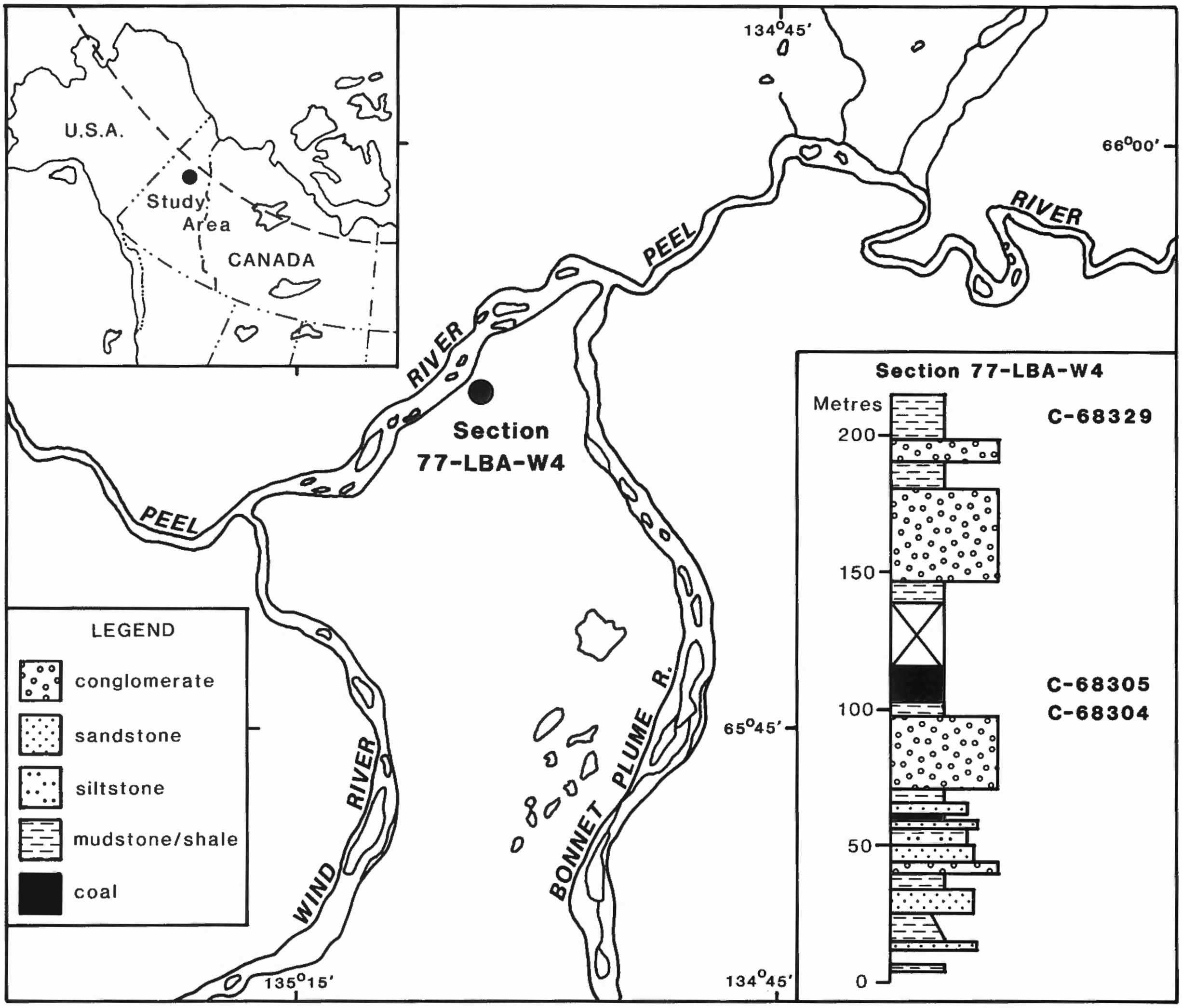

Figure 4.1. Location and lithological sequence of Section 77-LBA-W4 in the Bonnet Plume Formation, Yukon Territory (NTS 106 E). Sample horizons with fungi are indicated by GSC locality numbers.

of the 18 samples collected from the section contained abundant fungal remains consisting of a variety of spores, fragments of vegetative hyphae, portions of mycelia, and fructifications from Microthyriaceae and Meliolaceae. The fungal material in these samples is well preserved and comparatively better represented than pollen and other spores.

GEOLOGICAL FRAMEWORK OF THE STUDY AREA

The Bonnet Plume Formation is a thick, predominantly clastic and nonmarine sequence of Cretaceous and Tertiary deposits occupying the structural depression called the Bonnet Plume Basin. The basin is located within the Columbian Orogen of the Cordilleran orogenic system of northern Yukon Territory (Norris and Hopkins, 1977). Accounts of the structural and geological framework of the Bonnet Plume Basin have been published (Mountjoy, 1967; Norris and Hopkins, 1977; Long, 1978).

Four major fining-upward depositional sequences occur within the Bonnet Plume Formation, each starting with a coarse conglomeratic unit and ending with fine grained, often coal-bearing sediments. The first of these cycles, of Albian to Campanian age, and the second, of latest Campanian to late Maastrichtian age, yield diverse pollen and spore assemblages (Rouse and Srivastava, 1972; Nichols and Sweet, pers. comm.), but fungal spores are infrequent. The shale and mudstone from the third and fourth Paleocene to possibly Eocene depositional sequence

(Rouse and Srivastava, 1972; Kalgutkar, 1985) are the focus of this paper. The third sequence starts with a conglomerate about 25 m thick overlain by a 45 m thick recessive interval of mudstone capped by lignite. Overlying the recessive interval of the third sequence is a conglomerate approximately 35 m thick, which in turn is overlain by mudstone and thinner conglomeratic beds, which together form the fourth fining-upward sequence.

The Paleocene (zone 3) assemblage of Rouse and Srivastava (1972) from the third fining-upward sequence was characterized by the presence of mainly triporate species representing the families Betulaceae and Myricaceae, an abundance of conifer pollen, and the presence of individual species, including *Extratriporopollenites* sp., *Paraalnipollenites alterniporus* (Simpson) Srivastava, 1975 and *Pistillipollenites macgregorii* Rouse, 1962. A more recent study of the third and fourth fining-upward sequence (Sweet, pers. comm.) established the presence of species additional to those reported by Rouse and Srivastava, including *Caryapollenites inelegans* Nichols and Ott, 1978, *Caryapollenites wodehousei* Nichols and Ott, 1978, *Tilia vescipites* Wodehouse, 1933, and cf. Acanthaceae A *in* Rouse (1977) in samples C-68304 and C-68305 from the base of the first recessive interval (Fig. 4.1). The sample from GSC loc. C-68329, the stratigraphically highest mudstone in the section, yielded *Momipites triradiatus* Nichols, 1973, *Caryapollenites imparalis* Nichols and Ott, 1978, *C. wodehousei* and *Pterocarya stellatus* (R. Potonié) Martin and Rouse, 1966. This combination of species indicates that the samples are no older than the late Paleocene P5 zone of Nichols and Ott (1978). However, a single specimen of *Juglans* sp. was observed within the same stratigraphic interval of another section. An earliest Eocene age therefore cannot be excluded.

The lithology and stratigraphic position of the samples from GSC locs. C-68304 and C-68305 suggests a depositional environment marginal to a coal swamp. The sample from GSC loc. C-68304 is a mudstone devoid of macroscopically visible plant material, directly overlain by a mudstone containing abundant plant material, probably leafy tissue (GSC loc. C-68305). The organic rich mudstone is in turn overlain by a thick bed of lignite. This sequence of lithotypes suggests a shift from a well-oxygenated floodplain environment (GSC loc. C-68304) to a reducing environment marginal to a coal swamp (GSC loc. C-68305). There is no coal directly associated with GSC loc. C-68329, but like GSC loc. C-68305 it also contains abundant plant material. Therefore, a water saturated, reducing floodplain environment can also be inferred for the former locality.

SAMPLE PREPARATION

The samples were macerated by standard palynological procedures using 25% hydrochloric acid (HCL), concentrated hydrofluoric acid (HF), light oxidation with Schulze's solution, base treatment with 10% ammonium hydroxide (NH_40H) and heavy liquid separation of palynomorphs with zinc bromide ($ZnBr_2$) of sp. gr. 2. Greater control on the rate of oxidation was accomplished by using a weak or diluted Schulze's solution, which improved the recovery of fungal spores. A small quantity of "Javex" or "Clorox" bleach was added to residues in Schulze's solution and allowed time to react before the solution was heated in a hot water bath. This proved effective in obtaining better, cleaner preparations. The final residues containing the palynomorphs were stained with safranine 0. Spores with relatively thin walls and less melanin became stained.

Macerals were spread on coverslips using polyvinyl alcohol. The dry coverslips were attached to labelled slides using bio-plastic epoxy. Slides of unsieved, +45 μm, -45 μm, +20 μm, and -20 μm fractions were prepared.

TYPE SLIDES

Coordinates of the figured specimens were taken using Leitz Wetzlar transmitted light microscope no. 646202 with attached camera. All slides bearing figured specimens, including holotypes, are permanently stored in the National Type Collection of Plant and Invertebrate Fossils of the Geological Survey of Canada, Ottawa. The sample residues and duplicate slides are maintained with the Geological Survey of Canada at the Institute of Sedimentary and Petroleum Geology in Calgary.

PRESERVATION AND RECOVERY

Fungal spores are generally considered more resistant to maceration techniques than pollen and other spores. This is probably due to a presence of a rigid and inelastic melanin-pigmented layer in the spore wall. It was observed, however, that fungal spores do show a tendency to disappear suddenly and abruptly with oxidation. Over-oxidation can result from either long treatment with a weak Schulze's solution or short treatment with a strong solution. It was also noted that fruiting bodies are not affected nearly as much as spores. This could be due to the more complex wall layers of the fruiting bodies, which makes them more resistant to excessive oxidation. Pollen and other plant spores were also affected by over-oxidation. However, their elimination during the process seems to occur gradually with apparent initial swelling and ultimate destruction of their walls in the ammonium hydroxide base. The effect of extreme oxidation and subsequent alkali treatment resulting in the progressive destruction and loss of dinocysts was also pointed out by Jain, Kar and Sah (1973) and Schrank (1988).

ANALYSIS OF FUNGAL PALYNOMORPHS

Identification

Spore is a general term applied to fossil fungal palynomorphs; they are either asexual spores like conidia, mainly produced by Ascomycetes and Deuteromycetes, or sexual spores like ascospores and basidiospores, produced respectively by Ascomycetes and Basidiomycetes. They also include an assortment of fungal hyphae.

The fossil fungal palynomorphs in this paper are generally referred to as "spores" for sporomorphs, irrespective of their affinity to modern asexual or sexual spores; or as "hyphae" when they represent fragments of mycelial tissue.

The so-called "pores" at the ends of fungal paleospores may either be real pores or points of attachments of the spores (Elsik et al., 1983). In fossil fungal studies, an apparent opening or aperture in a spore is referred to as a "pore" regardless of its function.

Taxonomy and nomenclature

The observed dispersed spores are compared with known form species, or described as new taxa by virtue of their morphological characters. These features include spore size and shape; septal nature and thickenings; wall sculpture; absence or presence, and number and nature of apertures or pores; and any special characteristics of diagnostic significance.

A new species was named only after 20 or more specimens with similar morphological features were counted and measured. Some new spore taxa of rare occurrence but distinctive morphology are described but not named.

Comparison

A comparison of the Bonnet Plume fungal flora was made with Paleogene floras from North America to show similarities and differences in species composition. The spores were also compared to known Tertiary fungal assemblages from countries outside North America, to assess the extent of their geographical distribution.

The spores were compared wherever possible, with their modern equivalents to show their close similarity.

Statistical treatment

Each sample was examined for the total number of species present. The relative abundance of species was determined by systematically scanning the prepared slides and counting the spores of each species on all slides of each sample. The relative abundance, estimated by using descriptive terms based on a total count scale (Table 4.1), is described as: rare (R) 1 to 10 counts; fairly common (F) 11 to 25 counts; common (C) 26 to 50 counts; very common (VC) 51 to 75 counts; abundant (A) 76 to 100 counts.

A coefficient of similarity analysis was applied to the spore assemblages from each sample to determine the degree of floristic similarity between samples. The Sörensen Coefficient (K) used by Bird and Marsh (1972) and Kalgutkar (1973) expresses the degree of floristic similarity and gives a good indication of the affinity of two floras as it takes into account the total number of species recorded from both samples. The Sörensen Coefficient (K) is described by the formula $K = (200 \times c)/(a + b)$ where 'a' is the number of species in one sample, 'b' is the number of species in other sample, and 'c' is the number of species common to both samples. The K values obtained for the samples (Fig. 4.2) are compared to estimate the degree of similarity between the samples.

FOSSIL FUNGI — A BRIEF REVIEW

The inclusion of paleomycology in most palynological and paleobotanical studies is often neglected for various reasons. Tiffney and Barghoorn (1974)

TABLE 4.1

Relative abundance of species from three samples of the early Tertiary Bonnet Plume Formation

Genera and species	Sample C-68329	Sample C-68305	Sample C-68304
Brachysporisporites pyriformis	VC	VC	F
B. atratus sp. nov.	VC	R	R
B. sp. A	R	-	-
B. bullatus sp. nov.	VC	F	C
B. catinus	VC	R	R
B. sp. B	R	-	-
B. sp. C	-	-	R
B. sp. D	C	-	F
Chaetosphaerites sp.	R	-	-
Ctenosporites eskerensis	R	-	R
Desmidiospora sp.	R	-	R
Dicellaesporites sp. A	-	-	R
D. sp. B	-	-	R
D. cellaequalis sp. nov.	-	VC	-
D. septoconstrictus sp. nov.	R	VC	R
Dictyosporites sp. A	-	R	-
D. elsikii sp. nov.	R	F	-
D. sp. B	-	R	-
D. eccentricus sp. nov.	C	-	R
D. sp. C	R	-	R
D. sp. D	R	R	-
Didymoporisporonites discordis sp. nov.	C	C	-
Diporicellaesporites mediocoloratus sp. nov.	VC	C	R
D. navicularis sp. nov.	C	R	-
D. pluricellus	VC	C	-
D. aequabilis sp. nov.	VC	C	R
D. quaternarius sp. nov.	C	C	R
D. chitaleyae sp. nov.	C	R	-
D. sp. A	R	-	-
D. vermiculatus sp. nov.	-	C	-
D. scalaris sp. nov.	F	C	R
D. sp. B	-	R	-
D. jansonius sp. nov.	-	C	R
D. sp. C	-	-	R
D. hillsii sp. nov.	-	C	-
D. sp. D	-	-	R
D. sp. E	-	R	-
D. sp. F	R	-	-
D. sp. G	-	R	-
D. sp. H	-	-	R
Diporisporites anklesvarensis	VC	C	-
D. sp. A	-	R	-
D. hammenii	-	F	R
Dyadosporites urniformis sp. nov.	C	F	R
D. incisus sp. nov.	F	VC	R
D. inaequalis sp. nov.	-	VC	-
Exesisporites annulatus sp. nov.	-	-	C
Fractisporonites doliiformis sp. nov.	C	-	-
Fusiformisporites spp.	-	C	R
F. sp. A	-	R	-
Hyphal filament	R	-	-
Hypoxylonites sp. (?)	-	VC	-
Involutisporonites sp. A	R	-	-
I. trapezoides sp. nov.	F	C	R
Monoporisporites magnus sp. nov.	VC	R	-
M. singularis	VC	C	C
Multicellaesporites sp.	-	F	-
Palaeancistrus sp.	R	-	-
Pesavis tagluensis	-	R	C
Pluricellaesporites sp. A	R	R	-
P. sp. B	R	-	-
P. sp. C	R	-	-
P. apiculatus sp. nov.	-	VC	R
P. sp. D	R	-	-
P. sp. E	-	R	-
P. sp. F	-	-	R
P. sp. G	-	-	R
Polyadosporites suescae	C	C	-
Psilodiporites krempii	VC	VC	R
Reduviasporonites catenulatus	F	C	-
R. sp. A	-	R	-
R. ramosus sp. nov.	-	C	-
Staphlosporonites delumbus	R	C	-
Striadiporites irregularis sp. nov.	VC	-	-
Triporicellaesporites sp.	R	-	-

Relative abundance: rare (R): 1–10 counts; fairly common (F): 11–25 counts; common (C): 26–50 counts; very common (VC): 51–75 counts; abundant (A): 76–100 counts.

	C-68304	C-68305
C-68329	48	57
C-68305	49	
C-68304		

Figure 4.2. The coefficient of similarity (K) between species.

summarized these reasons by commenting that "Paleomycology has, to some extent, been ignored because of the numerous difficulties surrounding the identification of fossil fungi." Lange (1978b) found that spores of many living fungi share a limited range of basic and commonplace morphological, characteristics and those of a particular species are often variable, not stereotyped like pollen.

Pirozynski (1976b) expressed the view that fragments of mycelia or fructifications rarely provide satisfactory clues to their ordinal, or even their phyletic affiliation, and in modern classification, spores play an increasingly subordinate role to other, much more ephemeral characters. However, in the same paper, Pirozynski also suggested that studies of assemblages, and an interpretation of individual fossil fragments made in the light of contemporary biological and geological developments, promise to provide a stronger basis for speculation on the origin and phylogeny of fungi and their role in the evolution of present-day biota.

In recent years, however, fossil fungi have been attracting the attention of those palynologists interested in paleomycology as an important source of information in evaluating the geological record of plants and their environments. "Fungal spores are now a functional part of the paleontologic technique, standing alone on occurrence and relative abundance, or in conjunction with other palynomorphs" (Elsik, 1982). Evidence from the fossil record now implicates fungi in such processes as establishment of terrestrial plants, the degradation of lignin in Devonian forests, parasitic relationships with plants and animals, and the development of ancient soils (Stubblefield and Taylor, 1988). Unique fossil fungal spores like *Pesavis* and *Ctenosporites* are used quite frequently by palynologists as index fossils to substantiate age interpretations. Fossil microthyriaceous thyriothecia are generally considered as reliable indicators of paleoecological conditions.

FOSSIL RECORD OF FUNGAL SPORES

The interest in fossil fungi since the 1950's has been mainly due to the development of palynology. The remains of fungi are recorded in sediments ranging in age from Precambrian (Schopf and Barghoorn, 1979; others) to Recent, despite the delicate and fragile nature of most fungi. As early as the close of the Carboniferous, there is evidence for most of the major groups of the Eumycota, including the Chytridiomycetes, Oomycetes, Ascomycetes and Basidiomycetes (Stewart, 1983). However, most of the palynologically diverse assemblages of fungal palynomorphs consist of predominantly ascomycetous forms by the beginning of the Cretaceous (Elsik, 1992). Tiffney and Barghoorn (1974), Pirozynski (1976a, b, 1978), Elsik (1978), Pirozynski and Weresub (1979) and Stubblefield and Taylor (1988) reviewed the fossil fungal record through time with critical commentaries on their evolution. Active contributions to fossil fungi studies in India in recent years have added a great deal of literature and new taxa from strata ranging in age from Paleocene to Pleistocene.

MORPHOLOGY, TAXONOMY AND NOMENCLATURE

Pirozynski (1976b) suggested that "the fungi of the past are referable to extant orders and as of late Cretaceous or early Cenozoic (Eocene), they are essentially modern." According to Pirozynski and Weresub (1979), inclusion of fossil fungal spores under the modern classification along with their present-day counterparts showing close affinities, translate into a classification system for all fungal spores. They stressed the importance of sufficient knowledge of modern fungi in identifying fossil spores and relating them to their modern equivalents. They also laid emphasis on the use of mycological terms to convey information more precisely, and proposed the use of the Saccardoan System of Classification for Deuteromycetes (Saccardo, 1899) to classify fossil fungal spores. The Saccardoan System was based primarily on the conidial characters of shape, size, colour and septation. Kendrick and Nag Raj (1979) modified the Saccardoan System to eliminate some of the inconsistencies or ambiguities they detected in the logic of the system. They supplied the requisite demarcations between groups by introducing characters of specific importance.

In contrast to a taxonomy based on extant fungi, a formal but artificial classification of fossil fungal spores was proposed by Elsik (1976). He raised a new Form Order, Fungi Sporae Dispersae, for fossil fungal spores. The spores were further divided among eight form families. His classification was primarily based on the two most constant features, namely, septation and the presence or absence of apertures. The system followed in this paper is a compromise between the approaches of Elsik and Pirozynski.

Irrespective of whether fossil fungal spores are ordered using strictly utilitarian morphographic classification, or incorporated into the classification of living fungi, circumscription of genera and especially species can be difficult, in view of the fact that diagnostic features available are predominantly morphological and, therefore, are subject to possible variation (Smith, 1981).

The variability and overlap of characteristics also seem to create major problems in classifying dispersed fungal spores. Lange and Smith (1971) commented that "The problem is much worse than when dealing with pollen. Whereas species population of dispersed pollen may involve morphologies and size ranges so fixed that a single grain is typical, members of the one species population of dispersed fungal spores may be quite dissimilar, while individuals from different species populations may appear identical." In addition, attempts to identify dispersed fungal spores have proved difficult because mycologists seldom describe extant spores with the precision characteristic of a palynologist's analysis of the pollen and spores of fossil plants (Pirozynski, 1976b).

