Laubierinidae and Pisanianurinae (Ranellidae), Two New Deep-Sea Taxa of the Tonnoidea (Gastropoda: Prosobranchia)

by

ANDERS WARÉN

Naturhistoriska Riksmuseet, Box 50007, S-10405 Stockholm, Sweden

AND

PHILIPPE BOUCHET

Muséum National d'Histoire Naturelle,
55 Rue de Buffon, F-75005 Paris, France

Abstract. The classification of the Tonnoidea is discussed based on new information about deep-sea species. Representative radulae, opercula, and larval shells are described and figured. The conclusions agree mainly with earlier classification, with the following exceptions: Oocorythinae is moved from Tonnidae to Cassidae and its value as a subfamily is questioned. The gross anatomies of two Recent deep-water species of *Pisanianura* Rovereto, 1899, are described, and a new ranellid subfamily, **Pisanianurinae**, is described for *Pisanianura* Rovereto, 1899, formerly classified in the Buccinidae. The genera *Laminilabrum* Kuroda & Habe, 1961, presently in the Trichotropidae, *Kaiparanura* Laws, 1944, and *Nawenia* Ladd, 1977, presently in the Buccinidae, are considered synonyms of *Pisanianura*, which is known in the fossil record since the Oligocene.

A new family, **Laubierinidae**, is erected for **Laubierina** gen. nov. and *Akibumia* Kuroda & Habe, 1958 (formerly Trichotropidae) with three Recent deep-water species. **Laubierina peregrinator** gen. et sp. nov. is described from deep water in the tropical Atlantic and Indian oceans. Two large (5 mm) planktonic larvae belonging to the **Laubierinidae** are described and one of them is remarkable for being a sexually mature male at the time of settlement. All dissected adults are females and it is speculated that **Laubierina** is a protandrous hermaphrodite with neotenic males. The gross anatomies of **L. peregrinator** sp. nov., *A. orientalis* (Schepman, 1909), and *A. schepmani* (Habe, 1962) are described.

Akibumia reticulata Habe, 1962, is referred to the Epitoniidae and *Conradia minuta* Golikov & Starobogatov, 1986 (described in Fossaridae) is considered a larva of Neptunellinae.

Thalassocyon bonus Barnard, 1960, and *T. tui* Dell, 1967, are synonymized; their anatomies are briefly described and compared with that of *Ficus* and it is concluded that *Thalassocyon* has been correctly referred to the Ficidae. Attention is drawn to the fact that the morphology of the Ficidae conforms poorly with other Tonnoidea.

The value and use of larval shells as taxonomical criteria are discussed, and it is concluded that they are useful criteria, as long as clear distinction is made between "primary" (*i.e.,* planktotrophic) and "secondary" (*i.e.,* non-planktotrophic) types of larval shells and only "primary" ones are compared.

INTRODUCTION

During the last two decades, several French expeditions have been exploring the bathyal and abyssal parts of the Indo-Pacific area. During these expeditions, material of deep-water species of the Tonnoidea has been obtained. Such specimens are rare and each expedition has usually brought back only one or two samples. Among them were

some specimens that could not be classified in the normally accepted suprageneric taxa.

During the same time, much has been added to the knowledge of the tonnoids, mainly through the work of Dr. Alan Beu, Geological Survey of New Zealand (see Literature Cited), working on the recent and fossil tonnoids. In order to give a more complete picture of the superfamily, we have felt that it would be valuable to review also the deep-sea groups, which otherwise, through their deviate morphology, might easily be overlooked.

We have also studied the consequences that the new taxa may have on existing classification by comparing them with presently accepted groups, and we have supplemented existing information with new data about larval shell and radular morphology of the known groups.

We will start by giving a key to the families of Tonnoidea partly based on BEU's (1981, 1988b) characters of the families, supplemented by our own observations. Then we continue with a review of the families of the Tonnoidea, supplemented by new information and illustrations of features used in the discussions of the new taxa. We finish with a discussion about the larval shell of the Tonnoidea and its value as a taxonomic criterion.

Author names and dates not found in the text are given in the Appendix.

MATERIAL

Deep-water Tonnoidea are rare and the material studied here has been accumulated over a period of more than 20 years. The following expeditions contributed material that was essential to our understanding of the deep-water Tonnoidea. "Benthedi," 1977, on R/V *Suroit,* in the northern part of the Mozambique Channel, directed by B. Thomassin, collected the first lot of **Laubierinidae,** which puzzled us for several years. "Walvis," 1981, on R/V *Jean Charcot,* off southwestern Africa, directed by M. Sibuet, collected additional wet material of **Laubierinidae.** "Biocal," 1985, on R/V *Jean Charcot,* off southern New Caledonia, directed by C. Levi, brought back living representatives of the genus *Pisanianura.* Other expeditions yielded additional information and are cited when appropriate in the text.

In addition, described and undescribed material from AMS, ANSP, MOM, NMNZ, SAM, SMNH, USNM, ZMA, and ZMC was examined. When necessary, type material has been examined, and is referred to in the text or accompanying figures.

The author and date for the taxa discussed are given at appropriate places in the text, except for the species listed in the Appendix.

ABBREVIATIONS USED

AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; MNHN, Museum National d'Histoire Naturelle, Paris; MOM, Musée Océanographique, Monaco; NMNZ, National Museum of New Zealand, Wellington; NZGS, New Zealand Geological Survey, Lower Hutt; NZOI, New Zealand Oceanographic Institute; SAM, South African Museum, Cape Town; SMNH, Naturhistoriska Riksmuseet, Stockholm; USNM, U.S. National Museum of Natural History, Washington, D.C.; ZMA, Zoölogisch Museum, Amsterdam; ZMC, Zoologisk Museum, København.

SYSTEMATICS

Superfamily TONNOIDEA Suter, 1913

The superfamily Tonnoidea has been defined by THIELE (1929) and BOSS (1982). The only change in the criteria of this taxon that our investigations have necessitated is that the osphradium, which has been supposed to be bipectinate in all species, is monopectinate in the **Laubierinidae.** If future work shows that the Ficidae does not belong to the Tonnoidea (*cf.* p. 83), it should also be added that all Tonnoidea have large, complex salivary glands (small and simple in Ficidae).

Morphology of the Tonnoid Veliger

Veliger larvae belonging to species of Tonnoidea have been known since the mid-19th century oceanographic expeditions (FORBES, 1852; H. & A. ADAMS, 1853–1858), and these large larvae were then frequently described as distinct holoplanktonic species. The following generic names were thus based on tonnoid larvae: *Macgillivraya* Forbes, 1852, larva of *Tonna* Brünnich, 1772; *Calcarella* Souleyet, 1850, probably larva of *Distorsio* Röding, 1798; *Gemella* H. & A. Adams, 1858, a cassid; *Talisman* de Folin, 1884, a bursid larva; and *Dissentoma* Pilsbry, 1945 (see PILSBRY, 1949) and *Ethella* H. & A. Adams, 1858, neptunelline larvae. Empty larval shells in sediments were (and still occasionally are) given specific names before being recognized as larval shells.

CAZENAVETTE (1853) briefly and FISCHER (1863) in more detail described the young of *Tonna* and identified it with *Macgillivraya.* Several authors (*e.g.,* KESTEVEN, 1901, 1902; CLENCH & TURNER, 1957) then figured the larval shells of tonnoids, based on young benthic stages with preserved apical whorls. PELSENEER (1906) briefly described two ranellid larvae from the Bay of Biscay (as *Coralliophila* sp. A and B). SIMROTH (1911) described *Calcarella* in some detail, but did not see the connection with the adult stage. Finally, SCHELTEMA (1971, 1972) and LAURSEN (1981) on a larger scale identified and figured planktonic larvae by comparison with benthic stages. SCHELTEMA (1966) introduced the term "teleplanic" to characterize the long-lived veligers of Neptunellinae and demonstrated that trans-Atlantic dispersal could take place during their planktonic life. PECHENIK *et al.* (1984) have shown that planktonic larvae of *Cymatium parthenopeum* (von Salis, 1793) do not grow during their dispersal across the North Atlantic via the North Atlantic drift, but remain

competent for metamorphosis during periods extending over 300 days. This growth stasis and ability to delay metamorphosis explains the more or less circumtropical distribution for many species of Tonnoidea. (It does not explain, however, why many of them are absent in the tropical eastern Pacific, and most species despite having teleplanic larvae are not cosmopolitan.)

We have examined numerous species of Tonnoidea in order to find out to what extent and with what precision larval shells can be identified, because these frequently are encountered in samples of plankton and benthos, and also in order to find out if the larval shells give any clues about the systematic relations of the species. We have then supplemented comparison of larval shells from planktonic or benthic catches and young specimens with examination of opercula and radulae, which contain important information. Under each family we figure representative species, with operculum and radula.

A sculpture of thin axial and spiral cords that meet at right angles and are clearly set off from the smooth surface is present on protoconch II of at least some species in most families of Tonnoidea (Figures 79, 90, 92–96, 102–109, 110–113). This type of larval shell is here considered to indicate planktotrophic development. We are not convinced that certain other larval shells with reticulate sculpture built up by axial and spiral ribs, but lacking the smooth surface (*e.g.*, BEU, 1988b:fig. 1B), indicate planktotrophic development.

Key to the Recent Families and Subfamilies of Tonnoidea

A. Osphradium monopectinate, shell about as broad as high and without well-defined siphonal canal
     . . . . **Laubierinidae**
A. Osphradium bipectinate, distinct siphonal canal present . . . . B
B. Operculum absent or reduced in adult C
B. Operculum well developed . . . . D
C. Siphonal notch present, larval shell corneous; if calcified, disjunctly coiled . . . . Tonnidae
C. Siphonal canal formed by the drawn out aperture; larval shell calcified, not disjunctly coiled . . Ficidae
D. Aperture with a well-developed posterior siphonal canal, jaws reduced; incremental scars aligned along both sides of shell, separated by 180° . . . . Bursidae
D. Aperture without distinct posterior canal, jaws large . . . . E
E. Shell globular or triangular with short siphonal canal . . . . Cassidae
E. Shell fusiform or bucciniform, often with long canal . . . . F
F. Parietal shield strongly developed; proboscis very long, strongly coiled when retracted; posterior edge of central radular tooth evenly curved . . . . Personidae
F. Parietal shield not strongly developed; proboscis straight when retracted; posterior edge of central radular tooth straight . . . . G (Ranellidae)
G. Shell with regularly appearing varices . . . . H
G. Shell without varices . . . . **Pisanianurinae**
H. Varices separated about 240° . . . . Neptunellinae
H. Varices separated about 180° . . . . Ranellinae

Family RANELLIDAE Gray, 1854

(Figures 25–40, 52–55, 67–70, 85–95, 97–104, 123–127, 142–145, 153, 154)

BEU (1985) and BEU & CERNOHORSKY (1986) have pointed out the nomenclatorial reasons for using the name Ranellidae instead of the well-established and almost universally used name Cymatiidae, and Personinae instead of Distorsioninae. However, they have continued using Cymatiinae Iredale, 1913, as the name of the subfamily, referring to ICZN Article 40b. Because the Commission evidently refuses to consider invalidating the name Ranellidae, we can see no possibility to avoid using the name Neptunellinae introduced by GRAY (1854) at the same occasion as the Ranellidae. It is based on the generic name *Neptunella* Gray, 1854 (defined by citation of the name "[*Murex*] *cutaceum*" (Linné, 1758)) and is an objective junior synonym of *Cabestana* Röding, 1798. This is a regrettable consequence of the strict application of the Code.

BEU (1988b) convincingly separated the Personidae as a distinct family, present already in the Upper Cretaceous, and distinguished two subfamilies of Ranellidae:

Neptunellinae (=Cymatiinae), with a central radular tooth that is distinctly wider than high and is equipped with several lateral denticles; a periostracum with dense axial blades and varices separated by ⅔ of a whorl.

Ranellinae, with a central radular tooth equipped with a few lateral denticles and about as high as broad; a peri-

$\longrightarrow$

Explanation of Figures 1 to 8
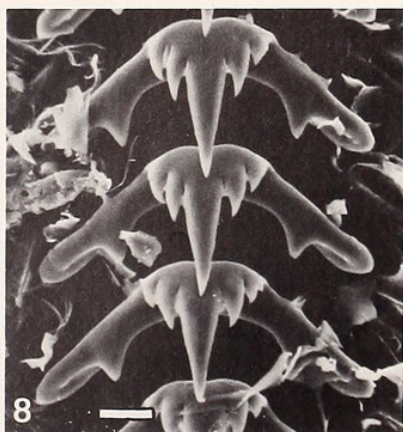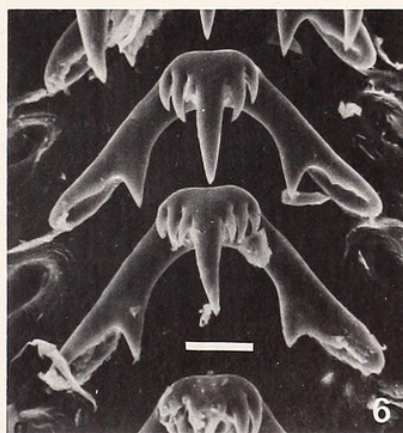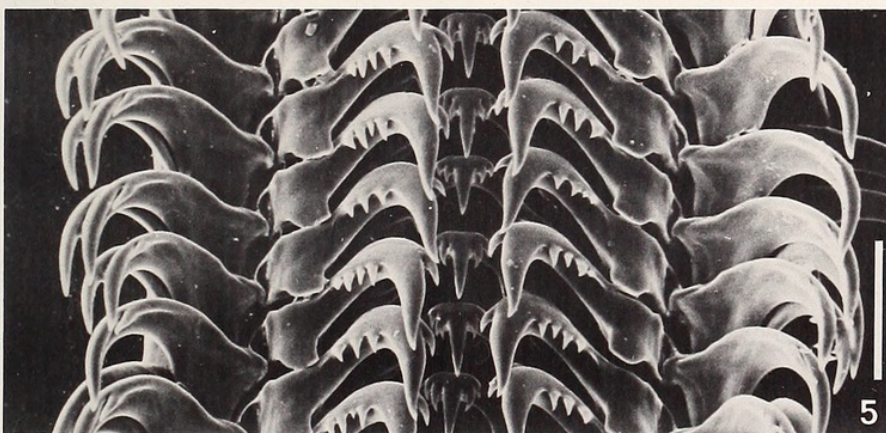
Radulae of Ficidae and Bursidae.
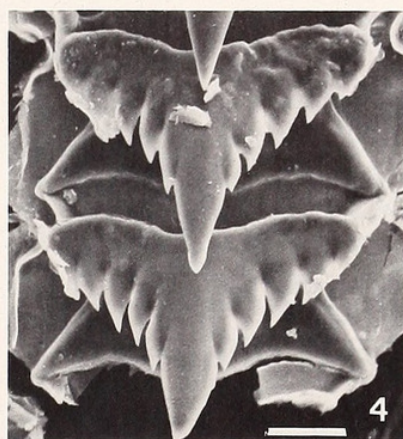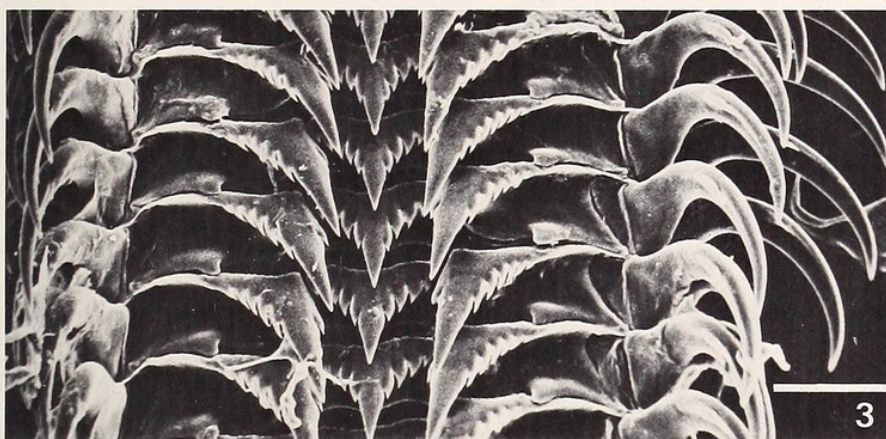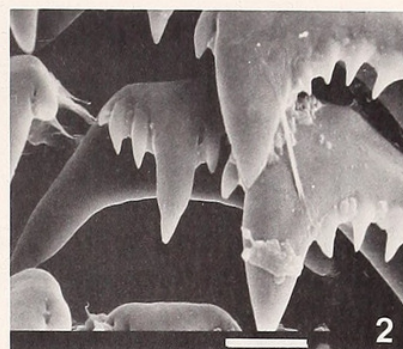
Figures 1 and 2. *Thalassocyon bonus* (New Zealand, NMNZ). Scale lines 25 and 10 μm.

