# Taxonomy of Gastropods of the Families Ranellidae (=Cymatiidae) and Bursidae
# Part 5.  Early History of the Families, with Four New Genera and Recognition of the Family Personidae

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## ABSTRACT

The origins and phylogeny of the Bursidae are obscure ; the only recorded Eocene species are ···q·.ahia washingtoniana (Weaver, 1912) (Late Eocene, western USA), proba.·i·y O. domenginica (Vokes, 1939) (Middle Eocene, western USA), and Marsupina yasila (Olsson, 1930), Late Eocene, Peru.

The oldest Ranellidae are six species of Sassia in Late Cretaceous rocks ; the earliest is S. innabensis (Stanton, 1893) (Turonian, western interior, USA) ; most others are Maastrichtian. Trachytriton Meek, 1864 is transferred to the neogastropod family Buccinidae, and Sassia is regarded as the stem group of all Ranellidae. The earliest recorded undoubted member of Ranellinae is Gyrineum (?) judithae Zinsmeister, 1983 (Danian, Early Paleocene, California) apparently a representative of the stem group of an Eocene radiation of Ranellinae in the north Pacific. A new species of Ranella is described from the late Paleocene Lodo Formation of California. Western USA Eocene Ranellinae are briefly reviewed, and the new genus Ameranella is proposed for Nyctilochus kewi Dickerson, 1915 (Late Eocene, Washington and California), "Fusitriton" terrysmithae Hickman, 1980 (latest Eocene, Oregon) and Triton verruculosum Sowerby, 1846 (Miocene, Chile).

The earliest recorded Cymatium species are C. (Monoplex) janetae Squires, 1983 (lower Middle Eocene, California) and C. (Monoplex) washingtonianum (Weaver, 1912) (Late Eocene, Washington). The new genus Eocymatium is proposed for Murex pyraster Lamarck, 1803 (Lutetian, Paris Basin) and an unnamed Late Paleocene species from the uppermost Ranikot beds of Pakistan.

The oldest recorded Distorsio species is D. praegranosa (Cottreau, 1922), a large, typical species from the early Campanian (Late Cretaceous) of Madagascar. Because of the appearance of Distorsio parallel to Sassia (so its inclusion in Ranellidae would make that a polyphyletic taxon) and because of its distinctive anatomy and radula, the small group of genera related to Distorsio is regarded as a sixth family of Tonnoidea, Family Personidae Gray, 1854. Personella Conrad, 1865 is an earlier name for Sassia (Byramia) MacNeil, 1984 (Ranellidae) and the new genus Personopsis is proposed for the small, weakly distorted Personidae that have previously been referred to Personella. The new genus and species Kotakaia simplex is proposed for a small personid from the Mid-Late Paleocene of the Chatham Island, New Zealand.

## INTRODUCTION

For several years I have been working towards understanding the classification and phylogeny of the tonnoidean gastropod families Ranellidae (=Cymatiidae) and Bursidae. Species in these families have very wide distributions, because of their very long-lived planktotrophic larvae, and so most species have received separate names in each of the different regions they occupy. Earlier taxonomists included a broad group of gastropods in Ranellidae, in particu-

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lar, because of the previously unrecognised convergent development of prominent varices and coarse sculpture in several unrelated gastropod groups. This is the fifth in a series of papers intended to revise the taxonomy of these families and to determine their phylogeny (Part 4: Beu & Kay, 1988).

The present paper is a brief summary of ideas developed during 20 years of considering the fossil record and possible phylogenies of these families. I do not attempt to document full phylogenies, but use the record of first appearances as evidence to begin sorting out phylogenies that, combined with morphology, can be used to recognize some genera that are incorrectly placed in the Ranellidae. The major conclusion from this study is that Ranellidae, as treated until now, is a polyphyletic taxon; the personid genus *Distorsio* evolved at about the same time as *Sassia* (the stem group of all other taxa included here in Ranellidae) and so Personidae is regarded as a family distinct from Ranellidae.

It is with great pleasure that I dedicate this paper, and the new genus *Kotakaia* proposed below, to my good friend and former professor (during his "New Zealand years"), Professor Tamio Kotaka, on the occasion of his retirement, and in commemoration of his association with New Zealand paleontology.

## ABBREVIATIONS

In lists of material, and figure captions and acknowledgements, institutions are abbreviated as follows:

BM(NH) — British Museum (Natural History), London.

CAS — California Academy of Sciences, San Francisco.

LACM — Los Angeles County Museum of Natural History.

LACMIP — Department of Invertebrate Paleontology, Los Angeles County Museum of Natural History.

NZGS — New Zealand Geological Survey, Lower Hutt.

UCMP — Museum of Paleontology, University of California, Berkeley.

USGS — United States Geological Survey (in Menlo Park, California and Washington, D.C.)

USNM — United States National Museum of Natural History, Washington D.C.

## TAXONOMY

### Superfamily Tonnoidea
### Family Bursidae Thiele, 1929

*Remarks*: The origins of the family Bursidae are obscure. No fossils of Eocene (or earlier) age are recorded from the European region or in Asia. The earliest taxon that has been referred to the family is *Bursa saundersi* Adegoke (1977, p. 209, pl. 31, fig. 27, 28), a small (22.0 mm × 14.4 mm), wide, generalised West African shell that is difficult to assign with certainty to either Ranellidae or Bursidae. Adegoke (1977) presumably assigned it to Bursidae because its varices are closely spaced and nearly aligned up the whorls (i.e., little more than 180° apart around the spiral), the sculpture is of coarse nodes, and the short spire more nearly resembles that of Bursidae than that of Ranellidae. However, the specimen clearly lacks all sign of the most distinctive character of Bursidae, the posterior siphonal canal at the top of the outer lip, and so has more the appearance of Ranellidae Ranellinae than of Bursidae. The significance of the specimen is therefore uncertain; it is earlier than all recorded Bursidae, and so suggests the possibility that Bursidae

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evolved from Ranellidae Ranellinae, but is likely to be a ranelline convergent on the bursid shell form, as the very different radulae and fore-gut anatomies of the Ranellidae and Bursidae (Beu, 1981) make a close phylogenetic relationship between them unlikely. The specimen is from the late Paleocene Ewekoro Formation of Nigeria, West Africa.

The only Eocene records of Bursidae I am aware of are from the western Americas: *Olequahia* Stewart, 1926 from the late Middle Eocene to Oligocene of western North America, and *Marsupina yasila* (Olsson, 1930) and *M. chira* (Olsson, 1930) from the Late Eocene (Stone, 1949) Talara Formation and Chira Formation, respectively, of Peru (Olsson, 1930, p. 62). The absence of Bursidae from Tethyan warm-water faunas, in which Ranellidae (notably *Sassia*) are so diverse, suggests that the Bursidae appeared only during Eocene time, and probably appeared first in the eastern Pacific during the Middle Eocene.

*Marsupina yasila* (Olsson) and *M. chira* (Olsson) have been well illustrated (Olsson, 1930, pl. 10, fig. 3-7, 12, 13) and clearly have the aligned, widely extended varices, distinctive posterior siphonal canal, and evenly granulous sculpture typical of modern species of *Marsupina* and *Bufonaria*. The earlier species, *M. yasila*, is a uniformly granulous species without prominent sculpture, but with a moderately low spire, with weak varices down the entire teleoconch, and with short anterior and posterior canals; it could well have been a stem taxon for all Miocene to modern Bursidae, with the possible exception of the western American endemic genus *Crossata* Jousseaume, 1881. Referral to *Marsupina* Dall, 1904 seems reasonable. I have previously regarded *Marsupina* as a subgenus of *Bufonaria* Schumacher, 1817 (Beu, 1981). However, further study has shown that, whereas *Marsupina bufo* (Bruguière, 1792) and *M.*

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*nana* (Broderip and Sowerby, 1829) have a calcareous intritacalx and a terminal opercular nucleus, the many Indo-West Pacific species of *Bufonaria* (most revised by Beu, 1987) have a finely bristled conchiolin periostracum and have the opercular nucleus mid-way down the columellar margin. *Marsupina* and *Bufonaria* are probably not closely related.

Species of *Olequahia* are far from typical Bursidae, having a long straight anterior siphonal canal with the columella continuing undeflected down its left edge; they more closely resemble cassine cassids, particularly *Galeodea*, than other Bursidae. The possibility therefore needs considering that the present concept of Bursidae is polyphyletic. Figures are provided here of the type species of *Olequahia* to enable evaluation of its relationships.

## Genus *Olequahia* Stewart, 1926

*Olequahia* Stewart, 1926, p. 382. Type species (by original designation): *Cassidaria washingtoniana* Weaver, 1912, Late Eocene, western USA.

*Remarks*: Important characters of the genus are its inflated, *Galeodea*-like form, its moderately long, straight columella and anterior siphonal canal, its prominent terminal varix, its narrow inner lip collar closely similar to that of many modern species of *Bufonaria*, and its relatively wide, moderately deep posterior canal cut into the outer lip extension, beyond the terminal varix. The oldest species referrable to *Olequahia* seems to be "*Ranella*" *domenginica* Vokes (1939, p. 147, pl. 19, fig. 6, 20), which has prominent varices over the entire teleoconch, and is taller and narrower than all younger species. The type species and the probably synonymous *O. hornii* (Gabb), from the Tejon Formation of California, have varices on the earliest 2-3 spire whorls, but none on
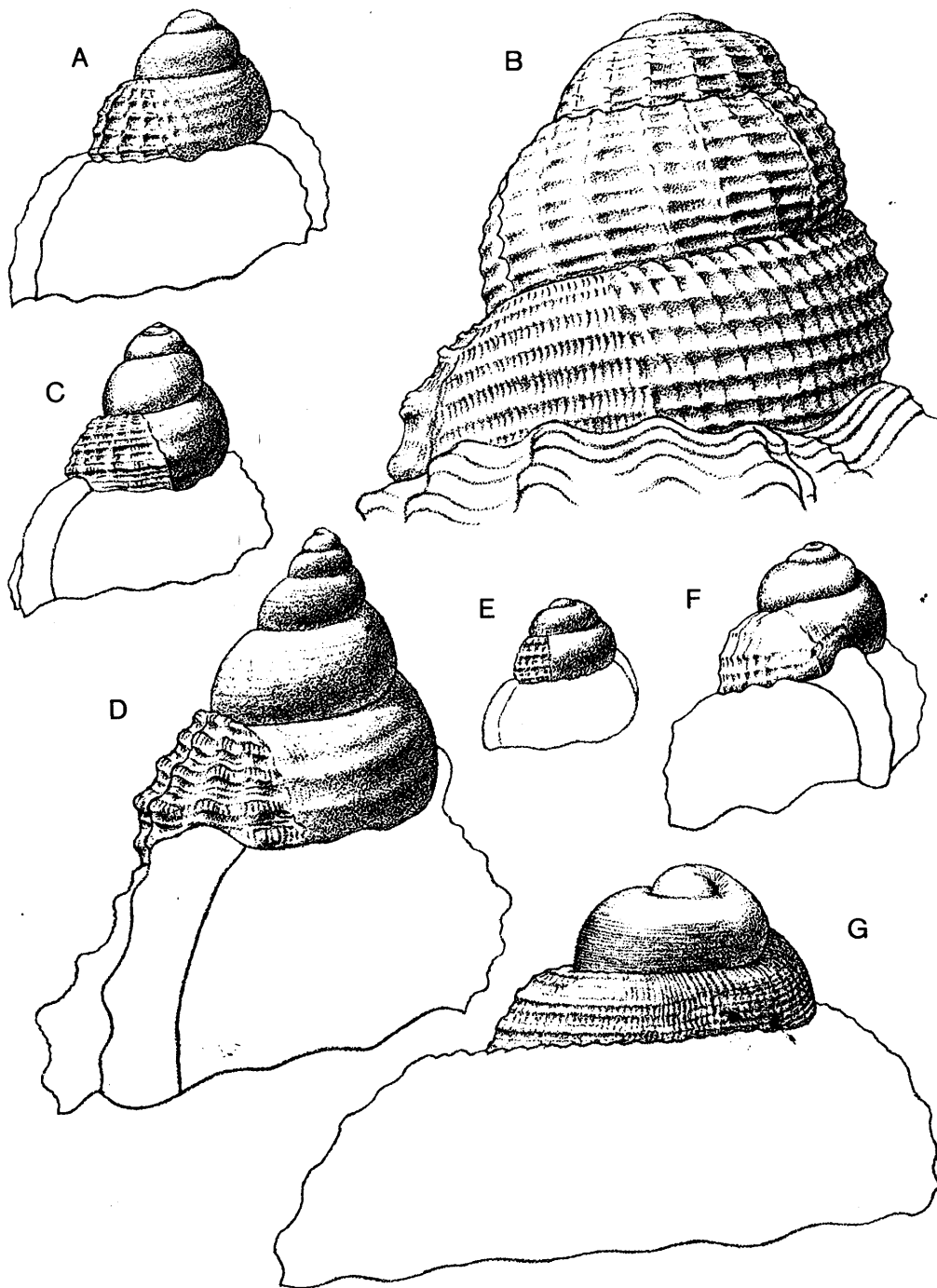
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the adult shell, other than the terminal one ; Oligocene species have only a terminal varix. *O. domenginica* (Vokes, 1939) is recorded from the early Middle Eocene (Squires, 1983) Llajas Formation in Simi Valley, California, and from the late Middle to early Late Eocene Domengine Formation of California. Examination of the two syntypes of *O. domenginica* (UCMP-672/15803, 15804, Domengine Formation, north of Coalinga, California) shows that the larger (40.3 × 22.5 mm) is similar in shape to *O. washingtoniana* (Weaver) ; Givens (1974, p. 79, pl. 9, fig. 4, 5) also included *O. domenginica* in *Olequahia*. Other species referrable to *Olequahia* are : *O. washingtoniana* (Weaver) from the Late Eocene Cowlitz Formation of Washington and Oregon, and its probable synonym *O. hornii* (Gabb, 1864) from the Late Eocene Tejon Formation in California ; *O. lincolnensis* (Weaver, 1916) from the Oligocene Lincoln Formation in Washington ; *O. schencki* Durham, 1944, from the latest Eocene Keasey and Oligocene Eugene formations of Oregon ; and *O. lorenzana* (Wagner and Schilling, 1923), from the Middle Oligocene of California (Hickman, 1969, p. 89, 90 ; Hickman, 1980, p. 48). The earliest species is therefore the relatively narrow, strongly varicate *O. domenginica* (Vokes), which suggests that the genus

could have evolved from a tall-spired, cymatiid-like ancestor.

## *Olequahia washingtoniana*
### (Weaver, 1912).

Fig. 1F ; Pl. 1, fig. 1-9.