Although higher plants are characterized by distinctive vegetative structures specific to genera and species, fungal mycelia are not taxonomically distinguishable. The presence of anamorphic forms in Ascomycetes, restricting their life cycles to imperfect processes, further compounds the issue. This generally leaves considerable gaps in establishing links and affinities of fossil taxa to modern taxa, except where older spores have a distinctive morphology that has changed little through time.

In fungi, both fossil and modern, spores and conidia are important criteria in classification. The use of conidial ontogeny is the basis of modern fungal classification. However, in modern fungi, anamorphosis and teleomorphosis have created controversies and problems in assigning taxa to their natural class when only asexual or sexual stages in their life cycles are known. A great many fungi have septate hyphae and reproduce only by conidia. These fungi have either lost the ability to produce sexually or their sexual stages have yet to be identified. All such taxa are grouped into a single form-class, namely, the Deuteromycetes, or the so-called "Fungi Imperfecti."

Dispersed fungal spores are somewhat similar to the modern taxa included in Fungi Imperfecti. However, species based on fossil spores, having been dispersed and detached, are incomplete, having lost their mycelial thalli. In modern classification of such forms, the taxa are complete when described with attached mycelial tissue producing the conidia.

MYCOSTRATIGRAPHY

Recent studies of fossil fungi have been used to correlate the results of fungal discoveries with stratigraphy. The ability to recognize dispersed ascospores and conidia increases with the complexity of their morphology. Some fungal spores such as *Ctenosporites*, *Dictyosporites*, *Fusiformisporites*, *Imprimospora*, *Pesavis*, and *Striadiporites* are so distinctive and unique that they can be identified with unquestionable reliability and can convincingly be used as index fossils in biostratigraphic studies (Elsik and Jansonius, 1974; Norris, 1986; Kalgutkar and Sweet, 1988). Coiled helicospores and stellate staurospores are generally more distinctive than two-celled didymospores or one-celled amerospores. Elsik (1970), in his comments on fungal spores in stratigraphy, observed that fossil fungal spores are rare to abundant in Cenozoic sediments; many morphological types were established by the late Mesozoic and others appeared at various intervals in the Cenozoic. He further observed that *Fusiformisporites* and related longitudinally ribbed forms appear to be restricted to the Cenozoic, and fungal spores of the extant *Hypoxylon*-type and the form genus *Exesisporites* are ubiquitous, especially in Neogene sediments.

Ramanujam (1982) indicated that the bulk of the fungal sporomorphs recorded from early Mesozoic and earlier strata are quite simple, being aporate, aseptate and essentially psilate. Ornamental spores had, however, appeared by the Late Cretaceous and even younger times. According to Elsik (1977), ornament is probably a late development in any morphological group of spores. He indicated that aporate, aseptate spores were not ornamented until the Paleocene or Eocene, whereas ornamented aporate, multicellular spores did not appear until the Miocene. Traverse (1988) pointed out that the fungi, especially Ascomycetes, evolved rapidly during the Cenozoic, and that their spores and spore-like bodies are useful stratigraphically.

Norris (1986), in the palynological investigation of Eocene to Pliocene strata in the Mackenzie Delta region of Canada, established a middle Eocene *Pesavis* zone within the lower part of the Richards Formation. Kalgutkar and Sweet (1988) documented the first occurrence of *Pesavis* in the Maastrichtian from northwestern Canada. The stratigraphic usefulness of *Pesavis* was further developed by Kalgutkar and Sweet with the documentation of a phylogenetic lineage starting in the Maastrichtian with *P. parva* and extending into the Eocene with *P. tagluensis*. White (1990) used the presence of *Ctenosporites eskerensis* and *Pesavis tagluensis* in combination with *Tilia* spp. to determine the age of an unnamed sedimentary unit in the Union Port Louis well and float from Mud Bay Creek, British Columbia, which was estimated to be between early Eocene and early Oligocene in age.

The value of using the relative abundance of major groups of taxa in identifying stratigraphic intervals was pointed out by Elsik (1969, 1976) and Jansonius (1976). Fournier and Elsik (1984) revealed the existence of hundreds of well preserved species of fungal spores from DSDP Site 493, LEG 66 and commented on the stratigraphic value of some characteristic spores in the assemblages from early Miocene to Recent sediments.

PALEOENVIRONMENT

The importance of fungal remains in paleoecological interpretations has been suggested by many authors. Dilcher (1971) commenting on the ecology of the fossil flora suggested that the paleoenvironment could be interpreted by comparing fossils to comparable living forms and basing paleoclimatic interpretations on the climatic range of these modern forms. Pirozynski (1976a) and Ramanujam (1982) stressed coordinated studies of fossil and modern fungi to realize the full potential of fossil fungal spores as indicators of past environments. Ramanujam (1982) indicated that only the types clearly related to modern taxa with known environmental requirements are particularly useful.

The fossil fungal spore assemblages reflect the flora that developed under certain environmental conditions. Ramanujam and Srisailam (1978) correlated the presence of the helicoid spores of *Palaeocirrenalia* from the Neogene sediments of Kerala, S. India, to conditions of brackish to marine waters. Jarzen and Elsik (1986) have shown how the known habitat and host preference of many of the identified fungal forms recovered from recently deposited sediments of the Luangwa River in Zambia could conceivably be used to deduce the environmental conditions of similar fossil fungal floras recovered from Neogene sediments. Kalgutkar and McIntyre (1991) described two helicosporous fungal types morphologically similar to present-day *Helicoön–Helicodendron* and *Helicosporium* genera from the Eocene Eureka Sound Formation in the Canadian Arctic, and used their presence to interpret the paleoenvironment. The unique and easily distinguishable spores like *Ctenosporites* and *Pesavis* could be good indicators of the paleoclimate if modern counterparts or comparable forms are recovered.

In recent years, paleomycological researchers have been trying to show the relationship of fossil fungal spores to their extant representatives (Lange, 1978c; Elsik, 1986; Ethridge Glass et al., 1986; Jarzen and Elsik, 1986; Prasad, 1986; Pirozynski et al., 1988; others). The importance of coordinated studies of megafossils and associated palynomorphs has been recognized by a few workers. Dilcher (1965) presented a comprehensive account on the epiphyllous fungi from Microthyriales, Erysiphales, and Meliolales in leaves from the middle Eocene of Tennessee. A study of this nature provides a potential source of data for determining the paleoclimatic conditions of the region. Chitaley (1978) and Chitaley and Yawale (1978) described fungal spores found associated with different parts of petrified plants from the Deccan Intertrappean beds of India and commented on the host-fungus relationship. Similarly, mycorrhizal relationship of fungi in the rhizomes and roots of carboniferous plants has been reported by Taylor (1981).

Gray (1985) compared the qualitative and quantitative relationship between microfossils (including pollen and fungal spores), and plant megafossils recovered from the same sequence of beds and from the same strata within that sequence. She commented on the usefulness of such a comparison involving close-spaced samples because of the different values determined for plant megafossils and pollen in paleoenvironmental interpretations. Pirozynski et al. (1988) investigated the palynology and mycology of organic clay balls accompanying mastodon bones found in New Brunswick, Canada, and reported the presence of numerous, taxonomically and ecologically diverse fungi. These fungi accounted for the organic component of the clay ball, which was derived from plants consumed by, and contained within, the animal near the time of death. Stubblefield and Taylor (1988) and Taylor (1990) discussed the significance of fossil fungi and their associations in the terrestrial paleoecosystem in a wide variety of interactions with plants, animals and the geological environment from the Paleozoic and Mesozoic.

The importance of paleogeography in correlation studies involving past vegetation and floristic composition from worldwide geographical localities was indicated by Bharadwaj (1967) and Lange (1976, 1978a). Lange (1978b) commented on the significant presence of *Pesavis tagluensis* and *Ctenosporites eskerensis* in establishing enigmatic and unique links between widely separated Paleogene floras in Australia and North America. Subsequent reports of these forms from England by Smith (1978) and Smith and Crane (1979), and more recently of *P. tagluensis* from Turkey (Ediger and Alisan, 1989) increase their importance in paleoclimatic correlations.

FOSSIL MICROTHYRIACEOUS FUNGI

The importance of fungal fructifications in biostratigraphy is mentioned by many workers in spite of the problems encountered in their comparison with modern taxa. Although dispersed fungal fructifications are not generally found associated with mycelia and spores, they can be referred to extant taxonomic groups with greater accuracy than can dispersed spores, due to their complex morphology (Kalgutkar, 1985). Indeed, quite a few families belonging to the Ascomycetes such as the Meliolaceae, Microthyriaceae, and Micropeltaceae are recognizable by their non-sporic, easily fossilized organs (Pirozynski and Weresub, 1979). However, most fructifications belong to microthyriaceous fungi; their distinctive and prevailing presence is especially prominent in the mid-Tertiary.

Microthyriaceous fruiting bodies are found in strata as old as Lower Cretaceous (Krassilov, 1967; Alvin and Muir, 1970; Singh, 1971; Bajpai and Maheshwari, 1987). Ramanujam (1982) mentioned the stratigraphic importance of *Plochmopeltinites*, *Euthythyrites*, *Trichopeltinites*, and to some extent *Parmathyrites*, in the Neogene strata of India, because of their limited geological ranges.

Compared to fossil fungal spores, fossil microthyriaceous fungi are generally preferred as paleoenvironmental indicators. The complex and peculiar morphological structures of their fructifications are distinctive. They are easily identifiable and therefore, unquestionably form a dependable source of information for the ecology of past vegetation. Palynological studies involving paleoclimatic discussions and conclusions are often substantiated by citing the presence of microthyriaceous ascocarps in sediments.

The occurrence of epiphyllous fungi has been correlated with moist, humid climates favouring the lavish growth of forest vegetation and ground vegetation flourishing under the canopy of trees (Kalgutkar, 1985). The abundance of microthyriaceous fungi indicates a floristic association of vegetational types favouring high precipitation and high temperatures (Prasad, 1986). They generally thrive best in tropical and subtropical forests consisting of broad-leaved vegetation and subject to heavy precipitation. However, Dilcher (1965) and Selkirk (1975) pointed out that ecological interpretations of warm, moist conditions based on the presence of epiphyllous fungi should be treated with caution. They further commented that although most fossil epiphyllous fungi have been found associated with warm or subtropical vegetation, isolated fruiting bodies do occur over a wide latitudinal range in Pleistocene deposits of North America (Rosendahl, 1943), and under a wide range of climatic conditions in Britain (Godvin and Andrew, 1951). According to Selkirk (1975) paleoenvironmental conclusions would be more dependable if the occurrences of microthyriaceous fungi were studied in conjunction with palynological assemblages. The classification and geological history of microthyriaceous fungi was given by Elsik (1978).

OTHER FOSSIL FRUCTIFICATIONS

Studies of fossil ascomycetes with ascocarps are fragmentary, although the literature on fungi with sporocarps has been increasing in recent years (Stubblefield and Taylor, 1983; Stubblefield et al., 1983; Taylor and White, 1989; White and Taylor, 1989).

Earlier discoveries of fruiting bodies resembling ascomycetous ascocarps have been recorded by a few workers (Hutchinson, 1955; Baxter, 1960; Davies and Leisman, 1962; Rothwell, 1972; Dennis, 1976; Singer, 1977). Of these, a discovery of clamp-bearing fungus, described as a fossil sclerotium, *Palaeosclerotium* from the middle Pennsylvanian by Rothwell (1972) attracted much attention from mycologists because of its likely significance in the evolution of fungi, particularly Basidiomycetes. Dennis (1976) re-examined these structures and observed that they contained asci and ascospores and indicated their similarity to the cleistothecia of Ascomycetes. Most importantly, Dennis reported clamp-connections and dolipores in the vegetative hyphae of the mycelium surrounding the cleistothecium. He therefore proposed that *Palaeosclerotium* represents an intermediate evolutionary stage between Ascomycetes and Basidiomycetes, thereby postulating the evolution of Basidiomycetes from Ascomycetes through transitory forms like *Palaeosclerotium*. McLaughlin (1976), however, was skeptical about this observation and interpretation and argued that dolipores are not restricted to Basidiomycetes and reports of clamp connections in Ascomycetes are not conclusive. He further pointed out that the hyphae in contact with the fruiting body are not convincingly organically connected. Singer (1977), however reaffirmed Dennis's (1976) conclusions and suggested a possible affinity of *Palaeosclerotium* to the Eurotiales. Pirozynski and Weresub (1979) questioned the validity of these conclusions and suggested that the so-called ''asci'' might be cavities in the stroma, while the ''ascospores'' resemble tetraspores with trilete markings. They concluded that *Palaeosclerotium* is neither an ascomycete nor a basidiomycete, but an early dikaryotic fungus and a representative of a group that links Basidiomycetes with extinct, possibly symbiotic, lichen-like nematophytes.

RESULTS AND DISCUSSION

OCCURRENCE

Three samples from the Bonnet Plume Formation yielded noteworthy and diverse fungal assemblages, with some common elements (Tables 4.1 and 4.2). The combined fungal population consists of 75 species, of which 26 are new; 26 form-genera are identified.

The total mycoflora is mainly characterized by species commonly found in samples C-68305 and C-68329 (Table 4.1). It is dominated by *Brachysporisporites pyriformis*, *Diporicellaesporites mediocoloratus* sp. nov., *D. pluricellus*, *D. aequabilis* sp. nov., *D. anklesvarensis*, *Monoporisporites singularis* and *Psilodiporites krempii*. The fungal assemblage of sample C-68329 was distinguished by more common taxa than those found in samples C-68305 and C-68304 (Table 4.2). The selective presence of some taxa in each sample (Table 4.2) is indicative of species diversity in the total fungal population from the Bonnet Plume Formation.

The K values of coefficient of affinity indicate that the three fungal assemblages were not significantly similar to each other. However, the K values (Fig. 4.2) indicate that fungal assemblages of samples C-68329 and C-68305 are more closely related to each other than they are to the fungal assemblage of C-68304. A closer affinity in distribution of fungal species between

TABLE 4.2
Distribution of genera and species in different categories

Genera and Species	Total number of species present in each sample ◎ very common			Species restricted to each sample			Species found in all samples	Species common to samples	Species common to samples	Species common to samples
	C-68329	C-68305	C-68304	C-68329	C-68305	C-68304		C-68329 C-68305	C-68329 C-68304	C-68305 C-68304
Brachysporisporites pyriformis	◎	◎	○				✳	+	+	+
B. atratus sp. nov.	◎	○	○				✳	+	+	+
B. sp. A	○			○						
B. bullatus sp. nov.	◎	○	○				✳	+	+	+
B. catinus	◎	○	○				✳	+	+	+
B. sp. B	○			○						
B. sp. C			○			○				
B. sp. D	○		○							
Chaetosphaerites sp.	○			○						
Ctenosporites eskerensis	○		○						+	
Desmidiospora sp.	○		○						+	
Dicellaesporites sp. A			○			○				
D. sp. B			○			○				
D. cellaequalis sp. nov.		◎			○					
D. septoconstrictus sp. nov.	○	◎	○				✳	+	+	+
Dictyosporites sp. A		○			○					
D. elsikii sp. nov.	○	○						+		
D. sp. B		○			○					
D. eccentricus sp. nov.	○		○						+	
D. sp. C	○		○						+	
D. sp. D	○	○						+		
Didymoporisporonites discordis sp. nov.	○	○						+		
Diporicellaesporites mediocoloratus sp. nov.	◎	○	○				✳	+	+	+
D. navicularis sp. nov.	○	○						+		
D. pluricellus	◎	○						+		
D. aequabilis sp. nov.	◎	○	○				✳	+	+	+
D. quaternarius sp. nov.	○	○	○				✳	+	+	+
D. chitaleyae sp. nov.	○	○						+		
D. sp. A	○			○						
D. vermiculatus sp. nov.		○			○					
D. scalaris sp. nov.	○	○	○				✳	+	+	+
D. sp. B		○			○					
D. jansonius sp. nov.		○	○							+
D. sp. C			○			○				
D. hillsii sp. nov.		○			○					
D. sp. D			○			○				
D. sp. E		○			○					
D. sp. F	○			○						
D. sp. G		○			○					
D. sp. H			○			○				
Diporisporites anklesvarensis	◎	○						+		
D. sp. A		○			○					
D. hammenii		○	○							+
Dyadosporites urniformis sp. nov.	○	○	○				✳	+	+	+
D. incisus sp. nov.	○	◎	○				✳	+	+	+
D. inaequalis sp. nov.		◎			○					
Exesisporites annulatus sp. nov.			○			○				
Fractisporonites doliiformis sp. nov.	○			○						
Fusiformisporites spp.		○	○							+
F. sp. A		○			○					
Hyphal filament	○			○						
Hypoxylonites sp. (?)		◎	○							+
Involutisporonites sp. A	○			○						
I. trapezoides sp. nov.	○	○	○				✳	+	+	+
Monoporisporites magnus sp. nov.	◎	○						+		
M. singularis	◎	○	○				✳	+	+	+
Multicellaesporites sp.		○			○				+	
Palaeancistrus sp.	○			○						
Pesavis tagluensis		○	○							+
Pluricellaesporites sp. A	○	○						+		
P. sp. B	○			○						
P. sp. C	○			○						
P. apiculatus sp. nov.		○	○							+
P. sp. D	○			○						
P. sp. E		○			○					
P. sp. F			○			○				
P. sp. G			○			○				
Polyadosporites suescae	○	○						+		
Psilodiporites krempii	◎	◎	○				✳	+		
Reduviasporonites catenulatus	○	○						+	+	+
R. sp. A		○			○					
R. ramosus sp. nov.		○			○					
Staphlosporonites delumbus	◎	○						+		
Striadiporites irregularis sp. nov.	○			○						
Triporicellaesporites sp.	○			○						
Total number Percentage	45 (60%)	47 (63%)	34 (45%)	14 (19%)	15 (20%)	9 (12%)	14 (19%)	26 (35%)	19 (25%)	20 (27%)

samples C-68329 and C-68305, although from different stratigraphic levels in the section, is possibly related to their similar lithotypes. Both these samples are of mudstone containing abundant plant leaf material; sample C-68304, however, is a mudstone devoid of macroscopically visible plant material. The lithology and stratigraphic position of the samples from GSC locs. C-68304 and C-68305 (Fig. 4.1) indicate a depositional environment marginal to a coal swamp, with a shift from the well oxygenated floodplain environment of sample C-68304, to the reducing environment marginal to a coal swamp as in C-68305. There is no coal associated with C-68329 which, however, like C-68305 also contains abundant plant material. This may suggest that environmental factors including substrate ecology and microclimate were at least partially important in the distribution of fungi in Bonnet Plume strata.

AFFINITY

Some fungal spores from the Bonnet Plume Formation appear closely similar in morphological characters to their probable modern equivalents generally as conidia of Hyphomycetes, or ascospores of Ascomycetes. In Table 4.3 is a list of fungal species from the Bonnet Plume with their comparable modern taxa.

AGE

A brief comparison of fungal spores from the Bonnet Plume Formation with those from strata of Tertiary age in Argentina, Australia, Africa, China, England, India, Malaya, and Russia indicates that there is some similarity between Tertiary fungal spore assemblages described from these countries and those investigated in the Bonnet Plume Formation. A few characteristic species like *Ctenosporites eskerensis*, *Diporicellaesporites pluricellus*, *Diporisporites anklesvarensis*, and *Pesavis tagluensis* are fairly common. However, most fungi, although represented widely by form-genera like *Brachysporisporites*, *Diporicellaesporites*, *Diporisporites*, *Exesisporites*, *Fusiformisporites*, *Pluricellaesporites*, *Polyadosporites*, and *Staphlosporonites* vary in differentiation at the species level. The distinctive spores *Ctenosporites eskerensis* and *Pesavis tagluensis* have not been encountered from India despite extensive paleomycological literature on its Tertiary sediments.

The fungal spore assemblages of the Bonnet Plume Formation had relatively more fungal spores in common with those from other Paleogene sediments from North America than elsewhere in the world. These North American fungal assemblages are often found to contain widespread spores like *Brachysporisporites pyriformis*, *Ctenosporites eskerensis*, *Diporicellaesporites pluricellus*, *Diporisporites anklesvarensis*, *D. hammenii*, *Monoporisporites singularis*, *Pesavis tagluensis*, *Polyadosporites suescae*, *Reduviasporonites catenulatus* and *Staphlosporonites delumbus*, which have also been recovered in the present fungal population.