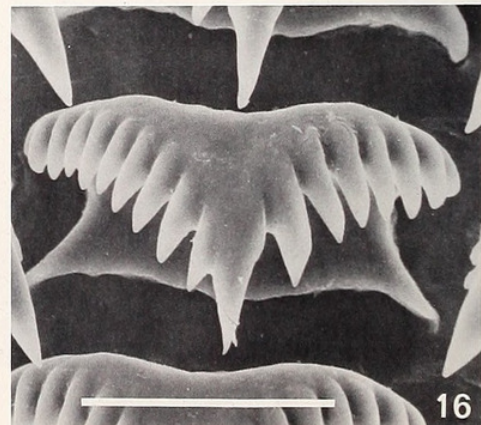Figures 3 and 4. *Ficus* sp. (Seychelles, MNHN). Scale lines 100 and 25 μm.
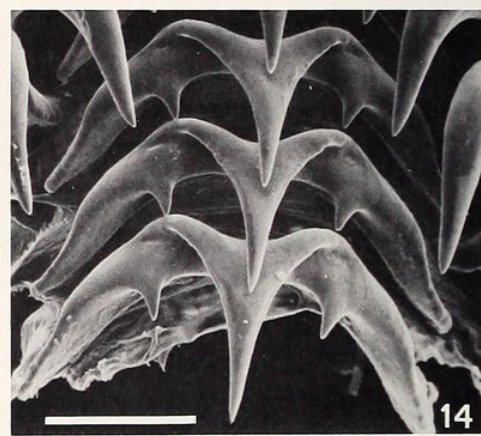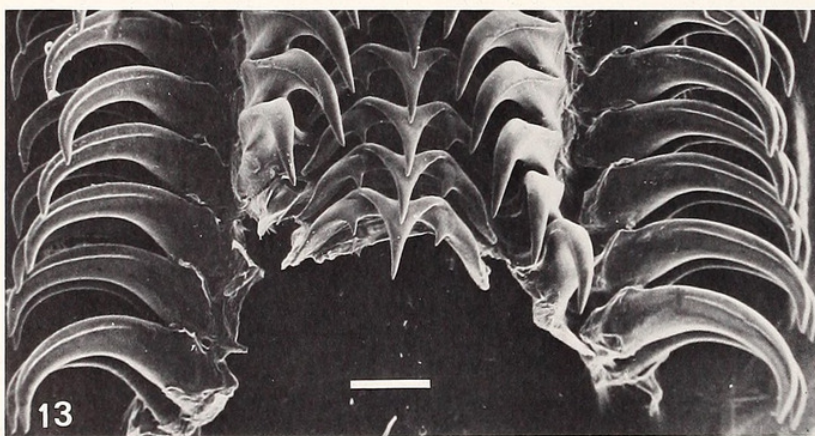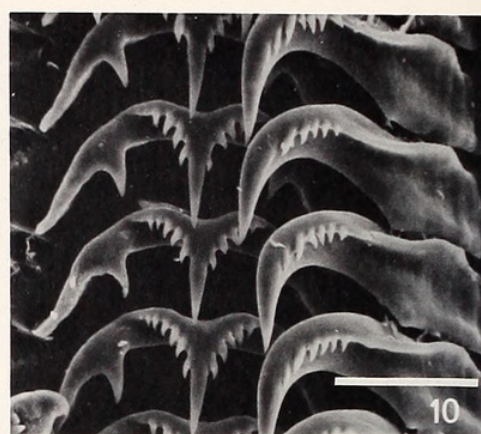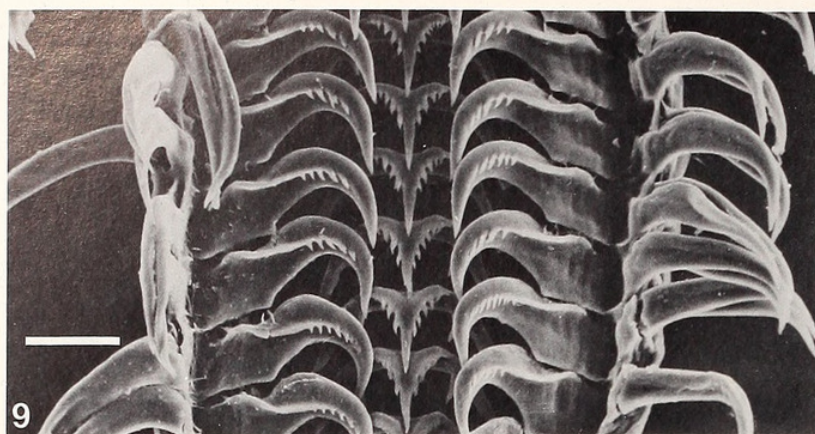
Figures 5 and 6. *Bursa* sp. (Gilbert Id., SMNH). Scale lines 100 and 25 μm.

Figures 7 and 8. *Bufonaria marginata* (Canaries, SMNH). Scale lines 100 and 25 μm.

ostracum without dense axial blades and varices aligned up the sides of the spire, *i.e.*, separated by 180°.

We will here add one additional subfamily, based on the genus *Pisanianura* Rovereto, 1899, previously classified in the Buccinidae. However, first we will give some background information about the protoconch of the Ranellidae.

The Ranellid Larval Shell

There is considerable variation in the morphology and development of the larval shell of this family. It is therefore outlined for the different subfamilies, and for species with planktotrophic development.

PILKINGTON (1974) described the early young of *Sassia* (*Cymatona*) *kampyla* (Watson, 1885) (Neptunellinae), which belongs to the oldest genus of Tonnoidea, dating back to the Late Cretaceous (Turonian, BEU 1988b). The planktonic stage of this species was mentioned by DELL (1956). In several papers Beu has later figured and described larval shells of many species of *Sassia*, which differ from other species of Neptunellinae in being calcareous, globular and often equipped with cancellate sculpture.

The morphology and biology of larvae belonging to *Cymatium* and *Charonia* (Neptunellinae) have been described by SCHELTEMA (1971), LAURSEN (1981), RICHTER (1984), and PECHENIK *et al.* (1984). Characteristic for these is that they are only partly, or not at all, calcified, and have a fairly tall spire, usually considerably higher than the aperture (Figures 97–104). The larval operculum has a characteristic shape, very slender, with a semicircular external and depressed bell-shaped inner margin (Figure 70). As in the Tonnidae the larval shell is, after settlement, filled by calcareous deposits, so that after destruction of the periostracum only a disjunctly coiled, internal mould remains. This internal mould shows the original sculpture also in species that resorb primarily deposited calcium carbonate (Figures 103, 104).

In species of *Sassia* (Neptunellinae)—*e.g., S. remensa* (Iredale, 1936), *S. parkinsonia* (Perry, 1811), and *Sassia raulini* (Cossmann & Peyrot, 1923) (Figure 90)—there is no interspace between the whorls of the protoconch II, even after treatment with bleach to remove remains of the periostracum. This can only be interpreted in one way, *viz.* that already the planktonic larva forms a calcareous shell, covered only externally by a periostracum.

We consider the sculpture of species of *Cymatium,* on the inside of the periostracum of the apical whorl (Figure 104) and on the remaining internal mould (Figure 103), of great interest and indicating that these species originate from species with a reticulate larval sculpture of the same type as in, *e.g., Sassia.*

The osphradium of the larva is usually bipectinate in species of *Cymatium,* but in one species we found a monopectinate osphradium (shell: see Figure 98).

The larvae of the Ranellinae are less well known, but PILKINGTON (1974, 1976) described the hatching young of *Argobuccinum pustulosum* (Lightfoot, 1786), *Fusitriton magellanicus,* and KESTEVEN (1901, 1902), IREDALE (1936), and BEU (1978a, b, 1988b) figured several protoconchs from juvenile specimens. To expand on this, we have examined some late larvae and early post-larvae. A specimen of *Ranella australasia* taken in surface plankton off southeastern Australia has a larval shell that shows only traces of an internal calcareous coating, which certainly is of no supporting function (Figure 89). The shell is perfectly smooth and unexpectedly solid, considering that it consists only of periostracum. Immediately after settlement the young starts to form an internal calcareous coating, and later a shell. When the post-larval growth continues, the periostracum starts to disintegrate and finally a perfectly smooth, calcareous, internal mould of the larval shell remains (as in Figures 86, 87), following the same pattern as in *Cymatium* and *Charonia.* We have examined young benthic stages of *Fusitriton magellanicus* (Figure 85), *Ranella olearia* (Figure 87), and *Argobuccinum pustulosum tumidum* (Figure 86) that have larval shells conforming with this developmental model. Usually one can see a distinct interspace between the whorls, where once there was periostracum (Figure 87).

The larval shell of the **Pisanianurinae** is characteristic in its large size (2.5–3.5 mm high), usually brown color, and globular shape without a distinct siphonal canal and especially in the perfectly reticulated sculpture with large smooth squares between raised axial and spiral ribs that meet at close to right angles (Figures 90, 96). It resembles that of the **Laubierinidae** (Figures 105, 106), but they have a still larger and proportionally broader larval shell (5–6 mm high) with an expanded aperture and a more regular spiral arrangement of the minute tubercles on protoconch I (*cf.* Figures 108 and 142).

Most competent ranellid larvae have a radula similar

←

Explanation of Figures 9 to 16

Radulae of Tonnidae and Cassidae.

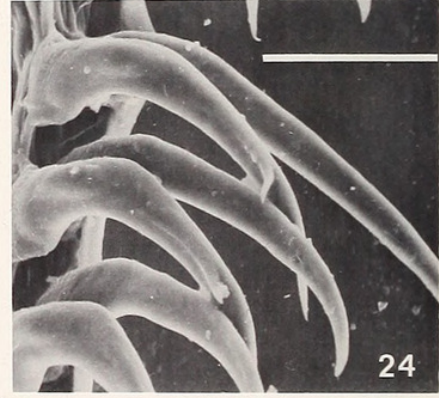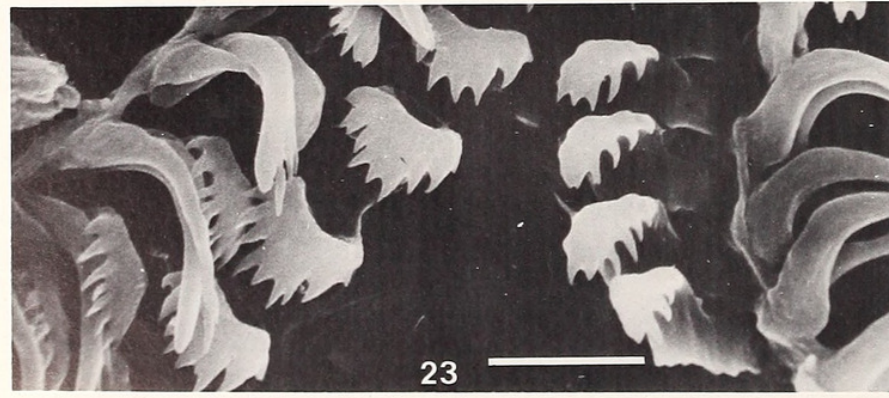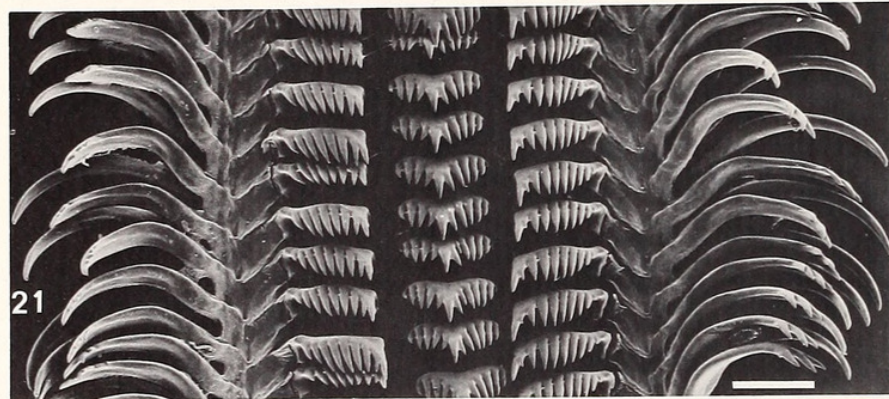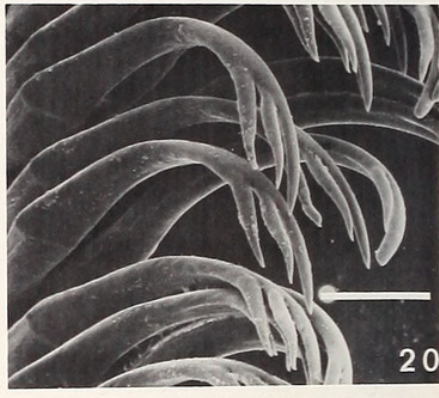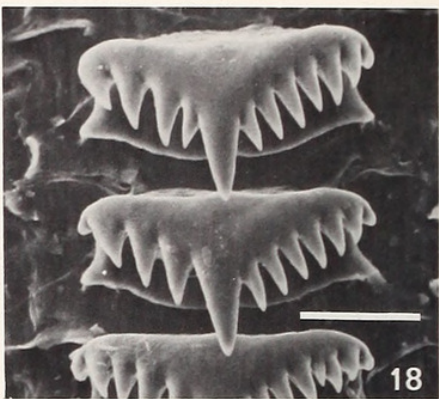Figures 9 and 10. *Tonna,* larva (off SE South Africa, SMNH). Scale lines 50 μm.

Figure 11. *Eudolium crosseanum* (the Azores, MNHN). Scale line 50 μm.

Figure 12. *Tonna* sp. (Madagascar, SMNH). Scale line 50 μm.

Figures 13 and 14. *Tonna allium* (Sumatra, SMNH). Scale lines 250 μm.

Figures 15 and 16. *Oocorys sulcata* (off S Portugal, MNHN). (For detail of marginal teeth, see Figure 24.) Scale lines 50 μm.

to adults of the species (Figures 30, 34, 36–38, 41, 42), but PELSENEER (1906:pl. 10, figs. 1–4) reported a species missing the radula and we noticed the same in a larva with a similar shell.

Subfamily PISANIANURINAE Warén & Bouchet, subfam. nov.

Diagnosis: Tonnoidea with a medium-sized *Buccinum*-like shell lacking varices, with poorly developed siphonal canal. Columella curved, contributing to giving the aperture a more rounded appearance. Operculum with corroded apical nucleus. Proboscis very short, broad, and muscular. Osphradium bipectinate with left row of leaflets less developed than inner ones.