? *Tritonium hornii* Gabb, 1864, p. 94, pl. 28, fig. 208 (in part) ; Gabb, 1869, p. 218 (in part).
? *Tritonium* (*Trachytriton*) *tejonensis* Gabb, 1869, p. 154, pl. 26, fig. 34.
*Cassidaria washingtoniana* Weaver, 1912, p. 38, pl. 3, fig. 28.
*Nyctilochus washingtoniana*, Dickerson, 1915, p. 90, pl. 7, fig. 9.
? *Bursa hornii*, Anderson and Hanna, 1925, p. 54, pl. 13, fig. 3, 4, 8.
? *Siphonalia tularensis* Anderson and Hanna, 1925, pl. 10, fig. 1 only (not p. 45).
*Olequahia washingtoniana*, Stewart, 1926, p. 383 ; Weaver, 1943, p. 425, pl. 84, fig. 6, 10, 11.
? *Olequahia hornii*, Stewart, 1926, p. 382, pl. 29, fig. 1, 4, 18.

*Remarks* : Stewart's (1926, pl. 29, fig. 1, 4, 18) figures of *Olequahia hornii* (Gabb) show no significant differences from the specimens of *O. washingtoniana* I have examined ; the two nominal taxa have the same shape, spiral sculpture, and varices on the top few spire whorls only. I show below that both *Ranella washingtoniana* (Weaver) (= *Gyrineum uvasilis* Anderson and Hanna) and *Ameranella kewi* (Dickerson) are present in the Late Eocene Tejon Formation of California and the at least partly coeval

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Fig. 1. Protoconchs of Ranellidae and Bursidae, at two different scales : Fig. A, C-F enlarged ×22 ; Fig. B, G, enlarged ×33.

A. *Ameranella kewi* (Dickerson, 1915), type species of *Ameranella* n.gen., Cowlitz Formation, Late Eocene, Cowlitz River, Washington, USA ; WM13325, NZGS.

B. *Sassia delafossei* (Rouault, 1850), Gan, near Pau, southern France, Cuisian, late Early Eocene ; Mississippi Bureau of Geology.

C. *Cymatium* (*Monoplex*) *cowlitzense* (Weaver, 1912), Cowlitz Formation, Late Eocene, Cowlitz River, Washington, USA ; LACMIP loc. 5654.

D. *Ranella washingtoniana* Weaver, 1912, same locality and collection as Fig. C.

E. *Sassia formosa* (Deshayes, 1865), Calcaire Grossier, Lutetian, early Middle Eocene, Chaussy, Oise, Paris Basin, France, ex Cloez Colln., UCMP-B5350.

F. *Olequahia washingtoniana* (Weaver, 1912), type species of *Olequahia* Stewart, 1926 ; Cowlitz Formation ; Late Eocene, Cowlitz River, Washington, USA ; UCMP-D8044/16071.

G. *Eocymatium pyraster* (Lamarck, 1803), type species of *Eocymatium* n.gen. ; Calcaire Grossier, Lutetian, early Middle Eocene, Amblainville, Oise, Paris Basin, France, ex Cloez Colln. ; UCMP-B5349.

Cowlitz Formation of Washington and Oregon; *O. hornii* may well be another species in common. As I am not sure of the synonymy in this case and as *O. washingtoniana* is the type species of *Olequahia*, the illustrated specimens from the Cowlitz River type locality of *O. washingtoniana* are identified by that name at present.

The specimens of *O. washingtoniana* examined show considerable variation in spire height, whorl inflation, prominence of spiral cords, width of the outer lip extension beyond the terminal varix, and width and depth of the posterior siphonal canal. The outer lip is crenulated into a series of rounded nodes and sinuses; as the lip margin grows forward after varix formation, it produces a complexly frilled outer lip not unlike that of some Muricidae. This complexly sculptured lip extension is notched by the posterior canal, which is widely, thickly and smoothly callused, with a wide, evenly rounded external flare. The canal is constricted by a large nodule on the top of the inner edge of the outer lip, and another on the parietal region. The two nodules seem to become progressively more callused as the outer lip extension grows forwards; of the specimens seen, the one with the widest outer lip is also that with the narrowest and deepest posterior canal (Pl. 1, fig. 5, 6, 9). Most specimens examined, however, have a widely open posterior canal.

The anterior siphonal canal is unusual among Bursidae in being straight; the very straight columella continues without deviation down the left edge of the canal. The complete length of the unbroken canal is not demonstrated by any specimens I have examined. All specimens examined have three prominently noded major spiral cords, low varices restricted to the first 2-3 teleoconch whorls, and a clearly raised collar on the left edge of the inner lip. The protoconch (Fig. 1F) is small, turbiniform, of about 3.5 apparently smooth, inflated whorls (the tip is abraded in most specimens), and similar in most characters to those of Cassidae (e.g., Abbott, 1968, pl. 5, 6) and all other Bursidae. All Bursidae have closely similar turbiniform protoconchs, differing only at the species level.

The posterior canal of *Olequahia* is closest to that of *Crossata californica* (Hinds, 1843). Immature specimens of *C. californica* (particularly of the thin-shelled form or geographic subspecies *Bursa californica sonorana* Berry, 1970, p. 118) are closely similar to *O. washingtoniana* in the following characters: the position of the major spiral cords (although only the upper two bear nodes in *Crossata*), the straight, continuous columella and left side of the anterior canal, the form of the outer lip, and the widely open, shallow posterior canal. The complex frills on the outer surface of the outer lip flare have been observed also on some specimens of *Crossata californica*. *Crossata* differs clearly from all *Olequahia* species younger than *O. domenginica* in having varices on all whorls. It seems feasible that, despite the lack of a fossil record in Miocene rocks of western America, *Olequahia* was either the direct ancestor of *Crossata*, or (to judge from the lack of varices in Oligocene *Olequahia* species), it branched from a lineage that led to modern *Crossata* species. The widely open anterior and posterior canals, the large aperture, and the subdued teleoconch sculpture certainly make *Crossata* a distinctive, endemic western American genus that appears to have had a long history of isolation in the area.

An important aspect of the morphology of *Olequahia* is the outer lip extension, a thin flange extending beyond the terminal varix. I am not aware of the existence of such a lip flange in any Cassidae, and its presence in *Olequahia*

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suggests strongly (along with the posterior apertural canal) that *O. washingtoniana* is convergent on the cassid shell form. Indeed, the morphology of *Olequahia washingtoniana* seems closest to that of *Bufonaria* in its elongate but inflated form, the presence of only three widely spaced, noded, primary spiral cords, and the straight columella. *Bufonaria* differs in being more dorsoventrally compressed, in having evenly granulous interstitial sculpture, varices on all whorls, and a longer, gutter-or tube-like posterior canal, but a close relationship appears feasible. It remains enigmatic that two such markedly different bursids as *Olequahia* and *Marsupina* should have appeared, apparently nearly simultaneously in North and South America respectively; the first appearance of *Bursa* occurred elsewhere, probably in the tropical Indo-West Pacific.

*Dimensions*: Most complete specimen seen (Pl. 1, fig. 1-3): height 55.1 mm, diameter 33.7 mm.

*Localities*: All examined well-preserved specimens are from the Cowlitz River near Vader, Lewis County, Washington, from the Cowlitz Formation (Late Eocene). Several specimens from this locality have been examined in USNM, UCMP, CAS, and LACMIP. The probably synonymous *O. hornii* (Gabb) occurs in the coeval Tejon Formation near Tejon, Kern County, California. *O. hornii* has also been recorded from the far eastern USSR by Schmidt (Stewart, 1926, p. 382, synonymy list) so this species seems to be widespread in Late Eocene rocks of eastern Asia and western North America.

## Family Ranellidae Gray, 1854
### Subfamily Ranellinae Gray, 1854

*Remarks*: The excellent monograph by Smith (1970) has greatly clarified the taxonomy and phylogeny of the

Oligocene and Neogene Ranellinae (particularly in genera *Argobuccinum* and *Fusitriton*) in the North Pacific, but Smith (1970) pointed out that the same treatment was needed for the Eocene taxa of western North America. A brief review is undertaken here of most Paleocene and Eocene ranelline taxa of western USA.

## Genus *Ranella* Lamarck, 1816

*Ranella* Lamarck, 1816, pl. 412-414, "Liste" p. 4. Type species (by subsequent designation, Children, 1823): *Ranella gigantea* Lamarck, 1816 ( = *Murex olearium* Linné, 1758), (Oligocene ?) Miocene to Pliocene, Europe; Recent, Mediterranean, eastern and western Atlantic, South Africa, St Paul & Amsterdam Islands, Réunion, New Zealand, and Kermadec Islands.

*Gyrina* Schumacher, 1817, p. 77, 253. Type species (by monotypy): *Gyrina maculata* Schumacher, 1817 ( = *Murex olearium* Linné, 1758) (not *Gyrina* Linné, 1767, Insecta).

*Eugyrina* Dall, 1904, p. 132. Type species (by original designation): *Ranella gigantea* Lamarck, 1816 ( = *Murex olearium* Linné, 1758).

*Mayena* Iredale, 1917, p. 324. Type species (by original designation): *Biplex australasia* Perry, 1811, late Miocene-Recent, New Zealand and southern Australia.

*Gyrinopsis* Dall, 1925, p. 18. Type species (by monotypy): *Gyrinopsis cowlitzi* Dall, 1925 ( = *Ranella washingtoniana* Weaver, 1912), Mid-Late Eocene, western USA.

### *Ranella washingtoniana* Weaver, 1912.

Fig. 1D; Pl. 2, fig. 1-3.

*Ranella washingtoniana* Weaver, 1912, p. 41, pl. 2, fig. 14.

*Bursa washingtoniana*, Dickerson, 1915, p. 64, pl. 4, fig. 4, 6.

*Gyrineum uvasilis* Anderson and Hanna, 1925, p. 57, pl. 6, fig. 1; pl. 10, fig. 5; pl. 13, fig. 13.

*Gyrinopsis cowlitzi* Dall, 1925, p. 18, pl. 18, fig. 4, 6.

*Cymatium* cf. *washingtoniana*, Turner, 1938, p. 90, pl. 16, fig. 17.

*Cymatium washingtonianum*, Weaver, 1943, p. 412, pl. 81, fig. 9, 11, 12 (in part).

*Remarks*: Beu (1976, p. 424), Hickman (1980, p. 48) and Squires (1983, p. 358) have previously referred this species

to *Ranella* sensu stricto; Weaver (1912) presumably intended to place the species in what is now called *Bursa*.

The shells of large, typical *Ranella washingtoniana* illustrated by Weaver (1943, pl. 81, fig. 9, 11, 12) are closely similar to both living species, *R. olearia* (Linné, 1758) (Pl. 4, fig. 4, 5) and *R. australasia* (Perry, 1811) (Pl. 4, fig. 7), in spire proportions, in sculpture, in having the varices aligned — or nearly so — down the entire teleoconch, and in apertural characters. These include a relatively long, straight, narrow canal deflected slightly to the left, the presence of several low nodules of transverse ridges on the columellar base (apparently a consistent character or Ranellinae), and the presence of a shallow posterior apertural notch. The interior of the outer lip is almost smooth and curves gently out over the terminal varix in *R. washingtoniana*. The type material of *Gyrinopsis cowlitzi* Dall, 1925 (examined, in USNM) consists of several large, excellent specimens of *R. washingtoniana*. The recently named *R. katherinae* Squires (1983, p. 358, fig. 2E-G) from the Llajas Formation (early Middle Eocene) of the Simi Valley, California, is still more like the living *R. olearia*, as it has a flat-faced terminal varix with many small nodules along the inner edge of the outer lip. Several Cowlitz Formation specimens of *R. washingtoniana* bear a well preserved protoconch (Fig. 1D); it is closely similar to that of *R. olearia* and *R. australasia*. The protoconch of *R. washingtoniana* is unusually large for a member of Ranellinae (4.5 mm high), rather narrowly turbiniform, with 5 almost smooth, weakly inflated whorls, faint signs of spiral threads and — unlike that of *R. olearia* — it develops three low, wide spiral cords over the last half-whorl. The much smaller protoconchs of modern *Argobuccinum* species and of *Ameranella kewi* (Fig. 1A) help confirm the relation-

ships suggested here.

The identification of material of *R. washingtoniana* and other Ranellidae figured by Weaver (1943, pl. 81, 82) is muddled. *Ranella washingtoniana* actually appears on pl. 81, fig. 6, 9, 11, 12, and 13; fig. 13 shows the distinctive large protoconch of *R. washingtoniana*, although it is identified as *Cymatium cowlitzense* (Weaver, 1912). Weaver's (1943) pl. 81, fig. 8, 10 and pl. 82, fig. 2, 3, and 10 show a single species of *Cymatium (Monoplex)* identified on pl. 81 as *C. cowlitzense*, and on pl. 82 as *C. etheringtoni* Weaver, 1943; as the specimen illustrated by Weaver (1943) in pl. 81, fig. 10 is the holotype of *C. cowlitzense* I conclude that this is the valid name for a species later also named *C. etheringtoni* by Weaver (1943). Examination of many collections of Cowlitz River fossils showed that only one species of *Cymatium (Monoplex)* occurs there. A third taxon, identified below by the name *Ameranella kewi* (Dickerson), was also identified as *C. cowlitzense* by Weaver (1943, pl. 81, fig. 7; pl. 82, fig. 1, 4) who seems to have regarded this as the adult form of his *C. cowlitzense*; the two are readily distinguished by the varices being nearly aligned in *A. kewi* but situated at each 0.66 whorls in *C. cowlitzense*.

*Dimensions*: height 96.5 mm, diameter 55.8 mm (USNM 333358, lectotype of *Gyrinopsis cowlitzi* Dall, 1925); largest specimen seen.

*Localities*: Examination of the types and of a series of topotypes of *Gyrineum uvasilis* Anderson and Hanna, 1925 showed that this taxon was based on specimens of *R. washingtoniana* from the Tejon Formation at Grapevine Canyon and nearby localities in Kern County, California. Turner (1938, p. 91) recorded what appears to be typical *Ranella washingtoniana* from the lower Coaledo Formation (which he thought coeval with the Tejon and Cowlitz formations)

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at the east side of the lighthouse reefs, Cape Arago, Oregon (UCMP loc. A715). Squires (1983, p. 358) identified a specimen from the lower Middle Eocene Ardath Shale in San Diego County, California, as *R. washingtoniana*. Numerous specimens (below) have been examined from the Cowlitz River, Washington, from the Cowlitz Formation (Late Eocene, approximately coeval with Tejon Formation). The species is therefore widespread in western North America, and occurs in rocks of lower Middle to Late Eocene age.

*Material examined* : USGS loc. 4026, USNM 333358, Dall's figured specimen (here designated lectotype) of *Gyrinopsis cowlitzi* Dall, 1925, from Little Falls, Cowlitz River, Washington, with 10 other specimens (all syntypes ?-not labelled as to status); USGS 18510, "type locality of Cowlitz Formation", 2 (USGS, Menlo Park, California, and 2 with no locality data) ; two syntypes of *Ranella washingtoniana* Weaver, 1912, Cowlitz River, Washington (CAS 488, 488a); holotype (CAS 829) and 2 paratypes (CAS 830, CAS 872) of *Gyrineum uvasilis* Anderson and Hanna, 1925, from Tejon, California; Cowlitz River below mouth of Drew Ck., 1.5 miles from Olequa, Washington, 9 (CAS 61656.01) ; Tejon Formation, Liveoak Canyon, Kern Co., California, 1 (CAS 61661.01) ; UCMP7162/33863, Weaver's (1943, pl. 81, fig. 12) figured specimen, Cowlitz River, Washington ; Cowlitz River Eocene general collections, Museum of Paleontology, University of California, Berkeley (many) ; UCMP loc. 7200, Tejon Formation, Tejon Quadrangle, Kern Co., California, 5 ; UCMP A452, Tejon, 3 ; UCMP A4522, Cowlitz River, Washington, several, including specimen with complete protoconch ; LACMIP loc. 5654, north bank Cowlitz River 1.5 miles E of Vader, Lewis County, Washington, 5.