Fungal species *Brachysporisporites catinus*, *Ctenosporites eskerensis*, *Diporicellaesporites pluricellus*, *Diporisporites anklesvarensis*, *Monoporisporites singularis*, *Pesavis tagluensis*, *Reduviasporonites catenulatus* and *Staphlosporonites delumbus*, found in the Bonnet Plume Formation,

TABLE 4.3

Affinity of Bonnet Plume fungi

FOSSIL TAXON	EXTANT TAXON	EXTANT GROUP	EXTANT FUNGAL TYPE
Brachysporisporites	*Brachysporium/Brachysporiella*	Dematiaceous Hyphomycetes	Conidium
Chaetosphaerites sp.	*Chaetosphaeria* sp.	Pyrenomycetous Ascomycetes	Ascospore
Ctenosporites eskerensis	*Dictyosporium toruloides*	Dematiaceous Hyphomycetes	Conidium
Desmidiospora sp.	*Desmidiospora* sp.	Dematiaceous Hyphomycetes	Conidium
Dicellaesporites sp. A	*Hypocrea* sp.	Pyrenomycetous Ascomycetes	Ascospore
Dictyosporites elsikii sp. nov.	*Septosporium bulbotrichum*	Dematiaceous Hyphomycetes	Conidium
Dictyosporites sp. B	*Pleospora* sp.	Loculoascomycetidae-Ascomycetes	Ascospore
Dictyosporites sp. D	*Monodictys* sp.	Dematiaceous Hyphomycetes	Chlamydospore/conidium
Diporicellaesporites jansonius sp. nov.	*Annellophora* sp.	Dematiaceous Hyphomycetes	Conidium
Diporicellaesporites sp. F	*Corynespora foveolata*	Dematiaceous Hyphomycetes	Conidium
Exesisporites	*Nigrospora*	Dematiaceous Hyphomycetes	Conidium
Fusiformisporites	*Cookeina*	Discomycetous Ascomycetes	Ascospore
Involutisporonites trapezoides sp. nov.	*Helicoma* sp.	Dematiaceous Hyphomycetes	Conidium
Monoporisporites singularis	*Gilmaniella humicola*	Dematiaceous Hyphomycetes	Conidium
Pluricellaesporites apiculatus sp. nov.	*Phaeodactylium alpiniae*	Dematiaceous Hyphomycetes	Conidium
Polyadosporites suescae	*Papulospora* sp.	Mycelia Sterilia	Sclerotium-like bulbil
Reduviasporonites catenulatus	Capnodiaceous hyphae	Loculoascomycetidae Ascomycetes	Mycelium
Triporicellaesporites sp.	*Triposporium* sp.	Dematiaceous Hyphomycetes	Conidium

have also been recorded from other Paleogene strata of Arctic Canada (Jansonius, 1976; Rouse, 1977; Norris, 1986). Of these, *Ctenosporites eskerensis*, (Rouse, 1977; *C. wolfei*, Pl. 2, fig. 48), *Diporicellaesporites pluricellus* (Rouse, 1977; *Multicellaesporites* spp., Pl. 2, fig. 47) and *Diporisporites anklesvarensis* (Rouse, 1977; *Punctodiporites* A, Pl. 2, figs. 44, 45) are mainly restricted to late Paleocene to Eocene. The presence of these forms in the Eocene of the Arctic and in the Bonnet Plume, is supportive of an Eocene age for the studied interval, as suggested by the presence of *Juglans*. In addition, the absence of the distinctive fungal taxon *Imprimospora tankensis* Norris 1986, which is present in Upper Eocene and possibly younger strata of the Arctic, may be considered indicative of the Bonnet Plume Formation being older than Late Eocene in age. Specific occurrences of *Brachysporisporites* sp. A, *Ctenosporites eskerensis*, *Diporicellaesporites* sp., *D.* sp. F, *Fractisporonites doliiformis* sp. nov., *Involutisporonites* sp. A, *Palaeancistrus* sp., *Pluricellaesporites* sp. B, *P.* sp. C, *P.* sp. D, *Sriadiporites irregularis* sp. nov., and *Triporicellaesporites* sp. A in sample C- 68329 indicate their first appearence in the upper level of the section, and their younger age. Similarly, species like *Dicellaesporites cellaequalis* sp. nov., *Diporicellaesporites vermiculatus* sp. nov., *Dyadosporites inaequalis* sp. nov., *Exesisporites annulatus* sp. nov. and others, which occur restricted to stratigraphically lower samples C-68304 and C-68305, suggest their occurrence is stratigraphically limited.

PALEOENVIRONMENT

The presence of noteworthy fungal populations in the Bonnet Plume is indicative of an environment conducive to the flourishing of these fungi. The fungal spores were generally found to be related to types belonging to extant Hyphomycetes and Ascomycetes. This indicates that the depositional environments of the Bonnet Plume Formation strata favoured the growth of both saprophytic and parasitic forms, along with epiphyllous fungi (Kalgutkar, 1985).

The occurrence and evolution of microthyriaceous fungi after the Cretaceous–Tertiary boundary event is usually correlated with the evolution of angiosperms that are modern in aspect. Extant microthyriaceous fungi appear to thrive in humid, tropical and subtropical environments, generally epiphyllic on broad-leaved angiosperms. Many of these fungi are resistant to extremes of temperature, but most are adversely affected by desiccation (Ramanujam, 1982). Their occurrence, therefore, is generally restricted to forests in wet tropical to subtropical climates.

The occurrence of microthyriaceous and *Meliola*-like fructifications (Kalgutkar, 1985) implies warm, wet, humid surroundings. The Meliolales are primarily tropical, although they also occur in the warmer regions of the temperate zones. They are generally absent from the arid areas of the subtropics, indicating that at least a minimum level of humidity is required for their growth (Hansford, 1961; as quoted *in* Alexopoulos and Mims, 1983). The fungal ascocarps, however, were less common than fungal spores. This may be related to the subordinate influence of angiosperms in a predominantly coniferous forest. Although epiphyllous fungi can occur on coniferous plants, they seem to flourish more vigorously on angiosperm leaves.

Genera related to modern hyphomycetous forms such as *Brachysporisporites*, *Dictyosporites*, *Diporicellaesporites*, *Dyadosporites*, and *Pluricellaesporites* occur generally as saprophytes on dead wood and other decaying organic substrata, and require moisture and warm temperatures. Although an extant form comparable to *Pesavis tagluensis* has yet to be found, its common occurrence in sample C-68304 suggests a swampy, probably lacustrine floodplain environment (Kalgutkar and Sweet, 1988). Helicosporous hyphomycetes occur commonly today on decaying substrata and always in damp situations (Ellis, 1971). The presence of helicoid *Involutisporonites* spores, which typically have been found in fossil aquatic habitats with open, marshy and waterlogged areas (Kalgutkar and McIntyre, 1991), indicate a similar depositional climate in the Bonnet Plume strata. *Ctenosporites* occurs in variable substrata and its association with other fungal remains are thought to be indicative of moist, warm climatic conditions (Smith, 1978).

Samples from the uppermost part of the Bonnet Plume Formation were dominated by the Cupressaceae–Taxodiaceae group. The angiosperm component of the palynoflora primarily included pollen of Betulaceae, Juglandaceae, Tiliaceae, and Ulmaceae.

The dominance of coniferous vegetation and abundance of fungal sporomorphs under the canopy of trees suggest the presence of swamp conditions in a forest biome. The climax taxodiaceous forest, therefore, presumably grew in a swamp environment and nearby associated presence of angiosperms in forested stands of mixed vegetation. The rich vegetation and presence of floodplains is indicative of a considerable amount of rainfall, suggesting a climate with mild, wet winters and warm, moist summers.

The presence of dominant conifers, associated with less conspicuous angiosperms, tends to indicate that there was no true tropical rain forest climate during deposition of the Bonnet Plume Formation. The climate may have been frost free with higher rainfall for the paleolatitude than today. The climate of the Bonnet Plume could be described as mesothermal — similar to modern subtropical climates, without freezing winter temperatures (McIver, pers. comm.).

This inference, based on the possible existence of a coniferous forest with associated fungi, agrees favourably with other paleoclimatic studies of the Arctic during the Tertiary (Wolf and Hopkins, 1967; Shackeleton and Boersma, 1981; McMillan, 1986; Francis and McMillan, 1987; Miller et al., 1987; Thomas and Spicer, 1987; Francis, 1991).

The ecology of fungi forms the basis for the study of their geographical distribution. The studies of comparison of fungal assemblages from geographically disparate localities are likely to allow evaluation of the degree of correlation in their distribution and ecology. This could be achieved by comparing the occurrences of distinctive and characteristic forms, or of sporomorphs that have not changed morphologically and ecologically, or by interpreting the effect of physical and biological variables on the distribution of particular fungi.

In conclusion, the striking presence of fungal spores and ascomycetous fructifications in uppermost Bonnet Plume Formation strata offers an important source of paleoenvironmental information and provides additional support for the palynological interpretation of an Early Eocene age for the samples.

SYSTEMATIC DESCRIPTIONS

The Saccardoan system of classification (Saccardo, 1899, adapted from Alexopoulos and Mims, 1983) for modern Deuteromycetes, and the nomenclatural system (adopted from Sheffy and Dilcher, 1971) are generally followed to classify these fossil fungal spores.

Form taxa of fungal spores are grouped into *Class* Fungi Imperfecti, *Order* Sporae Dispersae and *Sections* Amerosporae, Didymosporae, Phragmosporae, Dictyosporae, and Staurosporae. The distribution of genera and species in the *Sections* is shown graphically in keys (Figs. 4.3–4.9) prepared by choosing spore characters of particular diagnostic value that differentiate genera from each other, and separate each species within a genus. The helicosporous forms, represented by species of *Involutisporonites*, are included in Phragmosporae. A species of a hyphal filament and *Palaeancistrus* sp. found in the total fungal assemblage are described under the *Order* Mycelia Sterilia (Elsik, 1976).

Class FUNGI IMPERFECTI

Order SPORAE DISPERSAE

Genus *Brachysporisporites* Lange and Smith, 1971

Type species. *Brachysporisporites pyriformis* Lange and Smith, 1971.

Granatisporites Elsik and Jansonius, 1974.

Discussion. Wilson and Webster (1946) described and illustrated the genus *Brachysporium* to accommodate spores ranging widely in size that were composed of one to several cells, and that ranged from 30 to 76 μm in length, depending upon the number of cells in the spore. The width ranged between 28 and 48 μm. However, conidia in all extant forms of *Brachysporium* have a limited number of cells, have 2 to 5 septa, vary in shape and are much smaller in overall size (Ellis, 1971).

Trivedi and Verma (1970) included Tertiary multicellular spores with two to several cells in both *Pluricellaesporites* and *Brachysporium*. They distinguished *Brachysporium* from *Pluricellaesporites* by the former being multicellular, smaller, and with the distal cell rounded and the proximal cell gradually narrowing before ending in a stalk cell. However, the two genera were not clearly defined; there were overlapping characters ascribed to both genera.

Lange and Smith (1971) proposed a new genus *Brachysporisporites* to describe spores of *Brachysporium*-type with "obovate, turbinate or pyriform phaeophragmospores of several cells much broader than long in a sharply graded series of diminishing size from a large domed apical cell to a small hyaline attachment cell, with extremely dark thick bands at septa, similarly graded towards the attachment cell."

Elsik and Jansonius (1974) described a new genus *Granatisporites*. Lange and Smith (1975a) considered its type species *G. cotalis* to belong to *Brachy-*

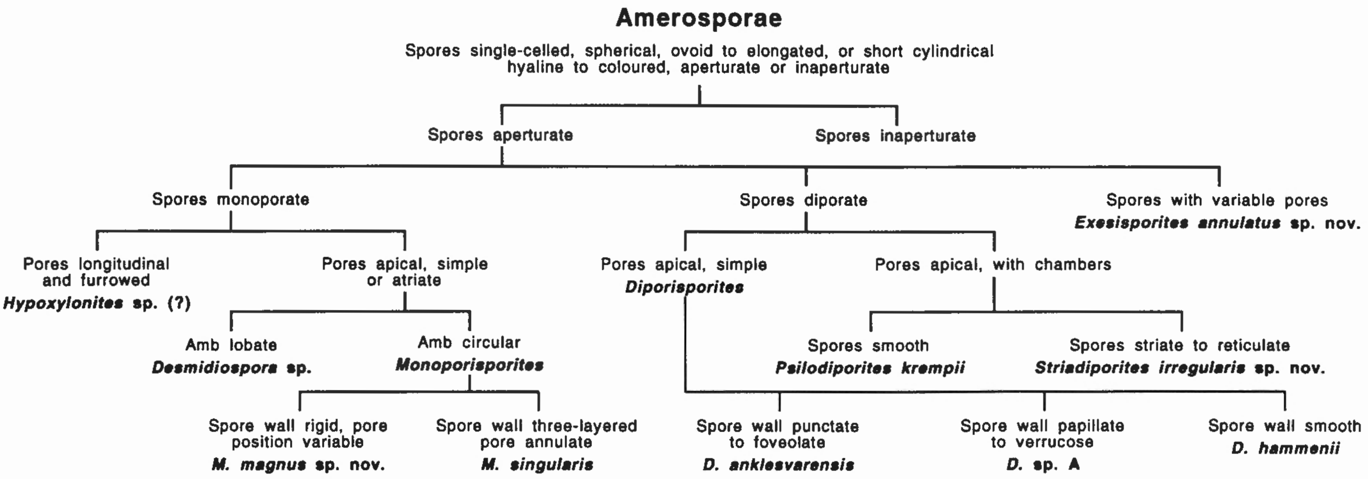

Figure 4.3. Key to the Amerosporae.

sporisporites. This makes *Granatisporites* a synonym of *Brachysporisporites*.

Affinity. Spores of *Brachysporisporites* are usually compared to the conidia of the modern hyphomycetous genus *Brachysporium*. However, they seem to appear closer to *Brachysporiella* in general appearance and morphology.

Brachysporisporites pyriformis Lange and Smith, 1971

Plate 4.1, figures 1, 2

Description. Spores pyriform with ovoid and prominently enlarged distal cells tapering gradually toward the basal end. Spores monoporate, smooth, having three to five cells, bulk of the spore consists of upper two cells. Spore walls thicker at the septa over the distal cells, reflected in dark bands; proximal cells paler with considerably thinner septa. Spore size 25–35 x 13–18 μm.

Occurrence. Very common in samples C-68329 and C-68305, fairly common in sample C-68304.

Brachysporisporites atratus sp. nov.

Plate 4.1, figure 4

Holotype. GSC 96392, GSC loc. C-68329.

Description. Spores smooth, clavate to ellipsoidal, typically four-celled, dark to opaque. Spores often with proximal two cells paler than the distal cells. Spores with thick distal septa; proximal cells with relatively thinner septa. Cell wall thick. Spore size 40–53 x 20–25 μm.

Occurrence. Very common in sample C-68329, rare in samples C-68305 and C-68304.

Etymology. From the Latin, *atratus*, dressed in black, referring to the dark colour.

Remarks. *Brachysporisporites atratus* sp. nov. is distinguished from *B. catinus* Elsik and Jansonius, 1974 by its narrowly ellipsoidal shape, uniformly dark distal portion and absence of conspicuous septal folds.

Brachysporisporites bullatus sp. nov.

Plate 4.1, figures 5, 6

Holotype. GSC 96394, GSC loc. C-68329.

Description. Spores brown to opaque, psilate, thick-walled, generally four-celled. Spore cells unequal with darker distal portion, either cylindrical to ellipsoidal or obovoid, made up of two cells, the next cell expanded or bulged, and hyaline, small, conical proximal cell. Two upper septa very much thickened forming broad transverse bands. The basal portion of the spore consist of two smaller proximal cells is distinguished from the upper portion made up of two distal larger cells by a distinct notch and a concave thickening at the septum between cells. Spore size 35–48 x 20–30 μm.

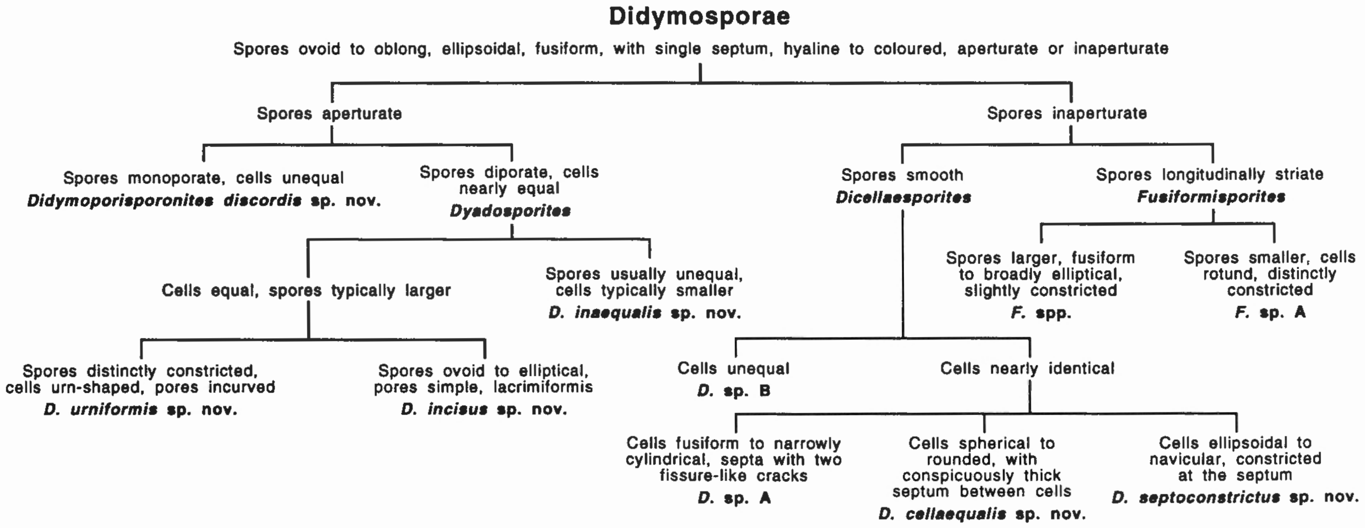

Figure 4.4. Key to the Didymosporae.

Occurrence. Very common in sample C-68329, fairly common in sample C-68305 and common in sample C-68304.

Etymology. From the Latin, *bullatus*, inflated, referring to the bulged cell.

Remarks. This species differs from *B. pyriformis* Lange and Smith, 1971 in its large size and broad distal portion. It is distinct from *B. catinus* Elsik and Jansonius, 1974 because of its expanded or bulged cell at the proximal end, and the absence of clear septal folds.

Brachysporisporites catinus Elsik and Jansonius, 1974

Plate 4.1, figures 7, 8

Description. Spores medium brown, psilate, ovate to broadly elliptical; generally four- to five-celled with lighter, hyaline, thin-walled proximal cell and a two-celled, brown, larger distal portion. Spores with a distinct incurving of the cell wall at the basal septum. Distal septa of the spore with septal folds and central pores. Spore size 37–58 x 22–35 µm.

Occurrence. Very common in sample C-68329, rare in samples C-68305 and C-68304.

Brachysporisporites sp. A

Plate 4.1, figure 3

Description. Spores unequally tricellate, medium brown, smooth. Spores with a predominantly large, rounded to turbinate apical cell, flattened central cell and a smaller protuberant lighter proximal cell subtending a pore or an attachment scar. Septum between the large distal cell and the central cell with a clear pore and septal thickening. Illustrated spore 22.5 x 17.5 µm.

Occurrence. Rare in sample C-68329.

Brachysporisporites sp. B

Plate 4.1, figure 11

Description. Spores limoniform, light brown, smooth-walled, four-celled; traversed by three curved septa. The septum at the distal end is thicker than the two proximal septa. The folds in the cell wall make the septa appear curved. Septa are porate and have septal folds. Illustrated spore 37.5 x 20 µm.

Occurrence. Rare and restricted to sample C-68329.

Brachysporisporites sp. C

Plate 4.1, figure 20

Description. Capsular, ellipsoidal, dark brown, smooth walled, pedicellate spores. Equatorial horizontal septum is a distinct, thick, opaque band nearly 3 µm thick. Spores with an external hyaline, thin layer were observed. Spore wall less than 1 µm thick, continuous

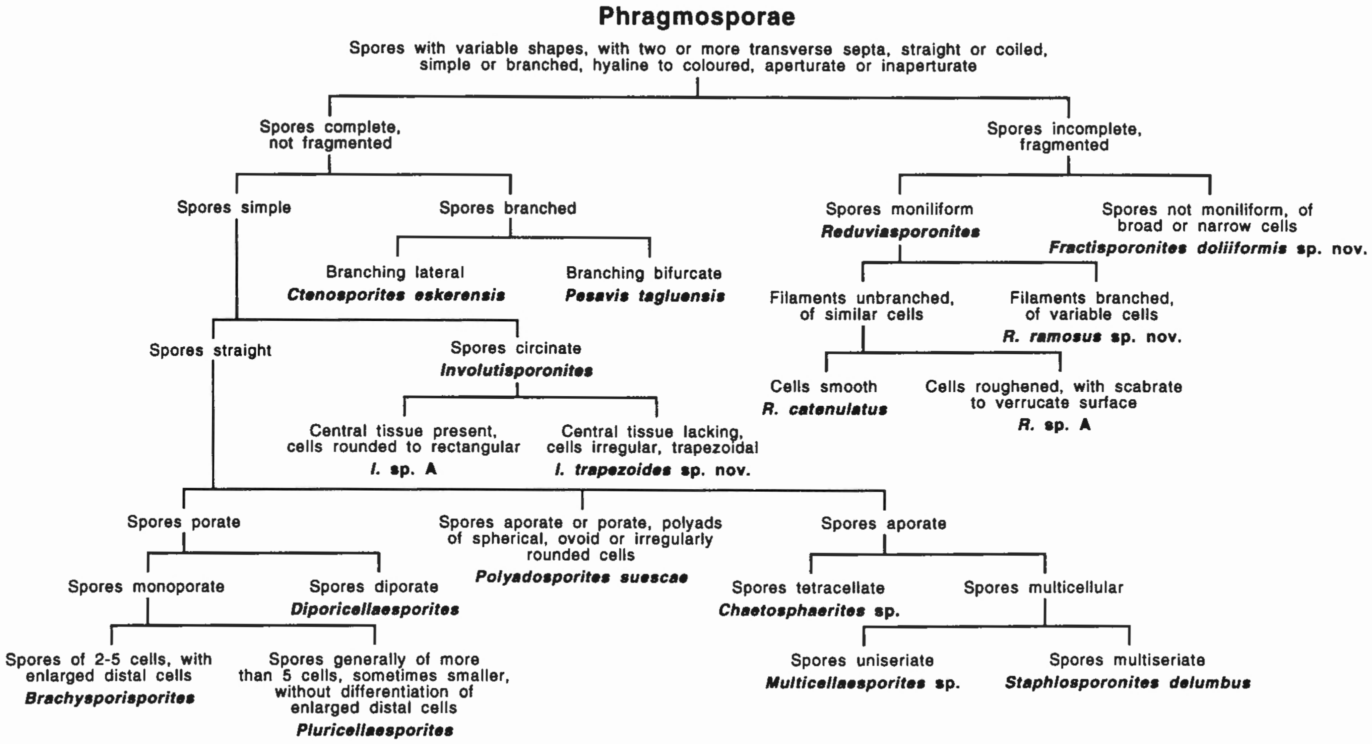

Figure 4.5. Key to the Phragmosporae.

from the appendicular pedicel making it a persistent part of the spore. The pedicel subtending the spore is pigmented. Illustrated specimen 40 x 17.5 μm.