Pisanianura Rovereto, 1899, has always been regarded as a buccinid genus, although FISCHER (1883) and LOCARD (1897) evidently had some doubts about it and compared *P. grimaldii* with *Oocorys*. We have had access to a few specimens preserved with soft parts and the anatomy (presented below) does not conform with a position in the Neogastropoda. The salivary glands have the typical structure that occurs only in Tonnoidea, and there is no deviation in other anatomical features from what is known in that superfamily. Therefore, we conclude that *Pisanianura* should be transferred to the Tonnoidea.

The shell morphology agrees well with the Ranellidae, except that it lacks varices (*i.e.,* it does not have periodical growth) and that the columella has a peculiar, curved shape. The anatomy is less useful for assigning *Pisanianura* to family because anatomical features, as far as they are known, are quite uniform throughout the superfamily and the differences so subtle and incompletely known that a detailed analysis can hardly be undertaken presently.

It is, however, obvious that the families are based on anatomical or shell morphological specializations, and because we are not suggesting anything better, we do not want to disturb this order. Therefore, we can exclude a position in the following families:

1. Ficidae. Salivary glands simple; proboscis pleurembolic, long and slender; buccal mass small and without large retractors.
2. Tonnidae. Foot large, operculum missing in adult;

distal part of proboscis suckerlike; jaw with a strong hook; shell globular and inflated.

3. Bursidae. Jaws reduced or absent. Varices present. Posterior canal strongly developed.
4. Personidae. Proboscis very long and slender, coiled when retracted. Varices present.
5. Cassidae. Central radular tooth broad and low. Shell globular with short canal.
6. **Laubierinidae**. Osphradium monopectinate. Shell with poorly developed siphonal canal.

The Ranellidae on the other hand consists of species with obviously less specialized or modified morphology and we can see no reason against a position therein. (This may give reason to suspect that the classification is based on grades rather than clades, with the Ranellidae to some extent constituting a less modified stock. This may be true, but this classification is practical and in the absence of detailed anatomical information that gives a better resolution, we prefer to keep it.)

The assignment of *Pisanianura* to subfamily offers more problems. In the Neptunellinae the proboscis is retracted by numerous small muscles attached to the sheath (HOUBRICK & FRETTER, 1969), whereas in *Pisanianura* there are two major muscles attached to the buccal mass and additional muscles are inconspicuous. Another difference from the Neptunellinae is the relative size of the buccal mass, which in the Neptunellinae is small in relation to the proboscis sheath, whereas in *Pisanianura* it is large (for drawings of this see, *e.g.*: PANCERI, 1869; HALLER, 1893; SIMROTH, 1896–1907; AMADRUT, 1898; HOUBRICK & FRETTER, 1969).

It is difficult to compare anatomically *Pisanianura* with the Ranellinae because few species of that group have been described anatomically (HALLER, 1893), but it seems that the species of Ranellinae closely resemble the Neptunellinae. Also the shell morphology contradicts a position in the Ranellinae. Beu (pers. comm.) considers this a uniform, monophyletic taxon, characterized by the neat alignment of the varices along the sides, separated by 180°.

We, therefore, supported by Beu (pers. comm.), consider *Pisanianura* a monophyletic group distinct from the Neptunellinae and Ranellinae, and erect a new subfamily for *Pisanianura,* the **Pisanianurinae**, in the Ranellidae.

←

Explanation of Figures 17 to 24

Radulae of Cassidae.

Figures 17, 18, and 22. *Galeodea echinophora* (Mediterranean, SMNH). Scale lines 100, 50, and 50 µm.

Figures 19 and 20. *Semicassis granulatum* (Mediterranean, SMNH). Scale lines 500 and 100 µm.

Figure 21. *Semicassis saburon* (West Africa, MNHN). Scale line 100 µm.

Figure 23. *Cypraecassis testiculus,* larva from plankton (Dana sta. 1286). Scale line 10 µm.

Figure 24. *Oocorys sulcata,* marginal teeth (off S Portugal, MNHN). (For a figure of the whole radula, see Figure 15.) Scale line 100 µm.

It is also possible that the **Pisanianurinae** should be considered a distinct family in the Tonnoidea, because it (1) lacks varices, which evidently is a primitive character in the group and (2) has the left row of leaflets in the osphradium less developed (equal size in all other tonnoids except the **Laubierinidae**). This view is supported by Beu (pers. comm.).

The subfamily Anochetinae Cossmann, 1901, was erected with *Pisanianura* as "type genus" (in the Buccinidae), but it is not based on a generic name and therefore has no nomenclatural status.

Pisanianura Rovereto, 1899

Anura BELLARDI, 1873:201 (not *Anura* Hodgson, 1841). Type species: *Murex inflatus* Brocchi, 1814, subsequent designation COSSMANN (1901:178).

Pisanianura ROVERETO, 1899:104, new name for *Anura* Bellardi, 1873 (preoccupied several times).

New synonyms:

Kaiparanura LAWS, 1944:309. Type species by original designation: *Phos spiralis* Marshall, 1918, Miocene, New Zealand (Figures 142–145).

Laminilabrum Kuroda & Habe *in* HABE, 1961, app.:13. Type species by original designation: *L. breviaxe* Kuroda & Habe, 1961, Recent, deep water, Japan.

Nawenia LADD, 1977:51. Type species by original designation: *N. bartholomewi* Ladd, 1977, Pliocene, west Pacific.

Remarks: *Laminilabrum* was described in the Trichotropidae, *Kaiparanura* in the Cominellidae (=Buccinidae), and *Nawenia* in the Buccinidae. These positions have not been questioned since. The soft parts of *Pisanianura* and *Laminilabrum* (described after the species, below) do not indicate differences other than of specific rank. The shells of all four genera have in common a multispiral protoconch with a large-meshed reticulate sculpture, a teleoconch without varices, and a stongly curved columella. They differ mainly in the degree of axial sculpture on the teleoconch, with *Laminilabrum* having no axial sculpture, *Nawenia* axial sculpture on the first two whorls, and *Pisanianura* and *Kaiparanura* on all the whorls. We regard these differences as of specific rank, and consequently treat the generic names as synonyms.

The type species of *Pisanianura* is a Pliocene fossil from northern Italy. Brocchi's type material has been figured

by ROSSI RONCHETTI (1955:201) and PINNA & SPEZIA (1978:pl. 34, fig. 3) and we have examined Pliocene material from Pradalbino, Bologna, Italy, kindly sent on loan by Mr. Della Bella (Figures 93, 125). The larval shell is multispiral with cancellate sculpture (Figure 93) and the teleoconch differs from the recent *P. grimaldii* mainly in the presence of a peripheral keel.

Beside the type species, BELLARDI (1873) included *Fusus borsoni* (Gené *in* Bellardi & Michelotti, 1840) in *Anura* and described *A. ovata, A. striata, A. craverii, A. pusilla,* and *A. sublaevis* from the Italian Miocene and Pliocene. We have not examined these species, some of which recently have been figured by FERRERO MORTARA *et al.* (1981:pl. 7). Judging from the figures it seems certain that the Miocene *A. craverii* belongs to *Pisanianura;* the status of the other species is more doubtful.

The genus is furthermore represented in the European Tertiary deposits by *Pisanianura aturensis* Peyrot, 1927, and *P. benoisti* Peyrot, 1927, from the Oligocene and Miocene of southwestern France respectively. (*P. degrangei* Peyrot, 1927, is probably a young cerithid related to *Gourmya* Fischer, 1884 [Cerithidae]; P. Lozouet, pers. comm.)

The type species of *Kaiparanura* is a Lower Miocene fossil from New Zealand; the teleoconch has a sculpture of coarse axial ribs. LAWS (1944) introduced this new genus because he had been misled by COSSMANN's (1901) description of the protoconch of *Pisanianura inflata,* which erroneously had been described as sculptured with weak spiral threads and with a smooth and depressed nucleus. This synonym was pointed out to us by Dr. A. Beu.

Finally, the type species of *Nawenia* is a Pliocene fossil from Fiji, similar to *Pisanianura breviaxe* but differing in having stronger axial sculpture on the first two teleoconch whorls.

Pisanianura is thus known from at least two Paleogene and two Neogene North Atlantic species, two Neogene South Pacific species, and two Recent (sub)tropical deepwater species. The taxonomy and distribution of the Recent species only are here treated in detail.

Pisanianura grimaldii (Dautzenberg, 1889)

(Figures 25, 26, 55, 68, 94, 95, 126, 127)

Hindsia grimaldii DAUTZENBERG, 1889:33, pl. 2, fig. 4.
Anura clathrata DAUTZENBERG & FISCHER, 1906:25, pl. 3, figs. 6–8. (New synonym.)

→

Explanation of Figures 25 to 32

Radulae of Ranellidae.

Figures 25 and 26. *Pisanianura grimaldii* (New Caledonia, MNHN). Scale lines 50 µm.

Figure 27. *Pisanianura breviaxe* (New Caledonia, MNHN). Scale line 50 µm.

Figure 28. *Sassia kampyla,* very young (New Zealand, NMNZ 9196). Scale line 25 µm.

Figure 29. *Sassia parkinsonia* (New South Wales, AMS C 50074). Scale line 50 µm.

Figure 30. *Ranella australasia,* planktonic larva (New South Wales, AMS C 147218). Scale line 25 µm.

Figures 31 and 32. *Ranella olearia* (the Azores, MNHN). Scale lines 200 and 100 µm.
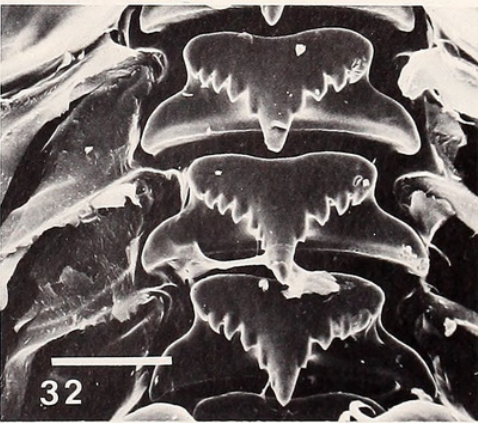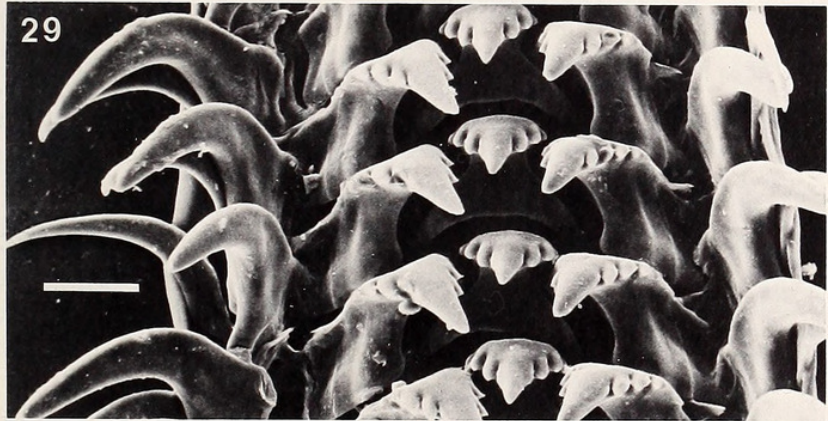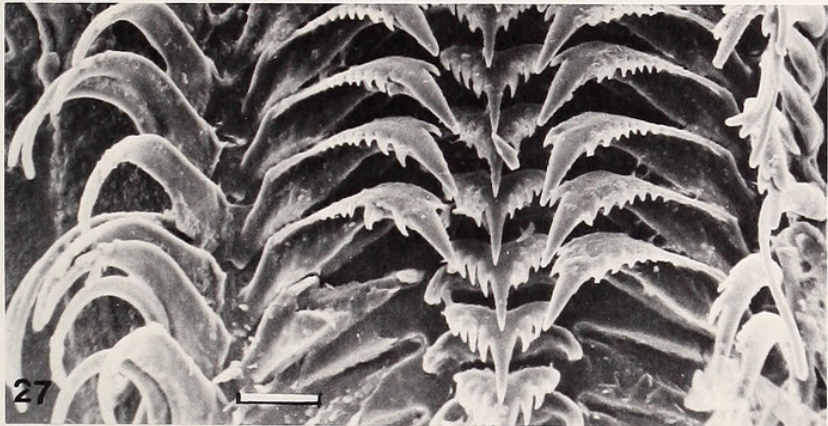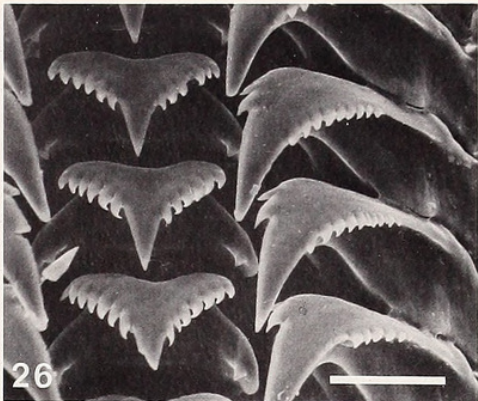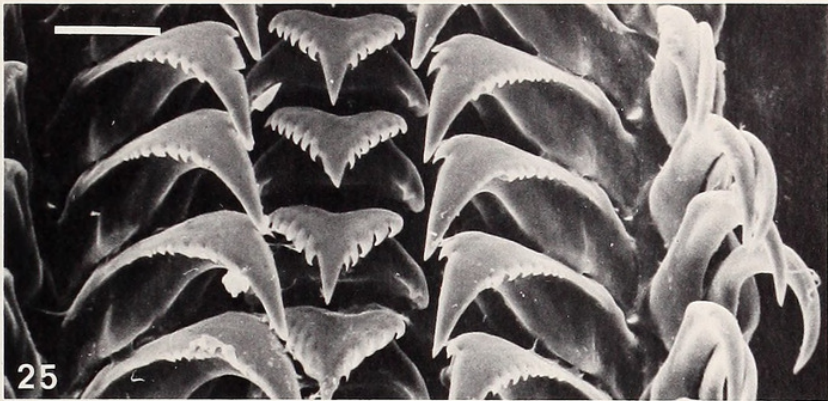
Type material: *Hindsia grimaldii,* holotype in MOM; *Anura clathrata,* lectotype here selected, the specimen figured by Dautzenberg & Fischer (figs. 6, 8), in MOM.

Type localities: *Hindsia grimaldii,* Monaco Expeditions sta. 112, 38°39'N, 28°06'W, 1287 m (Azores); *Anura clathrata,* Monaco Expeditions sta. 719, 39°11'N, 29°06'W, 1600 m (Azores).

Material examined: The type material and: Talisman Expedition 1883, dragage 72, 25°39'N, 15°38'W, 882 m (off S Morocco), 1 shell (LOCARD, 1897:323), MNHN; Monaco Expeditions sta. 1116, 31°43'N, 10°47'W, 2165 m (off Morocco), 1 shell, MOM; Monaco Expeditions sta. 1236, 32°43'N, 17°03'W, 1500 m (S of Madeira), 1 shell, MOM; R/V *Vauban* sta. CH22, 12°27'S, 40°10'E, 680–700 m (off N Mozambique), coll. A. Crosnier, 1 specimen, MNHN; Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (S New Caledonia), 2 specimens, MNHN.

Distribution: Only known from the material examined, northeastern Atlantic, southwestern Indian Ocean, and southwestern Pacific, in 700–2200 m.