## *Ranella tuomeyi* Aldrich, 1886.

Pl. 2, fig. 4-6.

*Ranella* (*Argobuccinum*) *tuomeyi* Aldrich, 1886, p. 20, pl. 3, fig. 3.
*Triton tuomeyi*, Harris, 1899, p. 64, pl. 8, fig. 12.
*Ranella tuomeyi*, Palmer and Brann, 1966, p. 873 (with further synonymy).

*Remarks* : Figures are provided of the holotype of *Ranella tuomeyi*, which is among the earliest species I am aware of in *Ranella* (sensu stricto). The holotype is small (39.0 mm × 24.1 mm) and superficially resembles a large, very finely sculptured form of the living Western Pacific *Gyrineum bituberculare* (Lamarck, 1816), but its apex bears the last fragments of a formerly large, smooth protoconch, much larger than that of *Gyrineum* species. The aligned, narrow varices, the long anterior canal, the form of the outer lip (with 8 interior nodules along an inner ridge, forming an almost flat outer face) and the simple spiral sculpture of narrow cords are all characters in common with *Ranella*. *R. tuomeyi* and the following new species differ from *Ameranella* n. gen. in their much larger protoconch and weaker sculpture, and particularly in the lack of prominent nodules on the varices. Aldrich (1886) and Harris (1899, p. 64) mentioned several specimens, and Harris (1899, pl. 8, fig. 12) figured one that is more complete than the holotype, bearing a large protoconch similar to that of *R. olearia*.

*Locality* : Woods Bluff, Tombigbee River, Clarks County, Alabama, USA ; Bashi Member, Hatchetigbee Formation, upper Wilcox Group, Early Eocene (Palmer and Brann, 1966, p. 873) ; USNM registered no. 638755.

*Remarks* : The only other Eocene species I am aware of that seems referable to *Ranella* is *Triton eogassinense* Sacco (1904, pl. 10, fig. 12), from Gassina, Italy, Bartonian (Late Eocene), based on a poor internal mould resembling *R.*

*olearia* (Linné).

## *Ranella louellae* n. sp.
### Pl. 4, fig. 1-3.

? *"Fusitriton"* sp. aff. *Murex (Argobuccinum) mansfieldi* Gardner; Smith, 1975, p. 469.

*Description* : Shell very small for genus, very prominently sculptured, with prominent varices aligned down at least last few whorls of teleoconch (spire missing). Sutural ramp wide, steeply descending at first, then strongly concave. Sculpture of narrowly crested, widely spaced spiral cords, five on penultimate whorl (lowest immediately above suture), nine on last whorl, and at least five further weak ones on anterior canal (which is very incomplete); interspaces crowded with fine spiral threads of several orders, at least four secondary threads in each interspace; crossing prominent, closely spaced, rounded axial costae that rise on centre of sutural ramp, become very prominent around periphery (and are raised into low nodules where crossed by spiral cords), and fade out over lower half of last whorl; five costae on each of the last three intervariceal intervals. Varices high and narrow, hollowed abaperturally and buttressed by spiral cords, but spiral cords only slightly raised where they cross outer surfaces (i.e., varices lack nodules). Aperture subcircular; outer lip flared over inner two-thirds of terminal varix, weakly digitate around outer rim, bearing eight prominent, narrowly rounded nodules on angulation at inner edge of outer lip; inner lip thick, with squarely elevated rim along posterior margin of aperture and alongside columella, smooth except for a single prominent parietal nodule and five low, narrow, transverse ridges on base of columella. Anterior canal only narrowly open, deflected to left, with very low fasciole and narrow pseudumbilical groove, but

length unknown (broken off below junction of outer lip). Spire apex and protoconch missing.

*Dimensions* : height (very incomplete) 34.1 mm, (estimated) 52 mm, diameter (slightly incomplete) 27.0 mm.

*Repository* : holotype (LACMIP 7689) in LACMIP.

*Locality* : University of California at Los Angeles (UCLA) locality no. 6456, basal Lodo Formation shellbed, abrupt hill slope on south side of road, south side of Panoche Creek, 0.75 miles east of junction with Silver Creek (3450′S, 500′ E of NW corner section 21, T15S, R12E), Tumey Hills, Fresno County, California, coll. L.R. Saul, 10 June 1977; holotype only; Late Paleocene (see below).

*Remarks* : *Ranella louellae* differs clearly from all other *Ranella* species other than *R. tuomeyi* Aldrich in its small size, and from all other species, in its very prominent sculpture. *R. tuomeyi* is closely similar in size and general appearance, differing from *R. louellae* in its weaker sculpture (particularly the much less prominent axial costae), its much lower varices, and its thinner but more complexly sculptured inner lip. The concave sutural ramp, the abaperturally hollowed and buttressed varices, the nodules on the inner angulation of the outer lip, and the squarely raised, thickened posterior apertural margin and left edge of the inner lip are characters that *R. louellae* shares with the living type species, *Ranella olearia* (Linné) (Pl. 4, fig. 4, 5). Apart from the much smaller size, the main differences from *R. olearia* are the slightly more prominent spiral cords, the markedly more prominent axial costae, and the fewer, more prominent nodules on the outer lip of *R. louellae*. Thus, although the lack of knowledge of the protoconch and spire proportions make a position in *Ranella* tentative, I am reasonably confident that is nevertheless the correct position for *R. louellae*.

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Illustrations of specimens from the basal Lodo Formation shellbed shown to me by Dr J. Terry Smith (Palo Alto; during August 1987), identified by her as "*Fusitriton*" close to *Murex* (*Argobuccinum*) *mansefieldi* Gardner (Smith, 1975, p. 469), are too fragmentary to be identified with certainty, but have varices situated at each 0.66 whorls and appear to belong in *Sassia*. A single well preserved spire of a tall, narrow *Sassia* species in LACMIP collection 7044 (road cut on east bank of Silver Creek, 0.25 miles south of Panoche Creek, Tumey Hills, Fresno County, California, coll. C.E. Weaver, 1949; not now exposed) from the basal Lodo Formation shellbed resembles juvenile specimens of *Charonia lampas* (Linné) in sculpture and proportions, and also resembles *Sassia mansfieldi* (Gardner) (1935, p. 258, pl. 23, fig. 3-6) in sculpture. It is likely the specimen belongs in the species referred to by Smith (1975, p. 469).

*Etymology* : I have great pleasure in naming the new species in honour of Dr LouElla R. Saul (LACMIP), for her many valuable contributions to Californian Cretaceous and early Cenozoic paleontology.

*Relative ages of Lodo Formation and Simi Conglomerate* : The authors of faunal revisions of the Lodo Formation (Smith, 1975) and the Simi Conglomerate (Zinsmeister, 1983) both considered the faunas they revised to be Thanetian (early Late Paleocene) in age. For understanding the apparent first appearances of ranelline genera it is desirable to refine the relative ages of these formations as closely as possible. Saul (1983) has reviewed the micropaleontological evidence for age and the turritellid and *Venericardia* biostratigraphy of several important Californian Paleogene sequences, concluding that the basal Lodo Formation shellbed (type formation of *Ranella louellae* n. sp.) contains

Foraminifera of zone P4 (late Montian-early Thanetian). According to Zinsmeister (1983, p. 1282-3) and Saul (1983, fig. 2) the Simi Conglomerate (type formation of *Gyrineum judithae* Zinsmeister, 1983) partly underlies and is partly a lateral facies equivalent of the Las Virgenes Sandstone, which in turn underlies (in ascending order) the "Martinez marine member" and the Santa Susana Formation. Saul (1983, p. 71) regarded the unnamed molluscan stage (including both the Las Virgenes Sandstone and the Santa Susana Formation) below the Martinez stage as Danian in age, so it is likely that the still lower Simi Conglomerate it also Danian (Early Paleocene). Age assignment is complicated by the fact that LouElla Saul (LACM; letter 21 Sept. 1987), who has investigated the location of Zinsmeister's fossils, reports that his locality appears to be in a tongue of Santa Susana Formation, but that it is nevertheless of late Danian or perhaps early Montian age. Although refinement of the ages of the earliest Cenozoic formations of California is clearly needed, there is little doubt that *Gyrineum judithae* is significantly older than *Ranella louellae*.

Genus *Ameranella* n. gen.

*Diagnosis* : Shell small for the subfamily (about 40-60 mm high), with small protoconch similar to that of modern *Argobuccinum* species. Varices aligned, or nearly so, down initial 3-4 teleoconch whorls, becoming separated by 5°-10° on later whorls of some species, bearing 3 moderately to very prominent, rounded nodules where crossed by the major spiral cords. Intervariceal sculpture of 3 or 4 rows of small to large, rounded nodules on the major spiral cords, and of interstitial spiral threads.

Aperture similar to that of *Ranella*, but with outer lip interior gently rounded and weakly sculptured or with low nodules along inner edge, lacking the prominent angulation of *Ranella* species; a row of small nodules on base of columella; parietal tubercle constricts a shallow posterior sinus; anterior canal rather short, moderately narrow, straight or weakly deflected dorsally and to the left.

*Remarks*: The definitive generic characters are: a rather small, *Ranella*-like teleoconch, an aperture close to that of *Ranella*, but lacking the angulation along the inner edge of the outer lip that is present in most *Ranella* species, sculpture dominated by prominent rounded nodules (in particular, strongly protruding on the varices), and a small protoconch (much smaller than that of *Ranella*) resembling that of *Argobuccinum*. Combined, these characters define a species group that does not fit into any ranellid genus I am aware of. This was also the opinion of Hickman (1980, p. 47). At present I know of only three species that belong here: the western North American Eocene *Nyctilochus kewi* Dickerson, 1915, "*Fusitriton*" *terrysmithae* Hickman, 1980, from the latest Eocene Keasey Formation in Oregon, and the Chilean Miocene *Triton verruculosum* G.B. Sowerby I, 1846. Although the two Eocene species are similar to and presumably congeneric with the Miocene one, it seems likely that the Eocene and Miocene species did not have a simple ancestor-descendent relationship.

The earliest undoubted ranelline I am aware of is *Gyrineum judithae* Zinsmeister (1983, p. 1294, fig. 3R-U) (Pl. 4, fig. 6) (gender emended to that of the person the species was named after; ICZN Articles 31 (a) ii, 32 (c) ii), a small species from the ? Danian (early Paleocene) Simi Conglomerate, Simi Hills, Ventura County, California (see above for age discussion). It is uncertain whether this should be placed in *Gyrineum*, or should

be considered an early species of the *Argobuccinum* group of lineages (which include *Mediargo* Terry, 1968) and included in *Argobuccinum*. *G. judithae* certainly is a small (30.5 mm high), moderately proportioned, evenly granulous species that seems to be a suitable member of a stem group for all the known later ranelline Ranellidae.

The next youngest named ranelline taxa in western North America that resemble *Argobuccinum*, rather than *Ranella*, are *Argobuccinum* (?) *californicum* (Gabb) and the species here identified as *Ameranella kewi* (Dickerson). The identity and taxonomic position of *Argobuccinum* (?) *californicum* (Gabb) (1866, p. 154; Gabb, 1869, pl. 26, fig. 33) are obscure. Gabb's holotype (Stewart, 1926, pl. 30, fig. 6; Smith, 1970, pl. 49, fig. 11) is a small, immature, slightly incomplete specimen with finely and evenly granulous sculpture, from the Late Eocene Tejon Formation at Tejon, California. The available material does not make it clear whether *Argobuccinum* (?) *californicum* (Gabb) is a distinct taxon occurring in the Tejon Formation with *A. kewi* (the opinion of Dickerson, 1915 and of Anderson and Hanna, 1925) or whether only one variable taxon occurs there. *Argobuccinum* (?) *californicum* is tentatively accepted as the name for the finely and evenly granulous, *Argobuccinum*-like shell illustrated by Clark (1938, p. 717, pl. 2, fig. 32) and Smith (1970, p. 522, pl. 49, fig. 1, 2) and *Ameranella kewi* (Dickerson) is tentatively accepted as the earliest name for the species discussed below, but it should be realised that these names may refer to a single species, the earliest name for which would be *Ameranella californica* (Gabb).