Occurrence. Found in sample C-68304 only.

Brachysporisporites sp. D

Plate 4.3, figure 16

Description. Spores subglobose to globose, smooth, monoporate, with two or more cells, dark pigment. Cells unequal; small cell light coloured and thin. Larger portion of the spore dome shaped, opaque, consisting of one or two cells. Pore slightly excrescent, with a thick-walled collar beneath it but no pore chamber. Some specimens were wider than long. Spore size 20–38 x 20–43 μm. Illustrated specimen 42.5 x 27.5 μm.

Occurrence. Common in sample C-68329 and fairly common in sample C-68304.

Remarks. This species is generally similar to *Brachysporisporites tenuis* Kumar, 1990 except for its wide range in size.

Genus *Chaetosphaerites* Felix 1894

Type species. Chaetosphaerites bilychnis Felix, 1894.

Discussion. On the diagnosis of the genus *Chaetosphaerites,* Jansonius and Hills (1976) comment, "All those remains of fossil pyrenomycetes that are so similar in appearance to the living genus *Chaetosphaeria,* that they possibly could belong there. But such assignment would be questionable, for example when only isolated sporidia are found, because in several related genera the dispersed sporidia are similar in structure and appearance, such as e.g. *Lophiostoma, Massaria,* and *Melanomma.* The name *Chaetosphaeria* was selected for the construction of the generic name for the fossil remains, however, because in it the relationship of the Sphaeriaceae is indicated. Dispersed sporidia should only be assigned to the genus when central cells are dark or colored whilst the terminal cells have a hyaline appearance."

Chaetosphaerites sp.

Plate 4.1, figure 9

Description. Spores tetracellate, smooth, aporate, broadly ellipsoidal; central cells brown, thick-walled;

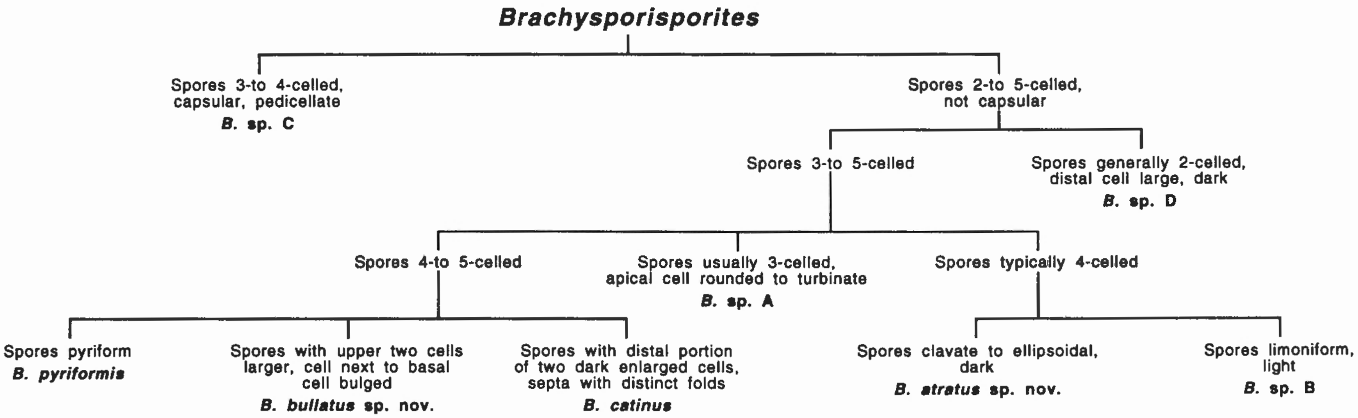

*Figure 4.6. Key to the **Brachysporisporites** species.*

terminal cells light brown to hyaline, thin-walled, cylindrical with rounded ends. Septa thick with folds and pores. Observed specimen 62.5 x 27.5 µm.

Occurrence. Rarely found in sample C-68329.

Remarks. The type species, *C. bilychnis* Felix, 1894, differs markedly from this species in being much smaller (23.8 x 8.5 µm). Also, in *C. bilychnis* a central septum cannot be discerned, whereas in this species septa with central pores, are clearly evident. This species appears more like *C. mohgaoense* reported by Chitaley (1978) from the Deccan Intertrappean beds of India.

Genus *Ctenosporites* Elsik and Jansonius, 1974

Type species. Ctenosporites eskerensis Elsik and Jansonius, 1974 emend. Smith, 1978.

Discussion. Ctenosporites is of special interest in palynological studies due to its complex, multicellular structure, and unique, distinctive and easily recognizable appearance. Its limited stratigraphic range in the Paleogene, and geographical distribution restricted to the northwest Pacific and Arctic regions of Canada, to South Australia and England could be of potential value in stratigraphic palynology and palaeoenvironmental research.

Elsik and Jansonius (1974) first described *Ctenosporites* from the Paleogene of the Pacific northwest. They proposed two species, *C. eskerensis* and *C. wolfei,* based on the pattern of curvature exhibited by the lateral branches, presence or absence of an unbroken rounded apical cell, and the number of nonhyaline, thick-walled cells of the basal filament. Lange and Smith (1975b) described a fungal mycelium-bearing *Ctenosporites* from a fossil angiosperm anther containing *Proteacidites asperopolus* Stover and Evans from the Maslin Bay Flora, South Australia. The recovery of large numbers of *Ctenosporites*-type structures led them to suggest that the entire known range of variation of *Ctenosporites* can be produced by the same mycelium. Later, Smith (1978) concluded that the variants within this highly distinctive taxon do not necessarily warrant their distinction into two species. He therefore placed *C. wolfei* in synonymy with *C. eskerensis.*

Ctenosporites eskerensis

Plate 4.1, figure 10

Synonym. Ctenosporites wolfei Elsik and Jansonius, 1974 *in* Smith (1978, p. 719–720).

Description. A multicellular fungal spore. Main stem constitutes a basal or primary filament from one side of which arise lateral branches or secondary filaments. Basal filament made up of six cells or more. The lateral branches seem to show a tendency to curve upward and toward the apical cell of the basal filament. The lateral branches are of a few to several cells in downward progression from the apical end. The apical cell of the basal filament is devoid of a lateral branch. The illustrated specimen of *Ctenosporites eskerensis* is noticeably larger (65 x 45 µm) than the holotype described by Elsik and Jansonius (1974, Pl. 1, fig. 1).

Occurrence. Rare in samples C-68329 and C-68304.

Remarks. Lange and Smith (1975b), on the basis of their observation that *Ctenosporites* grew from a

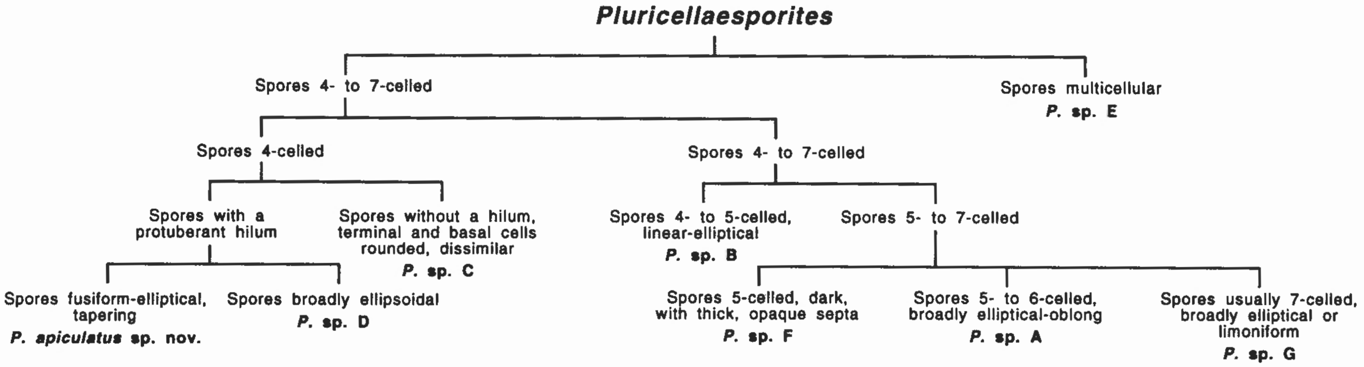

Figure 4.7. Key to the ***Pluricellaesporites*** *species.*

hyphal pedicel, concluded that *Ctenosporites* represents spores rather than a specialized branched hyphae.

Affinity. Smith (1978) suggested *Ctenosporites* to have affinities with the conidia of the extant saprophytic dematiaceous fungus *Dictyosporium toruloides*.

Genus *Desmidiospora* Thaxter, 1891

Type species. *Desmidiospora willoughbyi* (Bradley, 1967) Ethridge Glass, Brown and Elsik, 1986.

Discussion. Specimens similar in appearance to *Desmidiospora willoughbyi* have been reported by various authors under different identifications. They have been described as microthyriaceous germlings (Dilcher, 1965), as chytrids (Bradley, 1967), as hyphopodia (Vishnu-Mittre, 1973; Lange, 1976) and as algae (Davis, 1916; Bradley, 1931; Kock, 1939). Their similarity in appearance has been likened to morphological structures from algae and fungi, and their occurrences associated with different habitats have sparked debate as to their exact taxonomic position. However, more recently, there has been a general acceptance that they are fungal in nature.

Dilcher (1965) reported several spore-like stages of microthyriaceous fungi and observed their development to mature forms. These microthyriaceous germlings appear to show close similarity to *Desmidiospora*. Martin and Rouse (1966) reported similar spores from upper Tertiary sediments of the Queen Charlotte Islands, British Columbia, citing their affinity to those of the extant fungal genus *Desmidiospora*.

Bradley (1967) and Jain and Gupta (1969) described the same type of spores from the Eocene of the Green River Formation of Wyoming, and the Tertiary of the Kerala Coast, India, respectively, as *Entophlyctis willoughbyi*, an aquatic fungus belonging to Chytridiales. Elsik (1968) and Gaponoff (1984) reported such fungal bodies as microthyriaceous germlings, and Elsik in the same paper further suggested their similarity to the macroconidia of *Desmidiospora*. Vishnu-Mittre (1973) encountered identical fungal bodies along with multicellular spores attached to hyphae as fossils. He described them as *Clasterosporium caricinum*-type suggesting their affinity to the lobed hyphopodia of this modern hyphomycetous fungus. Lange (1976) presented an extensive study of the Tertiary epiphyllous "germlings" from Australia. He concluded that epiphyllous microfossil populations, like the microthyriaceous germlings in question, involve many fungi that were epiphytic in life. Accordingly, not only microthyriaceous fungi but other epiphyllic organisms are thoroughly implicated, and functionally and taxonomically unrelated structures of similar appearance could be confused with "germlings" at various points in the morphological continuum. According to Elsik (1981) the presence of a pore and general lack of septa differentiate *Desmidiospora* from "microthyriaceous germlings", if such exist. Ethridge Glass et al. (1986) reassigned *Entophlyctis willoughbyi* Bradley, 1967 to *Desmidiospora willoughbyi*. They further commented that structures of this type, though fungal in origin, cannot be assigned with certainty.

Desmidiospora sp.

Plate 4.1, figure 15

Description. Monoporate, flattened, brown, smooth fungal bodies or spores. Spores outline wavy, indented or distinctly convoluted with equatorial projections or narrow invaginations. Spore wall smooth, less than

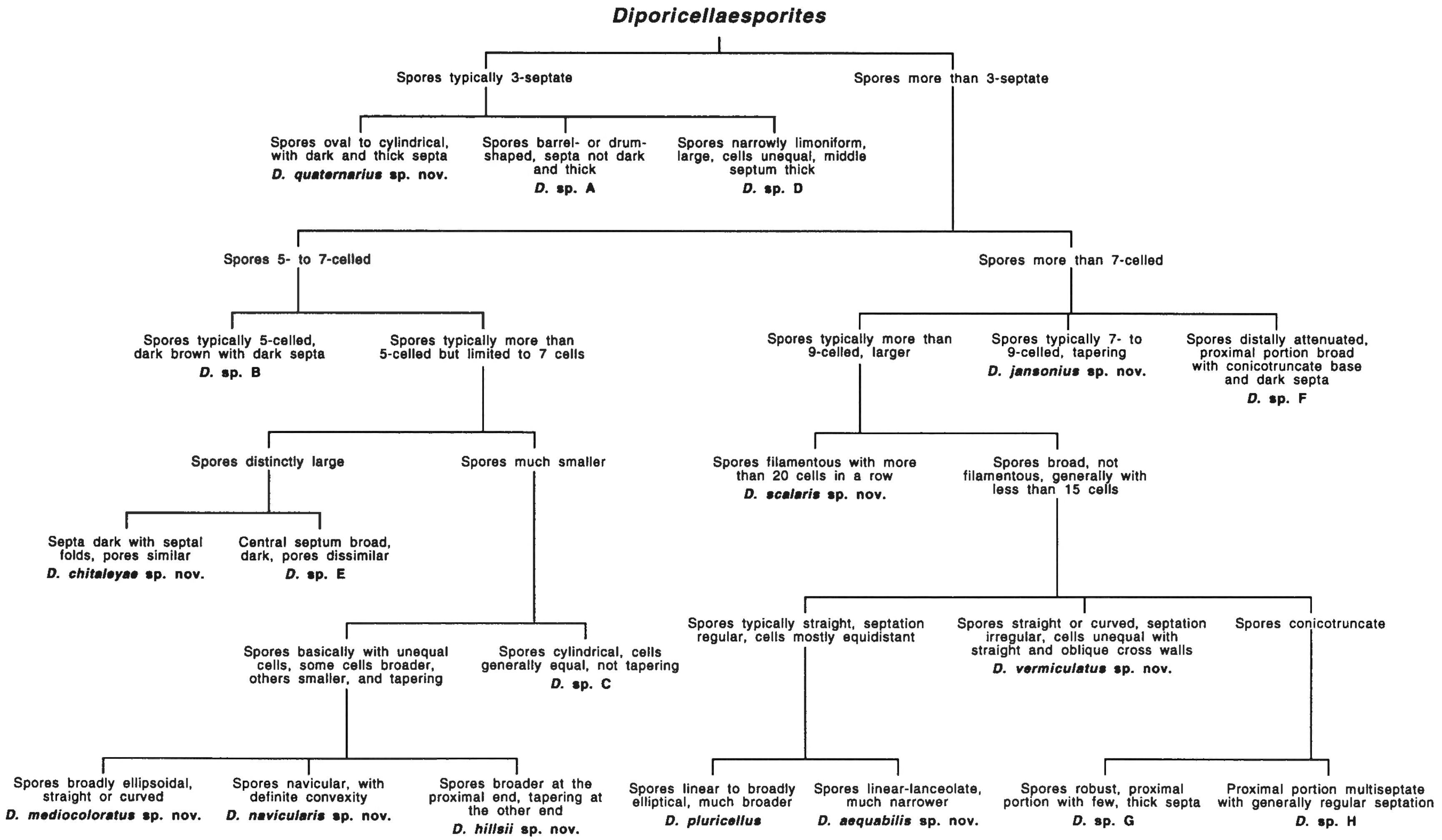

Figure 4.8. Key to the ***Diporicellaesporites*** species.

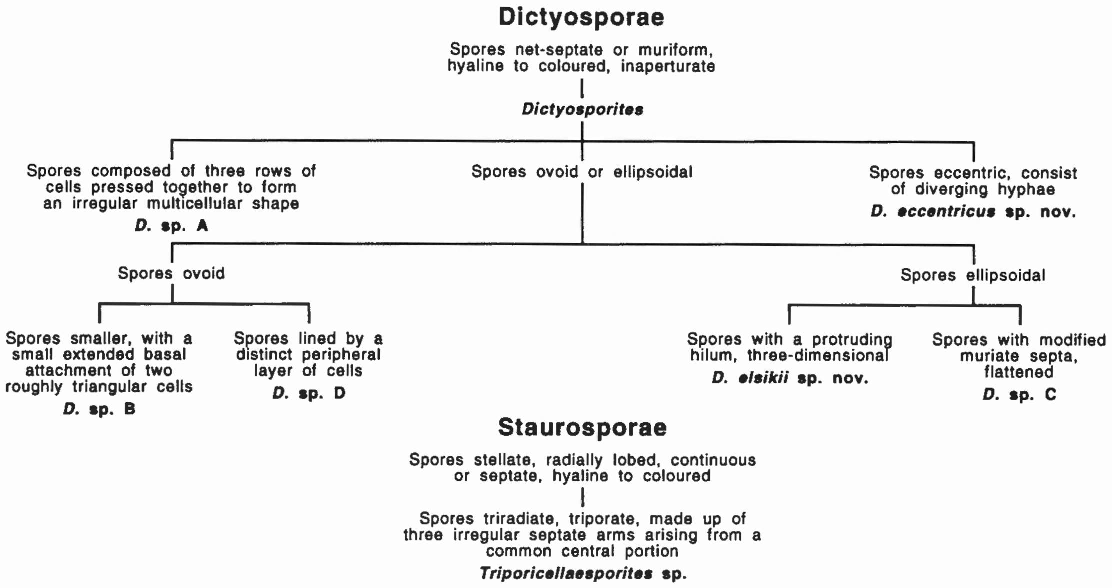

Figure 4.9. *Key to the Dictyosporae and Staurosporae.*

1 μm thick. The pore is in the form of an opening more or less centrally located, and may represent a point of attachment to the mycelium. Exine may be thickened equatorially around the pore as an annulus. Diameter from 12 to 18 μm.

Occurrence. Rare in samples C-68329 and C-68304.

Remarks. This species appears similar in appearance to *Desmidiospora willoughbyi* (Bradley, 1967) Ethridge Glass, Brown and Elsik, 1986 but lacks its secondary bilobate invaginations at the periphery.

Genus *Dicellaesporites* Elsik, 1968 emend. Sheffy and Dilcher, 1971

Type species. Dicellaesporites popovii Elsik, 1968.

Dicellaesporites sp. A

Plate 4.1, figure 12

Description. Spores brown, aporate, fusiform to narrowly cylindrical, broad in the middle, gradually tapering at the ends. Spore wall smooth; septum 2.5–3 μm thick dividing the spore into slightly unequal parts. Septum with two fissure-like cracks in the middle. Spores 70–85 x 17–23 μm in size. Illustrated spore 85 x 22.5 μm with halves 40 and 45 μm long.

Occurrence. Rare in sample C-68304.

Remarks. This spore strongly resembles *Dyadosporonites inequalis* Varma and Patil, 1985 in shape, size, appearance and even in having two pore-like cracks in the septum. The latter species is described as diporate. However, the pores are not clearly evident in the specimen illustrated by Varma and Patil (1985, Pl. 1, fig. 7). The spores resemble the ascospores of *Hypocrea,* a typical genus of the extant family Hypocreaceae (Ascomycetes).

Dicellaesporites cellaequalis sp. nov.

Plate 4.1, figure 13

Holotype. GSC 96404, GSC loc. C-68305.

Description. Aporate, monoseptate, psilate, dark brown fungal spores; spores dicellate, cells nearly equal, spherical to rounded; spore divided into two cells by a conspicuously thick septum; spore outline clearly indented at the septum. Septum about 2 μm thick, black. Spore size 18–23 x 7–13 μm.

Occurrence. Very common in sample C-68305.

Etymology. From the Latin, *cella*, cell; *aequalis*, equal, referring to the spores having both cells equal.

Remarks. The spores resemble *Dicellaesporites granuliformis* Sheffy and Dilcher, 1971 except for their larger size and typically rounded cells. They show similarity to the dicellate spores described by Prasad

(1986, Pl. 3, fig. 15), which were commonly found in the Paleogene and Neogene sediments of India.

Dicellaesporites septoconstrictus sp. nov.

Plate 4.1, figure 18

Holotype. GSC 96405, GSC loc. C-68305.

Description. Dicellate, aporate, dark brown, simple, smooth-walled spores; slightly tapering at both ends; noticeably constricted in the middle at the septum; septum about 3 μm thick. Both cells ellipsoidal to navicular. Spore size 20–28 x 7–10 μm.

Occurrence. Very common in sample C-68305, rare in samples C-68329 and C68304.

Etymology. From the Latin, *septum*, wall; *constrictus*, contracted, referring to the cells being constricted at the septum.

Remarks. This species is somewhat similar to *D. aculeolatus* Sheffy and Dilcher, 1971, but differs in being larger in size, and in having a thick wall without small irregular folds. However, the size range of *D. aculeolatus* was based on only two specimens.