Remarks: Despite the considerable geographical distribution, *Pisanianura grimaldii* shows little morphological variation, and we have no indication that the specimens from the northeastern Atlantic and the Indo-Pacific areas are not conspecific. Such a wide distribution seems to be well documented among the Tonnoidea (DELL & DANCE, 1963; SCHELTEMA, 1971, 1972; SCHELTEMA & WILLIAMS, 1983).

DAUTZENBERG & FISCHER (1906) enumerated several differences between *Pisanianura grimaldii* and *P. clathrata,* but direct comparison of the types proved them to be much smaller than appears from the text.

Pisanianura breviaxe (Kuroda & Habe, 1961)

(Figures 27, 123, 124, 153, 154)

Laminilabrum breviaxe Kuroda & Habe *in* HABE, 1961:36, app.:13, pl. 15, fig. 24 (Japanese edition); 1964:55, pl. 15, fig. 24 (English edition).

Type material: Lectotype, here selected, the shell figured

in references above, National Science Museum, Tokyo, Reg. No. 38611.

Type locality: Tosa Bay, Shikoku, Japan, 150–200 m.

Material examined: The lectotype; 1 paralectotype from Tosa Bay, USNM 658749; Biocal sta. DW36, 23°09'S, 167°11'E, 650–680 m, 1 specimen, MNHN; Biocal sta. CP52, 23°06'S, 167°47'E, 540–600 m (S New Caledonia), 1 specimen, MNHN; Fukura, Awaji, Japan, 1 shell, USNM 607197; Tosa Bay, Japan, 1 shell, USNM 617812; North of New Zealand, 28°39.5'S, 173°01'E, 837 m, 1 shell, A. Beu, NZGS (46 mm high).

Remarks: One of the New Caledonian specimens was found on a stem of a stalked crinoid, but no scar was visible and the animal fell off when preserved, which probably means that the association was fortuitous. There were no crinoid remains in the stomach of the dissected specimens.

Anatomy of *Pisanianura* (Figures 153, 154)

We have investigated the soft parts of the two recent species *Pisanianura grimaldii* and *P. breviaxe.* They are quite similar anatomically and we do not question that they belong to the same genus. The description below is based on *P. breviaxe;* differences from *P. grimaldii* are pointed out.

Most of the visceral mass was poorly preserved and not suitable for dissection. The foot is rather small and fleshy, with a conspicuous propodium, no median furrow on the ventral side, and no epipodial tentacles or flaps. The sides of the foot are strongly wrinkled close to the sole, with a constriction or furrow demarcating the smoother area above this furrow.

Operculum. See Figure 68.

The head is large and broad with two conical, blunt tentacles and large black eyes situated in lateral, basal bulges. There is no snout, only a thin membrane between the tentacles, over the proboscis opening. The presence of a penis is not known, because only females were examined.

The pallial cavity is rather deep, ca. 0.4 whorls, and spacious. The pallial edge is finely "crenulated," thick and muscular with a well-developed siphonal fold. A row of

→

Explanation of Figures 33 to 40

Radulae of Ranellidae.

Figure 33. *Cymatium muricinum* (Hawaii, SMNH). Scale line 50 μm.

Figure 34. *Cymatium* sp., larva (Dana sta. 3940:Ib). Scale line 10 μm.

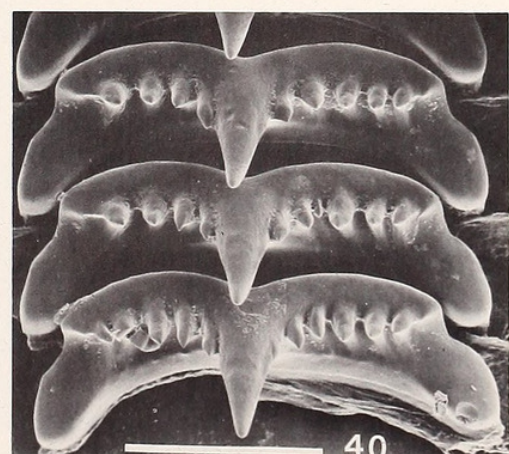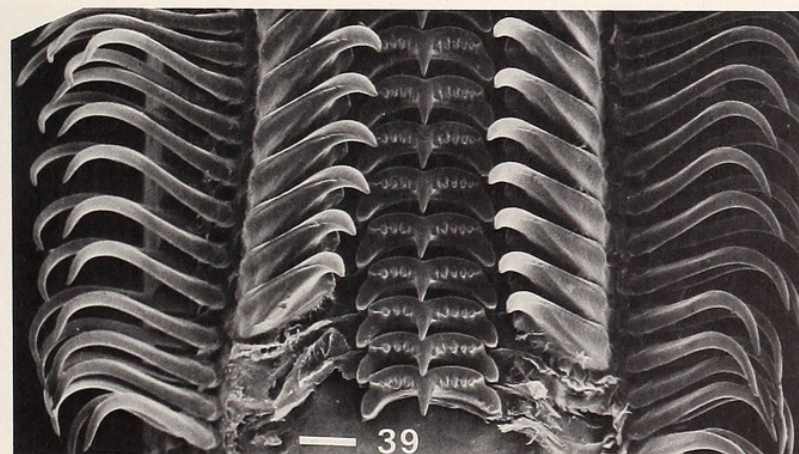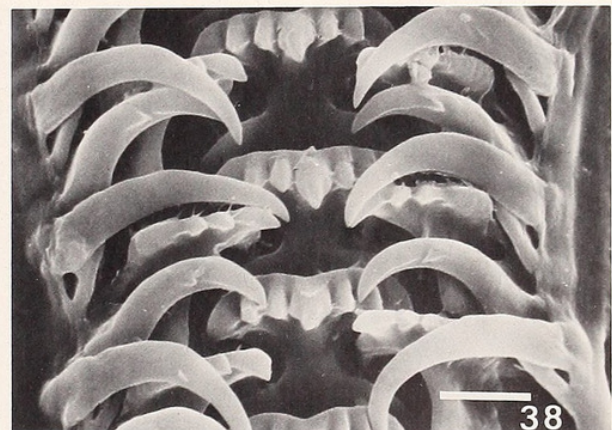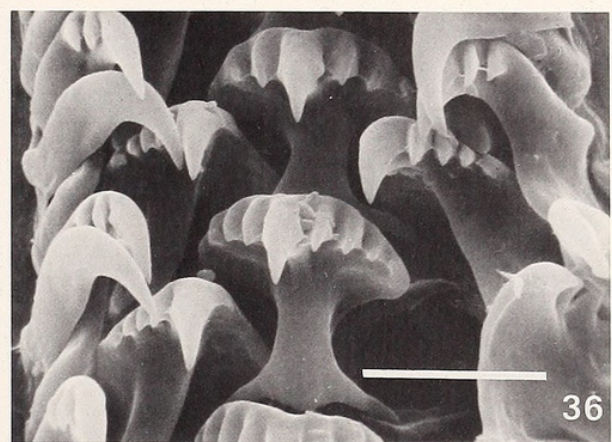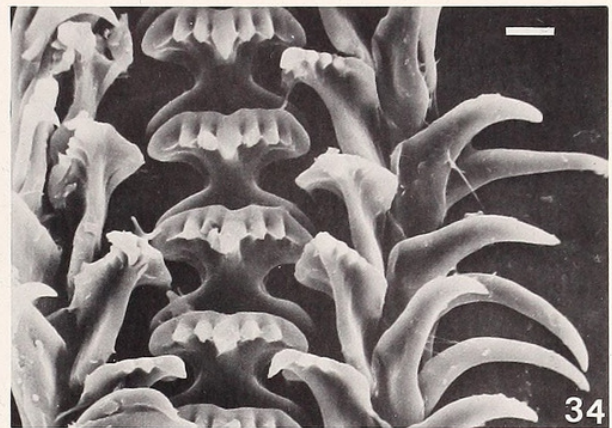Figure 35. *Cabestana cutacea* (Mediterranean, SMNH). Scale line 50 μm.

Figure 36. *Cymatium* sp., larva (Dana sta. 1253). Scale line 10 μm.

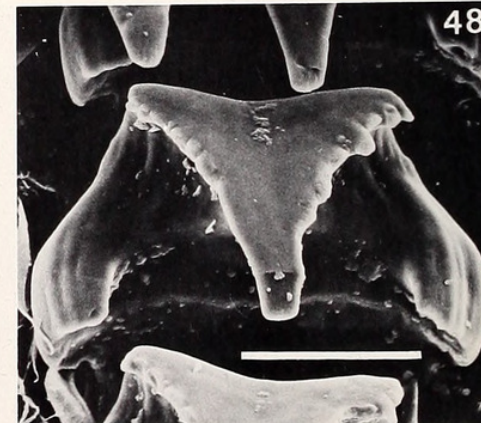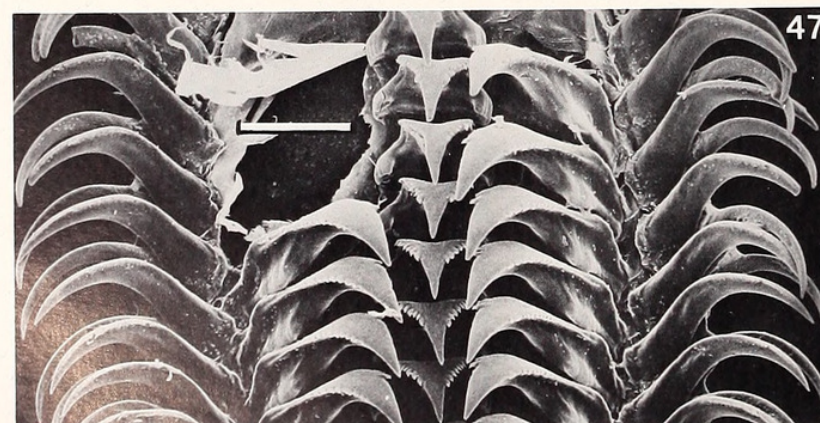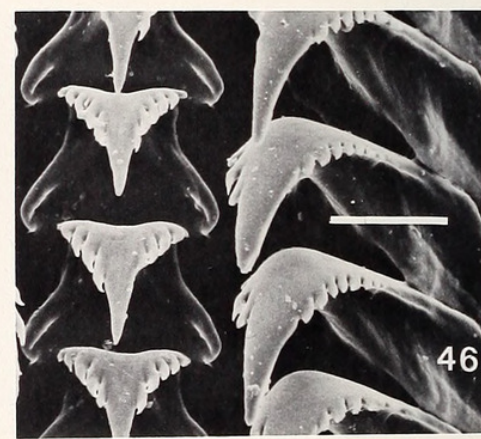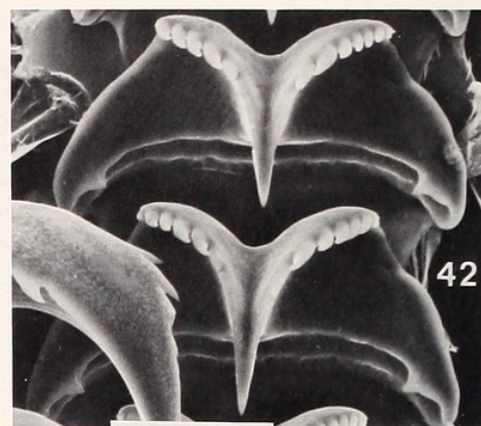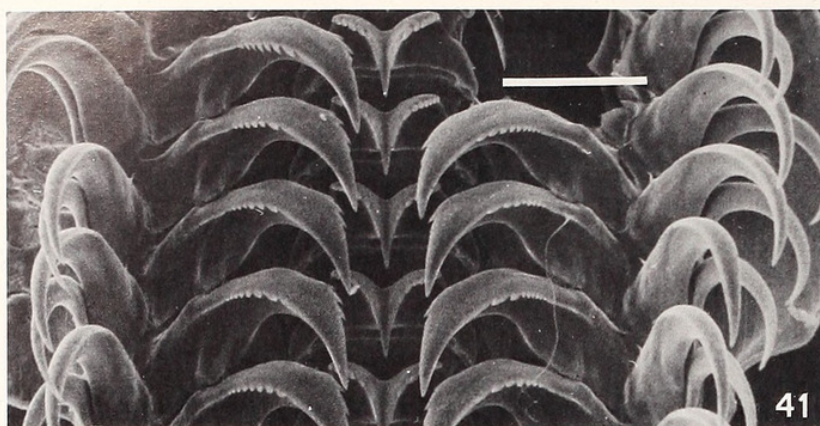Figure 37. *Charonia* sp., larva (Dana sta. 1247). Scale line 10 μm.

Figure 38. *Cymatium* sp., larva (Dana sta. 3940:Ib). Scale line 10 μm.

Figures 39 and 40. *Charonia lampas* (SW Spain, SMNH). Scale lines 250 μm.

about 12 small papillae, parallel to the pallial edge, is present just in front of the gill. The osphradium is bipectinate, with the left lamellae half as long as the inner ones, and is situated along the central half of the gill. Its surface area corresponds to ¼ of that of the gill. No fine details were discernible because of poor preservation and a cover of tough mucus. The gill consists of 60–80 tongue-shaped leaflets, about 4 times as high as broad, and occupies the whole distance from the bottom of the pallial cavity to just to the right of the siphon. The hypobranchial gland is well developed and forms large quantities of mucus when placed in water (at least in preserved specimens).

The pallial oviduct is sausage-shaped, 2.5 times as long as broad, with a simple lumen. It is closed and opens through a pore ⅙ of its length from the distal end. There are six simple sac-shaped receptacula seminis situated dorsally along the posterior part of the oviduct, joining to a common duct leading towards the ventral, posterior part of the oviduct.

The rectum is almost hidden in the wall of the oviduct and opens just in front of the oviduct.

The proboscis sheath is broad, short, and thin-walled. The buccal mass is cylindrical, about twice as long as broad, connected to the anterior part of the proboscis sheath by a system of numerous thin retractor muscles. Two large retractor muscles attach to the posterior, ventral part of the buccal mass, pass through the nerve ring and attach in the floor of the cephalo-pedal haemocoel. The salivary glands are large, of normal tonnoid type (which was described in more detail by DAY, 1969), with a smaller, solid-looking part close to the thick ducts, which pass through the nerve ring, follow the laterodorsal sides of the buccal mass and become narrow before opening into the buccal cavity. The openings were not found. The prismatic jaws (Figure 55) are roughly semicircular and situated well in front of the radula.

Radula. Central tooth with a large median cusp and 5 or 6 smaller lateral denticles on each side. Lateral tooth thin, with a major cusp, two inner denticles, and external serrations. Marginals undifferentiated, simple, claw-shaped. Figures 25–27.

The nervous system is highly concentrated; the pleural ganglia are indiscernibly fused to the cerebral ones, which are short, broad, flat, and united by a short and broad commissure. The pedal connectives are long and slender, about 1.5 times the width of the two cerebral ganglia together. The pedal commissure is short. The suboesophageal-pleural connective leaves the ventral side of the cerebro-pleural ganglion and runs along the floor of the body cavity to the suboesophageal ganglion, which is situated ventrally to the right cerebro-pleural ganglion, in the floor of the body cavity. A large nerve from the suboesophageal ganglion forms a zygoneury. The supraoesophageal ganglion is situated in a median position, between the two salivary glands; a zygoneury to the left cerebro-pleural ganglion was not verified.

Faecal pellets from the rectum contain sand, detritus, sponge spicules, remains of crustaceans, and calcareous particles or needles.

Pisanianura grimaldii differs mainly in having a more thin-walled proboscis sheath and a short, roughly globular buccal mass, a difference that, however, may be the result of contraction. Another difference is that the gill leaflets of *P. grimaldii* are semicircular instead of tongue-shaped.