*Phylogeny*: A feasible scenario for the phylogeny of the Ranellinae (suggested graphically in Fig. 2), taking into account recorded first appearances, suggests that *Gyrineum* (?) *judithae* Zins-
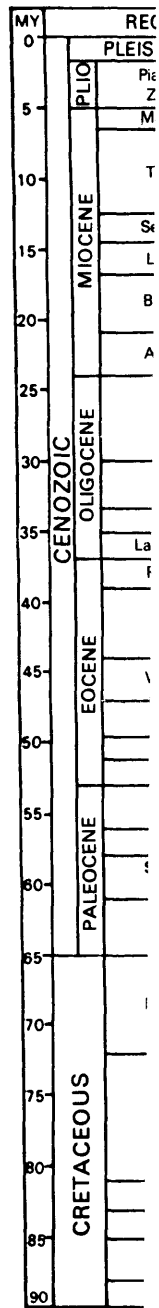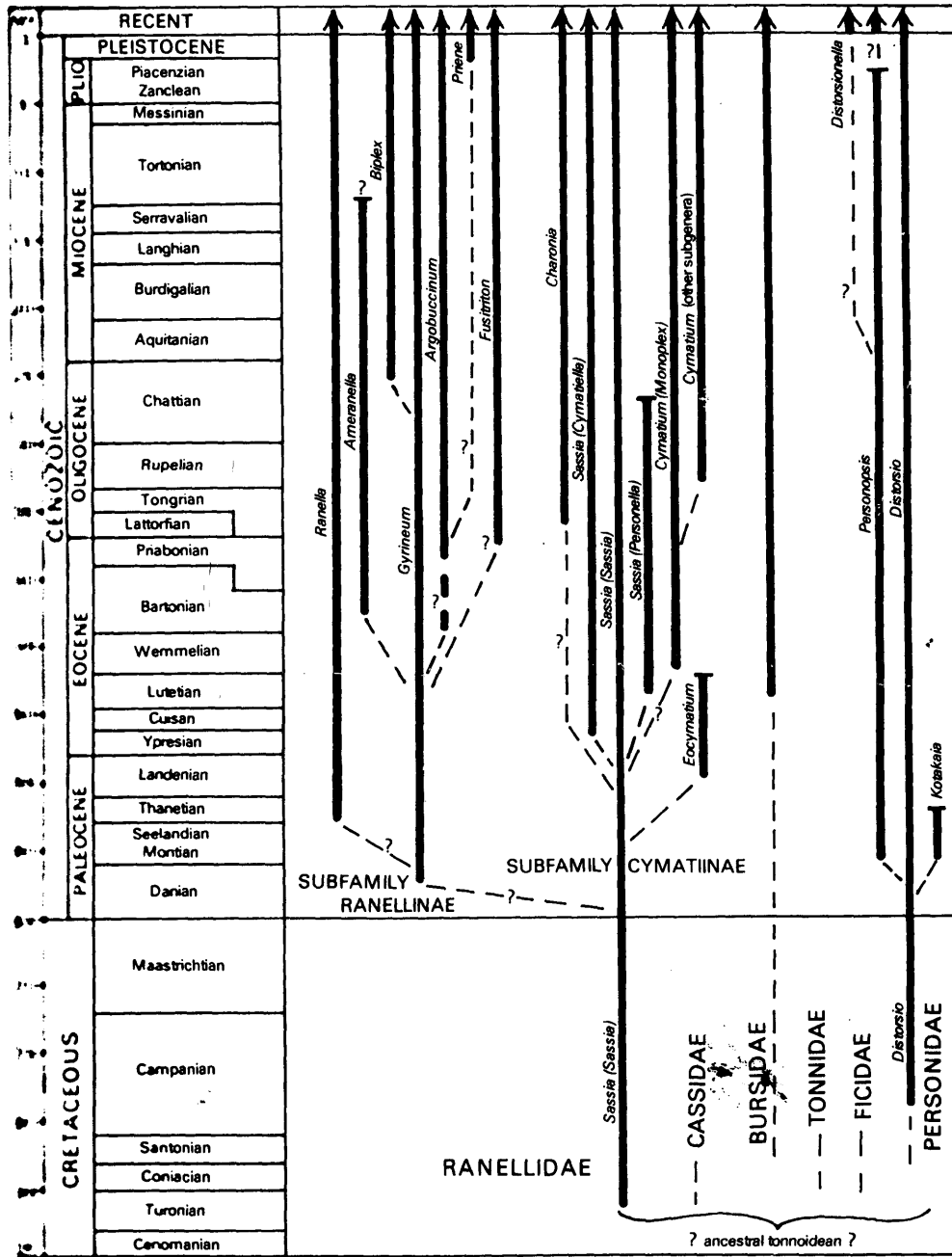
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Recorded time ranges of the family Bursidae and of the genera of Ranellidae and Personidae, with a tentative phylogeny. Time ranges are shown against the European "standard" stage sequence and an approximate time scale in years (at left), correlated largely from Stevens (1981). Heavy vertical bars show recorded time ranges; narrow dashed lines suggest ancestries but not necessarily times of origin. Only part of Late Cretaceous time is included.

meister was a member of an Early Paleocene species group ancestral to all younger Ranellinae. *Ranella* had evolved by Late Paleocene time and occurred from western North America to the Tethys by Late Eocene time; it has remained little-changed since that time. *Argobuccinum* seems likely to have evolved directly from small, generalised, early species resembling *Argobuccinum* (?) *californicum* (Gabb). *Priene* similarly is little different from Oligocene North Pacific *Argobuccinum* species, has only a Pleistocene fossil record in South America, and perhaps represents a stock of *Argobuccinum* that crossed the tropics to the eastern South Pacific early in Cenozoic time. *Fusitriton* also seems likely to have evolved from an early evenly granulous species group similar to *Gyrineum judithae* and *Argobuccinum* (?) *californicum*, by lengthening of the spire and anterior canal. Another minor line here named *Ameranella* n. gen., had branched off the finely granulous stem group similar to *Gyrineum judithae* by Late Eocene time and developed large, rounded variceal nodules, and ultimately gave rise to the Chilean Miocene *Triton verruculosum* Sowerby.

### *Ameranella kewi* (Dickerson, 1915)

Fig. 1A; Pl. 2, fig. 7-13.

*Nyctilochus kewi* Dickerson, 1915, p. 64, pl. 7, fig. 5a, 5b.
*Gyrineum kewi*, Anderson and Hanna, 1925, p. 56, pl. 10, fig. 4; pl. 13, fig. 12.
*Cymatium washingtonianum*, Weaver, 1943, p. 412, pl. 81, fig. 7 (only), pl. 82, fig. 1, 4 (only) (in part).
"*Mayena*" *kewi*, Smith, 1970, p. 523, pl. 49, fig. 3, 4.
? NOT *Gyrineum kewi*, Clark, 1938, p. 717, pl. 2, fig. 32 (*Argobuccinum ? californicum* (Gabb)).

*Remarks*: Examination of a series of topotypes from the Tejon Formation of California and of a large series of well preserved Cowlitz River specimens shows that this is a highly variable species. Specimens vary in the prominence of

spiral cords (particularly the interstitial ones), and in the prominence of the sparse hemispherical nodules on the varices and on the major spiral cords. All specimens have the nodules arranged in axial rows, continuing further down onto the base than on *A. verruculosa*. All specimens bear the row of small nodules on the base of the columella that characterises the subfamily Ranellinae. The inner surface of the outer lip is curved gently out over the terminal varix, and bears nodules that range from small, rounded denticles to short, narrow, transverse ridges. All specimens have a low spiral cord on the sutural ramp raised into a fourth low variceal nodule that is absent from *A. verruculosa*. The best-preserved Tejon Formation topotype examined (UCMP 7200; Pl. 2, fig. 8) has relatively coarse interstitial spiral cords, but these can be matched in the Cowlitz sample; it also has relatively low nodules on the cords and varices, but these are little different from those on the more finely sculptured shells examined from the Cowlitz Formation, including the finely sculptured specimens illustrated by Weaver (1943, pl. 81, fig. 7; pl. 82, fig. 1, 4). There seems little doubt that populations from the Tejon and Cowlitz Formations are conspecific. The coarsely sculptured specimens illustrated here (Pl. 2, fig. 9, 10) are uncommon in the Cowlitz Formation population, and are illustrated to demonstrate the similarity of this species to *Ameranella verruculosa* (Sowerby).

*Dimensions*: height 37.8 mm, diameter 23.3 mm (WM13325, NZGS; Pl. 2, fig. 11-13); height 41.6 mm, diameter 25.0 mm (not including attached polychaete tube) (LACMIP 5654; Pl. 2, fig. 9); height 39.3 mm (apex incomplete), diameter 26.7 mm (UCMP-A3787, largest seen; Pl. 2, fig. 10).

*Material examined*: UCMP 7200, Tejon, Kern County, California, Tejon Formation, Late Eocene, 1; UCMP-

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A971, Tejon (as above), 2; UCMP-A452, Tejon (as above), 3; USGS loc. 4026, Little Falls, Cowlitz River, Washington, Cowlitz Formation, 1 (USGS, Menlo Park, California); USGS loc. 18511, Cowlitz Formation, Cowlitz River, 1 (USGS, Menlo Park, California); "plesiotypes" of Anderson and Hanna (1925), Tejon, California (CAS 827, CAS 828); Tejon Formation, Cañada de las Uvas, 1 mile E of Grapevine pumping station, Kern Co., California 1 (CAS 61665.01); Tejon Formation, east side Grapevine Canyon, Kern Co., California, 1 (CAS 61663.01); holotype of *Gyrineum kewi* Dickerson, 1915, Tejon, California, UCMP 458/11052; Weaver's (1943) illustrated specimens ident. as "*Cymatium cowlitzense* (Weaver)", Cowlitz River, Washington, UCMP-7163/33868; UCMP-B5838, type section Cowlitz Formation, Cowlitz River, several; USGS loc. 4026, Cowlitz Formation, Cowlitz River, Washington, with syntypes of *Gyrinopsis cowlitzi* Dall, 1 (USNM 333358); LACMIP loc. 5654, north bank of Cowlitz River 1.5 miles east of Vader, Lewis County, Washington, Cowlitz Formation, 3.

### *Ameranella terrysmithae* (Hickman, 1980)

*Fusitriton"* terrysmithae Hickman, 1980, p. 47, pl. 6, fig. 4-6.

*Remarks*: The description and clear figures by Hickman (1980) make it clear that "*Fusitriton*" *terrysmithae* is a second western North American Late Eocene species of *Ameranella*. The holotype of "*Fusitriton*" *terrysmithae* has varices aligned to form two continuous ridges down early teleoconch whorls, although they become a little separated over the last whorl in the same manner as most specimens of *A. kewi* (e.g., Pl. 2, fig. 12). The holotype is similar in size, proportions, apertural characters, anterior siphonal canal, and sculpture to the more

coarsely sculptured specimens of *A. kewi*, although it does not appear to have the same prominent variceal tubercles as are present on *A. kewi* and *A. verruculosa* (Sowerby); more material is needed to clarify this character. The holotype of *A. terrysmithae* differs from all specimens of *A. kewi* I have seen in its more numerous rows of nodules on whorl surfaces; the mid-sutural ramp cord in raised into a row of nodules as large as those below (it is weaker in all *A. kewi*) and there are five lower rows of nodules in *A. terrysmithae*, rather than the three rows and weak fourth row in *A. kewi*. The paratype of "*Fusitriton*" *terrysmithae* (Hickman, 1980, Pl. 6, fig. 4) has widely separated varices and appears to be a specimen of a *Sassia* species close to *S. bilineata* (Dickerson, 1916, p. 493, pl. 37, fig. 6a, b).

*Dimensions*: height 36.5 mm, diameter 20.0 mm (holotype; Hickman, 1980, p. 47).

*Locality*: USGS loc. 15268, upper part of Middle Member of Keasey Formation (latest Eocene; Hickman, 1980, p. 6), in the upper Nehalem River Basin, northwestern Oregon; holotype only (USNM 251369).

### *Ameranella verruculosa* (Sowerby, 1846)

Pl. 3, fig. 1-4, 6, 7

*Triton verruculosus* G.B. Sowerby I, 1846, p. 260, pl. 4, fig. 23.
? *Tritonium exiguum* Philippi, 1887, p. 57, pl. 3, fig. 23 (juvenile?).
"*Tritonium*" (*Ranella* ?) *verruculosum*, Tavera Jerez, 1979, p. 90, pl. 19, fig. 67a, b.
NOT *Tritonium verruculosum*, Philippi, 1887, p. 57, pl. 4, fig. 10 [ = *Sassia armata* (Hupé, 1854)].

*Remarks*: The illustration by Sowerby (1846, pl. 4, fig. 23) and Sowerby's type (BM(NH) Department of Palaeontology, no. G26396) show that this is an unusual *Bursa*-like species with aligned lateral varices, each varix

bearing 3 large, hemispherical nodules; the intervariceal surface bears a few large nodules on the major spiral cords, similar to those on the varices. It lacks a bursid posterior siphonal canal, and clearly belongs in Ranellidae Ranellinae. Examination of W.J. Zinsmeister's collections of Chilean Miocene fossils showed that this is a reasonably common species in the Middle Miocene Navidad Formation in the Navidad-Matanzas area, near the mouth of Rio Rapel, Chile. Few complete, well preserved shells have been seen, but many are complete enough to demonstrate that *Triton verruculosum* resembles *Ameranella kewi* closely in critical characters, and is referable to *Ameranella*.

*Ameranella verruculosa* differs from *A. kewi* and *A. terrysmithae* in its slightly larger size (complete large shells probably reached about 60 mm high), its considerably narrower form and taller spire, its weaker interstitial spiral cords, its lack of a raised cord on the sutural ramp and its much more prominent nodules, particularly on the varices.

Philippi (1887, pl. 3, fig. 23) figured as *Tritonium exiguum* a very small, undiagnostic specimen of a taxon with aligned varices and large nodules. The only Chilean ranelline taxon this shell can be referred to is *Ameranella verruculosa*. As Philippi (1887, pl. 4, fig. 10) misidentified the common Chilean *Sassia armata* (Hupé) (1854, p. 22) by the name *Tritonium verruculosum*, it is feasible that he renamed a juvenile specimen of *A. verruculosa*.

*Dimensions*: Height (incomplete) 46. 9 mm, diameter (incomplete) 26.3 mm (estimated originally ca. 32 mm) (most complete large specimen seen, WJZ loc. 286); height 34.3 mm, diameter 25.2 mm (Sowerby's very incomplete holotype, BM(NH), G26396).

*Material examined* : holotype, BM(NH) Palaeontology Department, no. G26396, from Navidad, Chile, Middle Miocene, collected by Charles Darwin (but note that Darwin's locality "Navidad" is neither at the present site of Navidad nor in Topocalma Bay, where the locality is said to be by modern Chilean geologists (e.g., Cecioni, 1978, p. 3); Darwin's locality is that now known as Matanzas, about 15 km south of the mouth of Rio Rapel; see Cecioni, 1978, fig. 1; pers. comm. W.J. Zinsmeister, letter 1987). Department of Earth and Atmospheric Sciences, Purdue University, Indiana, collections from the Chilean Middle Miocene Navidad Formation (Group ?) (Punta Perro-La Era Formation of Cecioni, 1978) by W.J. Zinsmeister : loc. 145, float material from Rio Rapel-Navidad area, 1; loc. 264, sandstone 10 m above beach, Punta Perro, southern point of mouth of Rio Rapel, (33°55'10"S, 71°50'20"W), 1; loc. 286, base of seacliff 1 km north of mouth of Rio Rapel (33°52'50"S, 71°49'40"W), 1 (Pl. 3, fig. 1, 2); loc. 326, base of sea cliff 200 m south of loc. 286, North Rio Rapel (33°52'59"S, 71°49'40"W), 4; loc. 327, base of sea cliff 100 m south of loc. 326, North Rio Rapel (33°53'00"S, 71°49'49" W), 2; loc. 331, 3 m above beach, seacliff 150 m north of loc. 286, North Rio Rapel (33°52'40", 71°49'40"W), 2; loc. 332, seacliff 3 m higher than loc. 331, 9 (Pl. 3, fig. 4, 5, 6, 7); loc. 335, north side of mouth of Rio Rapel (33°52'55"S, 71°50'26"N), 1.

*Remarks* : It may be added that a species of *Ranella* (sensu stricto), closely resembling both short-spired specimens of *R. washingtoniana* (Weaver) and the New Zealand early Miocene *R. kaiparaensis* (Finlay), occurs in the Chilean Miocene Navidad Formation; W.J. Zinsmeister's locality 254, fossiliferous lens at low tide ca. 100 m north of Matanzas township (33°57'30"S, 71°52'20"W), 3 km south of Navidad, Chile (Darwin's original "Navidad" locality; pers. comm. W. J. Zinsmeister), 2 specimens; neither *Sassia armata* (Hupé) nor *Ameranella verruculosa* are present in this collection.

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## Subfamily Cymatiinae Iredale, 1913 (1891)
## Genus *Sassia* Bellardi, 1872

*Sassia* Bellardi, 1872, p. 219. Type species (by subsequent designation, Cossmann 1903, p. 93): *Triton apenninicum* Sassi, 1823, Miocene and Pliocene, Europe.

*Synonymy*: Beu (1987, p. 307).