Dicellaesporites sp. B

Plate 4.1, figure 16

Description. Spores two-celled, dark brown, aporate. Cells unequal, one cell much smaller; both cells thick-walled, large cell 2 μm and small cell 1 μm thick. Cells separated by a prominently thick, opaque septum 4.5 μm thick. Both cells generally rounded and flattened at the septum. Cell size: large cell 25–35 x 25 μm, small cell 10–12 x 17.5 μm.

Occurrence. Rare in sample C-68304.

Genus *Dictyosporites* Felix, 1894

Type species. *Dictyosporites loculatus* Felix, 1894.

Discussion. Different species of *Dictyosporites* are comparable to some modern genera like the conidia of *Dictyosporium*, *Stemphylium*, *Septosporium*, and *Alternaria* belonging to dematiaceous hyphomycetes, and the ascospores of *Pleospora*. Also, the fossil form genus described as *Pleosporonites* Lange and Smith, 1971 appears to be closely related to *Dictyosporites*. *Pleosporonites hyalinus* Lange and Smith, 1971 resembles the ascospores of the extant genus *Pleospora*. Vishnu-Mittre (1973) reported various fungal remains from Flandrian deposits in the Whittlesey Mere Region, Hunts, England and compared multicellular spores with both parallel and cross walls (Pl. 2, figs. 38–40) with conidia of the modern genus *Stemphylium*. Spores comparable to the ascospores of modern *Pleospora* have been identified from the Holocene of the Netherlands (Van Geel, 1978), and from East African lake sediments and alluvial deposits of the Late Pleistocene and Eocene (Wolf, 1966a, b, 1967a, b, 1968, 1969a, b, 1970), and the Deccan Intertrappean beds of India (Chitaley, 1978).

Ramanujam and Srisailam (1978) described a *Dictyosporium* spore type (Pl. 2, fig. 29) and illustrated the striking resemblance of this fossil form to the conidia of the living *Dictyosporium*.

Dictyosporites elsikii sp. nov.

Plate 4.1, figure 22

Holotype. GSC 96408, GSC loc. C-68305.

Description. Spores muriform, aporate, light brown, solitary, simple, usually broadly ellipsoidal with a protruding hilum and rounded apex. Some three-dimensional spores were noted (Pi. 4.1, fig. 22). Spore wall smooth, thin; spores divided by longitudinal and cross walls to form an irregular, multicellular, reticulate pattern of thin walled, squarish to rectangular cells. Spore size 55–73 x 30–38 μm. Not common but distinctive.

Occurrence. Fairly common in sample C-68305, rare in sample C-68329.

Etymology. Named in honor of Dr. William C. Elsik.

Remarks. *Dictyosporites elsikii* sp. nov. differs from other known species of *Dictyosporites* in its size, shape and general morphology.

Affinity. This species appears analogous to the extant conidia of *Septosporium bulbotrichum*.

Dictyosporites sp. A

Plate 4.1, figure 21

Description. Spores broadly oblong or irregular, brown, slightly curved, multicellular, smooth-walled. Spores tristichous, composed of three rows of cells of approximately the same length; each row of five to six rounded to rectangular cells, often constricted at the septa; cells 7–8 μm wide. Illustrated spore 40 x 15 μm.

Occurrence. Rare in sample C-68305.

Remarks. The spore resembles the conidia of the extant genus *Dictyosporium* but seems to be different in morphology from the fossil forms included in *Dictyosporites*, which is characterized by a multicellular body consisting of transverse and longitudinal septa forming an irregular muriform pattern. Varma and Patil (1985) described two *Dictyosporium*-type spores (Pl. 1, figs. 23, 24), of which figure 24 resembles the present form.

Dictyosporites sp. B

Plate 4.1, figure 17

Description. Spores muriform, aporate, dark brown, ellipsoidal to ovoid; multiseptate, with regular transverse and irregular longitudinal septa, three-dimensional. Cells form a somewhat brick-like pattern made up of thick-walled cells. Spores with a small extended basal attachment of two roughly triangular cells. Illustrated specimen 25 x 17.5 μm.

Occurrence. Rare in sample C-68305 only.

Remarks. These spores appear similar to the spores of *Pleosporonites* Lange and Smith, 1971 but differ from *P. hyalinus* Lange and Smith, 1971 in having noticeably thick-walled cells. The spores also show close resemblance to the modern ascospores of *Pleospora*, except for their thick-walled cells. The basal attachment of extended cells may be comparable to a claw-like basal scar found in the ascospores of *Pleospora*.

Dictyosporites eccentricus sp. nov.

Plate 4.3, figure 4

Holotype. GSC 96449, GSC loc. C-68329.

Description. Spores eccentric, laterally flattened in one plane, variable in shape, brown, smooth; spores appear muriform with juxtaposed rows of cells radiating and diverging from the hilum to form a loose pseudoparenchymatous tissue or a fascicle of square to rectangular cells. The rows of cells are of unequal length and held close together in a somewhat semicircular shape; the middle ones being generally longer than those at the sides. Illustrated specimen 55 x 35 μm in size.

Occurrence. Common in C-68329 and rare in sample C-68304.

Etymology. From the Latin, *eccentricus*, lateral, referring to the lateral spores.

Remarks. *Dictyosporites eccentricus* sp. nov. is distinguished from other species of *Dictyosporites* by its eccentric and diverging rows of cells from the hilum.

Affinity. These spores show some similarity to the conidia of most species of the modern genus *Dictyosporium* in having rows of cells flattened in one plane.

Dictyosporites sp. C

Plate 4.3, figure 5

Description. Fungal body, oval-ellipsoidal, mid to light brown, consisting of two central longitudinal ribs and eight to ten lateral septa on either side. Spores pluricellate with modified muriate septa; the edges of the septa are thickened. External wall smooth, moderately thick, with slight notches at the point of contact between lateral septa. Spore size 30–63 x 22–33 μm.

Occurrence. Rare in samples C-68329 and C-68304.

Dictyosporites sp. D

Plate 4.3, figure 7

Description. Fungal spores made up of many cells to form an unevenly muriate spherical group. Spores brown, smooth, aporate; differentiated into a clear central tissue of irregular cells and a distinct, peripheral layer of elongated, rectangular cells on the outside. Basal cell conspicuously inflated, protruding, coarsely triangular. Central cells squarish, rhomboid to polyhedral, thicker and darker than outer cells and the basal cell. Spore size between 37 and 43 μm in diameter.

Occurrence. Rare in samples C-68329 and C-68305.

Affinity. The multicellular spores in this species may be compared to the terminal chlamydospores resembling those of *Monodictys* as illustrated by Pirozynski and Weresub (1979; Pl. 2, fig. 18) or to the conidia of *Monodictys* (Ellis, 1971).

Genus *Didymoporisporonites* Sheffy and Dilcher, 1971

Type species. *Didymoporisporonites psilatus* Sheffy and Dilcher, 1971.

Didymoporisporonites discordis sp. nov.

Plate 4.1, figure 14

Holotype. GSC 96410, GSC loc. C-68305.

Description. Spores monoporate, dicellate, smooth. Cells of unequal size and shape, one cell much smaller than the other. Larger cell dark brown, robust, spherical to ovoid; smaller cell light brown to hyaline, spherical to dome-shaped, porate. Cell wall slightly thicker in large cell than in small cell. Spores constricted and thickened at the septum. Septum centrally porate. Pore in the small cell simple. Diameters: large cell 12.5–20 μm, small cell 5–10 μm.

Occurrence. Common in samples C-68329 and C-68305.

Etymology. From the Latin, *discordis*, different, referring to the unequal cells.

Remarks. This species is different from *D. psilatus* Sheffy and Dilcher, 1971 in being larger and in the shape of both large and small cells. It also differs from *D. inaequalis* Sheffy and Dilcher, 1971 in general morphology and absence of disk-shaped septum.

Genus *Diporicellaesporites* Elsik, 1968

Type species. *Diporicellaesporites stacyi* Elsik, 1968.

Diporicellaesporites aequabilis sp. nov.

Plate 4.2, figure 2

Holotype. GSC 96415, GSC loc. C-68329.

Description. Spores multicellular, psilate, brown, linear-lanceolate, nine- to thirteen-celled. Central cells slightly broader than end cells. Spores brown or mid-brown except for two smaller terminal hyaline cells subtending simple, incurved pores. Spore wall smooth, thin, two-layered and slightly incurved at the septa; septa thick, straight, with septal flaps and pores; septation regularly even, dividing the spore into roughly symmetrical cells. Spore size 40–75 x 10–13 μm.

Occurrence. Very common in sample C-68329, common in sample C-68305 and rare in sample C-68304.

Etymology. From the Latin, *aequabilis*, equal, referring to spores with symmetrical cells.

Remarks. *Diporicellaesporites aequabilis* sp. nov. is distinguished from *D. pluricellus* Kar and Saxena, 1976 by its narrow slender spores, compared to the generally broad spores in the latter.

Diporicellaesporites chitaleyae sp. nov.

Plate 4.1, figure 26

Holotype. GSC 96417, GSC loc. C-68329.

Description. Spores large, variable but distinctive, dark brown, broadly elliptical to irregularly limoniform, usually six-celled, smooth; cells unequally coloured, end cells colourless or pale, intermediate cells dark brown; of the four central cells, two centralmost cells are larger and darker than the two on either side. Cells traversed by dark thick bands at the septa; septa straight or slightly curved, with septal folds and central pores; two end cells lighter, dissimilar, rounded to conical or cylindrical, with pore-like attachment scar at one end and pedicel-like portion of the hypha at the other end. Spore size 62–108 x 30–50 μm.

Occurrence. Common in sample C-68329, rare in C-68305.

Etymology. In honour of Dr. Shya Chitaley.

Remarks. *Diporicellaesporites chitaleyae* sp. nov. is separated from other known species of *Diporicellaesporites* by its notably large size and central dark cells.

Diporicellaesporites hillsii sp. nov.

Plate 4.2, figures 8, 9

Holotype. GSC 96426, GSC loc. C-68305.

Description. Spores pale brown, thin walled, obclavate or fusiform, six- to eight-celled, smooth, diporate. Cells unequal, two proximal cells immediately above the basal cell are relatively larger and broader than the smaller, tapering upper cells. Cell wall and septa roughly of the same thickness. Basal cell hyaline or subhyaline. Spore size 35-53 x 7-13 μm; one unusually large specimen was 72.5 x 15 μm (Pl. 4.2, fig. 9).

Occurrence. Common in sample C-68305.

Etymology. In honour of Dr. L.V. Hills.

Remarks. Spores of *Diporicellaesporites hillsii* sp. nov. show some similarity to spores of *D*. sp. F, *D*. sp. G, and *D*. sp. H in being proximally broad and distally tapering, but they are not distally filamentous and lack the conico-truncate base.

Diporicellaesporites jansonius sp. nov.

Plate 4.2, figures 5, 17

Holotype. GSC 96423, GSC loc. C-68305.

Description. Multicellular, fusiform-ellipsoidal, brown, smooth fungal spores. Spores generally with six to nine septa, diporate with regular septation. Cell wall, about 1 μm thick. Spores broad in the centre, gradually narrowing at the ends; with a distinct band and flaps of triangular dark brown thickenings at the septa. Pores simple, incurved. Spore size 35-45 x 10-13 μm.

Occurrence. Common in sample C-68305 and rare in sample C-68304.

Etymology. In honour of Dr. Jan Jansonius.

Remarks. Some specimens were observed with serial spores in succession. This may be attributed to germination of spores in situ at the apex to form a short, percurrent secondary conidiophore that bears secondary, singular spores at the apices of successive proliferations (Pl. 4.2, fig. 17).

Affinity. The tendency for these spores to form in succession and their morphological similarity are comparable to conidia encountered in species of modern *Annellophora*, a dematiaceous hyphomycetous fungus.

Diporicellaesporites mediocoloratus sp. nov.

Plate 4.1, figures 23, 24

Holotype. GSC 96411, GSC loc. C-68329.

Description. Spores broadly ellipsoidal, five- to seven-celled, diporate, levigate, pigmented in the centre; end cells hyaline to pale brown. Cells unequal in size and shape; central cells larger than the end cells. Some spores distinctly asymmetrical with one side straight and the other side slightly convex in the middle (Pl. 4.1, fig. 24). Cell wall thin, smooth, superficially indented at the septa; central septa conspicuously thicker than the terminal ones; septa with clear septal folds and pores. End cells porate; pores simple. Spore size 52-75 x 15-20 μm.

Occurrence. Very common in sample C-68329, common in sample C-68305, and rare in C-68304.

Etymology. From the Latin, *medius*, middle; *coloratus*, coloured, referring to the middle cell pigment.

Remarks. This species resembles *Diporicellaesporites reticulatus* Elsik and Dilcher, 1974 in general appearance and size, but differs in lacking an irregular reticulate surface in the centre of the spores.

Diporicellaesporites navicularis sp. nov.

Plate 4.2, figure 1

Holotype. GSC 96413, GSC loc. C-68329.

Description. Spores navicular, or broadly fusiform, arched or curved on one side, straight on the other; spores broad in the middle, gradually tapering at the ends, smooth. Spores generally with six cells, pale brown, with two large central cells of almost equal size and shape, and with central septum noticeably thicker than the other septa. Two end cells pointed, hyaline, terminally porate. Cell wall thin. Spore size 55-80 x 15-20 μm.

Occurrence. Common in sample C-68329, rare in sample C-68305 .

Etymology. From the Latin, *navicularis*, boat-shaped, referring to the shape of the spores.

Remarks. The curved and navicular shape of this spore separate it from other spores of *Diporicellaesporites* described herein.

Diporicellaesporites pluricellus Kar and Saxena, 1976

Plate 4.1, figure 25

Description. Spores, generally 10-celled, linear to broadly elliptical, porate, brown; spores with distinctly thickened septa and more or less equally spaced cells forming a regular, scalariform pattern. Pores at each end of the spore, well developed and distinct. Spore size 45–80 x 15–28 μm.

Occurrence. Very common in sample C-68329, and common in sample C-68305.

Remarks. *Diporicellaesporites*(?) sp. described by Elsik (1968, Pl. 3, fig. 12) and *Diporicellaesporites* sp. (Kar, Singh and Sah, 1970, Pl. 2, fig. 27) appear similar to *D. pluricellus*.

Diporicellaesporites quaternarius sp. nov.

Plate 4.2, figure 3

Holotype. GSC 96416, GSC loc. C-68329.

Description. Spores tetracellate, diporate, psilate, oval to cylindrical, unevenly pigmented and noticeably incurved at the septa; septa conspicuously thickened. Two central cells larger, broad, dark brown, thick walled and generally of equal size; the two terminal cells light brown to hyaline, thin walled, subtending the terminal pores; generally rounded and gradually tapering at the pore end, similar or dissimilar in shape. Pores apical, simple, incurved. Spore size 25–30 x 12–15 μm.

Occurrence. Common in samples C-68329 and C-68305 rare in sample C-68304.

Etymology. From the Latin, *quaternarius*, consisting of four, referring to the spores being typically four-celled.

Remarks. These spores differ from *Diporicellaesporites stacyi* Elsik, 1968 in being constricted at the septa, in the absence of a granular to punctate inner surface of cells, and having end cells clearly different from the central cells. The spores also differ from tetracellate spores of *D. puryearensis* Sheffy and Dilcher, 1971 and *D. tetralocularis* Sheffy and Dilcher, 1971 by their generally large size and dark central cells.

Diporicellaesporites scalaris sp. nov.

Plate 4.2, figure 13

Holotype. GSC 96421, GSC loc. C-68305.

Description. Spores filamentous, scalariform, multicellular with typically 25 cells arranged in a row; spores brown, straight, slightly tapering toward the base. Cells usually equally spaced with regular transverse septation; broader than long, except those at the tapering end, with prominent triangular or wedge-shaped septal folds and clear perforations. Spore wall thin. Spores much longer than broad, generally with length greater than eight or nine times the width. Spores with a simple pore at one end and a hyaline, small pedicel-like attachment cell at the other end. Illustrated spore size 137.5 x 12.5 μm.

Occurrence. Common in sample C-68305, fairly common in sample C-68329 and rare in sample C-68304.

Etymology. From the Latin, *scalaris*, scalariform, referring to the ladder-like appearance of the spores.

Remarks. Lange and Smith (1971) separated extended linear phragmospores of more than 10 cells, and typically with length greater than four times the breadth, from other linear phragmospores. They included scoleco-phragmospores of length 15–30 times the breadth with ladder-like septa under the new genus *Scolecosporites* (type species *S. maslinensis*). However, it was not clear if they intended to include in it spores with or without pores. The present forms appear similar in general appearance to spores included under *Scolecosporites* except for their much smaller size and a distinct pore at one end. These spores appear similar to *D. aequabilis* sp. nov. in being regularly septate, but differ from it in their noticeably large size.

Diporicellaesporites vermiculatus sp. nov.

Plate 4.2, figures 10, 14

Holotype. GSC 96419, GSC loc. C-68305.

Description. Spores medium brown, diporate, straight or curved, ellipsoidal, multicellular, smooth to granular (Pl. 4.2, figs. 10, 14), of 7–12 cells; mature spores usually of 12 cells. Spores divided into unequal cells by irregular straight cross walls that are perpendicular to the (curved) longitudinal axis, with larger and broader cells in the middle and gradually smaller cells toward either end. Cell wall smooth to punctate, thin, slight constriction at the septa. Septa slightly thicker than the cell wall, with septal thickenings and perforations. Terminal cells thin-walled and paler to hyaline with a simple pore at each end. Some spores occur in chains. Spurious vertical septation was also noticed in some specimens (Pl. 4.2, fig. 14). Spore size 57–93 x 15–20 μm.

Occurrence. Common in sample C-68305.

Etymology. From the Latin, *vermiculatus*, like worms, referring to the worm-like spores.

Remarks. This species is somewhat similar to *D. mediocoloratus* sp. nov. in size and general appearance but is distinguished from the latter by its irregular shape and smooth to granular surface.

Diporicellaesporites sp. A

Plate 4.1, figure 19

Description. Diporate, tetracellate, smooth, brown fungal spores. Spores barrel- or drum-shaped with two noticeably large central cells and two much smaller end cells. Both central and end cells similar in colour; septa and cell wall of even thickness, slightly notched. Pores simple, large and terminal. Spore size 22.5 x 10 μm.

Occurrence. Rare in sample C-68329.

Diporicellaesporites sp. B

Plate 4.2, figure 4

Description. Spores dark brown, smooth, diporate, linear-oblong, five-celled. Central three cells almost rectangular, dark to olivaceous brown, thick walled; two end cells hemispherical to orbicular, thin walled, pale brown. Cell wall about 1 μm thick; septa broad, dark, more than twice as thick as the cell wall. Pores simple, circular. Illustrated specimen 25 x 7.5 μm in size.

Occurrence. Rare in sample C-68305.

Diporicellaesporites sp. C

Plate 4.2, figure 16

Description. Spores cylindrical, ellipsoidal, pale golden brown, smooth, with three to four septae, diporate, thin-walled. Observed spores catenulate; spores irregularly septate with somewhat unequal cells. Cell wall thin, continuous. Pores simple, round. Spore size: upper 40 x 7.5 μm, lower 45 x 10 μm.

Occurrence. Rare in sample C-68304.

Diporicellaesporites sp. D

Plate 4.2, figure 15

Description. Spores brown, diporate, three septate, isopolar, bilateral, narrowly limoniform. Medium septum thicker than the cell wall, 2.5 μm thick, with a central pore; other two septa subterminal and one beneath each pore. Spores pigmented in the middle portion and light brown to hyaline at the ends. Pores simple, formed probably by the rupture of fragile portions of the exine at apical ends. Spore size 37–43 x 20–25 μm.

Occurrence. Noted rarely in sample C-68304.

Diporicellaesporites sp. E

Plate 4.3, figure 3

Description. Spores with prominently wide and solid band of thickening at the septum. Spores brown, with five to six cells, smooth walled, broad, oval-elliptical, slightly indented at the middle septum. Middle septum broadly thickened, about 7–10 μm wide; other septa thin and at extremities beneath the pores. Cell wall 2 μm thick centrally, gradually thinning toward the pores. Pores apical, and dissimilar; larger pore about 17 μm wide. Smaller pore, around 12 μm wide. Spores 80–118 μm long and 40–70 μm wide.

Occurrence. Spores rare in sample C-68305.

Diporicellaesporites sp. F

Plate 4.4, figure 7

Description. Spores multicellular, dark brown, smooth walled, straight to slightly curved, uniseriate, filamentous, about 42 μm long, obclavate with lower part of the spore broader and darker, and apical part narrower, attenuated, thin walled, incomplete and with septation at longer intervals. The broad proximal portion of the spore four-celled, about 22 μm long and 7.5 μm wide; basal cell conico-truncate, other three cells thick-walled and with thick, opaque septa.

Occurrence. Rarely found in sample C-68329.

Remarks. This form appears similar to *Pluricellaesporites alleppeyensis* Ramanujam and Rao, 1978 in general morphology, but the latter is larger and has a scabrate to finely granular lower part. It also resembles *Quilonia typica* Jain and Gupta, 1969 in general appearance, but differs in the absence of a basal thick-walled stalk cell. The irregular furrow in the central region of the illustrated specimens of *Quilonia typica* and ostiolate bodies were not observed in *Diporicellaesporites* sp. F, but these may only be artifacts of preservation (i.e., a compressional rupture of the cell walls and septal plates, respectively).