Family LAUBIERINIDAE Warén & Bouchet, fam. nov.

(Figures 41–48, 56, 57, 71, 72, 96, 105–109, 128–131, 136–141, 155–162)

Diagnosis: Tonnoidea with a low-spired, fragile shell with poorly developed siphonal canal. Osphradium monopectinate, very large in the larva, of normal size in the adult. Proboscis short with large buccal mass.

Remarks: This new family is erected for the new genus *Laubierina*, and for a few species belonging to the genus *Akibumia* Kuroda & Habe, 1959, which previously have been classified (on the basis of shell and radula only) in the Trichotropidae. They differ from all other known Tonnoidea in having a fragile, more or less globular or weakly biconic, depressed shell with an indistinct siphonal canal, and in having a monopectinate osphradium (bipectinate in other adult Tonnoidea).

The shell provides little information about the relations of the **Laubierinidae** to other tonnoid families; unless typical salivary glands had been present, we should have been hesitant to include the **Laubierinidae** here. The radula, however, is similar to that of *Sassia* and *Pisanianura* in the Ranellidae. This is especially the case with the supporting ridge on the lateral tooth, which abuts the tooth in front, and the deeply excavated anterior base of the central tooth, which is equipped with basal denticles.

←

Explanation of Figures 41 to 48

Radulae of **Laubierinidae**.

Figures 41 and 42. **Laubierina** sp., recently metamorphosed young, (Mozambique Channel, MNHN). Scale lines 100 and 50 μm.

Figures 43 and 44. **Laubierina peregrinator** (Mozambique Channel, MNHN). Scale lines 100 μm.

Figure 45. *Akibumia orientalis* (Japan, USNM). Scale line 100 μm.

Figure 46. *Akibumia orientalis* (New South Wales, AMS). Scale line 100 μm.

Figures 47 and 48. *Akibumia schepmani* (Queensland, AMS). Scale lines 100 and 50 μm.

The fact that the osphradium deviates from all other adult tonnoids in being monopectinate may be connected with the morphological or functional causes that have led to its hypertrophy in the larva (see "laubierinid larva sp. 1," page 79). This hypertrophy is caused by some biological trait during the larval or early post-larval life, because adult and half-grown specimens have an osphradium of normal size, although it is also here monopectinate. This may result from the late larva or early post-larva needing to use the osphradium for localization or recognition of females (see discussion, page 81) or for finding a rare or restricted habitat for settlement.

There may be further anatomical criteria beside those of the osphradium, but the knowledge of variation among other Tonnoidea is not detailed enough to allow further comparisons. One difference, however, is that no sexually mature specimens of Tonnoidea without post-larval growth are known, despite numerous late larvae having been investigated (SIMROTH, 1911; and own examinations of *Tonna* spp., *Bursa* sp., *Semicassis* sp., *Cymatium* spp., *Sassia* sp., *Ranella australasia,* and *Argobuccinum pustulosum tumidum* (Dunker, 1862)).

Laubierina Warén & Bouchet, gen. nov.

Type species: *Laubierina peregrinator* Warén & Bouchet, sp. nov.

Diagnosis: Larval shell large, multispiral, with strong reticulate sculpture and expanded outer lip formed soon before metamorphosis. Teleoconch fragile, biconic, low-spired with short, shallow siphonal canal. Periphery with strong keel; weaker spiral cords and dense sharp incremental lines below and above keel.

Remarks: A search of the literature and museum collections has failed to reveal any described species even remotely similar to *Laubierina peregrinator.*

The genus is named after Dr. L. Laubier (IFREMER, Paris), to whom we owe great thanks for his support of our work on deep-sea mollusks.

Laubierina peregrinator Warén & Bouchet, sp. nov.

(Figures 43, 44, 128, 129, 159–161)

Type material: Holotype in MNHN.

Type locality: Walvis sta. 13, 32°18′S, 13°16′E, 3550 m, off SW Africa.

Material examined: The holotype and: Benthedi sta. CH13, 12°13′S, 46°40′E, 2300–2500 m (Mozambique Channel), 2 specimens, MNHN.

Distribution: Known only from the material listed, the southeastern Atlantic, and southwestern Indian oceans, between 2300 and 3550 m.

Description: Shell thin, fragile, strongly depressed, somewhat angular. Larval shell and first teleoconch whorls dissolved or damaged in holotype. In other specimens, larval shell of 3.5 brown, convex whorls with symmetrically reticulate sculpture of axial and spiral ribs of about same strength. Axial ribs straight on the uppermost whorls, becoming somewhat flexuous and prosocline on last two whorls. Four spiral ribs visible above suture in middle whorls, of which lower one partially concealed by last whorl. Total height of larval shell 5.5 mm, of which 3.6 mm visible above suture. Teleoconch with strong keel, situated just above suture and giving impression of strongly channelled suture. Whorls slightly convex above and below keel. Sculpture of sharp, regular incremental lines and stronger spiral ridges, 8 on first teleoconch whorl and 12 on last whorl, above keel; on body whorl below keel, ca. 20 ridges. Outer lip thin, regularly convex. Inner lip a thin parietal callus, forming narrow umbilicus. Siphonal canal short and open. Shell white, thin, covered by brownish beige periostracum with numerous axial lamellae parallel to growth lines.

Dimensions. Height of holotype 18.8 mm, diameter 19.5 mm, height of aperture 14.5 mm, breadth 11 mm.

Remarks: No gastropod known to us can be confused with *Laubierina peregrinator* except perhaps a young *Modulus* Gray, 1842 (Modulidae, Cerithioidea), but the species of that genus have a much more solid, strongly sculptured shell, and a columellar denticle.

The name *peregrinator* means migrant, alluding to a supposed long planktonic life.

In addition to the type species we have examined several young specimens and larval shells that we consider to belong to *Laubierina,* but they are too young to be determined accurately at the specific level.

←

Explanation of Figures 49 to 57

Jaws of Tonnoidea. Scale lines 250 μm.

Figure 49. *Tonna allium* (Sumatra, SMNH).

Figure 50. *Oocorys sulcata* (off Portugal, MNHN).

Figure 51. *Galeodea echinophora* (Mediterranean, SMNH).

Figure 52. *Argobuccinum pustulosum* (New Zealand, NMNZ).
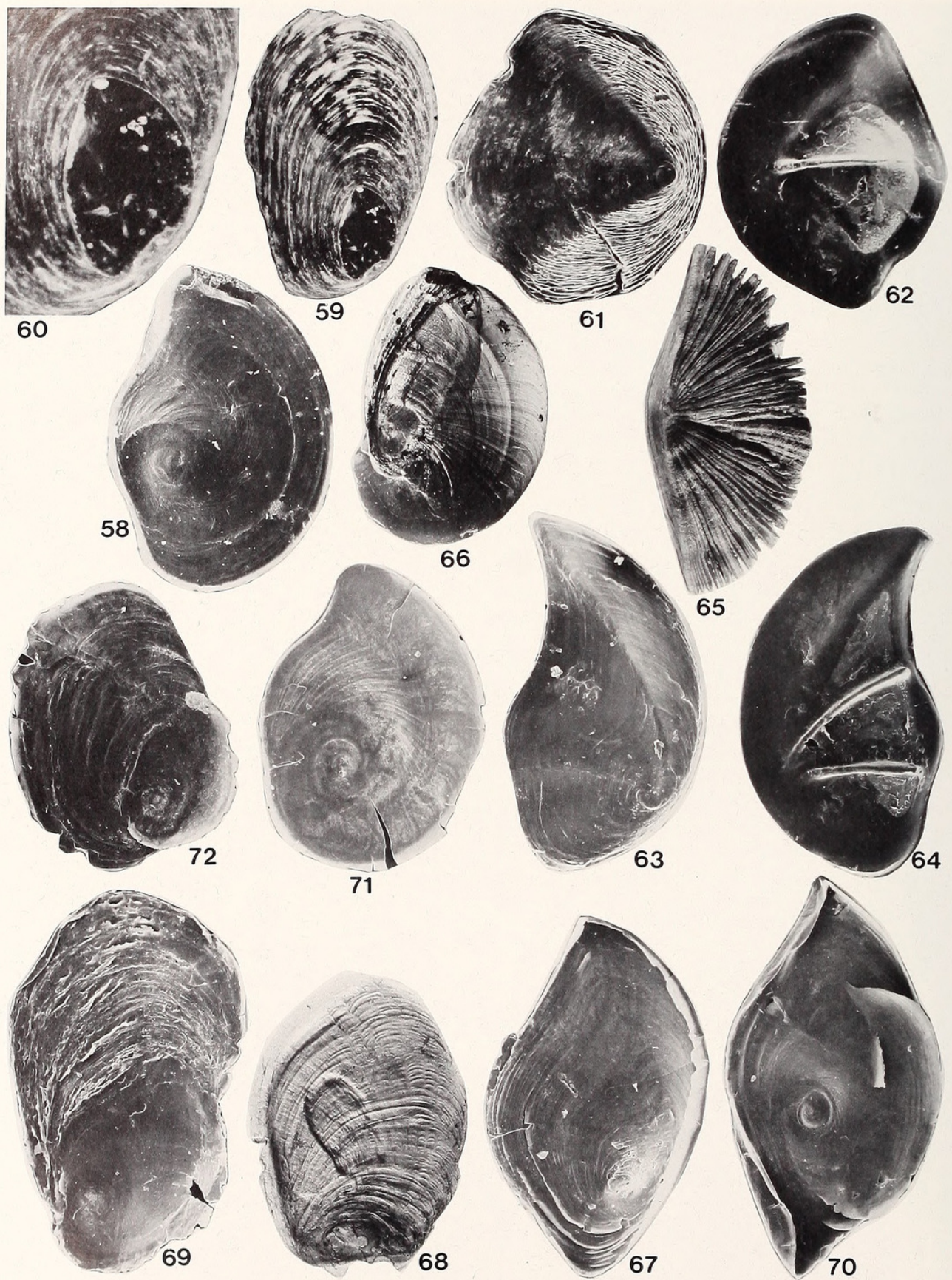
Figure 53. *Fusitriton magellanicus* (SMNH).

Figure 54. *Cabestana cutacea* (Sicily, SMNH).

Figure 55. *Pisanianura grimaldii* (New Caledonia, MNHN).

Figure 56. *Laubierina* sp., recently metamophosed benthic stage (Mozambique Channel, MNHN).

Figure 57. *Akibumia orientalis* (New South Wales, AMS).

60

59

61

62

58

66

65

72

71

63

64

69

68

67

70

Laubierina sp. A

R/V *Jean Charcot*, 1969, Madere sta. 13, 32°34′N, 17°07′W, 1970 m, 1 shell with ⅔ of a teleoconch whorl, MNHN. See Figure 106.

Cancap 2, Canaries, sta. 2.067, 27°58′N, 14°12′W, 2067 m, 2 larval shells, no post-larval growth, RMNH.

Biacores sta. 195, 37°56′N, 24°49.5′W, 1700–1776 m, 1 shell with no post-larval growth, MNHN. See Figures 105, 107, and 108.

Gulf of Mexico, 21°35′N, 96°54.6′W, 937 m, 1 young shell with ⅔ of a teleoconch whorl, MNHN. See Figures 130 and 131.

These specimens may represent a single species; the two specimens with post-larval growth certainly do.

Laubierina sp. B

Biocal sta. DW48, 23°00′S, 167°29′E, 775 m, 1 young shell with 1.4 post-larval whorls, MNHN. See Figure 96.

Off Broken Bay, New South Wales, 1000 m, 1 shell without post-larval growth, AMS C 150186.

NZOI sta. P941, 41°15.2′S, 167°07.2′E, 1457–1463 m, 1 shell without post-larval growth, NZOI.

These three specimens probably represent a third species, differing by the sculpture of protoconch II, which is more dense than in the North Atlantic specimens.

Anatomy of *Laubierina* (Figures 159–161)

The description is based on two females of ***Laubierina peregrinator***. The visceral mass was not extracted because of the risk of damaging the shell.

The foot is small, strongly contracted and muscular, blunt anteriorly, and rounded posteriorly. The propodium is well developed. The wrinkled, lower side of the foot is demarcated by a distinct furrow. There are no epipodial tentacles or folds.

Operculum. Similar to that of *Pisanianura* (Figure 68), but the apical part is more corroded.

The head is large and broad. The tentacles are slender and cylindrical with the eyes in large latero-basal bulges. The presence of a penis is not known, because only females were examined.

The pallial cavity is rather shallow, occupying 0.3 whorls. The pallial edge is simple and slightly thickened. A poorly developed siphon is indicated by the left corner of the pallial edge being more muscular. The osphradium is large, about ⅔ of the length of the gill, monopectinate, and has the leaflets directed towards the gill axis. The gill has about 85 low, triangular leaflets, and the free corner of each leaflet is drawn out into a tongue-shaped process.

The pallial oviduct is simple, closed, and sausage-shaped. A receptaculum seminis was not found. The rectum runs along the pallial oviduct in the pallial roof.

The proboscis sheath is short, thin-walled, and broad, and is evidently fully everted in one of the specimens (Figure 152). The buccal mass is large, globular, solid, and muscular. The salivary glands are large, of normal tonnoid type, and with the ducts passing through the nerve ring. The jaws were not examined.

Radula. Central tooth with a daggerlike median cusp and 8 or 9 lateral denticles. Lateral teeth fairly solid and robust and with 2 inner denticles, a median cusp, and a serrated external margin. Marginal teeth undifferentiated, simple, claw-shaped. Figures 43 and 44.

The anterior oesophagus is thin-walled and spacious; the posterior oesophagus forms an oesophageal gland, which is smaller than in other tonnoids.

The cerebral ganglia are large, connected by a slender commissure and well separated from the pleural ganglia, which are connected by short connectives. Two major nerve stems arise from the anterior edge of the cerebral ganglia and innervate the proboscis sheath; a third nerve leaves the anterior ventral side of the cerebral ganglion and forms the buccal connective; a fourth nerve leaving the lateral part leads to the tentacle. The suboesophageal ganglion is situated shortly to the right of behind and below the corresponding cerebral ganglion; the suboesophageal ganglion

---

←

Explanation of Figures 58 to 72

Opercula of Tonnoidea.

Figure 58. *Bursa* sp., larva (off Brasil, MNHN), max. diam. 1.33 mm.

Figures 59 and 60. *Bursa* sp., adult (Gilbert Id., SMNH), max. diam. 5.5 mm, and detail of the nucleus.

Figures 61 and 62. *Tonna* sp., larva (off SE South Africa), max. diam. 3.2 and 3.6 mm respectively.

Figures 63 and 64. *Semicassis* sp. aff. *granulatum,* larva (Dana sta. 1353), max. diam. 1.8 and 2.0 mm respectively.

Figure 65. *Semicassis granulatum* (no loc., SMNH), max. diam. 37 mm.

Figure 66. *Oocorys abyssorum* (SE Atlantic, MNHN), max. diam. 11.6 mm.

Figure 67. *Charonia* sp., larva (Dana sta. 1247:II), max. diam. 2.3 mm.

Figure 68. *Pisanianura grimaldii* (New Caledonia, MNHN), max. diam. 4.8 mm.
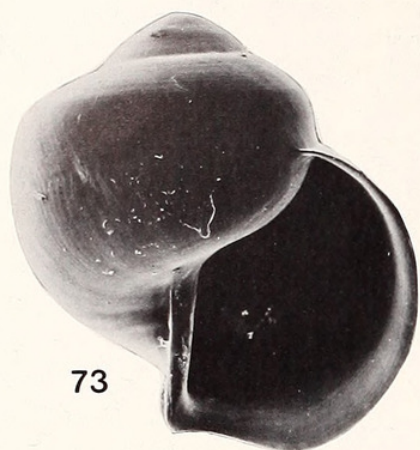
Figure 69. *Argobuccinum pustulosum* (New Zealand, NMNZ), very young specimen, max. diam. 3.7 mm.