*Remarks*: *Sassia* is very much the most diverse, the most widespread, and the longest-ranging genus of Ranellidae; it is the only undoubted ranellid genus I am aware of that occurs in Cretaceous rocks (*Distorsio*, formerly placed in the Ranellidae, is removed below to the separate Family Personidae). More than half of the named species of Ranellidae belong in *Sassia*.

I have previously (Beu, 1987, p. 308) suggested that three groups of *Sassia* species were sufficiently distinctive to be recognized as subgenera, but I have recently recognized that there is confusion about one of these subgenera, and it is desirable to rectify current usage, as one of the names has been incorrectly applied to a genus (or subgenus) of Personidae (discussed below). Two subgenera are distinctive enough to be easily recognized, and are not discussed further: *Sassia* (*Austrotriton*) Cossmann, 1903 (p. 98), containing southern Australian fossil and living species with caricelloid apices or no protoconch at all, reflecting direct development; and *Sassia* (*Cymatiella*) Iredale, 1924 (p. 253), containing Paris Basin Eocene, North American Oligocene, Caribbean Miocene, and southern Australian Miocene to Recent species of small size (few over 20 mm high), with tall spires, short anterior canals, and proportionally small protoconchs.

It is the third subgenus, identified previously as *Sassia* (*Byramia*) MacNeil in MacNeil and Dockery (1984, p. 118), that needs reconsideration. I have previously followed earlier workers

(Dall, 1904, p. 130; later usages listed by MacNeil and Dockery, 1984, p. 120) in regarding *Personella septemdentata* (Gabb, 1860) (type species of *Personella* Conrad, 1865, p. 21) as a member of the group of small Personidae with only weakly distorted coiling and with the basal columellar nodules situated directly on the columella, rather than elevated on a prominent callous ridge as in *Distorsio* and in *Kotakaia* n.gen. MacNeil and Dockery (1984, p. 118) and I previously thought there were no taxa resembling *Byramia* in the American Middle Eocene, but comparison of figures and specimens recently brought to light the real relationship of *Personella septemdentata*: it is the earliest recorded species of the subgenus previously known as *S.* (*Byramia*). Relatively small (immature?), complete specimens of *P. septemdentata* (Pl. 3, fig. 9) share with *Byramia* species a small size, regular coiling, similar low, cancellate sculpture with relatively widely spaced, flat-topped spiral cords, a moderately long, straight, narrow, open anterior canal, 4 or 5 low basal columellar ridges, a slightly enlarged second nodule from the top inside the outer lip, and a prominent angulation at the top of the outer lip and terminal varix, formed at the junction of near-horizontal and near-vertical segments of the lip. They differ from the genus of small Personidae previously confused with *Personella* (renamed *Personopsis* n.gen. below) by the following characters: the second, rather than third, outer-lip nodule is enlarged, coiling is almost completely regular, spiral cords are more distinct, the anterior canal is long and narrow, rather than an anterior spout at the end of a gradually tapered last whorl as in *Personopsis*, and the characteristically personid, widely spread inner lip of *Personopsis* is absent. I regard *Sassia* (*Personella*) as an earlier name for *S.* (*Byramia*), and *S. caseyi* MacNeil in MacNeil and Dockery (1984,

p. 120) as a second North American Oligocene species of *S. (Cymatiella)* (see also *S. fuscicava* MacNeil in MacNeil and Dockery, 1984, p. 118). The following is a single, very uniform American lineage of *Sassia (Personella)* species, apart from an apparent speciation event that produced two Oligocene members: *S. septemdentata* (Gabb), Middle Eocene; *S. jacksonensis* (Meyer) (see Harris and Palmer, 1947, p. 336, p. 44, fig. 7-9), Late Eocene; and *S. abbreviata* (Conrad, 1848) and *S. mississippiensis* (Conrad, 1848), both Oligocene. Whether any European fossil species are referable to *Sassia (Personella)* requires reevaluation. The following discussion refers entirely to species of *Sassia (Sassia)*.

*Sassia (Sassia)* species are mostly of small size (20-50 mm high), although several lineages have given rise to much larger species. They have a small turbiniform protoconch, although it varies from vary small (about 2 mm in diameter) and smooth, in the majority of species (e.g., the European Eocene *S. formosa* (Deshayes, 1865); Fig. 1E) to a little larger and coarsely cancellate, in species closely related to *S. apenninica* (Sassi) (Beu, 1978, fig. 6, 9), to 4 mm wide, with fine, close, conspicuously cancellate sculpture (in the European Eocene *S. delafossei* (Rouault, 1850); Fig. 1B). *S. delafossei* is the earliest species I am aware of with cancellate protoconch sculpture, and seems likely to have given rise to the lineage of *S. apenninica*. The *Sassia* teleoconch is a very generalised ranellid one, of moderately elongate shape, with an equally long spire and anterior canal, a relatively small muriciform aperture with small, even denticles inside the outer lip, and evenly convex whorls with sculpture of similar spiral cords and axial costae. To judge from morphology, it is the most likely stem group from which all other Ranellidae were derived. Stratigraphic evidence also strongly suggests that it

was the stem group of Ranellidae, as noted above. Two typical European Eocene species are illustrated as examples of *Sassia* teleoconch (Pl. 3, fig. 5, 8) and protoconch (Fig. 1B, E) morphology: the very finely sculptured, elongate *S. formosa* (Deshayes) (to which the New Zealand and southern Australian living species *S. parkinsonia* (Perry, 1811) is closely convergent) and the coarsely cancellate *S. delafossei* (Rouault).

Several other genera that occur in Cretaceous rocks have traditionally been placed in the Ranellidae, but in my opinion belong in several other families. Beu and Maxwell (1987) have removed the *Plesiotriton* group of genera, along with *Semitriton* and *Tatara*, to the family Cancellariidae; it is now clear that no Ranellidae have columellar plaits. *Trachytriton* Meek, 1864 (type species: *Buccinum ? vinculum* Hall and Meek, 1856; Pierre Shale, Late Cretaceous, USA) was discussed by Sohl (1967, p. 28, pl. 6, fig. 10, 14-17) who considered that *T. vinculus* is the sole species of the genus; his illustrations show clearly that this is a thin-shelled, fusiform, finely cancellate taxon without any varices, but with internal dentate thickenings at growth pauses. It is quite unlike all Ranellidae, and appears to belong in the Buccinidae. "*Charonia ?*" *univaricosum* (Wade, 1926) may be a buccinid neogastropod related to *Ranellina* Conrad, 1865, as the holotype (USNM32916, from the Ripley Formation, Maastrichtian, at Coon Creek, Tennessee) has a subsutural fold and concave sutural ramp, a shallow shoulder sinus, and only a terminal varix; but it has much more prominent axial sculpture than *Ranellina* and possibly belongs in *Sassia*. The holotype of *Tintorium pagodaeforme* Sohl, 1960 (type species of *Tintorium* Sohl, 1960), also from the Maastrichtian Ripley Formation at Coon Creek, Tennessee (USNM 128570), is a small shell (9.6 mm high) with a tall

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spire, short last whorl, no varices, and a coronate shoulder; it clearly belongs near *Cerithioderma* in the mesogastropod family Trichotropidae. With the removal, below, of *Distorsio* to the distinct family Personidae, *Sassia* remains as the only Cretaceous ranellid.

The earliest undoubted species of *Sassia* I am aware of is *Tritonium kanabense* Stanton (1893, p. 150, pl. 31, fig. 12) (holotype examined, USNM 22919), from the upper Kanab Valley, Utah. The holotype was collected from the *Inoceramus fragilis* zone of the Colorado Group, of Turonian age (Cobban and Reeside, 1952, table 10b). Most other Cretaceous *Sassia* species are of Maastrichtian age : *Triton konincki* Binckhorst (1861, p. 4, pl. 1, fig. 10a-c), Europe ; *Tritonium tuberculosum* Kaunhowen (1898, p. 77, pl. 9, fig. 3, 3a-d), Europe ; *Triton sauryi* Basse (1933, p. 74, pl. 10, fig. 1, 1a), Madagascar ; *Tritonium (Sassia)* sp. of Douvillé (1904, pl. 40, fig. 25), Iran ; and possibly *Tritonium univaricosum* Wade (1926, p. 147, pl. 51, fig. 9, 10 ; see also Sohl, 1960, pl. 18, fig. 44), USA ; this last species more closely resembles the group of Buccinidae related to *Ranellina* (see above). Abdel-Gawad (1986, p. 115-166) recently recorded *S. tuberculosa* (Kaunhowen) from early Late Campanian and Maastrichtian localities in the Vistula Valley, Poland. The specimen illustrated as *"Charonia" multicostata* (Favre, 1869) by Abdel-Gawad (1986, pl. 14, fig. 11, 12) is in my opinion not a tonnoidean and the taxonomic position of the poorly preserved material is enigmatic. *"Biplex" cretaceus* Abdel-Gawad (1986, p. 115, pl. 15, fig. 1) is similarly enigmatic, possibly a muricacean neogastropod, but certainly not tonnoidean. Several other very poorly known Maastrichtian species named in *"Triton"* could possibly belong in *Sassia*, but cannot be evaluated from published figures. Most other Mesozoic taxa assigned to *"Triton"* belong in the

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of the subfamily Ranellinae has been discussed above ; by Late Paleocene-Early Eocene time other genera of Cymatiinae were beginning to radiate from *Sassia*. The earliest species referrable to *Cymatium* is *C. (Monoplex) janetae* Squires (1983, p. 355, fig. 2A-D) from the lower Middle Eocene Llajas Formation in the Simi Valley, California. (Although *Cymatium janetae* Squires and *C. amnicretum* MacNeil (in MacNeil and Dockery, 1984, p. 116, pl. 18, fig. 4, 5) were placed in *Cymatium (Septa)* at my suggestion, I have since (Beu, 1987, p. 274) advocated subdivision of the broad subgenus *C. (Septa)* into several subgenera and now refer these fossil species to *C. (Monoplex)).* The next earliest species is *C. (Monoplex) cowlitzense* (Weaver, 1912) (Weaver, 1943, pl. 81, fig. 8, 10 ; pl. 82, fig. 2, 3, 10) [ = *C. etheringtoni* Weaver, 1943 ; distinguished above from *Ameranella kewi* (Dickerson)] from the Late Eocene Cowlitz Formation at the Cowlitz River, Washington. These seem reasonably typical of *C. (Monoplex)* in all characters ; the protoconch (Fig. 1C) is well preserved on many Cowlitz specimens, and confirms that it was already taller than those of any known *Sassia* species. This species group, then, is a suitable stem group for the large variety of later Cenozoic to Recent Cymatiinae. This long preamble on the apparent first appearances of early Cymatiinae is necessary to make clear my opinion on the phylogeny and taxonomic positions of the named taxa, and to reveal the distinctive characters of the following new

genus.

## Genus *Eocymatium* n. gen.

Type species: *Triton pyraster* Lamarck, 1803, Lutetian (lower Middle Eocene), France and Italy.

*Diagnosis*: Teleoconch shape and sculpture much as in *Cymatium* (*Ranularia*) Schumacher, 1817, with only a terminal varix or in addition one earlier varix to left of aperture on last whorl; spire short; anterior canal long, narrow, deflected slightly dorsally and to the left. Whorls evenly inflated. Sculpture dominantly of prominent, narrow, flat-topped, spiral cords crossed by narrow-crested, widely spaced axial folds. Aperture subcircular, lips thickened; inner edge of outer lip prominently denticulate, uppermost nodule largest, constricting a shallow posterior sinus. Protoconch very small, low-turbiniform, slightly inclined to the axis of the teleoconch on most specimens, of 1.8 inflated whorls, with a relatively large, in-rolled apex; the first half-whorl is microscopically reticulate, merging imperceptibly into a succeeding whorl with about 20 very fine, well raised spiral threads, in turn gradually developing fine, very weak axial costellae (initially only below the upper suture) that become more prominent over the last quarter-whorl; demarcated only weakly from the teleoconch, by increase in spacing of axial riblets and the development of more prominent, more widely spaced spiral cords on the early teleoconch.

*Remarks*: I know of no other ranellid with a short spirally lirate protoconch resembling that of *Eocymatium pyraster* (Lamarck); its form and lack of obvious demarcation from the teleoconch suggest that this species had lecithotropic development, a rare mode in this family of "ultradispersalists". The unique protoconch demonstrates conclusively that the resemblance in teleoconch mor-phology to Oligocene to Recent *Cymatium* (*Ranularia*) species results from convergence. The protoconch characters and the teleoconch form justify, the proposing of a new genus *Eocymatium* for *Triton pyraster* Lamarck, 1803; the only other taxon that seems to belong here is "*Ranularia* ?" of Cossmann and Pissarro (1909, p. 37, pl. 3, fig. 35, 36), a more finely sculptured but as yet unnamed species from the Late Paleocene uppermost Ranikot beds at Jhirak, Pakistan (Vredenberg in Coss-mann and Pissarro, 1909, p. xi, xii). The early Middle Eocene age and the unique protoconch morphology of *Eocymatium pyraster* indicate that *Eocymatium* represents an early, brief lineage with no apparent descendants; it is unlikely to have descended directly from *Sassia*.

### *Eocymatium pyraster* (Lamarck, 1803).

Fig. 1G; Pl. 3, fig. 10, 12, 13

*Murex pyraster* Lamarck, 1803, p. 225; Lamarck, 1822, p. 575; Palmer, 1977, p. 15, pl. 4, fig. 9a, b.
*Triton pyraster*, Deshayes, 1835, p. 616; Deshayes, 1837, pl. 80, fig. 36–38.
*Triton piraster* [sic], Deshayes, 1865, p. 303; Coss-mann, 1899, p. 121.
*Triton* (*Gutturnium*) *pyraster* var. *bilineatum* Gregorio, 1880, p. 102, pl. 4, fig. 18.
*Lampusia* (*Gutturnium*) *piraster*, Cossmann and Pissarro, 1900, p. 131, pl. 14, fig. 12.
*Tritonium* (*Ranularia*) *piraster*, Cossmann, 1903, p. 97, pl. 3, fig. 21.
*Eutritonium* (*Ranularia*) *piraster*, Cossmann and Pissarro, 1913, pl. 35, fig. 167-22.
*Eutritonium piraster*, Furon and Soyer, 1947, p. 119.

*Remarks*: The important taxonomic criteria are stated in the diagnosis above. The Paris Basin Lutetian specimens I have examined are variable in size, width, spire height, length of anterior canal, and prominence of the axial folds; the two illustrated specimens indicate the range of variation. Gregorio's (1880, p. 102, pl. 4, fig. 18) description and illus-

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tration of his "bellissima varietà del *pyraster*" show no significant differences from Paris Basin shells other than having only a terminal varix, an individual character.

*Dimensions* : height 26.7 mm, diameter 16.7 mm ; height 24.0 mm, diameter 12.6 mm (the 2 illustrated specimens).