Diporicellaesporites sp. G

Plate 4.4, figure 18

Description. Spores robust, brown, multicellular, smooth, straight, uniseriate. Proximal portion broad, consisting of three large cells with basal cell conico-truncate; upper part narrower, incomplete, of longer cells but firm. Illustrated specimen 80 μm long with broad, proximal portion 30 μm in length and 15 μm wide.

Occurrence. Rarely encountered in sample C-68305.

Diporicellaesporites sp. H

Plate 4.4, figure 1

Description. Spores pale to mid brown, multicellular, smooth walled, straight, uniseriate, obclavate; with numerous transverse septa at more or less regular interval giving them a somewhat scalariform appearance. Basal portion slightly bulged, five-celled; with basal cell lighter and conico-truncate. Upper portion slightly narrower, traversed by many septa and nearly symmetrical cells; uppermost narrow part incomplete. Cell wall and septa thin throughout the spore; septa with perforations. Observed spore 60 μm long (basal portion 22 μm long), 12.5 μm wide.

Occurrence. Rare in sample C-68304.

Remarks. The above three species *Diporicellaesporites* sp. F, *D*. sp. G, and *D*. sp. H have spores with common morphological characters; they all possess an enlarged proximal portion with a distinct conico-truncate basal cell and extended, sometimes attenuated upper part. Elsik and Dilcher (1974) have described similar spores from Lawrence Clay Pit, Tennessee (Pl. 27, figs. 42, 43).

Affinity. These spores appear generally similar to the conidia of some dematiaceous hyphomycetes with a typically conico-truncate base, e.g., *Acarocybella jasminicola*, *Corynespora foveolata*, *Clasterosporium* spp., and *Pseudocercospora* spp.

Genus *Diporisporites* Van der Hammen, 1954 emend. Elsik, 1968

Type species. *Diporisporites elongatus* Van der Hammen, 1954.

Diporisporites anklesvarensis (Varma and Rawat, 1963) Elsik, 1968

Plate 4.2, figure 11

Foveodiporites anklesvarensis Varma and Rawat, 1963.
Punctodiporites harrisii Varma and Rawat, 1963.

Description. Spores diporate, bilateral, isopolar, aseptate, broadly fusiform, medium to dark brown, typically with complex pore structure. Outer spore wall punctate to foveolate with dot-like markings in some specimens modified into pit-like openings in others, and some showing both. Pores about 7.6 μm wide, protruding, elevated by collar and compounded with a block or a pair of thickenings within the pore and at the base of the collar leaving a slit-like space in the centre of the collar extended to the pore. Spore size 52–65 x 22–33 μm.

Occurrence. Very common in sample C-68329 and common in sample C-68305.

Remarks. It was observed that the presence of punctate and foveolate exines in this species is only a morphological variation. Specimens with either punctate or foveolate exines, and with exines showing both these ornamentations were noticed. Elsik (1981), in his description of these spores, wrote, ''Exine apparently psilate, though appear to be punctate to foveolate due to underlying scabrae, grana, verrucae or rugulae.'' *Diporisporites anklesvarensis* is easily recognized from other fossil fungal spores by its complex pore structure and general appearance. *Diporisporites* sp. described by Singh et al. (1986, Pl. 1, fig. 16) and *Punctodiporites* A illustrated by Rouse (1977, Pl. 2, figs. 44, 45) appear similar to *D. anklesvarensis*.

Diporisporites hammenii Elsik, 1968

Plate 4.2, figure 7

Description. Spores elongate, broadly ellipsoidal, dark brown, thick and smooth walled, diporate, with truncated ends. Spore wall less than 1 μm thick, bulging out at the pores. Spore size 12–18 x 7–10 μm.

Occurrence. Fairly common in sample C-68305 and rare in sample C-68304.

Diporisporites sp. A

Plate 4.2, figure 6

Description. Diporate, aseptate, spores of ellipsoidal, oblong or barrel shape. Spores light brown with papillate to verrucose spore wall; papillae on the wall up to 1 μm in diameter in the centre of the spore, becoming finer and more densely packed toward extremities. Pores simple to annulate. Illustrated specimen 27.5 x 15 μm.

Occurrence. Rare in sample C-68305.

Genus *Dyadosporites* Van der Hammen, 1954 ex Clarke, 1965

Type species. *Dyadosporites ellipsus* Clarke, 1965.

Dyadosporonites Elsik, 1968.

Dyadosporites inaequalis sp. nov.

Plate 4.2, figures 20, 21

Holotype. GSC 96434, GSC loc. C-68305.

Description. Diporate, dicellate, smooth-walled, broadly pyriform or subspherical spores. Cells generally unequal; larger one broadly ovoid, rounded, brown; smaller one roughly dome-shaped, broadly rounded in the middle and gradually tapering apically, light brown to hyaline. Spore wall levigate, thin, slightly notched at the medium cross wall separating the two cells. Septum more than twice the cell wall in thickness, traversed by about 2 μm thickened band with a pore in the centre. Pores slit-like, apical. Spore size 15–23 x 7–13 μm. Illustrated spore 20 x 12.5 μm with large cell 12.5 μm and small cell 7.5 μm in length.

Occurrence. Very common in sample C-68305.

Etymology. From the Latin, *inaequalis*, unequal; *fissilis*, split, referring to the cells being unequal and the pores fissure-like.

Remarks. The spores of this species agree with spores of *Dyadosporites incisus* sp. nov. in the nature of their pores but differ markedly in size, being much smaller, and in being made up of mostly unequal cells.

Dyadosporites incisus sp. nov.

Plate 4.2, figures 12, 19

Holotype. GSC 96432, GSC loc. C-68305.

Description. Spores dicellate, diporate, monoseptate, broadly ovoid to elliptical, medium to dark brown. Each cell of the spore nearly equal in size, broad toward the centre and gradually pointed toward the apex, somewhat hemispherical to dome-shaped. Each cell separated by a prominently thick septum, about 2 μm thick and with thickened triangular flanges and central pores. Cell wall, psilate, little constricted at the septum, less than 1 μm thick. Pores apical, simple, lacerate with slit-like openings. Spore size 30–48 x 17–28 μm.

Occurrence. Very common in sample C-68305, fairly common in sample C-68329 and rare in sample C-68304.

Etymology. From the Latin, *incisus*, cut, referring to the pores pulling apart.

Remarks. This species resembles *Dyadosporites ellipsus* Clarke 1965 in its general appearance, but is differentiated from it by its greater size and simple, slit-like pores.

Dyadosporites urniformis sp. nov.

Plate 4.2, figure 18

Holotype. GSC 96431, GSC loc. C-68329.

Description. Spores diporate, monoseptate, psilate, broadly ovoid, medium to dark brown. Cell wall thin, smooth, clearly constricted at the septum; central septum thicker than cell wall. Spore cells urn-shaped, with apical pores. Pores annulate, circular, incurved. Spore size 25–40 x 12–23 μm.

Occurrence. Common in sample C-68329, fairly common in sample C-68305 and rare in sample C-68304.

Etymology. From the Latin, *urniformis*, urn-shaped, referring to the shape of the cells.

Remarks. This species shows a close resemblance to *Dyadosporonites constrictus* (Kar, 1979, Pl. 3, figs. 54, 55), but is much smaller in size. Also, its urn-shaped cells and annulate pores separate it from the latter.

Genus *Exesisporites* Elsik, 1969

Type species. *Exesisporites neogenicus* Elsik, 1969.

Exesisporites annulatus sp. nov.

Plate 4.2, figure 22

Holotype. GSC 96438, GSC loc. C-68304.

Description. Monoporate or diporate, spherical to discoid, psilate, unicellular, darkly pigmented fungal spores. Spore wall thin but appears darkly pigmented in polar view. Pore circular, about 1 μm in diameter and with a thin annular ring. Spores 17–30 μm in diameter.

Occurrence. Common in sample C-68304.

Remarks. The spores resemble *Exesisporites neogenicus* Elsik, 1969 in general morphology but show greater variation in size, are somewhat larger, and have a definite ring around the pore.

Affinity. Ethridge Glass et al. (1986) cited possible affinity of *Exesisporites* to the extant imperfect fungus *Nigrospora*.

Genus *Fractisporonites* Clarke, 1965

Type species. *Fractisporonites canalis* Clarke, 1965.

Fractisporonites doliiformis sp. nov.

Plate 4.3, figure 2

Holotype. GSC 96439, GSC loc. C-68329.

Description. Multicellular, fragmented, indeterminate, uniseriate, dark brown fungal spores. Fragments consist of many cells of different lengths, and are easily distinguishable. Central cells are longer and wider than the terminal cells on either side. Each cell is somewhat barrel-shaped with slightly bulged sides. Septa between cells noticeably thick. Cells with smooth to lightly rough wall, less than 1 μm thick; indented at the septa, about 15–23 x 10–18 μm in size. Septa 2–3 μm thick, with dark band and central pores. Spore size of the observed specimen 177.5 x 12.5 μm, size range 137–237 x 12–23 μm.

Occurrence. Common in sample C-68329.

Etymology. From the Latin, *doliiformis*, vessel-shaped, referring to the cells being barrel-shaped.

Remarks. Differentiated from *Alternoseptites* Rouse, 1962 by cells being indented at each septum and not at alternate septum. This species differs from *Fractisporonites canalis* Clarke, 1965 in being much smaller and in having constricted septa. It is distinguished from *F. moniliformis* Clarke, 1965 in being made up of cells with variable size range.

Genus *Fusiformisporites* Rouse, 1962

Type species. *Fusiformisporites crabbii* Rouse, 1962 emend. Elsik, 1968.

Discussion. Elsik (1968) emended the genus to include forms with less obvious parallel elements of ornamentation. *Fusiformisporites pseudocrabbii* described by Elsik (1968) differs from *F. crabbii* mainly in having fine inner striae made up of rows of punctae parallel to the coarse ribs. Salujha et al. (1972) described *F. foedus*, which is similar to *F. pseudocrabbii* in general appearance and size, but has ridges extending from one pole to the other, continuous across the dividing septum. Elsik (1968, Pl. 2, fig. 11) also reported another species of *Fusiformisporites* with smaller size, slightly thickened and apparently smooth apices, and septum of two layers; Gaponoff (1984) reported similar spores from the Silverado Formation of the Late Paleocene, California.

In *Fusiformisporites lineolatus* Sheffy and Dilcher, 1971, the longitudinal ribs seem to be continuous through the septum. Ramanujam and Rao (1978) described *F. keralensis* from the Miocene of Kerala, India. It is slightly larger than *F. crabbii*, but has a conspicuously thick septum and distinctly truncated or arched ends. Spores reported under *F. keralensis* by

Pathak and Banerjee (1984) are much shorter in size than the holotype (Ramanujam and Rao, 1978; Pl. 3, fig. 42) and their general size range is also smaller. Kumar (1990) described *F. acutus* from the Miocene of Kerala, India. The spores are characterized by their large size and tapering acute ends. Although *Fusiformisporites* is generally known from the Late Paleocene to Recent (Elsik, 1992), Martinez-Hernandez and Tomasini-Ortiz (1989) reported *F. striaoctoformis* from the Fuentes–Rio Escondido Carboniferous Basin, Mexico, in Maastrichtian strata.

Affinity. Spores of *Fusiformisporites* show a close resemblance to the ascospores of the modern genus *Cookeina* Wolf and Cavaliere, 1966. Wolf (1970) also reported nonpetrified spores from Pleistocene and Eocene sediments that were very similar in appearance to *Cookeina.*

Fusiformisporites spp.

Plate 4.2, figures 24, 29, 30

Description. Inaperturate, monoseptate, dicellate, fusiform to broadly elliptical, dark brown, fungal spores. Spore wall sculptured with longitudinal costae, ridges, ribs or grooves spreading out along and parallel to the wall subterminally from either end like a spindle. The wall immediately beneath the apical ends is distinctly thickened. Striae extend to the equatorial septum, or to only a short distance from the apex in each cell, sometimes splitting irregularly and longitudinally. Spores are divided into two equal halves with or without a slight constriction by an equatorial wall or septum that appears to be continuous, sometimes double-layered and noticeably much thicker than the exine. Septum about 2–3 μm thick, and apical ends 1–3 μm thick; apices rounded to pointed. Spore size 22–43 x 12–23 μm.

Occurrence. Common in sample C-68305 and rare in sample C-68304.

Remarks. Spore size range given by Rouse (1962) for *F. crabbii* is between 45–52 μm. Those spores, therefore, appear to be little larger and with more limited size range than observed for *F.* spp. It was observed that the striate nature of the exospore and the apical thickenings were more distinct in spores 35 μm or larger (Pl. 4.2, fig. 24). Spores with less conspicuous striations and apical thickenings were apparently smaller and smooth (Pl. 4.2, figs. 29, 30).

Fusiformisporites sp. A

Plate 4.2, figure 28

Description. Spores aporate, two-celled, smooth-walled, dark brown, elliptical to ovoid, rounded at the ends. Cells equal; each cell rotund due to obvious constriction at the equatorial septum. Spores ornamented with eight to ten elongate, parallel striae or ridges extending from either end to the middle cross wall; striae seem to develop within the cells and not from the cell wall. Spore wall not so clearly thickened at the apices as in mature spores of *F. crabbii.* Equatorial septum prominently thick banded, about 3–4 μm thick, opaque and much thicker than the relatively thin spore wall. Observed specimen 25 x 12.5 μm.

Occurrence. Rare in sample C-68305.

Remarks. This species is distinguishable from *F. crabbii* Rouse, 1962 emend. Elsik, 1968 in general morphology, relatively small size, and peculiar shape, but also in having noticeable bunched strands within each cell. The spores appear to be closely related to those of *F. marii* Elsik, 1968 in overall size, shape and general morphology, but differ from them in the number and orientation of ridges. These spores differ from the Maastrichtian form, *F. striaoctoformis* Martinez-Hernandez and Tomasini-Ortiz, 1989 by their thick equatorial septum, nature of striae and the shape.

Genus *Hypoxylonites*(?) Elsik, 1990

Type species. *Hypoxylonites brazosensis* Elsik, 1990.

Discussion. Elsik (1990) found a taxonomic solution for classifying generally dark coloured fungal amerospores with a single furrow that occurred in the Eocene to Pleistocene by incorporating all such spores into two form genera, *Hypoxylonites* and *Spirotremesporites*. This he did after reviewing their relationship to the modern genera, *Arthrinium, Hypoxylon*, and *Xylaria*, which are known to produce these two morphotypes. After extensive research into these modern genera and similar fossil spores, he established the new form genus *Hypoxylonites* for those fossil fungal spores that have one longitudinal furrow, and emended *Spirotremesporites* Duenas, 1979 to include only those fossil fungal spores with one furrow oblique to the longitudinal axis.

In the same year, Kumar (1990) erected a new form-genus *Hypoxylonsporites* with the type species *H.*

miocenicus to include fossil fungal spores that resembled spores of the extant genera *Hypoxylon* and *Endocalyx*. His description of *Hypoxylonsporites* is based on a few fungal spores similar to *Hypoxylon* from the Miocene Quilon deposits in Kerala, India and may in the future prove to be synonymous with *Hypoxylonites*.

Hypoxylonites sp.(?)

Plate 4.2, figure 23

Description. Spores inaperturate; characterized by a distinct, folded, longitudinal fissure, furrow, or slit at the junction of the two sides and extending for the full length between the apices. Spores single-celled, flattened, bilateral, dark brown, psilate, aseptate, elliptical to lenticular, or spindle shaped with rounded to pointed apices. Spore wall less than 1 μm thick. Spore size 17–28 x 7–13 μm.

Occurrence. Very common in sample C-68305.

Genus *Involutisporonites* Clarke, 1965 emend. Elsik, 1968

Type species. *Involutisporonites foraminus* Clarke, 1965.

Discussion. Jain and Kar (1979) raised a new genus *Colligerites* for multicellular, coiled spores differentiated into a central region consisting of generally smaller, rounded cells and an outer region with bigger, rectangular cells. They compared *Involutisporonites* Clarke, 1965 emend. Elsik, 1968 with *Colligerites* and pointed out that coiling in the former is not perfect and it has hyaline cell at the tip. They also suggested that *Pluricellaesporites hillsii* Elsik, 1968 appeared to be similar to species represented by *Involutisporonites*. However, in *P. hillsii* (Elsik, 1968, Pl. 3, fig. 5) the spores are multicellular, monoporate and not coiled. In the same paper, Jain and Kar emended *Involutisporonites kutchensis* Kar and Saxena, 1976 and placed it under *Colligerites* because the spores were perfectly coiled, had a prominent central tissue and the apical cell was not hyaline.

Affinity. *Involutisporonites* spores have been considered to show some affinity with the extant fungal spores of *Cirrenalia* (Pirozynski and Weresub, 1979), *Hobsonia mirabilis, Helicoma mulleri, Helicomyces roseus* and *Vanbeverwijkia spirospora* (Jain and Kar, 1979) belonging to Hyphomycetes. Pirozynski and Weresub (1979) suggested broad similarities in the morphology of modern conidia of marine *Cirrenalia tropica* or *Zalerion maritima* and *Involutisporonites foraminus*.

Involutisporonites trapezoides sp. nov.

Plate 4.2, figures 25, 26

Holotype. GSC 96447, GSC loc. C-68305.

Description. Distinctive, multicellular, porate, dark brown, helicoid, tightly curled, smooth spores without middle cells. Ten or more cells forming a conical helix are irregularly elongated, trapezoids with outer cell wall much longer than the inner and both traversed by two thick cross walls. Cells generally not constricted at the septa, 10–12 μm in diameter. Apical cell porate but not hyaline; pore simple, rounded. Septa about 2 μm thick, with folds and central slit-like openings. Spore size range 33–43 x 28–35 μm.

Occurrence. Common in sample C-68305, fairly common in sample C-68329 and rare in sample C-68304.

Etymology. From the Latin, *trapezoideus*, irregularly four-sided, referring to the trapezoid cells.

Remarks. This species differs from *Involutisporonites* sp. A in general appearance, being lighter in colour and lacking central cells. It is distinguished from *I. foraminus* Clarke, 1965 in being larger, porate, and having cells distinctly trapezoid and without strong septal notches.

Affinity. The single-layered coiled nature of the spore is comparable to spores of living dematiaceous genus *Helicoma*.

Involutisporonites sp. A

Plate 4.2, figure 27

Description. Multicellular, porate, involute, psilate, brown, helicoid spores made up of eight to ten cells. Individual cells rounded to rectangular, arranged in a conical helix with two to three middle cells lined spirally by eight peripheral cells, each 9–10 μm in diameter. Apical cell somewhat elongate and porate but not hyaline. Illustrated spore size 37.5 x 27.5 μm.

Occurrence. Rare in sample C-68329.

Remarks. This species differs from *I. foraminus* Clarke, 1965 mainly in cells not being indented at the septa, the presence of central cells, and in being porate. Septal folds and perforations are also not obvious in this species, whereas in *I. foraminus* they are evident. *Involutisporonites wilcoxii* Elsik, 1968 resembles this species in being coiled, psilate, and porate, but is distinguished by its smaller size, absence of central tissue, dark, thick-walled cells, and a hyaline apical cell.

Genus *Monoporisporites* Van der Hammen, 1954

Type species. Monoporisporites minutus Van der Hammen, 1954.

Monoporisporites magnus sp. nov.

Plate 4.3, figure 9

Holotype. GSC 96451, GSC loc. C-68329.

Description. Monoporate, aseptate, psilate, spherical to circular, thin-walled, light brown spores. Spore wall rigid, sometimes folded, smooth. Pore simple, may occur at different locations on the surface wall. Spore size 30–43 x 25–33 μm.

Occurrence. Very common in sample C-68329, and rare in sample C-68305.

Etymology. From the Latin, *magnus*, large, referring to the size of the spores.

Remarks. The notably large size of the spores separate this species from other known species of *Monoporisporites*.

Monoporisporites singularis Sheffy and Dilcher, 1971

Plate 4.3, figures 10, 12

Description. Aseptate, psilate, monoporate, dark fungal spores of spherical to circular shape. Spore wall thick; pore single, annulate. Spore diameter between 12.5 and 15 μm.

Occurrence. Very common in sample C-68329, common in samples C-68305 and C-68304.

Affinity. This species is nearly similar to the conidia of *Gilmaniella humicola*, an extant hyphomycetous fungus. Spores of *M. singularis*, however, are slightly larger than the conidia of *G. humicola*.

Genus *Multicellaesporites* Elsik, 1968 emend. Sheffy and Dilcher, 1971

Type species. Multicellaesporites nortonii Elsik, 1968.

Multicellaesporites sp.

Plate 4.3, figure 17

Description. Spores oblong-elliptical, smooth, thin-walled, generally six-celled, light brown. Septa and cell wall of uniform thickness; septal folds and perforations at the septa distinct. Spore size 37–43 x 17–20 μm.

Occurrence. Fairly common in sample C-68305.

Genus *Pesavis* Elsik and Jansonius, 1974

Type species. Pesavis tagluensis Elsik and Jansonius, 1974.

Discussion. Kalgutkar and Sweet (1988) described the morphology, taxonomy and phylogeny of this fossil fungus genus from northwestern Canada and discussed its biostratigraphic significance. They described a new species *Pesavis parva*, which is restricted to the Maastrichtian and Early Paleocene. *Pesavis tagluensis* was separated from *P. parva* because of the morphological variation in form and size associated with time and evolution. Because of its uniqueness, *Pesavis tagluensis*, in articular, has been cited as an important species in palynological and stratigraphic studies (Fournier et al., 1976; Jansonius, 1976; Ioannides and McIntyre, 1980; Norris, 1982, 1986; Young and McNeil, 1984), often occurring together with diverse fungal spore assemblages.