Figure 70. *Cymatium* sp., larva (Dana sta. 3940:Ia), max. diam. 1.8 mm.
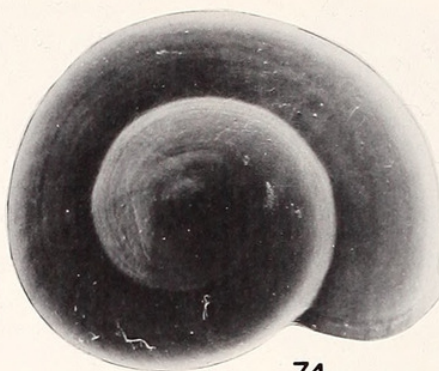
Figure 71. ***Laubierina*** sp., larva (Mozambique Channel, MNHN), max. diam. 2.9 mm.

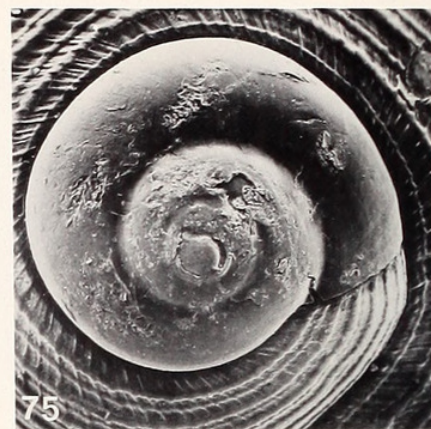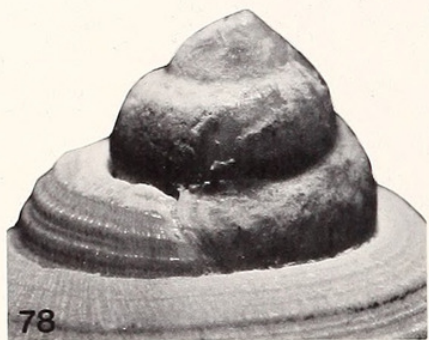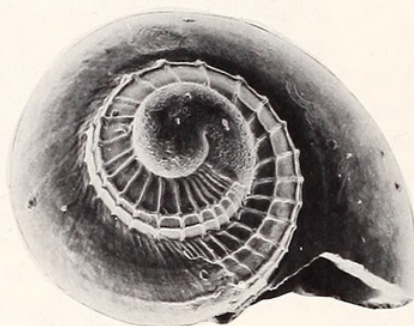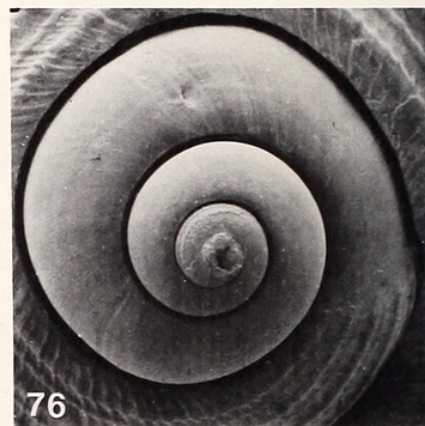Figure 72. *Akibumia orientalis* (Japan, USNM), max. diam. 2.9 mm.
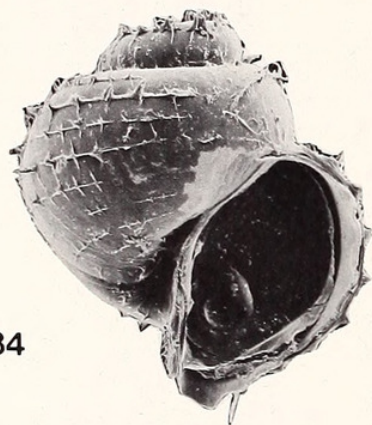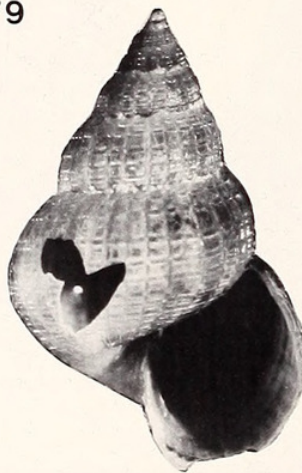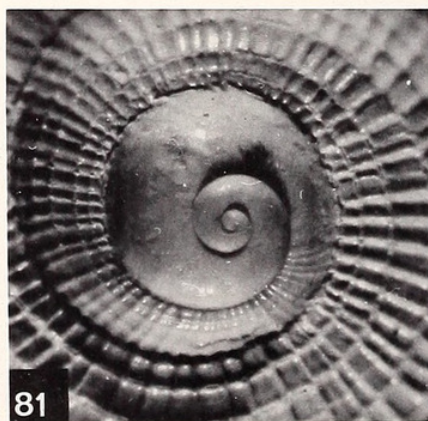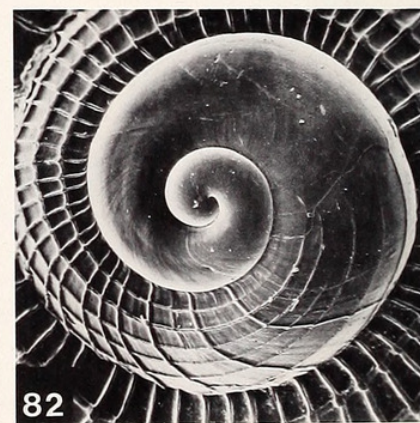
is connected to the right pleural ganglion by a solid nerve, and to the left pleural ganglion via a long slender connective. The supraoesophageal ganglion is situated to the left of and behind the left pleural ganglion; no zygoneury was found, only a connection to the right pleural ganglion. The buccal ganglia are large, situated ventrally at the posterior part of the buccal mass.

The rectum contained radiolarian tests, fragments of crustaceans, scattered sponge spicules, polychaete bristles, unidentified organic matter, scattered diatom skeletons and very few mineral particles.

Akibumia Kuroda & Habe, 1959

Akibumia Kuroda & Habe *in* KURODA, 1958:pl. 20, fig. 4. (Not available, ICZN Article 13a, e.)
Akibumia Kuroda & Habe *in* KURODA, 1959:317.

Type species: *Akibumia flexibilis* Kuroda & Habe, 1959, by monotypy.

Remarks: Beside the three species here included in the genus, HABE (1962) described *Akibumia reticulata* from Honshu, Japan. We have examined the holotype (Figure 83) and conclude that it is an epitoniid as also is indicated by it being found attached to coelenterates (HABE, 1962). It may provisionally be classified in *Epitonium*.

HABE (1962:74) also suggested that *Fossarus cereus* Watson, 1880, from 2580 m, off northeastern Australia is related to *Akibumia*. He had evidently overlooked PELSENEER's (1888) note on this species, based on the soft parts of the holotype, which Pelseneer placed in the "Pleurotomidae" (=Turridae). Pelseneer, however, did not describe the soft parts, but rather remarked only that the animal lacks eyes and "cervical lobes" (=the lobes between the tentacles?) and is therefore probably not a *Fossarus*. We have examined the holotype in BMNH and are uncertain about its systematic position as all the apical parts are corroded; however, the absence of eyes and presence

of a snout in WATSON's figure (1886:pl. 43, fig. 4d) are good indications that it does not belong to the **Laubierinidae**. GOLIKOV & STAROBOGATOV (1986) referred *Fossarus cereus* to *Conradia* (*Gottiana*) [*sic*!; should be *Gottonia* A. Adams, 1863], together with a new species, described as *Conradia minuta* Golikov & Starobogatov, 1986, from the North Pacific. Judging from the figure, the new species actually is a veliger larva of a ranellid, whereas both *Gottonia* and *Conradia* are based on type species belonging to the Trochoidea (Warén, examination of type material of the type species).

Akibumia orientalis (Schepman, 1909)

(Figures 45, 46, 57, 72, 136–138, 157, 158)

Trichotropis orientalis SCHEPMAN, 1909:176, pl. 12, fig. 2.

Type material: Holotype ZMA 3.02.041.

Type locality: Siboga Expedition sta. 211, 05°41'S, 120°46'E, 1158 m (Banda Sea).

Material examined: The holotype and: Albatross Expedition sta. 4919, 30°34'N, 129°19'E, Kagoshima Gulf, Japan, 805 m, 1 female, USNM 206835; 33°36'S, 152°05'E, 1106–1143 m (off Sydney, Australia) 1 female, AMS C 150223; Three Kings Rise, New Zealand, 31°19.9'S, 173°05.1'E, 1563–1570 m, 1 shell, NZOI.

Distribution: Known only from the material examined, western Pacific in 805–1570 m.

Remarks: *Akibumia orientalis* is well characterized by the strong spiral keels. We do not know any Recent gastropod that even resembles it. In addition to this, there is a distinct sculpture of strong, close-set incremental lines and finer spiral ribs, which is especially strong on the keels. The specimen from off Sydney was dissected and the results are presented below. The Japanese female had been dried and could not be used for detailed examination.

←

Explanation of Figures 73 to 84

Larval shells of Tonnidae and Ficidae.

Figures 73 and 74. *Tonna* sp., larvae (off SE South Africa, SMNH), height 4.5 mm, diameter 3.6 mm.

Figure 75. *Tonna galea,* apical view with complete protoconch (Malta, SMNH), diameter of the larval shell 3.2 mm.

Figure 76. *Tonna galea,* apical view; the periostracum of the protoconch has been dissolved in bleach and the calcareous internal mould of the protoconch, with disjunct whorls, is now visible (Brasil, SMNH), diameter of the larval shell 3.3 mm.

Figure 77. Same specimen as Figure 76, close-up view of protoconch I and early part of protoconch II, width of photo 1.0 mm.

Figure 78. *Eudolium crosseanum,* side view of apex with complete protoconch (Azores, MNHN), height of larval shell 3.1 mm.

Figure 79. Same specimen as Figure 78, protoconch I and initial part of protoconch II; the periostracum has been removed in bleach; max. diam. 1.0 mm.

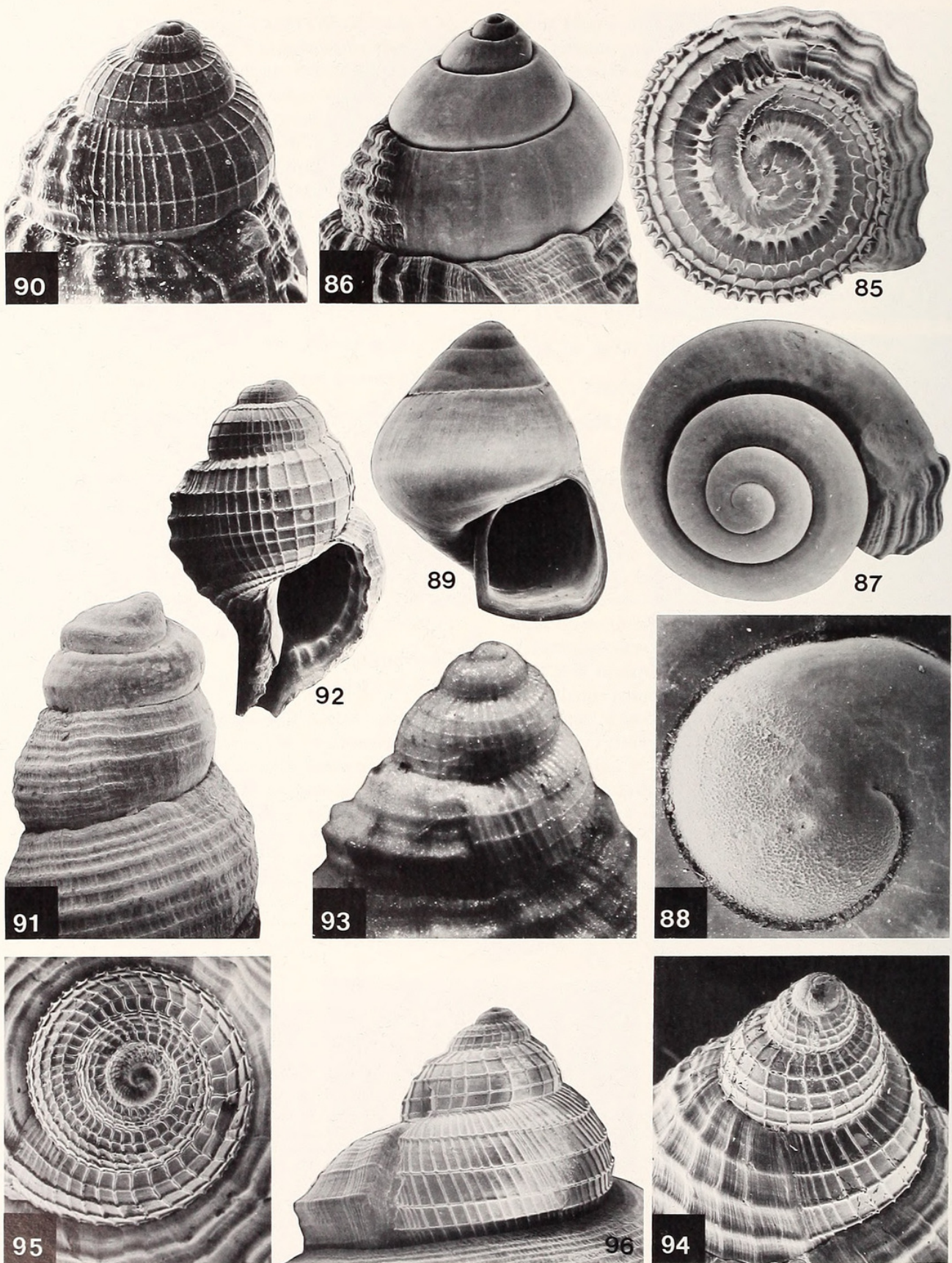Figure 80. *Ficus communis* (Florida, SMNH). Scale line 250 μm.

Figure 81. *Ficus conditus* (Lower Miocene, France), diameter of the protoconch 1.8 mm.

Figure 82. *Ficus* sp. (Philippines, MNHN), diameter of the protoconch 2.2 mm.

Figure 83. *Akibumia reticulata,* holotype, height 7.55 mm.

Figure 84. *Distorsio* sp. (Philippines, MNHN), larval shell with traces of post-larval growth, diameter 1.2 mm.

Akibumia flexibilis Kuroda & Habe, 1959

(Figures 109, 140, 141)

Akibumia flexibilis Kuroda & Habe *in* KURODA, 1958:pl. 20, fig. 4 (not available, ICZN Article 13a, e).
Akibumia flexibilis Kuroda & Habe *in* KURODA, 1959:317.

Type material: Two syntypes in Kuroda's private collection; the shell figured as "holotype" by ANONYMOUS, 1986: pl. 17, figs. 3–5, is not to be considered a lectotype according to ICZN art. 74(b) because a nomenclatural act published anonymously after 1950 is not available (ICZN art. 14).

Type locality: "Deep bottom off Tosa, Shikoku, Japan."

Material examined: The type material and: 06°52′S, 39°54′E, off Tanzania, 1 shell, USNM 718939; Tosa, Japan, 270 m, 1 shell, ANSP 234711.

Remarks: We are not convinced that this species can be distinguished from *Akibumia schepmani,* although the spire gives an impression of being lower in that species. This difference is probably caused by the larval shell being almost completely eroded away in the holotype of *A. schepmani.* The lack of material, in combination with the presumed wide distribution, makes synonymization unsafe and we have preferred to keep the two species separate.