*Localities* : Lamarck (1803) and most subsequent authors seem to have recorded the species only from the Calcaire Grossier (Lutetian, early Middle Eocene) at Grignon and nearby localities in the Paris Basin, where it seems to be reasonably common. Cossmann and Pissarro (1900, p. 131) recorded it from Fresville, near Valognes, Normandy, presumably also Lutetian. Gregorio (1880, p. 102-3) did not state a specific locality for his Italian specimen, but stated in the preface (p. XV) that the four fossil localities at S. Giovanni Ilarione are Ciupio, Pozzani, Bosco del Prete, and Croce Grande, and most specimens came from the first or last of these. The age is given only as "Parisian".

## Family Personidae Gray, 1854

*Phylogeny* : The earliest species I am aware of that is referrable to *Distorsio* Röding, 1798 or to closely related genera is *Eutritonium* (*Sassia*) *praegranosum* Cottreau (1922, p. 66, pl. 9, fig. 4-7). This is a moderately large (to 34 mm high ; but the two illustrated internal moulds lack anterior canals and spire apices and probably represent shells 45-50 mm high), highly distorted, coarsely cancellate species, with coiling distortion and sculpture similar to those of Neogene and Recent *Distorsio* species. It particularly resembles the Caribbean *Distorsio clathrata* (Lamarck, 1816), and I am in no doubt that it belongs in *Distorsio*. The specimens are from two localities in Madagascar (Province of Mananjaray : range of hills west- south-west of Antanihody ; Province of Vatomandry : third

col southwest of Lokia), close to localities where specimens of an *Inoceramus* species were collected that were later identified by Sornay (1968, p. 10) as *I. pseudoregularis* Sornay, of lower to lower middle Campanian (Late Cretaceous) age.

As *Distorsio praegranosa* (Cottreau) had already evolved typical *Distorsio* morphology by lower Campanian time, older than all known undoubted Ranellidae of the genus *Sassia* other than the Turonian *S. kanabensis* (Stanton) (see above), it is clear that *Distorsio* and related genera (*Distorsionella* Beu, 1978 ; *Personopsis* n.gen. ; *Kotakaia* n.gen.) represent a distinct monophyletic group that evolved independently of Ranellidae ; inclusion of this group (even as subfamily Personinae) would make Ranellidae a polyphyletic taxon.

The concept of Personidae as a distinct family of Tonnoidea is strengthened by the distinctive fore-gut anatomy of *Distorsio* (Lewis, 1972), resembling that of *Ficus* (Beu, 1981, p. 251) more than the Ranellidae. Beu (1981, p. 251) also pointed out that the small, black, subcircular operculum of the ficid *Thalassocyon* Barnard, 1960 more closely resembles that of *Distorsio* than of any other tonnoidean.

The anatomical evidence therefore suggests that Personidae could be more nearly related to Ficidae than to Ranellidae, but the very different shell form of Ficidae (elongate and fig-shaped, with weak sculpture and no varices) from that of Personidae suggests that the relationship is more distant than at the family level. Another distinctive character of *Distorsio* and *Distorsionella* is the unique radula with a crescentic rachidian tooth (Clench and Turner, 1957, pl. 132 ; Beu, 1978, fig. 30) that is not closely similar to the almost uniform radulae of Ranellidae, all easily derived from the equidimensional rachidian tooth of *Sassia*. (The radula of *Personopsis* (?)

*pusilla* (Pease) is unknown, and must be examined to confirm its placement.) The combination of a first appearance parallel with that of *Sassia* with a distinctive, distorted shell form and an anatomy and radula more like those of Ficidae than of Ranellidae necessitate recognizing Personidae as a sixth family of the Tonnoidea. Evolutionary stasis is exemplified by the remarkably low generic diversity of the family and the long time range of unchanged shell form in the most diverse genus, *Distorsio*, which has existed from at least lower Campanian to Recent.

The genera now included in Family Personidae are: (1) Genus *Distorsio* Röding, 1798 (synonymy: Beu, 1987, p. 310); (2) Genus *Distorsionella* Beu, 1978 (p. 38; type species: *Distorsio* (*Distorsionella*) *lewisi* Beu, 1978, Recent, Reinga Ridge, Norfolk Ridge and Kermadec Islands, north of New Zealand); (3) Genus *Personopsis* n. gen.; (4) Genus *Kotakaia* n. gen.

### Genus *Personopsis* n. gen.

Type species: *Triton grasi* Bellardi, 1872, Pliocene, Italy.

*Diagnosis*: Shell small (to 25 mm high in *P. grasi*; not over 20 mm high in other species), with slightly irregular whorl coiling; sculpture of regularly cancellate spiral cords and axial costae, all relatively low and closely spaced, with several orders of closely spaced interstitial spiral threads; terminal varix low and narrow but obvious, earlier varices low and indistinct, situated regularly at each 0.66 whorls; last whorl tapering gradually to a moderately short, open anterior canal that curves gently to left and dorsally; inner lip spread widely (but much less so than in *Distorsio*) to form a thin, adherent shield over parietal area, over lower third to half of last whorl to left of aperture, and over columella, smooth except for one or two

low parietal ridges, and four or five low transverse ridges (the uppermost the largest) on the basal columellar area and left edge of anterior canal; interior of outer lip bearing a row of seven of eight short radial ridges, all low and narrow except for the third from top, which is elevated into a large, rounded nodule.

*Remarks*: The new genus *Personopsis* has formerly been confused with *Sassia* (*Personella*), from which it differs in having slightly distorted (rather than regular) coiling, more strongly cancellate sculpture with more closely spaced spiral cords, a shorter anterior canal and more gradually tapered last whorl and, in particular, a much more widely spread inner lip shield and a more enlarged third (rather than second) outer lip nodule. These apertural characters give *Personopsis* a close resemblance to *Distorsio*, and are assumed to express a close phylogenetic relationship between the two genera. *Personopsis* differs from *Distorsio* in its markedly smaller size, its less distorted coiling, its less widely flared inner lip, its less prominently armed aperture, and in bearing the basal columellar ridges directly on the columella, rather than on the highly elevated basal columellar callus-ridge that is characteristic of *Distorsio*. *Personopsis* differs from *Distorsionella* in its smaller size (*D. lewisi* (Beu) reaches 38 mm high), its shorter and wider form and less gradually tapered last whorl, its shorter and much narrower anterior canal, and its more widely flared inner lip; the two genera have similar apertural armature, except that the second (rather than third) inner lip nodule is enlarged in *Distorsionella*.

Species referred to *Personopsis* at present are:

1. *Personopsis rutoti* (Vincent, 1930), Montian (Mid-Paleocene), Belgium and Poland. See Krach (1963, p. 102, pl. 23, fig. 6) for reference and apertural characters.

2. *Perso* 1956, p. 1 Lutetian-ea Eocene), b Pyrenees ( scribed in although t suggests a tall spire m as likely. visible on t determined clear.

3. *Perso* p. 135), Lat well (1968) the distribu name *Disto*

4. *Persc* 1894, p. 17 Torquay, *interposit* differentiat ridge (bear ules) and s than other in size, sc characters

5. *Persc* p. 262, pl. 1 3, fig. 11) which, how Oligocene s characters.

6. *Persc* 1861, p. 39 (Amami Isl *pusilla* re species in s ance but i mm high; and differs its smaller longer and very narro "basal" col situated on lar area, an (the upper

2. *Personopsis* ?   *alvaradoi* (Villalta, 1956, p. 182, pl. 7, fig. 4a, b), late Lutetian-early Bartonian (Middle-Late Eocene), blue marls at Isún, Spanish Pyrenees (Villalta, 1956, p. 120). Described in the genus *Distorsio*, and although the weakly distorted coiling suggests a position in *Personopsis*, the tall spire makes a position in *Sassia* just as likely. Apertural characters (not visible on the broken holotype) must be determined before the family position is clear.

3. *Personopsis beui* (Maxwell, 1968, p. 135), Late Eocene, New Zealand. Maxwell (1968) provided a useful review of the distribution of *Personopsis*, under the name *Distorsio* (*Personella*).

4. *Personopsis interposita* (Tate, 1894, p. 172, pl. 10, fig. 3), Oligocene, Torquay, Port Phillip, Victoria. *P. interposita* has a very weakly differentiated, elevated basal columellar ridge (bearing the basal columellar nodules) and slightly more distorted coiling than other *Personopsis* species, but agrees in size, sculpture, and most apertural characters with *Personopsis*.

5. *Personopsis grasi* (Bellardi, 1872, p. 262, pl. 14, fig. 18), Pliocene, Italy (Pl. 3, fig. 11); a relatively large species which, however, agrees with Paleocene to Oligocene species in all other significant characters.

6. *Personopsis* (?) *pusilla* (Pease, 1861, p. 397), Recent, western Pacific (Amami Islands to New Caledonia). *P. pusilla* resembles other *Personopsis* species in sculpture and general appearance but is still smaller (rarely over 9 mm high; largest seen 12.5 mm high) and differs in its much narrower shape, its smaller and narrower aperture, its longer and narrower anterior canal, its very narrow inner lip, in having the "basal" columellar nodules enlarged and situated on the middle to basal columellar area, and in having only five nodules (the uppermost the largest) inside the outer lip. It is assumed tentatively that the small size has necessitated the loss of the uppermost two outer lip nodules and adapical movement of the columellar nodules in *P. pusilla*, but another new genus might prove necessary for this distinctive species.

## Genus *Kotakaia* n. gen.

Type species:   *Kotakaia simplex* n. sp., mid-Late Paleocene, Pitt Island, Chatham Islands, New Zealand.

*Diagnosis*:   Shell small (to 20 mm high), with regularly coiled whorls; sculpture of simple low spiral cords (no axial sculpture visible); low, wide varices every 0.66 whorls; a short, straight, widely open anterior canal deflected strongly to the left; and a heavy apertural armature of high, narrowly rounded ridges, four inside the outer lip, one on the parietal area, and two (and, on some specimens, a very weak third) on a large, protruding callus-pad at the top of the anterior siphonal canal.

*Remarks*:   The new genus *Kotakaia* bears the large basal columellar-upper siphonal canal callus-pad, coarsely nodulous and protruding strongly into the aperture, that is the primary character of *Distorsio* Röding, 1798, and is absent from its close relatives *Personopsis* n. gen. and *Distorsionella* Beu, 1978, in which the small basal columellar ridges are situated directly on the columella. *Kotakaia* differs from all other Personidae in having completely regular coiling (not strongly distorted, with a large bulge opposite the aperture in each intervariceal interval, as in *Distorsio*). It has sculpture of simple spiral cords (prominent axial costae cancellate the spiral cords in all other Personidae); a short, wide teleoconch, with evenly rounded whorls and a short, widely open anterior siphonal canal; and a much more coarsely and simply armed aperture than all other Personidae, strongly con-

stricted by similar large, simple ridges protruding from both lips. The apertural ridges extend as far into the aperture of the three prepared specimens as the hard matrix has been removed (at least 5 mm).

*Etymology* : I have great pleasure naming the new genus *Kotakaia* in honour of Professor Tamio Kotaka ("Tam" to his many New Zealand friends) of Tohoku University, Sendai.

## *Kotakaia simplex* n.sp.

Pl. 3, fig. 14-17.

*Description* : Most important characters are stated above. There are six main spiral cords, all low, wide and with convex surfaces, on the spire whorls, 12 on the last whorl and base; low, wide secondary cords fill all spiral interspaces on well preserved specimens (the holotype is slightly abraded). The varices are very low, but have an abruptly raised abapertural margin; the adapertural margin is low, wide, and descends gradually. The inner lip is narrow and strongly thickened, with a squarely raised, adherent left edge. The outer lip also is strongly thickened inside, and tapers rapidly outwards to a smooth margin. The uppermost and largest ridge on the basal columellar callus-pad is a truly spiral ridge, extending as far into the aperture as the matrix has been removed. The parietal ridge and the uppermost ridge inside the outer lip constrict an obvious, narrowly rounded posterior siphonal canal, and the edge of the outer lip is shallowly embayed at this point on the holotype; it appears that the embayment is largely due to breakage of the lip, which is thinnest at this point. The parietal ridge and the uppermost basal columellar ridge constrict

another rounded "channel" only slightly larger than the upper one. The protoconch is missing from all specimens.

*Dimensions* : height (spire incomplete) 18.2 mm, diameter 12.9 mm (holotype); height (incomplete) 19.5 mm, diameter (incomplete) 12.4 mm (paratype, TM6787); height (incomplete) 15.7 mm, diameter (incomplete) 10.5 mm (paratype, TM6786).

*Repository* : Holotype (TM6785) and four paratypes (TM6786-TM6789) in NZGS.

*Locality* : NZGS loc. 12173, N.Z. National Fossil Record no. CH/f478, calcareous Red Bluff Tuff beneath Matanginui Limestone in northern cliff of Rocky Side Bay, on west side of neck of Tarawhenua Peninsula, Pitt Island, Chatham Islands; collected A.G. Beu, P.A. Maxwell, H.J. Campbell, February 1977 ; age at this locality mid-late Teurian (Montian-Landenian), Mid-Late Paleocene (*Fasciculithus tympaniformis* total range zone; pers. comm. A.R. Edwards, NZGS).

*Remarks* : The volcanogenic matrix at Rocky Side Bay and nearby localities on northern Pitt Island contains an unusual fauna of epifaunal gastropods, a few bivalves and brachiopods, common barnacles in a few places, and diverse ahermatypic corals, helping to fill what is otherwise a partial faunal vacuum in the extensive sequences of early Cenozoic rocks exposed in New Zealand. Several other striking taxa remain to be described from this fauna, which includes diverse Cyraeacea for a New Zealand fauna (four taxa); this is the source of *Bernaya chathamensis* Cernohorsky (1971, p. 117), from Flowerpot Bay, nearby on northern Pitt Island (P.A. Maxwell, pers. comm.) ; Red Bluff Tuff crops out also in Flowerpot Bay.

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Beu, A.G.,
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## REFERENCES

Abbott, R.T., 1968, The helmet shells of the world (Cassidae). Part 1. *Indo-Pac. Moll.*, v. 2 (9), p. 7-202, pl. 1-187.

Abdel-Gawad, G.I., 1986, Maastrichtian non-cephalopod mollusks (Scaphopoda, Gastropoda and Bivalvia) of the Middle Vistula Valley, central Poland. *Acta Geol. Polonica*, v. 36, p. 69-224, pl. 1-48.

Adegoke, O.S., 1977, Stratigraphy and paleontology of the Ewekoro Formation (Paleocene) of southwestern Nigeria. *Bull. Am. Paleont.*, v. 71 (295), p. 1-379, pl. 1-50.

Aldrich, T.H., 1886, Preliminary report on the Tertiary fossils of Alabama and Mississippi. *Geol. Surv. Alabama Bull.*, v. 1, p. 15-60.

Anderson, F.M. and Hanna, G.D., 1925, Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. *Occas. Pap. Cal. Acad. Sci.*, v. 11, p. 1-249, pl. 1-16.

Basse, E., 1933, Paléontologie de Madagascar. XVIII. Faune malacologique du Crétacé supérieur du sud-ouest de Madagascar. *Ann. Paléont.*, v. 21, p. 89-168, pl. 1-10.