Pesavis tagluensis

Plate 4.3, figure 18

Description. Unique fungal spore-like body consisting of a central stalk cell with two lateral arms, which curve around to form a central cavity. The lateral arms consist of a variable number of cells with terminal cells of the opposing lateral arms either overlapping or meeting at their distal ends. Secondary hyphae-like projections arise in pairs from two pores in the central stalk cell and all primary cells except the terminal one. Secondary hyphae are thin-walled, septate and project inward to converge in the central cavity. The central cell bears a stalk with a circular peripheral thickening and a flattened distal end, interpreted as an attachment scar. The lateral arm arising nearest the attachment scar is generally shorter by one cell than the other lateral arm. Overall diameter usually within the range of 20–50 µm. Illustrated specimen is larger than the average and has a diameter of 57.5 µm.

Occurrence. Common in sample C-68304, rare in sample C-68305.

Genus *Pluricellaesporites* Van der Hammen, 1954 emend. Elsik and Jansonius, 1974

Type species. *Pluricellaesporites typicus* Van der Hammen, 1954.

Discussion. *Pluricellaesporites* as illustrated by Van der Hammen (1954) includes five species distinctly different from each other. Clarke (1965) restated the diagnosis of *Pluricellaesporites*, using *P. psilatus* as the type species. The dispersed fungal fragments, which are uniseriate and consist of many rectangular to square cells with generally parallel sides, are described under the genus *Fractisporonites* (Clarke, 1965). Elsik (1968) emended the genus to accomodate monoporate, psilate fungal or algal spores with three or more cells and two or more septa, cells being symmetrical or nearly symmetrical around one long axis. At the same time he also formed a new genus *Multicellaesporites* to encompass inaperturate spores. Sheffy and Dilcher (1971) emended Elsik's (1968) description of *Pluricellaesporites* to incorporate spores with psilate to scabrate ornamentation. In the same paper, they also emended the description of *Multicellaesporites* Elsik, 1968 to introduce a wider range of ornamentation. Lange and Smith (1971) concluded that Van der Hammen's circumscription was unacceptably broad. Later, in their paper on *Ctenosporites* and other paleogene fungal spores (1975a), they stated that, "*Pluricellaesporites* is at risk of becoming a terminological catchall for few-celled linear phragmospores, unless an effective revision of this group is accomplished soon."

Elsik and Jansonius (1974) further emended *Pluricellaesporites* to include monoporate, symmetrical or nearly symmetrical fungal spores of three or more cells showing different characteristics of shape, size, ornamentation, and septation and made its description more complete.

In this study, monoporate, nonlinear and linear phragmospores are broadly grouped in *Brachysporisporites* and *Pluricellaesporites*, and differentiated by shape, size and septation. Spores with ovoid, turbinate, pyriform or spathulate cells having a distinct gradation in size from larger apical cell to a small basal attachment cell, and with two to five cells separated by dark septa are included in *Brachysporisporites*. Larger ellipsoidal, linear to cylindrical spores without clear gradation in shape, generally of more than five cells but also smaller types, with or without septal thickening are placed in *Pluricellaesporites*.

Affinity. Pirozynski and Weresub (1979) likened *Pluricellaesporites* to the conidia of the modern dematiaceous hyphomycetous fungus *Sporidesmium*.

Pluricellaesporites apiculatus sp. nov.

Plate 4.3, figure 11

Holotype. GSC 96462, GSC loc. C-68305.

Description. Spores light brown, fusiform-elliptical, tapering to a fine point at the base. Spores tetracellate, transversely septate, two central cells larger than the end cells. Septa thicker than the cell wall; septal folds and pores present. Some specimens with an intact hilum or a small portion of a subtending conidiophore were noted (Pl. 4.3, fig. 11). Spore size 25–38 x 7–13 µm.

Occurrence. Very common in sample C-68305, and rare in sample C-68304.

Etymology. From the Latin, *apiculiformis*, with a point, referring to the spores being pointed at their base.

Remarks. This species is distinct from other species of *Pluricellaesporites* in its smaller size and pointed base.

Affinity. This species shows a close affinity to the conidia of the extant dematiaceous fungus *Phaeodactylium alpiniae* in general morphology.

Pluricellaesporites sp. A

Plate 4.3, figure 15

Description. Spores light brown, thin, smooth, five- to six-celled, broadly elliptic-oblong, with a simple pore at the proximal end. Distal cells may be darker, central cell or cells tend to be largest. Septa thin, with septal folds and central perforations. Spore size 37–55 x 15–20 μm.

Occurrence. Rare in samples C-68329 and C-68305.

Pluricellaesporites sp. B

Plate 4.3, figure 8

Description. Spores dark brown, thin, smooth-walled, four- to five-celled. Cells unequal, almost as wide as long, with bulging sides. Cell wall less than 1 μm thick, slightly but clearly constricted at the septa; septa much thicker than the cell wall, 2.5 μm thick, with septal flaps and central openings. Pore simple, situated at the proximal end. Middle cells larger and darker than terminal and basal cells. Terminal cell somewhat dome-shaped. Spore size 42–53 x 15 μm.

Occurrence. Found rarely in sample C-68329.

Remarks. This species differs from *Pluricellaesporites* sp. A in being conspicuously notched at the septa, narrower, and in having thicker septa.

Pluricellaesporites sp. C

Plate 4.3, figure 14

Description. Spores light brown, oblong, tetracellate. Cells distinctly unequal; proximal and distal cells rounded but distal cell larger than the proximal cell; two central cells nearly similar. Cell wall thin, smooth, slightly indented at the septa. Septa about 2 μm thick, subtended by septal folds and pores. Illustrated specimen 47.5 μm long and 15 μm wide.

Occurrence. Rare in sample C-68329.

Pluricellaesporites sp. D

Plate 4.3, figure 13

Description. Medium to dark brown, broadly elliptical, thin, smooth-walled, four-celled fungal spores. Two middle cells much darker and broader than the terminal cells. Both cells at proximal and distal ends typically conical to orbicular in shape. A remnant of an attached conidiophore or conidiogenous cell or hilum subtending a single terminal spore is apparent. Spores are provided with well developed septal folds and pores. Upper and basal septa slightly curved, middle septum straight. Observed spore 57.5 x 25 μm.

Occurrence. Rare in sample C-68329.

Pluricellaesporites sp. E

Plate 4.4, figure 6

Description. Distinctive, dark brown, elongate-ellipsoidal, pluriseptate, smooth, porate spores. Septa nearly equidistant making cells appear more or less equal in size, and giving the spores a scalariform appearance. Septa dark, about 2 μm thick, much thicker than the spore wall; with dark septal flaps and central pores. Spores with a prominent, light coloured, protuberant basal cell and a rounded apex. The intact attachment cell in spores like this is another indicator that the so-called "pore" at one end in species of *Pluricellaesporites* is actually an attachment point and the spore is developed terminally on a conidiophore or conidiogenous cell subtending it. Spore size 78–95 x 10–25 μm.

Occurrence. Rare in sample C-68305.

Pluricellaesporites sp. F

Plate 4.4, figure 2

Description. Spores, dark brown, smooth, oblong-ellipsoidal, rounded at the apex, thick-walled, five-celled. Spores traversed by four opaque, dark, transverse, septa about 5 μm thick. Central three cells with thicker septa and septal thickenings extending within these cells forming distinct inner circular layers. Proximal cell lightly pigmented and thin-walled. Pore circular and lateral on the proximal cell. Illustrated specimen 52.5 x 20 μm.

Occurrence. Rare in sample C-68304.

Remarks. This species resembles *Pluricellaesporites ovatus* Sheffy and Dilcher, 1971, except for its shape and much larger size.

Pluricellaesporites sp. G

Plate 4.4, figure 15

Description. Spores light brown, broadly elliptical or limoniform, smooth, thin-walled, seven-celled; septation generally regular with more or less equally spaced cells; septa thin, with septal folds and perforations. Illustrated spore size 57.5 x 27.5 μm.

Occurrence. Rare in sample C-68304.

Genus *Polyadosporites* Van der Hammen, 1954 emend. Ediger, 1981

Type species. *Polyadosporites suescae* Van der Hammen, 1954.

Discussion. Vishnu-Mittre (1973) recorded spherical or globose spore masses (Pl. 2, fig. 49) from Flandrian deposits in England and found them similar to the spore masses in the extant dematiaceous fungus *Coniothecium glumarum*. They also closely resemble the polyads of *Polyadosporites*.

Ediger (1981) emended the genus *Polyadosporites* and assigned the type species *Staphlosporonites conoideus* Sheffy and Dilcher, 1971 to *Polyadosporites conoideus* (Sheffy and Dilcher, 1971) Ediger, 1981, thereby cancelling the genus *Staphlosporonites*. However, spores of *S. conoideus* Sheffy and Dilcher, 1971 appear different in general appearance and morphology from the polyads of *Polyadosporites*. They seem to agree with the description of *Staphlosporonites*. Moreover, the transfer of *S. conoideus* to *Polyadosporites* was not valid because sufficently detailed bibliographic references were not provided, as required by the International Code of Botanical Nomenclature (Jansonius and Hills, 1976).

Polyadosporites suescae

Plate 4.4, figures 3–5

Description. Clumps of aporate fungal spores or cells arranged in a more or less spherical mass forming a polyad. Cells similar, spherical, ovoid or rounded, inaperturate, 5–7 μm in diameter, brown, appressed together, smooth. Polyad diameter ranges between 12 and 45 μm.

Occurrence. Common in samples C-68329 and C-68305.

Remarks. A fair number of polyads with similar cell morphology were found scattered in samples C-68329 and C-68305. However, they had a wide range of sizes. The consistently uniform nature of these polyads, apart from the variation in size, may indicate that the observed variability is not the result of pleomorphism, but can most likely be attributed to stages in development. *Polyadosporites suescae* has been described with polyads of a size range 40–55 μm.

Affinity. Clusters of *Polyadosporites suescae* are comparable to sclerotium-like bulbils found in *Papulospora*, a genus of Mycelia Sterilia. Although seemingly hypothetical, they also appear analogous to the spore balls of some smut fungi, which consist of aggregates of either teliospores (e.g., *Sorosporium*) or both teliospores and sterile cells (e.g., *Urocystis*).

Genus *Psilodiporites* Varma and Rawat, 1963

Type species. *Psilodiporites krempii* Varma and Rawat, 1963.

Psilodiporites krempii

Plate 4.4, figures 8–11

Description. Spores distinctive, diporate, isopolar, bilateral, generally limoniform, light to dark pigmented, aseptate, psilate. Spores with pore chambers formed by a basal septum beneath each pore at both ends. Spore wall thin, sometimes irregularly folded. Spores surrounded on the outside by a thin, hyaline layer were observed. Pores 5–10 μm in diameter. Spore size 37–55 x 15–30 μm.

Occurrence. Very common in samples C-68329 and C-68305 and rare in C-68304.

Remarks. Because a large number of specimens were found, some serial stages in pore development were observed. In one young spore, the spore wall was complete all around with no sign of pores, but thin at either end; small perforations were about 2–3 μm from the tip at both ends (Pl. 4.4, fig. 8). At a later stage these thinned patches become more distinct, and slightly curved basal septa begin to appear roughly 7 μm from both tapering ends of the spore (Pl. 4.4, fig. 9). In a still later stage, small, thin portions of the cell wall at either end start to separate from the rest of the wall (Pl. 4.4, fig. 10) and at maturity these are absent, resulting in the formation of a pore at each end (Pl. 4.4, fig. 11).

Diporicellaesporites bellulus (Sung et al., 1978, Pl. 5, figs. 4, 5; Norris, 1986, Pl. 2, figs. 32–34) and *D.* sp. cf. *D. bellulus* (Norris, 1986, Pl. 2, fig. 31) appear similar to *Psilodiporites krempii*. Elsik (1981) described such spores under the genus *Psilonites* and the type species *P. californicus* (Elsik, unpubl). He classified the spores as diporate and aseptate, and considered the basal septa as part of the pore chambers.

Genus *Reduviasporonites* Wilson, 1962

Type species. Reduviasporonites catenulatus Wilson, 1962.

Discussion. Wilson (1962) discovered the type species in the Upper Permian marine deposits from the Flowerpot Shale of Oklahoma. He suggested a resemblance of spores of *Reduviasporonites* with conidiospores of some species in the living genera like *Aspergillus*, *Penicillium*, *Monilia*, *Torula*, but also pointed out their marked differences in size and details of the spore walls. He further inferred that *Reduviasporonites* might be a terrestrial fungus because of its occurrence with pteridophyte spores and gymnosperm pollen in the Flowerpot Shale, of the absence of an equivalent extant fungus from the marine deposits, and its resemblance to many soil-inhabiting extant fungi. *Aspergillus torulosus* Trivedi and Verma, 1970 from a Tertiary coal bed in Malaya appears to be similar to *Reduviasporonites catenulatus*, except for its basal stipe-like attachment.

Pirozynski and Weresub (1979) pointed out that the short moniliform chains of *Reduviasporonites* somewhat resemble the mycelium of modern sooty moulds, in particular, of *Ophiocapnocoma* of the Metacapnodiaceae. However, they also remarked, "although it is tempting to take the fossil fragments as evidence of the antiquity and once wide distribution of ancestral sooty moulds, again the possibility of the algal character of the fossil cannot be ruled out."

Reduviasporonites catenulatus

Plate 4.4, figure 19

Description. Spores or thallus occurring in uniseriate, simple, straight or curved chains with variable number of cells; cells subspherical, circular to ovoid, smooth, brown, slightly flattened at the contacts with adjacent cells; cells approximately of equal size, varying between 7 to 12 μm in diameter; size variation in a filament is probably due to the occurrence of young and growing cells borne terminally; cells with septal folds and pores. Illustrated specimen has more than 20 cells. The number of cells in a chain may vary subject to the conditions at the time of deposition and subsequent preservation, and during laboratory treatment.

Occurrence. Common in sample C-68305 and fairly common in sample C-68329.

Affinity. This species shows some resemblance to the hyphae of the Metacapnodiaceae (Ascomycetes).

Reduviasporonites ramosus sp. nov.

Plate 4.4, figure 13

Holotype. GSC 96479, GSC loc. C-68305.

Description. Spores distinctive, dark to mid brown, branched, uniseriate, comprising many cells of variable sizes arranged in rows of moniliform chains. Cells smooth, spherical to ovoid, barrel-shaped to elongate, varying between 7 and 15 μm in length; cells somewhat flattened, thickened and little indented at contact between cells.

Occurrence. Common in sample C-68305.

Etymology. From the Latin, *ramosus*, branched, referring to the branched spores.

Remarks. This species differs from *Reduviasporonites catenulatus* Wilson, 1962 and *R*. sp. A by its branching habit and variable cells.

Reduviasporonites sp. A

Plate 4.4, figure 17

Description. Spore or thallus pigmented, consists of simple, serially arranged and distinctly constricted cells forming a moniliform or torulose chain. Cells somewhat barrel-shaped, roughened with scabrate to verrucate surface. Septa indistinct, probably due to deep constrictions and continuous broad passage between cells. Cells about 10–12 μm in diameter. Observed specimen 90 μm long.

Occurrence. Rare in sample C-68305.

Remarks. Differs from *R. catenulatus* Wilson, 1962 in the general cell morphology and in having conspicuously roughened cell walls. The general appearance of the species seems to show an affinity to the hyphal morphology of some living species of the Capnodiaceae.

Genus *Staphlosporonites* Sheffy and Dilcher, 1971

Type species. *Staphlosporonites conoideus* Sheffy and Dilcher, 1971.

Transeptaesporites Ediger, 1981.

Discussion. Ediger (1981) replaced *Staphlosporonites* with the new genus *Transeptaesporites* after transferring its type species *S. conoideus* to the genus *Polyadosporites*. Spores of *Transeptaesporites* are considered to resemble the conidia of the extant genus *Alternaria*. *Transeptaesporites irregularis*, the type species described by Ediger (1981), although similar to *Alternaria*, is not shown to be sufficiently related to it (Jansonius and Hills, 1976). Moreover, cancellation of *Staphlosporonites* and transfer of *S. conoideus* was not properly validated (Jansonius and Hills, 1976; see comments on *Polyadosporites* in this text). If these comments are acceptable, then the creation of *Transeptaesporites* Ediger, 1981 in place of *Staphlosporonites* Sheffy and Dilcher, 1971 seems unnecessary and is nomenclaturally superfluous. Sheffy and Dilcher (1971) had also suggested affinity of *Staphlosporonites allomorphus* Sheffy and Dilcher, 1971 to the conidia of *Alternaria*.

Staphlosporonites delumbus Norris, 1986

Plate 4.4, figure 14

Description. Multicellular, dark brown spores composed of two or three rows of irregularly formed cells. Tiers of cells appressed together to form an extended and elongated pseudoparenchymatous tissue of anastomosing cells. Spores about 20 µm in width and of variable length. The longest spore noted was 287.5 µm. Cells smooth, thin, rounded to polygonal, irregular, overlapping. A number of specimens were observed of variable length, indicating gradation in spore development with continuing division of cells in rows.

Occurrence. Common in sample C-68305, and rare in sample C-68329.

Genus *Striadiporites* Varma and Rawat, 1963 emend. Elsik and Jansonius, 1974

Type species. *Striadiporites reticulatus* Varma and Rawat, 1963.

Discussion. The genus *Psilodiporites* resembles *Striadiporites* in size, shape, pore development and presence of basal septa beneath the pores, but lacks the striate ornamentation so characteristic of *Striadiporites*. It may be postulated that *Striadiporites* and similar striate forms diverged as offshoots from the main line of *Psilodiporites* in the course of evolution. Elsik (1976) suggested the origins of diporate, aseptate, and diporate, monoseptate spores were distinct offshoots of the *Fusiformisporites* line, both possessing prominent longitudinal ribs.

Striadiporites irregularis sp. nov.

Plate 4.4, figure 12

Holotype. GSC 96481, GSC loc. C-68329.

Description. Diporate, aseptate, brown, broadly ellipsoidal to limoniform, smooth, bilateral, isopolar spores with a few but distinct irregular longitudinal striae partially extending from one end to the other. Striae bifurcating and branching randomly; traversed by small, clear oblique or transverse arteries to form an irregular loose reticulum. Spore wall thin, less than 1 µm thick. Pores simple, narrow, not more than 5 µm in diameter, with basal septa about 7 to 8 µm beneath them. Spore size 40–50 x 17–28 µm.

Occurrence. Very common in sample C-68329.

Etymology. From the Latin, *irregularis*, irregular, referring to the spores being irregularly striate.

Remarks. This species differs from *S. reticulatus* in the pores being much smaller in diameter, in the partial and irregular formation of striae with a loose reticulum, and spores having light pigmentation. In *S. reticulatus,* spores are conspicuous by their dark colour and the presence of strong striations running the whole length between the pores. *Striadiporites irregularis* sp. nov. is distinguished from *S. sanctaebarbarae* Elsik and Jansonius, 1974 and *S. californicus* Elsik and Jansonius, 1974 by its much larger size, shape and nature of the reticulum.

Genus *Triporicellaesporites* Ke et Shi, 1978

Type species. *Triporicellaesporites triangulus* Ke et Shi, 1978

Triporicellaesporites sp.

Plate 4.4, figure 16

Description. Staurospores, triradiate, psilate, triporate. Spores made up of three smooth, irregular, septate arms joined by their wide bases to form a common, central dark portion from which they appear to originate. The arms are dark brown and thick near the centre of the spore and hyaline or subhyaline and thin at the apical cells. Each radiating arm di-to tricellate, 25 μm wide at the base and narrow at the tip. Septa with septal folds and central openings.

Occurrence. Rare in sample C-68329.

Remarks. Pores in this species, although not quite revealing, are likely present terminally on apical cells. This spore is roughly similar to *Triporicellaesporites multicellatus* (Sung et al., 1978, Pl. 5, fig. 16), except that it is slightly larger and has a smaller number of cells in the arms.

Affinity. It shows some affinity to the conidia (aleuriospores) of the extant dematiaceous fungus *Triposporium elegans.* However, in the latter, the conidial arms are multiseptate.

Class FUNGI IMPERFECTI

Order MYCELIA STERILIA

Hyphal filament

Plate 4.3, figure 1

Description. Multicellular, branched, incomplete, generally dark brown fungal hyphae. Hyphal cells much longer than wide, specifically thickened at the septa; septa with distinct, lateral, thickened nodular areas formed by inward extension of the septal and wall elements from the subtending cells reaching the central pore.

Occurrence. Rare in sample C-68329.

Genus *Palaeancistrus*

Type species. Palaeancistrus martinii Dennis, 1970.

Palaeancistrus sp.

Plate 4.3, figure 6

Description. Portion of the fossil septate fungal hypha presumably with clamp cell, and belonging to Basidiomycetes. Hypha thin-walled, narrow, hyaline to light coloured; terminal cell undergoing nuclear division shows a presence of a small hook-shaped clamp connection. Illustrated specimen 72.5 x 2.5 μm.

Occurrence. Rare in sample C-68329.

Remarks. There was not enough material of this species for a comparison with *P. martinii*. However, it is noted that *P. martinii* is a Basidiomycetous mycelium that was found within the wood of a Middle Pennsylvanian fern, *Zygopteris illinoiensis*, (Dennis, 1970), while the present hyphal fragment was recovered from sediments in the Lower Tertiary. More recently, Osborn et al. (1989) reported the clamp-bearing fungus *Palaeofibulus antarctica* from the Triassic of Antarctica.