Akibumia schepmani Habe, 1962

(Figures 47, 48, 139, 155, 156)

Akibumia schepmani HABE, 1962:74.

Type material: Holotype ZMA 3.62.001.

Type locality: Siboga Expedition sta. 211, 05°41′S, 120°46′E, 1158 m (Banda Sea).

Material examined: The holotype and: 28°01′S, 153°59′E, 550 m (off Gold Coast, southern Queensland), coll. K. Graham, 1 specimen, AMS 150192.

Distribution: Known only from the two specimens examined.

Remarks: The name *Akibumia schepmani* is based on SCHEPMAN's (1909:177, pl. 12, fig. 3; pl. 16, fig. 3) description and figures of an unnamed gastropod of doubtful family position. Schepman had two specimens; we have regarded the figured shell as the holotype; the second specimen was probably destroyed by Schepman when he extracted the radula.

We find it remarkable that the Siboga Expedition obtained two species of this otherwise rare genus in the same dredge-haul, but other gastropods obtained in the same haul give no indication of any special character of the biotope.

Anatomy of *Akibumia* (Figures 155–158)

The description is based on *Akibumia orientalis*; the differences from *A. schepmani* are pointed out below. Most of the visceral mass was poorly preserved and unsuitable for dissection, but it consists of about 3.5 whorls, mainly occupied by the ovary.

The foot is small, strongly contracted, and muscular, without a median furrow or any epipodial appendages, but with a distinct propodium. The sides of the foot are strongly wrinkled close to the ventral edge and with a furrow demarcating this area from the smoother, higher parts.

Operculum. Fairly solid, yellowish brown, fan-shaped, with the larval operculum remaining apically. Figure 72.

The head is large and broad with short, stout (contracted) tentacles with the eyes situated in large latero-basal bulges. The snout is short and inconspicuous, and consists mainly of a thin membrane between the tentacles, covering the proboscis opening. The penis is not known, as only females were examined.

←

Explanation of Figures 85 to 96

Larval shells of Ranellidae and **Laubierinidae**.

Figure 85. *Fusitriton magellanicus* (New Zealand, NMNZ), young post-larva with periostracum of the larval shell intact, diameter 3.2 mm.

Figure 86. *Argobuccinum pustulosum* (New Zealand, NMNZ), internal mould of larval shell obtained by removal of the periostracum (see text for explanation); note the slightly disjunct whorls; width of photo 4.2 mm.

Figure 87. *Ranella olearia* (SW Europe, MNHN), very young post-larva with internal mould of larval shell with disjunct whorls, diameter 3.6 mm.

Figure 88. Same specimen as Figure 87; close-up view of protoconch I, diameter 560 μm.

Figure 89. *Ranella australasia* (plankton off Sydney, AMS), height 3.8 mm.

Figure 90. *Sassia raulini* (Miocene of France), width of photo 3.4 mm.

Figure 91. *Sassia textilis* (Miocene of Victoria, AMS), height 4.3 mm.

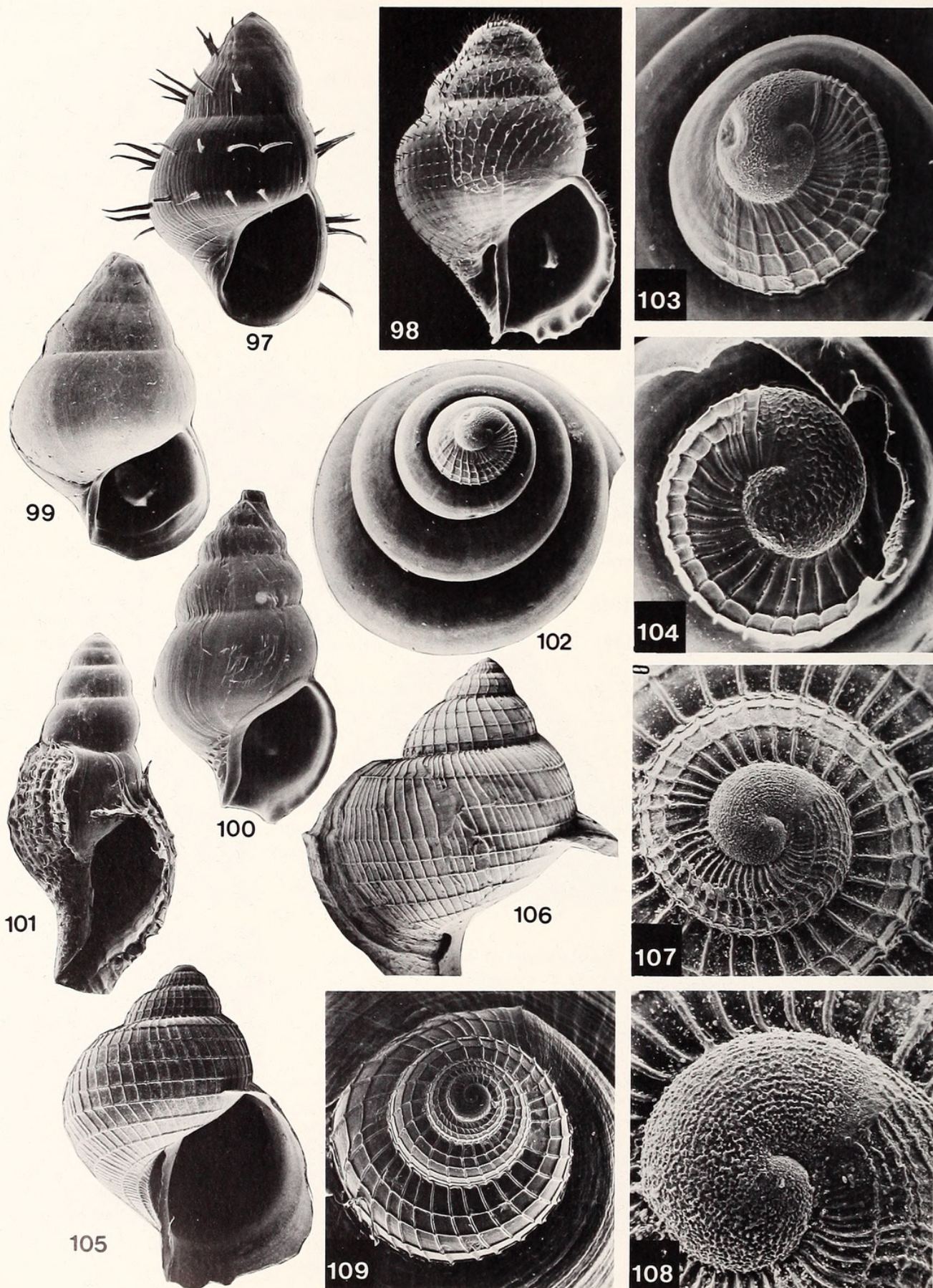Figure 92. *Sassia remensa* (Queensland, AMS), height 3.2 mm.

Figure 93. *Pisanianura inflata* (Pliocene of Italy), height of the protoconch 2.2 mm.

Figure 94. *Pisanianura grimaldii* (Madagascar, MNHN), width of photo 3.4 mm.

Figure 95. *Pisanianura grimaldii* (New Caledonia, MNHN), diameter of larval shell 2.3 mm.

Figure 96. **Laubierina** sp. (New Caledonia, MNHN), height of larval shell 3.0 mm.

The pallial cavity is shallow, occupying 0.25 whorls, and spacious. The pallial edge is slightly thickened in *Akibumia orientalis*, with indistinct internal crenulation. The right corner of the pallial edge (in *A. schepmani* and *A. orientalis*, both females) is equipped with a thin, muscular skin-fold, hanging down as a protective curtain, just in front of the pallial oviduct and the rectum. This skin-fold starts 2 mm in front of the left edge of the anus (0.5 mm behind the pallial edge) from the roof, grows higher towards the right, to a height of about 2 mm just in front of the right edge of the oviduct, where it forms a 90° turn backwards and becomes gradually lower. The siphonal canal is only indistinctly indicated by a more muscular area around the left corner of the pallial edge. The osphradium is monopectinate, with about 40 leaflets covering most of the area between its axis and the gill axis. The axis of the osphradium runs parallel to the central part of the gill axis and is half as long. The gill occupies almost the entire distance from the innermost part of the pallial cavity to the pallial edge and consists of about 75 low, triangular leaflets of which the free corner is drawn out into a tongue-shaped projection, measuring 2.0 × 1.2 mm (high) in the central parts of the gill.

The pallial oviduct is closed and sausage-shaped, 1.5 times as long as broad and with a simple flat cavity. The opening was not found. A group of seven simple, sac-shaped receptacula seminis is situated just behind the proximal end of the oviduct, and the receptacula open to a single duct leading towards the oviduct. The rectum runs along the left side of the oviduct and opens on a small papilla, just behind the distal end of the oviduct.

The proboscis sheath is short and thick-walled. The buccal mass is long and cylindrical, almost twice as long as broad, and is connected to the proboscis sheath along its sides by numerous fine muscle fibres. A large, solid muscle is attached to each posterior side and connects to the floor of the body cavity shortly behind the nerve ring. (These seem to be the main muscles for retraction of the proboscis.) The salivary glands are large and occupy most of the space of the body cavity behind the nerve ring. They

consist of a large, distal, almost transparent part (accessory salivary gland) and a more solid, proximal part. The right gland is situated in front of and above the left one. The ducts are thick-walled, pass through the nerve ring, run dorsally on the buccal mass, and open rather far forwards. The anterior oesophagus is spacious and thin-walled and leads to a large oesophageal gland. The jaws (Figure 57) are large, rounded, and situated well in front of the radula.

Radula. Short, 40–50 transversal rows. Figures 45–48.

The nervous system is highly concentrated. The pleural ganglia are visible as bulges from the cerebral ones. The cerebral commissure is slightly more slender than the ganglia it connects. Three major nerves emerge from the anterior edge of the cerebral ganglia and innervate the proboscis; the most lateral one of these leads to the buccal mass, the inner one innervates the area around the true mouth, and the central one innervates the proboscis sheath. One large lateral nerve from each cerebral ganglion innervates the corresponding tentacle. The suboesophageal ganglion is situated shortly behind and below the right cerebral ganglion and is connected to the two pleural ganglia. The supraoesophageal ganglion is situated further posteriorly in the cavity, and is connected to the right pleural ganglion via a long connective and to the left pleural ganglion via a zygoneury to the osphradial nerve.

Akibumia schepmani differs mainly in having a slightly deeper pallial cavity, occupying about 0.4 whorls; in having long and slender tentacles; in having about 75 leaflets in the gill and 45 in the osphradium; and by having only five receptacula seminis and a more slender pallial oviduct, about 2.5 times as long as broad. The only specimen available was a female.

Undetermined Laubierinid Larvae

Larva Species 1

(Figures 41, 42, 56, 71, 162)

Material examined: One dried specimen with crushed shell in sample of benthic material, Benthedi 1977 sta. 87,

---

←

Explanation of Figures 97 to 109

Larval shells of Ranellidae and **Laubierinidae**.

Figure 97. *Cymatium* sp., young larva (Dana sta. 1337), height 1.85 mm.

Figure 98. *Cymatium* sp., larva (Dana sta. 1253), height 3.6 mm.

Figure 99. *Charonia* sp., larva (Dana sta. 1247), height 4.2 mm.

Figure 100. *Cymatium* sp., larva (Dana sta. 3940:Ia), height 4.1 mm.

Figure 101. *Cymatium problematicum* (Canaries, SMNH), young post-larva, height 5.6 mm.

Figures 102 and 103. *Cymatium* sp. (Madeira, SMNH), post-metamorphic larva; the periostracum has been removed; max. diam. 1.85 mm, diameter of protoconch I, 315 µm.

Figure 104. *Cymatium* sp., same larva as Figure 98; the larval shell is seen from inside and shows the periostracal mould of the sculpture of the young calcified larval shell; breadth of field 0.5 mm.

Figures 105, 107, and 108. *Laubierina* sp. (Azores, MNHN), larval shell, height 3.6 mm; detail of the protoconch I and initial part of protoconch II; breadth of field 0.75 mm (Figure 107), diameter of protoconch I, 300 µm (Figure 108).

Figure 106. *Laubierina* sp. (Madeira, MNHN), young benthic specimen with less that one post-larval whorl, height of the protoconch 5.4 mm.

Figure 109. *Akibumia flexibilis* (Japan, ANSP), width of photo 3.1 mm.
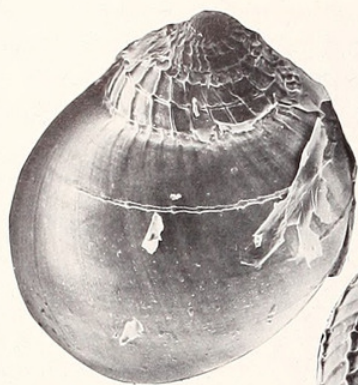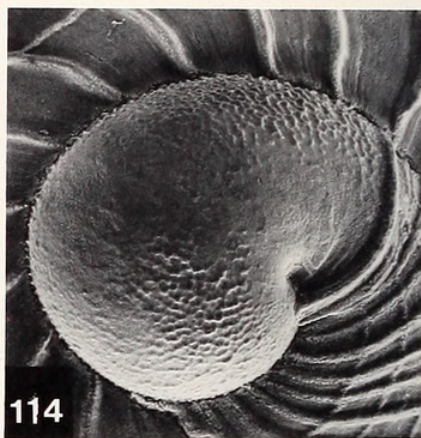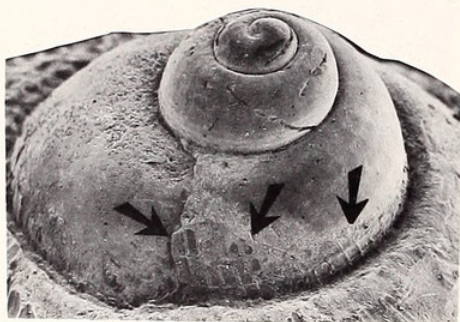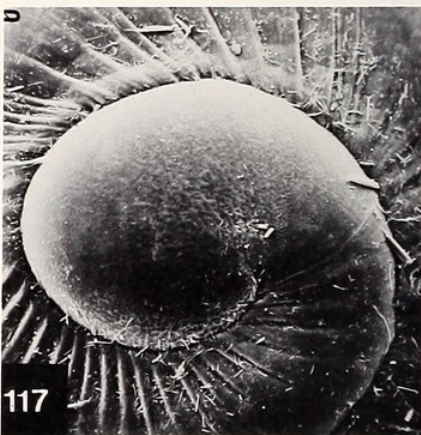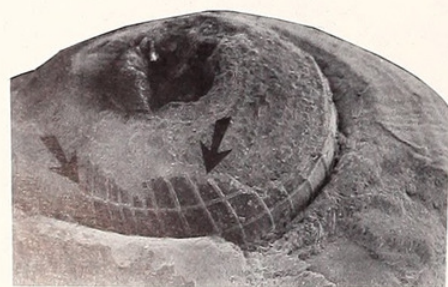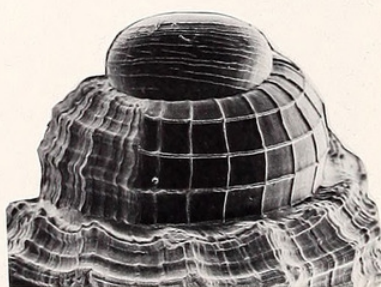
11°44'S, 47°35'E, 3716 m (northern Mozambique Channel), MNHN.
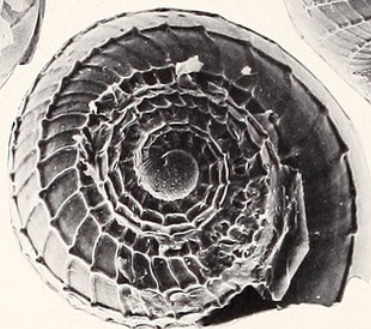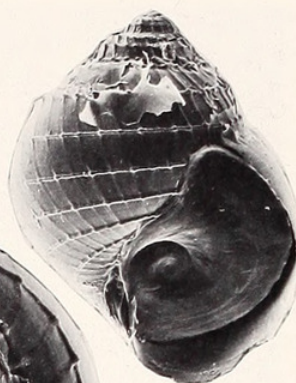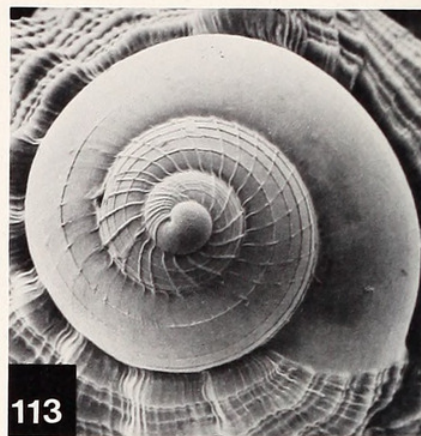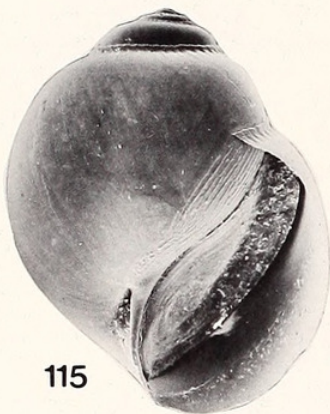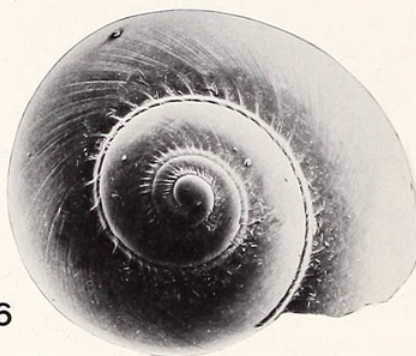
Remarks: This single specimen was badly broken, and the generic identification is uncertain. Several shell fragments were still attached to the soft parts, showing a sculpture of square and rectangular surfaces defined by sharp ridges. The radula (Figures 41, 42), which is similar to that of adult **Laubierina** and *Akibumia,* has a small denticle at the lateral part of the base of the central tooth, similar to *Pisanianura.* However, for several other Tonnoidea, minor changes in radular morphology may take place during the growth from larva to adult.