Bellardi, L., 1872, *I molluschi dei terreni terziari del Piemonte e della Liguria. Part 1: Cephalopoda, Pteropoda, Heteropoda, Gasteropoda (Muricidae et Tritonidae)*. Loescher, Torino, 264 p., 15 pl.

Berry, S.S., 1970, Notices of new eastern Pacific Mollusca-IV. *Leaflets in Malacology* [S.S. Berry, Redlands, Calif.], v. 1, no. 19, p. 113-122.

Beu, A.G., 1976, Arrival of *Semicassis pyrum* (Lamarck) and other tonnacean gastropods in the Southern Ocean during Pleistocene time. *Jour. Roy. Soc. N.Z.*, v. 6, p. 413-432, 18 fig.

——— 1978, New records and species of Cymatiidae (Gastropoda: Prosobranchia) from the Kermadec Islands, Norfold Ridge and New Zealand. *Jour. Malac. Soc. Aust.*, v. 4, p. 29-42, 30 fig.

——— 1981, Australian gastropods of the family Bursidae. Part 1. The families of Tonnacea, the genera of Bursidae, and revision of species previously assigned to *Tutufa* Jousseaume, 1881. *Rec. Aust. Mus.*, v. 33, p. 248-324, 22 fig.

——— 1987, Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 2. Descriptions of fourteen new modern Indo-West Pacific species and subspecies, with revisions of related taxa. *N.Z. Jour. Zool.*, v. 13, p. 273-355, 274 fig.

——— and Kay, E.A., 1988, Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 4. The *Cymatium pileare* complex. *Jour. Roy. Soc. N.Z.*, v. 18. p. 185-223, 86 fig.

——— and Maxwell, P.A., 1987, A revision of the fossil and living gastropods related to *Plesiotriton* Fischer, 1884 (Family Cancellariidae, Subfamily Plesiotritoninae n. subfam.). With an appendix: Genera of Buccinidae Pisaniinae related to *Colubraria* Schumacher, 1817. *N.Z. Geol. Surv. Paleont. Bull.*, v. 54, p. 1-132, pl. 1-30.

Binckhorst van den Binckhorst, J.T., 1861, *Monographie des gastéropodes et des céphalopodes de la Craie supérieure du Limbourg, suivie d'un description de quelques espèces de crustacées du même dépot . . .* C. Muquard, Bruxelles, and Müller frères, Maestricht, vi+83+44 p., 17 pl.

Cecioni, G.O., 1978, Petroleum possibilities of the

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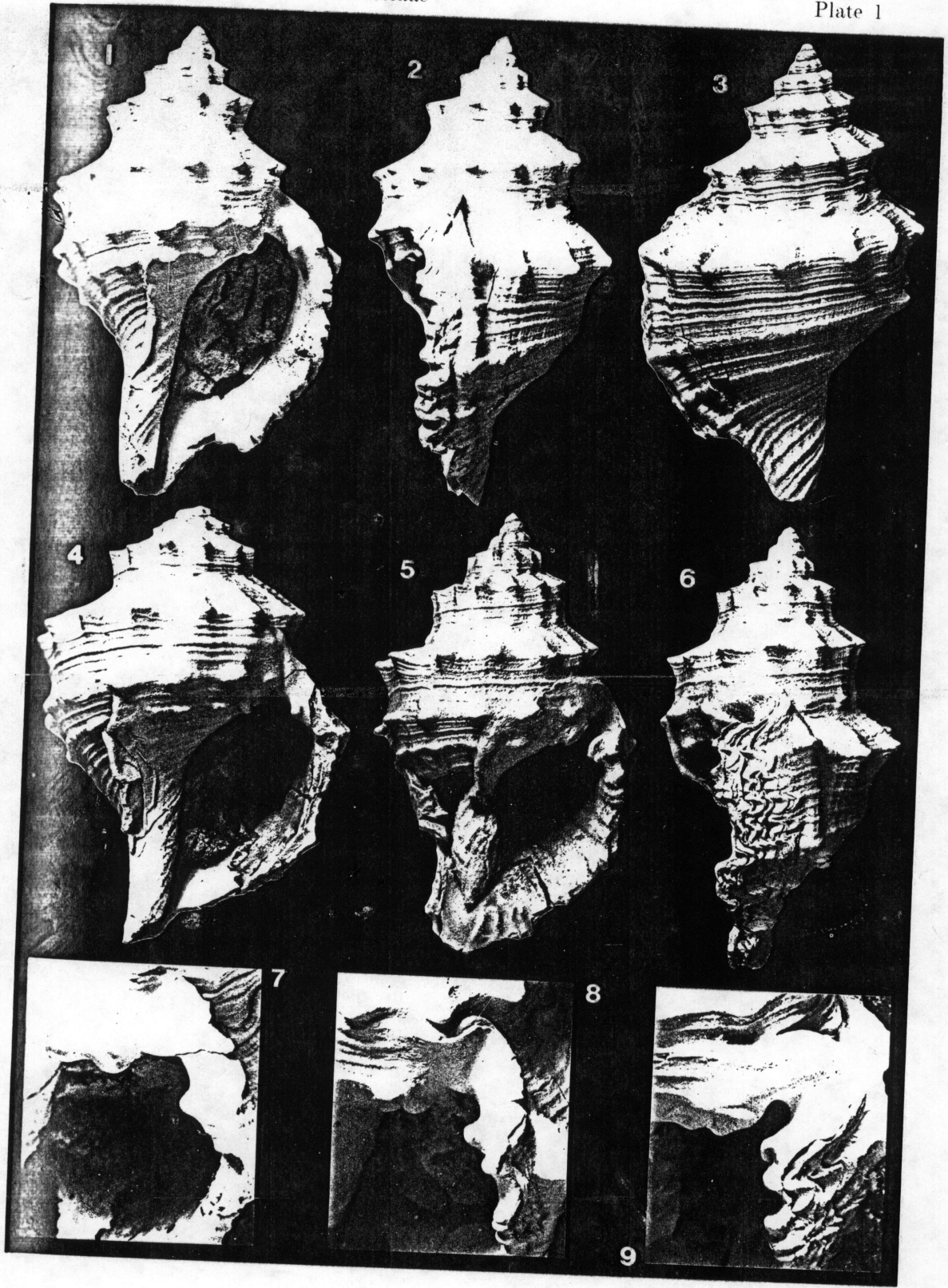*nic matrix y localities ains an un-stropods, a ls, common nd diverse to fill what vacuum in early Cen-v Zealand. main to be a, which for a New this is the nsis Cerno-Flowerpot itt Island Red Bluff pot Bay.*
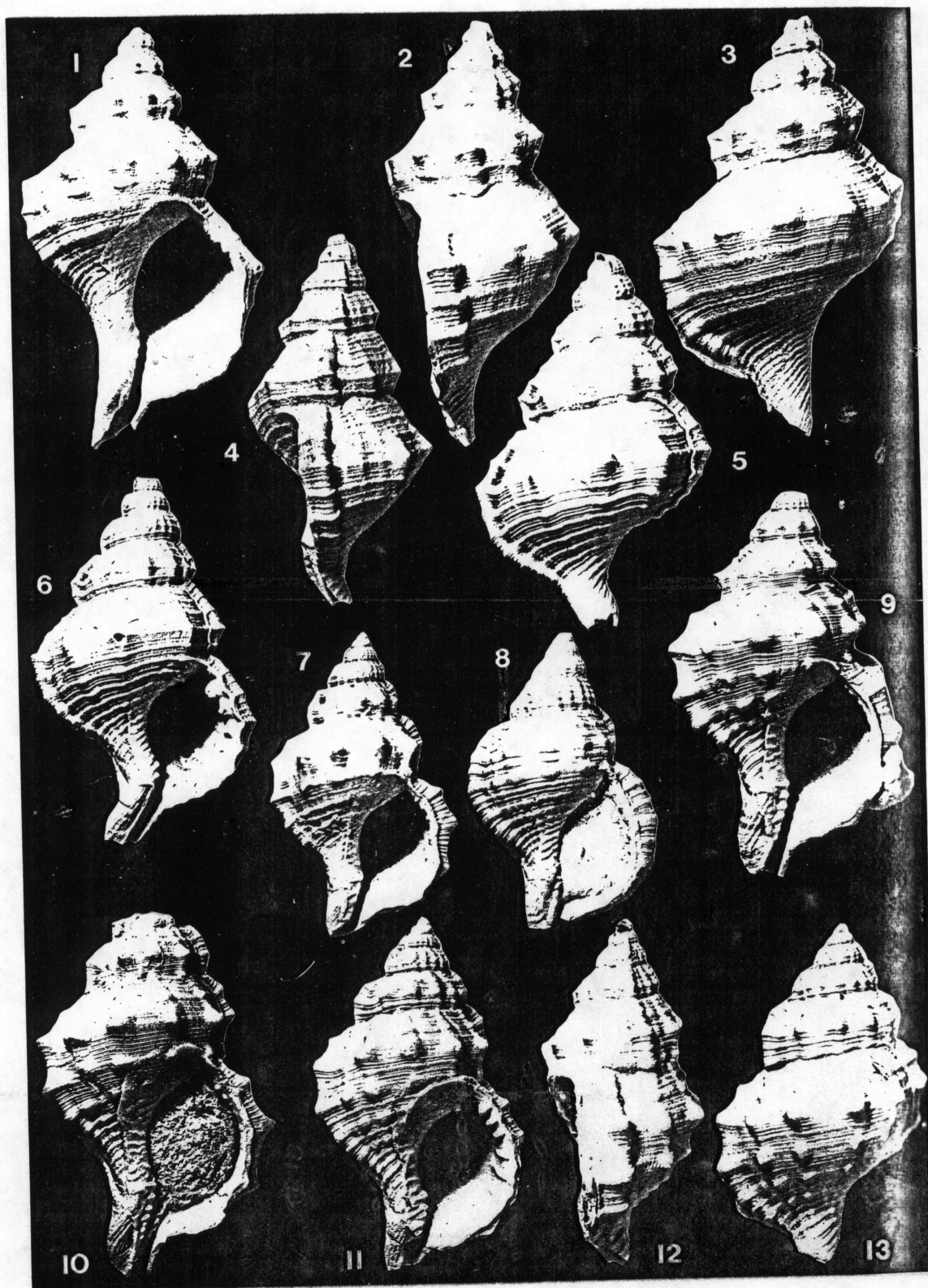
*California:*

Darwin's Navidad Formation near Santiago, Chile. *Mus. Nac. Hist. Nat. Santiago de Chile, Publ. Ocas.*, no. 25, p. 1-26, fig. 1, 2.

Cernohorsky, W.O., 1971, Fossil and Recent Cypraeacea (Mollusca: Gastropoda) of New Zealand with descriptions of new species. *Rec. Auckland Inst. Mus.*, v. 8, p. 103-129, 19 fig.

Children, J.G., 1823, Lamarck's genera of shells, translated from the French [part]. *Quart. Jour. Sci.*, v. 16, p. 49-79.

Clark, B.L., 1938, Fauna from the Markley Formation (upper Eocene) on Pleasant Creek, California. *Geol. Soc. Am. Bull.*, v. 49, p. 683-730, pl. 1-4.

Clench, W.J. and Turner, R.D., 1957, The family Cymatiidae in the western Atlantic. *Johnsonia*, v. 3, p. 189-244, p. 110-135.

Cobban, W.A. and Reeside, W.B., 1952, Correlation of the Cretaceous formations of the western interior of the United States. *Geol. Soc. Am. Bull.*, v. 63, p. 1011-1044, table 10.

Conrad, T.A., 1865, Catalogue of the Eocene and Oligocene Testacea of the United States. *Am. Jour. Conch.*, v. 1, p. 1-35.

Cossmann, M., 1899, Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris, faisant suite aux travaux paléontologiques de G. -P. Deshayes. Fasc. 4. *Ann. Soc. R. Malac. Belgique*, v. 24, p. 3-381, pl. 1-12.

————— 1903, *Essais de paléoconchologie comparée*, vol. 5. M. Cossmann, Paris, 215 p., 9 pl.

————— 1904, *Essais de paléoconchologie comparée*, vol. 6. M. Cossmann, paris, 151 p., 9 pl.

————— and Pissarro, G., 1900, Faune éocénique de Cotentin (mollusques) [part]. *Bull. Soc. Géol. Normandie*, v. 20, p. 61-140, pl. 7-15 [reprint pagination only].

————— 1909, The Mollusca of the Ranikot Series, Part I. -Cephalopoda and Gastropoda. With introductory note on the stratigraphy of the Ranikot Series by E.W. Vredenberg. *Palaeont. Indica*, new ser., v. 3, p. i-xix+1-83, pl. 1-8.

————— 1913 (in 1906-1913), *Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris. Vol. 2, Scaphopodes, gastropodes, brachiopodes, céphalopodes, supplément, avec titre, errata, 65 planches et une table alphébetique.* M. Cossmann, Paris, 20 p., 65 pl. [pl. 1-9, 1906; pl. 10-25, 1910; pl. 26-45, 1911; pl. 46-65, 1913].

Cottreau, J., 1922, Paléontologie de Madagascar. X. -Fossiles Crétacés de la Côte occidentale. *Ann. Paléont.*, v. 11, p. 109-192, pl. 9-19.

Dall, W.H., 1904, An historical and systematic review of the frog-shells and tritons. *Smithson. Misc. Collns.*, v. 47, p. 114-144.

————— 1925, Illustrations of unfigured types of shells in the collection of the United States National Museum. *U.S. Nat. Mus. Proc.*, v.

66 (17), p. 1-41, pl. 1-36.

Deshayes, G. -P., 1835 (in 1824-1837), *Description des coquilles fossiles des environs de Paris. Tome 2. Mollusques.* Chez l'auteur, Rue de Paradis... Paris, 814 p. [p. 1-80, 1824; 81-146, 1825; 147-290, 1832; 291-426, 1833; 427-498, 1834; 499-780, 1835; 781-814, 1837].

————— 1837, *Description des coquilles fossiles des environs de Paris. Atlas.* F. -G. Levrault, Paris and Strasbourg, 28 p., 65 pl.; 51 p., 106 pl.

————— 1865 (in 1864-1865), *Description des animaux sans vertèbres découverts dans le Bassin de Paris, pour servir de supplément à la description des coquilles fossiles des environs de Paris, comprenant une revue générale de toutes les espèces actuellement connues. Tome 3. Texte. Mollusques céphalopodes. Accompagné d'un atlas de 42 planches.* J. -B. Baillière et fils, Paris, p. 1-200, pl. 63-85, 1864; p. 201-685, pl. 86-107, 1865.

Dickerson, R.E., 1915, Fauna of the type Tejon: its relation to the Cowlitz phase of the Tejon Group of Washington. *Cal. Acad. Sci. Proc.*, ser. 4, v. 5, p. 33-98, pl. 1-11.

————— 1916, Stratigraphy and fauna of the Tejon Eocene of California. *Univ. Calif. Publ. Bull. Dept. Geol. Sci.*, v. 9, p. 363-524, pl. 36-46.

Douvillé, H., 1904, Mollusques fossiles. Etudes géologiques. Partie IV-Paléontologie. *In* de Morgan, J. (ed.) *Mission scientifique en Perse, par J. de Morgan.* Tome 3, p. 187-380, pl. 25-50. Ernest Leroux, Paris.