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PLATES 1 to 4

In the explanation of figures, the species name is followed by the GSC type number, the slide number, stage coordinates, and the GSC locality number. Magnification for all specimens is x1000.

PLATE 4.1

Figures 1, 2. *Brachysporisporites pyriformis*

1. GSC 96390, 2096-55-a, 46.1 x 108.3, GSC locality C-68329.
2. GSC 96391, 2096-55-a, 46.1 x 108.2, GSC locality C-68329.

Figure 3. *Brachysporisporites* sp. A

GSC 96393, 2096-55-g, 29.9 x 127.9, GSC locality C-68329.

Figure 4. *Brachysporisporites atratus* sp. nov.

Holotype, GSC 96392, 2096-55-a, 12.7 x 118.8, GSC locality C-68329.

Figures 5, 6. *Brachysporisporites bullatus* sp. nov.

5. Holotype, GSC 96394, 2096-55-b, 18.4 x 119.9, GSC locality C-68329.
6. GSC 96395, 2096-64-f, 18.0 x 115.4, GSC locality C-68304.

Figures 7, 8. *Brachysporisporites catinus*

7. GSC 96396, 2096-55-e, 38.0 x 117.1, GSC locality C-68329.
8. GSC 96397, 2096-55-a, 17.0 x 120.0, GSC locality C-68329.

Figure 9. *Chaetosphaerites* sp.

GSC 96399, 2096-55-g, 21.0 x 122.0, GSC locality C-68329.

Figure 10. *Ctenosporites eskerensis*

GSC 96400, 2096-64-c, 27.1 x 126.7, GSC locality C-68304.

Figure 11. *Brachysporisporites* sp. B

GSC 96398, 2096-55-g, 18.3 x 113.6, GSC locality C-68329.

Figure 12. *Dicellaesporites* sp. A

GSC 96402, 2096-64-e, 32.1 x 116.9, GSC locality C-68304.

Figure 13. *Dicellaesporites cellaequalis* sp. nov.

Holotype, GSC 96404, 2096-63-a, 31.7 x 117.1, GSC locality C-68305.

Figure 14. *Didymoporisporonites discordis* sp. nov.

Holotype, GSC 96410, 2096-63-e, 28.3 x 116.0, GSC locality C-68305.

Figure 15. *Desmidiospora* sp.

GSC 96401, 2096-64-f, 16.9 x 124.7, GSC locality C-68304.

Figure 16. *Dicellaesporites* sp. B

GSC 96403, 2096-64-e, 25.8 x 116.3, GSC locality C-68304.

Figure 17. *Dictyosporites* sp. B

GSC 96409, 2096-63-a, 29.5 x 112.0, GSC locality C-68305.

Figure 18. *Dicellaesporites septoconstrictus* sp. nov.

Holotype, GSC 96405, 2096-63-e, 18.2 x 116.1, GSC locality C-68305.

Figure 19. *Diporicellaesporites* sp. A

GSC 96418, 2096-55-g, 20.0 x 122.7, GSC locality C-68329.

Figure 20. *Brachysporisporites* sp. C

GSC 96406, 2096-64-f, 43.0 x 112.7, GSC locality C-68304.

Figure 21. *Dictyosporites* sp. A

GSC 96407, 2096-63-f, 15.7 x 122.1, GSC locality C-68305.

Figure 22. *Dictyosporites elsikii* sp. nov.

Holotype, GSC 96408, 2096-63-k, 36.1 x 126.2, GSC locality C-68305.

Figures 23, 24. *Diporicellaesporites mediocoloratus* sp. nov.

23. Holotype, GSC 96411, 2096-55-a, 24.9 x 112.0, GSC locality C-68329.
24. GSC 96412, 2096-55-b, 25.3 x 122.1, GSC locality C-68329.

Figure 25. *Diporicellaesporites pluricellus*

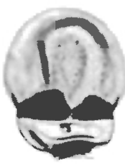
GSC 96414, 2096-55-a, 31.6 x 120.1, GSC locality C-68329.

Figure 26. *Diporicellaesporites chitaleyae* sp. nov.

Holotype, GSC 96417, 2096-55-e, 37.2 x 118.2, GSC locality C-68329.


1


2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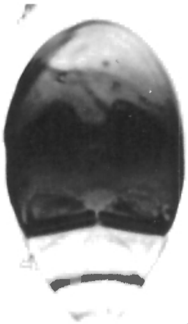
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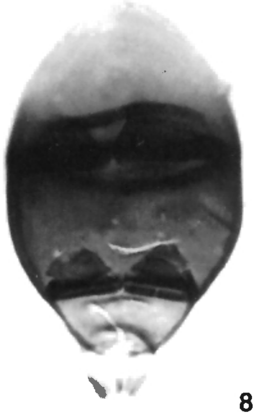
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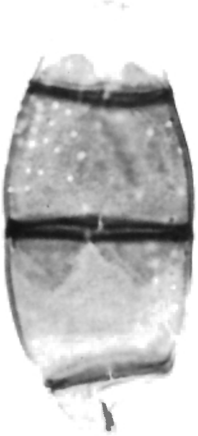
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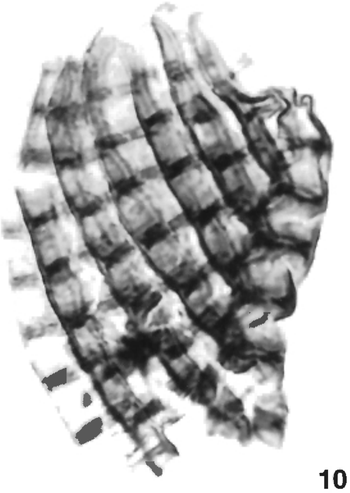
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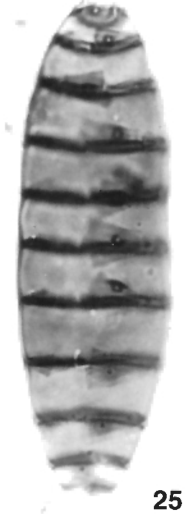
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PLATE 4.2

Figure 1. *Diporicellaesporites navicularis* sp. nov.
Holotype, GSC 96413, 2096-55-a, 21.2 x 120.9, GSC locality C-68329.

Figure 2. *Diporicellaesporites aequabilis* sp. nov.
Holotype, GSC 96415, 2096-55-a, 38.8 x 113.1, GSC locality C-68329.

Figure 3. *Diporicellaesporites quaternarius* sp. nov.
Holotype, GSC 96416, 2096-55-a, 26.5 x 114.3, GSC locality C-68329.

Figure 4. *Diporicellaesporites* sp. B
GSC 96422, 2096-63-f, 33.8 x 126.7, GSC locality C-68305.

Figures 5, 17. *Diporicellaesporites jansonius* sp. nov.
5. Holotype, GSC 96423, 2096-63-a, 14.8 x 114.0, GSC locality 68305.
17. GSC 96424, 2096-63-b, 21.1 x 117.0, GSC locality C-68305.

Figure 6. *Diporisporites* sp. A
GSC 96429, 2096-63-f, 36.9 x 121.0, GSC locality C-68305.

Figure 7. *Diporisporites hammenii*
GSC 96430, 2096-63-b, 26.2 x 110.0, GSC locality C-68305.

Figures 8, 9. *Diporicellaesporites hillsii* sp. nov.
8. Holotype, GSC 96426, 2096-63-b, 36.1 x 111.0, GSC locality C-68305.
9. GSC 96427, 2096-63-a, 18.3 x 121.2, GSC locality C-68305.

Figures 10, 14. *Diporicellaesporites vermiculatus* sp. nov.
10. Holotype, GSC 96419, 2096-63-a, 29.8 x 123.8, GSC locality C-68305.
14. GSC 96420, 2096-63-f, 22.2 x 116.0, GSC locality C-68305.

Figure 11. *Diporisporites anklesvarensis*
GSC 96428, 2096-55-a, 40.3 x 123.8, GSC locality C-68329.

Figures 12, 19. *Dyadosporites incisus* sp. nov.
12. GSC 96433, 2096-63-a, 24.0 x 118.0, GSC locality C-68305.
19. Holotype, GSC 96432, 2096-63-a, 14.2 x 121.1, GSC locality C-68305.

Figure 13. *Diporicellaesporites scalaris* sp. nov.
Holotype, GSC 96421, 2096-63-a, 17.2 x 117.9, GSC locality C-68305.

Figure 15. *Diporicellaesporites* sp. D
GSC 96437, 2096-64-e, 11.3 x 120.8, GSC locality C-68304.

Figure 16. *Diporicellaesporites* sp. C
GSC 96425, 2096-64-e, 12.0 x 112.5, GSC locality C-68304.

Figure 18. *Dyadosporites urniformis* sp. nov.
Holotype, GSC 96431, 2096-55-a, 46.7 x 109.9, GSC locality C-68329.

Figures 20, 21. *Dyadosporites inaequalis* sp. nov.
20. Holotype, GSC 96434, 2096-63-a, 35.0 x 113.0, GSC locality C-68305.
21. GSC 96435, 2096-63-a, 13.0 x 117.0, GSC locality C-68305.

Figure 22. *Exesisporites annulatus* sp. nov.
GSC 96438, 2096-64-e, 13.1 x 118.8, GSC locality C-68304.

Figure 23. *Hypoxylonites* sp.?
GSC 96445, 2096-63-a, 28.2 x 118.0, GSC locality C-68305.

Figures 24, 29, 30. *Fusiformisporites* spp.
24. GSC 96441, 2096-63-f, 25.0 x 123.4, GSC locality C-68305.
29. GSC 96442, 2096-63-b, 39.1 x 113.1, GSC locality C-68305.
30. GSC 96443, 2096-63-a, 30.3 x 120.0, GSC locality C-68305.

Figures 25, 26. *Involutisporonites trapezoides* sp. nov.
25. Holotype, GSC 96447, 2096-63-a, 23.1 x 125.5, GSC locality C-68305.
26. GSC 96448, 2096-63-l, 34.1 x 117.3, GSC locality C-68305.

Figure 27. *Involutisporonites* sp. A
GSC 96446, 2096-55-l, 39.8 x 114.4, GSC locality C-68329.

Figure 28. *Fusiformisporites* sp. A
GSC 96444, 2096-63-f, 35.5 x 114.9, GSC locality C-68305.

PLATE 4.2


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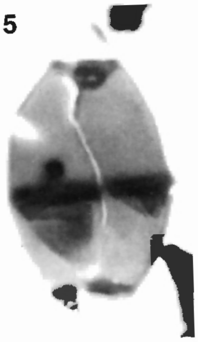


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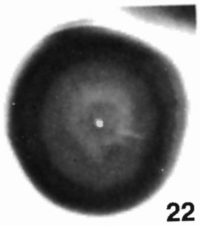
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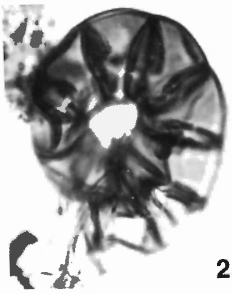
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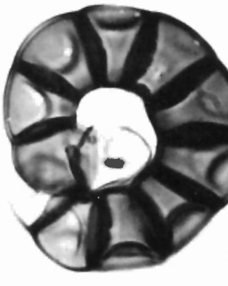
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PLATE 4.3

Figure 1. Hyphal filament

GSC 96440, 2096-55-g, 34.0 x 119.2, GSC locality C-68329.

Figure 2. *Fractisporonites doliiformis* sp. nov.

Holotype, GSC 96439, 2096-55-a, 24.2 x 120.9, GSC locality C-68329.

Figure 3. *Diporicellaesporites* sp. E

GSC 96436, 2096-63-c, 19.5 x 122.7, GSC locality C-68305.

Figure 4. *Dictyosporites eccentricus* sp. nov.

GSC 96449, 2096-55-g, 20.0 x 122.5, GSC locality C-68329.

Figure 5. *Dictyosporites* sp. C

GSC 96450, 2096-64-f, 22.0 x 112.0, GSC locality C-68304.

Figure 6. *Palaeancistrus* sp.

GSC 96456, 2096-55-g, 35.3 x 115.1, GSC locality C-68329.

Figure 7. *Dictyosporites* sp. D

GSC 96457, 2096-55-b, 15.0 x 119.8, GSC locality C-68329.

Figure 8. *Pluricellaesporites* sp. B

GSC 96460, 2096-55-a, 42.9 x 122.5, GSC locality C-68329.

Figure 9. *Monoporisporites magnus* sp. nov.

Holotype, GSC 96451, 2096-55-e, 26.0 x 112.9, GSC locality C-68329.

Figures 10, 12. *Monoporisporites singularis*

10. GSC 96452, 2096-64-e, 18.5 x 115.9, GSC locality C-68304.
12. GSC 96453, 2096-55-a, 40.9 x 111.8, GSC locality C-68329.

Figure 11. *Pluricellaesporites apiculatus* sp. nov.

Holotype, GSC 96462, 2096-63-a, 19.1 x 116.9, GSC locality C-68305.

Figure 13. *Pluricellaesporites* sp. D

GSC 96463, 2096-55-e, 36.0 x 124.2, GSC locality C-68329.

Figure 14. *Pluricellaesporites* sp. C

GSC 96461, 2096-55-g, 35.7 x 114.8, GSC locality C-68329.

Figure 15. *Pluricellaesporites* sp. A

GSC 96459, 2096-55-a, 29.3 x 111.1, GSC locality C-68329.

Figure 16. *Brachysporisporites* sp. D

GSC 96454, 2096-55-g, 24.5 x 116.0, GSC locality C-68329.

Figure 17. *Multicellaesporites* sp.

GSC 96455, 2096-63-e, 18.7 x 121.0, GSC locality C-68305.

Figure 18. *Pesavis tagluensis*

GSC 83359, 2096-63-c, 31.8 x 122.8, GSC locality C-68305.


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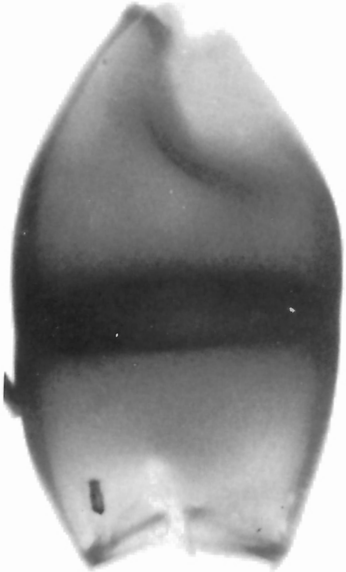
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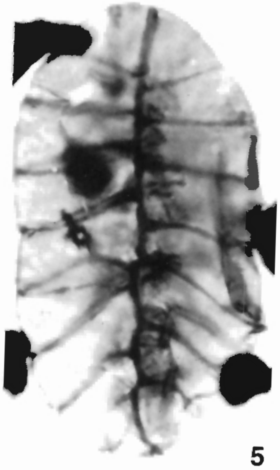
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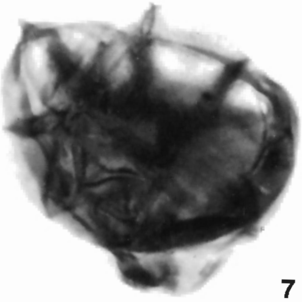
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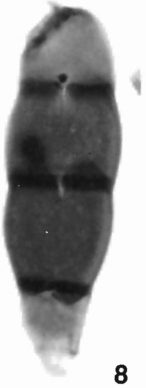
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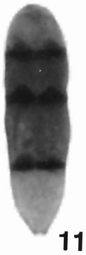
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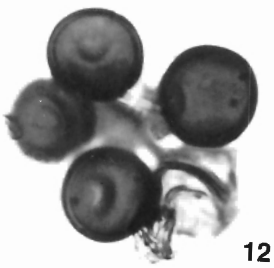
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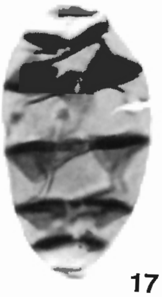
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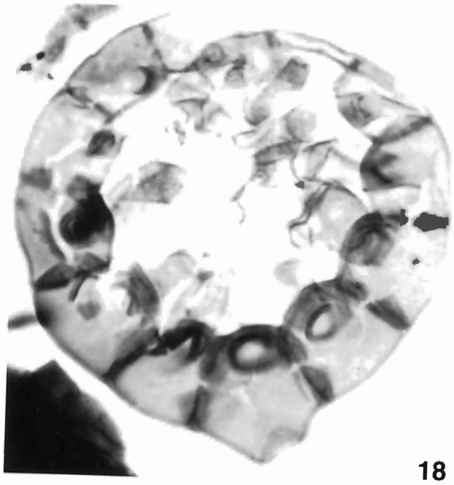
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PLATE 4.4

Figure 1. *Diporicellaesporites* sp. H

GSC 96469, 2096-64-e, 34.0 x 126.2, GSC locality C-68304.

Figure 2. *Pluricellaesporites* sp. F

GSC 96465, 2096-64-e, 45.3 x 120.9, GSC locality C-68304.

Figures 3–5. *Polyadosporites suescae*

3. GSC 96470, 2096-63-a, 15.9 x 113.9, GSC locality C-68305.
4. GSC 96471, 2096-55-a, 41.2 x 116.2, GSC locality C-68329.
5. GSC 96472, 2096-63-a, 29.3 x 114.0, GSC locality C-68305.

Figure 6. *Pluricellaesporites* sp. E

GSC 96464, 2096-63-e, 29.1 x 109.4, GSC locality C-68305.

Figure 7. *Diporicellaesporites* sp. F

GSC 96467, 2096-55-b, 44.5 x 115.4, GSC locality C-68329.

Figures 8–11. *Psilodiporites krempii*

8. GSC 96473, 2096-55-a, 41.5 x 113.1, GSC locality C-68329.
9. GSC 96474, 2096-55-a, 42.6 x 127.0, GSC locality C-68329.
10. GSC 96475, 2096-55-a, 12.2 x 114.9, GSC locality C-68329.
11. GSC 96476, 2096-55-e, 29.1 x 114.0, GSC locality C-68329.

Figure 12. *Striadiporites irregularis* sp. nov.

Holotype, GSC 96481, 2096-55-a, 27.0 x 113.7, GSC locality C-68329.

Figure 13. *Reduviasporonites ramosus* sp. nov.

Holotype, GSC 96479, 2096-63-b, 29.8 x 110.1, GSC locality C-68305.

Figure 14. *Staphlosporonites delumbus*

GSC 96480, 2096-55-b, 46.0 x 125.8, GSC locality C-68329.

Figure 15. *Pluricellaesporites* sp. G

GSC 96466, 2096-64-f, 20.0 x 109.1, GSC locality C-68304.

Figure 16. *Triporicellaesporites* sp.

GSC 96482, 2096-55-a, 42.2 x 115.2, GSC locality C-68329.

Figure 17. *Reduviasporonites* sp. A

GSC 96478, 2096-63-b, 39.1 x 123.1, GSC locality C-68305.

Figure 18. *Diporicellaesporites* sp. G

GSC 96468, 2096-63-a, 32.0 x 127.4, GSC locality C-68305.

Figure 19. *Reduviasporonites catenulatus*

GSC 96477, 2096-55-h, 42.6 x 123.6, GSC locality C-68329.

PLATE 4.4


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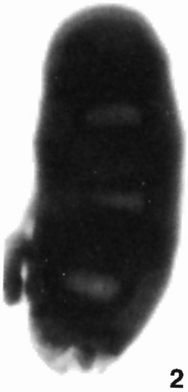
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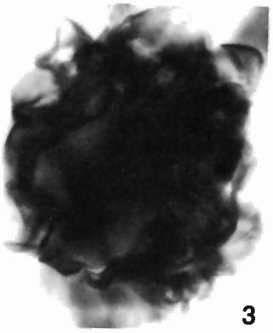
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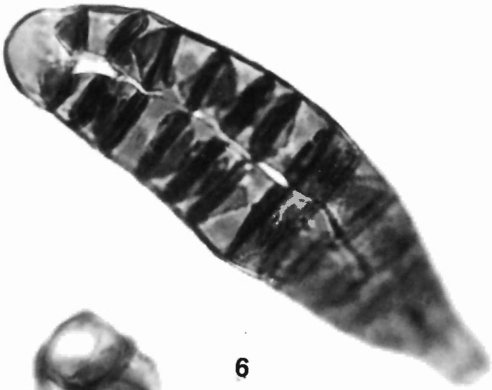
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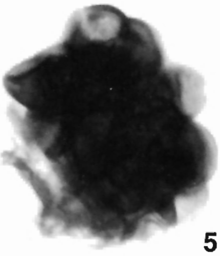
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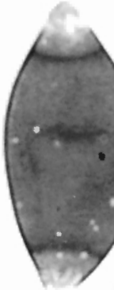
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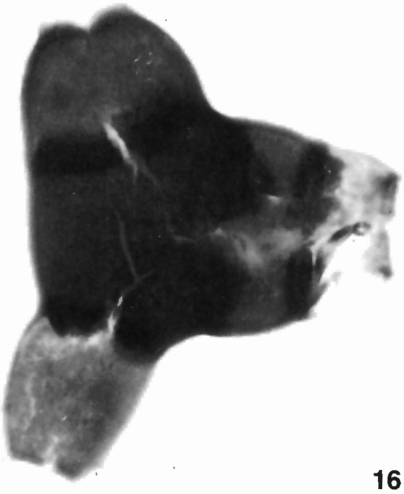
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