Furon, R. and Soyer, R., 1947, *Catalogue des fossiles Tertiaires du Bassin de Paris.* Savoir en histoire naturelle, no. 22. Lechevalier, Paris, 240 p., 31 pl.

Gabb, W.M., 1864, *Palaeontology of California, Vol. I, Triassic and Cretaceous fossils.* Published by authority of the legislature of California. Caxton Press of Sherman & Co., Philadelphia, 243 p., 32 pl.

————— 1866, *Palaeontology of California, Vol. II, part 1. Cretaceous and Tertiary fossils.* [as above]. p. v-xiv+299.

————— 1869, *Palaeontology of California, Vol. II, part 2. Cretaceous and Tertiary fossils.* [as above]. pl. 1-36.

Gardner, J. 1935, The Midway Group of Texas. Including a chapter on the coral fauna by T. Wayland Vaughan and Willis Parkison Popenoe. *Univ. Texas Bull.*, v. 3301, p. 1-403, pl. 1-28.

Givens, C.R., 1974, Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. *Univ. Cal. Publ. Geol. Sci.*, v. 109, p. 1-107, pl. 1-11.

Gregorio, A. de, 1880, *Fauna di S. Giovanni Ilarione*

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Harris, G.D.,
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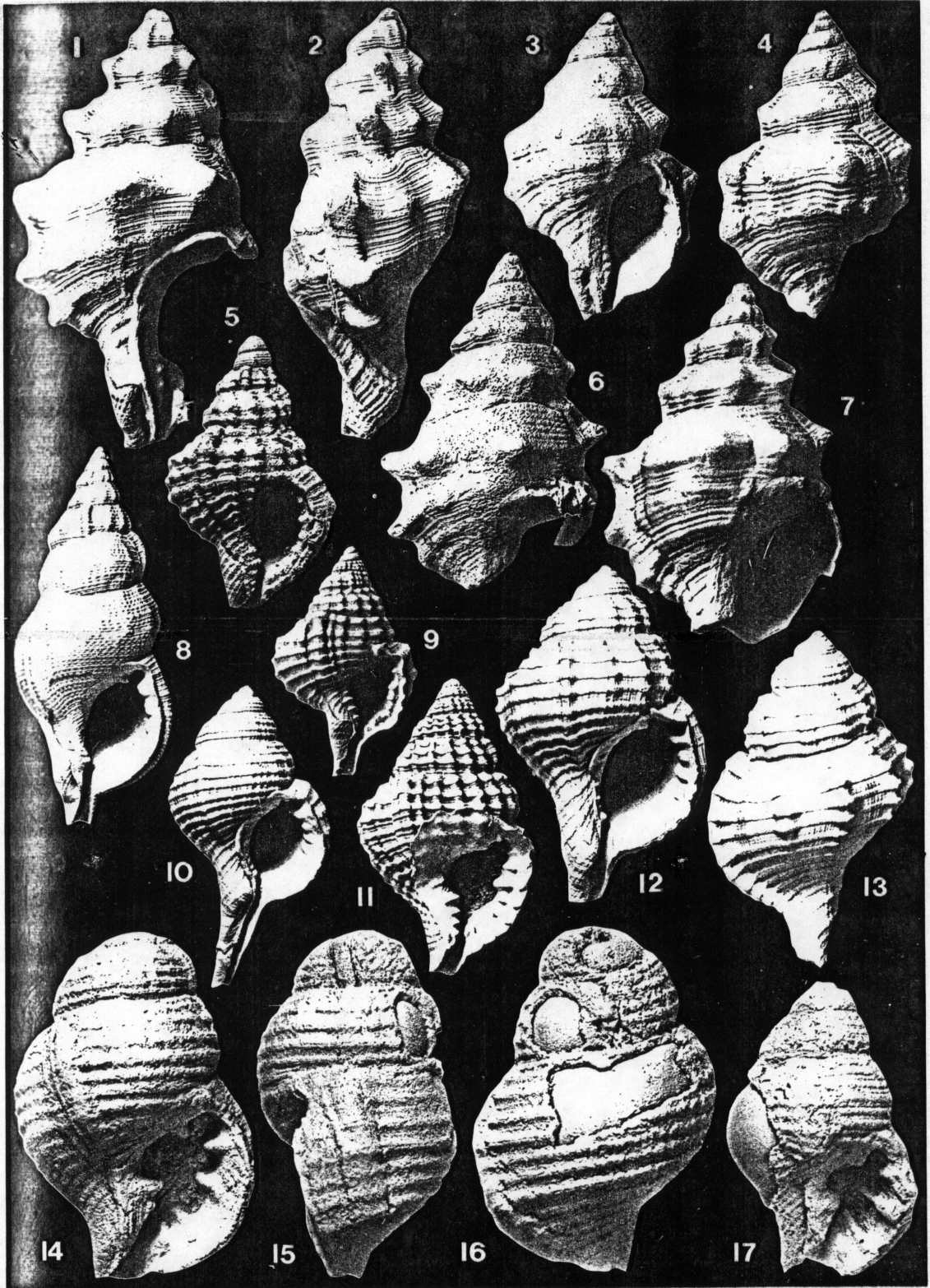(Cymatiida
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*Description s de Paris. ur, Rue de ), 1824; 81- 426, 1833; l-814, 1837]. s fossiles des l. Levrault, .; 51 p., 106*

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e Tejon: its the Tejon . Sci. Proc.,

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*ifornia, Vol.* Published California. hiladelphia,

*ornia, Vol. fossils.* [as

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of Texas. auna by T. Parkison )1, p. 1-403,

iostratigra- a, Ventura *Publ. Geol.*

*mi Ilarione*

(*Parisiano*). *Monografia de Antonio de Gregorio. Parte la : Cefalopodi e Gasteropodi. Fasc. 1.* Tipografia P. Montaina & C., Palermo, xxviii + 110 p., 9 pl.

Harris, G.D., 1899, The lignitic stage, Part II, Scaphopoda, Gastropoda, Pteropoda and Cephalopoda. *Bull. Am. Paleont.*, v. 3 (11), p. 1-128, pl. 1-12.

———— and Palmer, K.V.W., 1947, The Mollusca of the Jackson Eocene of the Mississippi embayment (Sabine River to the Alabama River), Sect. 2 : Univalves. *Bull. Am. Paleont.*, v. 30 (117), p. 209-564, pl. 26-65.

Hickman, C.S., 1969, The Oligocene marine molluscan fauna of the Eugene Formation in Oregon. *Mus. Nat. Hist. Univ. Oregon Bull.*, v. 16, p. 1-112, pl. 1-14.

———— 1980, Paleogene marine gastropods of the Keasey Formation in Oregon. *Bull. Am. Paleont.*, v. 78 (310), p. 1-112, pl. 1-10.

Hupé, L.H., 1854, Fauna Chilena. Moluscos. *In* Gay, C., *Historia fisica y politica de Chile, segun documentos adquiridos en esta republica durante doce anos ... Zoologia*, Tomo 8, p. 1-499, pl. malacologia 1-8, conquiliologia 1-6. En casa del autor, Paris; en el Museo de Historia Natural de Santiago, Chile.

Iredale, T., 1917, More molluscan name changes, generic and specific. *Proc. Malac. Soc. Lond.*, v. 12, p. 322-330.

———— 1924, Results from Roy Bell's molluscan collections. *Proc. Linn. Soc. New South Wales*, v. 49, p. 179-278, pl. 33-36.

Kaunhowen, F., 1898, Die Gastropoden der Maestrichter Kreide. *Pal. Abhand.*, v. 8, p. 1-132, pl. 1-13.

Krach, W., 1963, Mollusca of the Babica clays (Paleocene) of the middle Carpathians. Pt. I. Gastropoda. *Studia Geol. Polonica.*, v. 14, p. 1-152, pl. 1-27.

Lamarck, J.B.P.A. de M. de, 1803, Suite des mémoires sur les fossiles des environs de Paris. *Ann. Mus. Hist. Nat. Paris*, v. 2, p. 57-64.

———— 1816, *Tableau encyclopédique et méthodique des trois regnes de la nature. Vingt-troisième partie. Mollusques et polypes divers.* "Liste des objets représentés dans les planches de cette livraison", p. 1-16 ; pl. 391-488. Mme. Veuve Agasse, Paris.

———— 1822, *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux ...* Vol. 7. Chez l'auteur, au jardin du Roi, Paris, 711 p.

Lewis, H., 1972, Notes on the genus *Distorsio* (Cymatiidae) with descriptions of new species. *Nautilus*, v. 86, p. 27-50, 48 fig.

MacNeil, F.S. and Dockery, D.T. III, 1984, Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg Group in Missis-

sippi. *Miss. Dept. Nat. Resources Bur. Geol. Bull.*, v. 124, p. 1-415, pl. 1-72.

Maxwell, P.A., 1968, *Distorsio (Personella) beui*, a new species of the Cymatiidae (Gastropoda) from the upper Eocene of New Zealand. *Trans. R. Soc. N.Z., Geol.*, v. 6, p. 133-137, 3 fig.

Olsson, A.A., 1930, Contributions to the Tertiary paleontology of northern Peru : Part 3, Eocene Mollusca. *Bull. Am. Paleont.*, v. 17 (62), p. 1-96, pl. 1-12.

Palmer, K.V.W., 1977, *The unpublished vélins of Lamarck (1802-1809). Illustrations of fossils of the paris Basin Eocene.* Paleontological Research Inst., Ithaca, 67 p., 52 pl.

———— and Brann, D.C., 1966, Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part II. Gastropoda. *Bull. Am. Paleont.*, v. 48 (218), p. 471-1057.

Pease, W.H., 1861, Descriptions of seventeen new species of marine shells from the Sandwich Islands, in the collection of Hugh Cuming. *Proc. Zool. Soc. London*, 1860, p. 397-400.

Philippi, R.A., 1887, *Die tertiären und quaternären Versteinerungen Chiles.* Brockhaus, Leipzig, 266 p., 58 pl.

Sacco, F., 1904, *I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte XXX. Aggiunte e correzioni (con 1400 figure). Considerazioni generali. Indice generale dell'opera.* Carlo Clausen, Torino, 203 + xxxvi p., 30 pl.

Saul, L.R., 1983, Notes on Paleogene turritellas, venericardias, and molluscan stages of the Simi Valley area, California. *In* Squires, R.R. and Filewicz, M.V. (eds.), *Cenozoic geology of the Simi Valley Area, southern California*, Pacific Section, SEPM, Fall field trip volume and guidebook, p. 71-80, pl. 1, 2.

Schumacher, H.C.F., 1817, *Essais d'un nouveau système des habitations des vers testacés.* Le directeur Schultz, Copenhagen, 287 p., 22 pl.

Smith, J.T., 1970, Taxonomy, distribution and phylogeny of the cymatiid gastropods *Argobuccinum, Fusitriton, Mediargo* and *Priene. Bull. Amer. Paleont.*, v. 56 (254), p. 441-573, pl. 39-49.

———— 1975, Age, correlation, and possible Tethyan affinities of mollusks from the Lodo Formation of Fresno County, California. *In* Weaver, D.W., Hornaday, G.R., and Tipton, A. (eds.), *Conference on Future Energy horizons of the Pacific Coast : Paleogene symposium*, AAPG, Pacific Section, p. 464-483, pl. 1, 2.

Sohl, N.F., 1960, Archeogastropoda, Mesogastropoda and stratigraphy of the Ripley, Owl Creek and Prairie Bluff Formations. *U.S. Geol. Surv. Prof. Pap.*, v. 331-A, p. 1-151, pl. 1-18.

———— 1967, Upper Cretaceous gastropods from

the Pierre Shale at Red Bird, Wyoming.  *U.S. Geol. Surv. Prof. Pap.*, v. 393-B, p. B1-B46, pl. 1-11.

Sornay, J., 1968, Inocérames Senoniens du sud-ouest de Madagascar.  *Ann. Paléont.*, v. 54, p. 25-47, pl. A-H.

Sowerby, G.B. I, 1846, Appendix.  Descriptions of Tertiary fossil shells from South America.  *In* Darwin, C. *Geological observations on South America.  Being the third part of the geology of the voyage of the Beagle* ... , p. 249-264, pl. 2-4.  Smith Elder & Co., London.

Squires, R.L., 1983, New mollusks from the lower middle Eocene Llajas formation, southern California.  *Jour. Paleont.*, v. 57, p. 354-362, 2 fig.

Stanton, T.W., 1893, The Colorado Formation and its invertebrate fauna.  *U.S. Geol. Surv. Bull.*, v. 106, p. 1-288, pl. 1-45.

Stevens, G.R., 1981, Geological time scale, revised edition.  Wellington, Geol. Soc. New Zeal. (wall chart).

Stewart, R., 1926, Gabb's California fossil type gastropods.  *Acad. Nat. Sci. Philad. Proc.*, v. 78, p. 287-477, pl. 20-32.

Stone, B., 1949, Age of the Chira Group, northwestern Peru.  *Jour. Paleont.*, v. 23, p. 156-160.

Tate, R., 1894, Unrecorded genera of the older Tertiary of Australia, including diagnoses of some new genera and species.  *Proc. Roy. Soc.* *New South Wales*, v. 27, p. 167-197, pl. 10-13.

Tavera Jerez, J., 1979, Estratigrafia y paleontologia de la Formacion Navidad, Provincia de Colchagua, Chile (Lat. 30°50'34"S).  *Mus. Nac. Hist. Nat. Santiago de Chile Bol.*, v. 36, p. 1-176, pl. 1-21.

Turner, F.E., 1938, Stratigraphy and Mollusca of the Eocene of Western Oregon.  *Geol. Soc. Amer. Spec. Pap.*, v. 10, p. 1-130, pl. 1-22.

Villalta Comella, J.F. de, 1956, Los moluscos fósiles del Eoceno Pirenaico.  I.  Cuenca . del Basa.  Primera parte : Gasterópodos.  *Bol. Inst. Geol. Min. España*, vol. 67, p. 119-235, pl. 1-12.

Vokes, H.E., 1939, Molluscan faunas of the Domengine and Arroyo Hondo formations of the California Eocene.  *Ann. New York Acad. Sci.*, v. 38, p. 1-246, pl. 1-22.

Wade, B., 1926, The fauna of the Ripley Formation on Coon Creek, Tennessee.  *U.S. Geol. Surv. Prof. Pap.*, v. 137, p. 1-272, pl. 1-72.

Weaver, C.E., 1912, A preliminary report on the Tertiary paleontology of western Washington.  *Wash. Geol. Surv. Bull.*, v. 15, p. 1-80, pl. 1-15.

———— 1943, Paleontology of the marine Tertiary formations of Washington and Oregon.  *Univ. Wash. Publ. Geol.*, v. 5, p. 1-789, pl. 1-104.

Zinsmeister, W.J., 1983, New late Paleocene mollusks from the Simi Hills, Ventura County, California.  *Jour. Paleont.*, v. 57, p. 1282-1303, 4 fig.