We consider that the characteristic protoconch sculpture and the size, at least 5 mm, in combination with the monopectinate osphradium, the radula, and the operculum, make the identification reliable to family level.

Description: The larva (Figure 162) was soaked in 1% formalin with detergent added.

The foot is large, flat, blunt anteriorly, and rounded posteriorly, with a wrinkled zone just above the sole and a demarcating furrow above the wrinkled zone. The propodium is well developed. There are no pedal appendages.

Operculum. See Figure 71.

The head is large and broad with small, cylindrical tentacles. The huge eyes, twice the diameter of the tentacles, are attached laterally to the basal part of the tentacle. There is no snout, only a thin membrane between the tentacles covering the proboscis opening. The penis is long, simply finger-shaped and slender, reaching all the way back to the bottom of the pallial cavity, where it curves 180° and lies folded double for ¼ of its length. The pallial seminal furrow is open and runs along the right side of the pallial cavity to the left, bordered by a swollen rim, possibly a prostate; the furrow then curves to the left and reaches the penis, where it continues open along the dorsal side, up to the tip.

The pallial edge is simple and muscular, with a thickened left corner equipped with two ridges, which possibly function as a siphon. The osphradium is huge and mono-pectinate, with about 35 leaflets that are twice as high as broad and directed towards the gill. They cover ⅝ of the distance from the bottom of the pallial cavity to the pallial edge and cover about ⅔ of the total inner surface of the pallial skirt. The gill is much smaller, is situated along the posterior ⅓ of the osphradium, and corresponds to ⅓ of its width. The gill has about 10 low, triangular leaflets. The rectum opens far back in the pallial cavity, at about ⅓ of its depth from the pallial edge.

The buccal mass was partly everted and shows the true mouth with a pair of lateral jaws and a large glandular-looking bulge at each side of the mouth. These are presumed to be reduced velar lobes.

Radula. See Figures 41 and 42.

The visceral mass consists of 1.75 whorls, of which the stomach, kidney, and heart occupy the basal 0.2 whorls and the digestive gland the following 0.5. The remaining part is completely filled by the testis and the vesicula seminalis.

Larva Species 2

Material examined: Discovery sta. 10141, 24°34'N, 19°41'W, 3460–3470 m, 1 young specimen without post-larval growth, 4.2 mm.

Description: The head-foot is similar to that of the larva described above, except that the specimen lacks developed reproductive organs. Glandular pads similar to those in Figure 162, supposed to be the remains of the velum, were present. Osphradium monopectinate.

The rectum and the stomach contained some mineral particles and unidentified organic matter.

Reproductive Biology of the **Laubierinidae**

The laubierinid larva sp. 1, taken in a bottom sample from 3716 m depth, off Madagascar, is remarkable for the presence of a penis and a visceral mass full of sperm. This indicates that the specimen was ready to mate before post-larval growth had begun. This has not been known for tonnoid or other meroplanktonic gastropod larvae.

←

Explanation of Figures 110 to 122

Larval shells of Ranellidae, Bursidae, and Cassidae.

Figures 110 to 112. *Bursa* sp., young larvae (off Brasil, MNHN), heights 1.3 mm and 1.45 mm, and diameter 1.8 mm.

Figures 113 and 114. *Bufonaria marginata* (West Africa, MNHN), protoconch in apical view; diameter of protoconch II, 2.4 mm; of protoconch I, 330 μm.

Figures 115 to 117. *Cypraecassis testiculus* (Dana sta. 1286), height 3.1 mm (Figure 115), diameter 2.4 mm (Figure 116), diameter of protoconch I, 270 μm (Figure 117).

Figure 118. *Oocorys umbilicata,* apex, width of picture 2.4 mm. Note remains of protoconch II, indicated by arrows.

Figure 119. *Oocorys bartschi,* apex, width of picture 1.2 mm. Note remains of sculpture of protoconch II, indicated by arrows.

Figure 120. *Galeodea echinophora,* apex, height of larval shell 1.0 mm.

Figure 121. *Distorsionella lewisi,* apex, height of larval shell 1.1 mm.

Figure 122. *Distorsio* sp. (New Caledonia, MNHN), diameter of larval shell 1.07 mm.
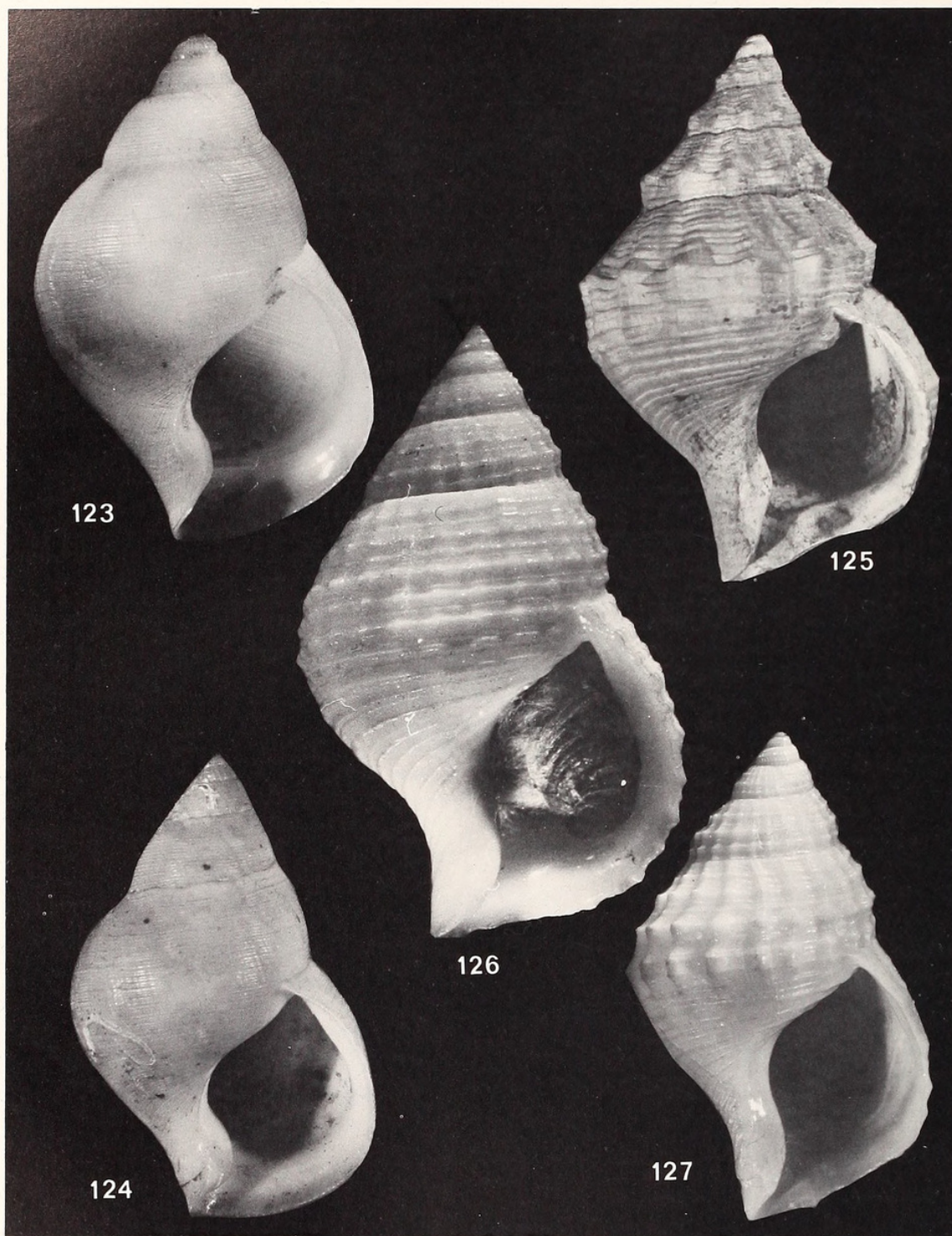
Explanation of Figures 123 to 127

Pisanianura species.

Figure 123. *P. breviaxe* (New Caledonia), 15.5 mm.

Figure 124. *P. breviaxe,* holotype, 20.7 mm.

Figure 125. *P. inflata* (Pliocene, Italy), 24.4 mm.

Figure 126. *P. grimaldii,* holotype, 27.6 mm.

Figure 127. *P. grimaldii* (off Madagascar, MNHN), 23.0 mm.

In connection with this sexually mature male larva, it is of interest to note that out of the six adult specimens of **Laubierinidae** that have been examined, all proved to be females (probability 1/64 assuming a 1:1 sex ratio). This gives reason to speculate that the species of **Laubierinidae** are protandrous hermaphrodites with neotenic males. No structure was found in the larva that could be a receptaculum seminis or bursa copulatrix, and therefore it seems unlikely that copulation takes place in the planktonic phase.

Family FICIDAE Meek, 1864

(Figures 1–4, 80–82, 132–135, 148, 149)

There is no good description of the anatomy of *Ficus* Röding, 1798, but scattered information is present in several papers, and does not conform well with a position in the Tonnoidea. The animal has been figured several times (ÖRSTED, 1850; H. & A. ADAMS, 1853–1858; KEEN, 1971; WILSON & GILLETT, 1971; ARAKAWA & HAYASHI, 1972). The pallial edge is greatly enlarged and forms a fold surrounding the shell, much more so in *F. ventricosa* (Sowerby, 1825), where it is so wide that it extends over the foot; at the same time the foot is reduced (ÖRSTED, 1850), thus giving a configuration similar to *Lamellaria* Montagu, 1815 (Lamellarioidea). The head part of the head-foot is small and slender, more so than in the Bursidae, where it is the smallest in the superfamily. The seminal duct is closed throughout its way to the penis (Boss, 1982) (open in other Tonnoidea, except some species of *Tutufa*, Bursidae; THIELE, 1929; BEU, 1981; and own observations). The proboscis is long and slender and lies coiled in the sheath, as in the Personidae, but in the Ficidae this occupies a large part of the cephalo-pedal haemocoel. The buccal mass is small, in preserved specimens not broader than the anterior oesophagus, and equipped with a pair of large jaws. The salivary glands are small and inconspicuous in *Ficus* (THIELE, 1929; AMADRUT, 1898; pers. obs.: 1.2 × 0.7 mm in a 40-mm *F. subintermedia*), situated far back in the body cavity and connected via long, slender ducts, whereas in other Tonnoidea they are complex and large. To what extent these differences are connected to differences in feeding is uncertain. The only published information about the diet of *Ficus* is that it feeds on sea urchins (WILSON & GILLETT, 1971), whereas of four specimens of *Ficus subintermedia* we examined, two had empty alimentary canals, one had remains of a polychaete, and one had a long tube-shaped cuticle in the rectum.

This information about the anatomy and feeding biology of *Ficus* agrees well with the new information about *Thalassocyon* presented below and confirms that BEU's (1969) transfer of *Thalassocyon* to Ficidae was justified.

This anatomical information also distinguishes the Ficidae from all other families of the Tonnoidea, but does not necessarily indicate that the Ficidae has to be separated from the superfamily. However, it can be assumed that they branched off before the hypertrophied salivary glands of other Tonnoidea were developed. It is more difficult to imagine that the salivary glands have been reduced. Fossil evidence also indicates that the Ficidae, morphologically similar to Recent *Ficus*, already existed in the Upper Cretaceous (WENZ, 1941).

A planktonic larva of *Ficus* has never been reported, but some information about the larval development of *Ficus* was given (in Japanese) by AMIO (1963), who figured egg capsules. WRIGLEY (1929) described the apical whorls of several species of *Ficopsis* Conrad, 1866, and *Ficus* from British Cenozoic deposits, and SMITH (1907) described those of some Recent and Cenozoic species. Interpretation of protoconchs in the Ficidae is presently impossible because there are no known reference cases. The calcified larval shell is smooth, except on the last part (Figures 80–82) (in Tonnoidea with calcified larval shell, protoconch I is usually sculptured with pits and minute tubercles; protoconch II is often with at least the initial part reticulated). The limits between protoconch I and II and between protoconch II and the teleoconch are indistinct, but the protoconch of *Ficus communis* (SMITH, 1945:pl. 1, figs. 1, 2, and this paper Figure 80) seems to indicate non-

→

Explanation of Figures 128 to 135

Shells of **Laubierina** (Figures 128 to 131) and *Thalassocyon* (Figures 132 to 135).

Figure 128. **L. peregrinator**, holotype, diameter 19 mm.

Figure 129. **L. peregrinator**, paratype (not adult), diameter 13.8 mm.

Figures 130 and 131. **L.** sp. (Caribbean, MNHN), height 13.2 mm.

Figure 132. *T. bonus,* holotype, 45 mm.

Figure 133. *T. bonus* (NMNZ 35293), diameter 12.6 mm.

Figure 134. *T. bonus* (NMNZ 75253), height 76 mm.

Figure 135. *T. bonus* (Amsterdam Id., MNHN), 28 mm.

Explanation of Figures 136 to 141

Shells of *Akibumia.*

Figure 136. *A. orientalis* (Japan, USNM), diameter 9.25 mm.
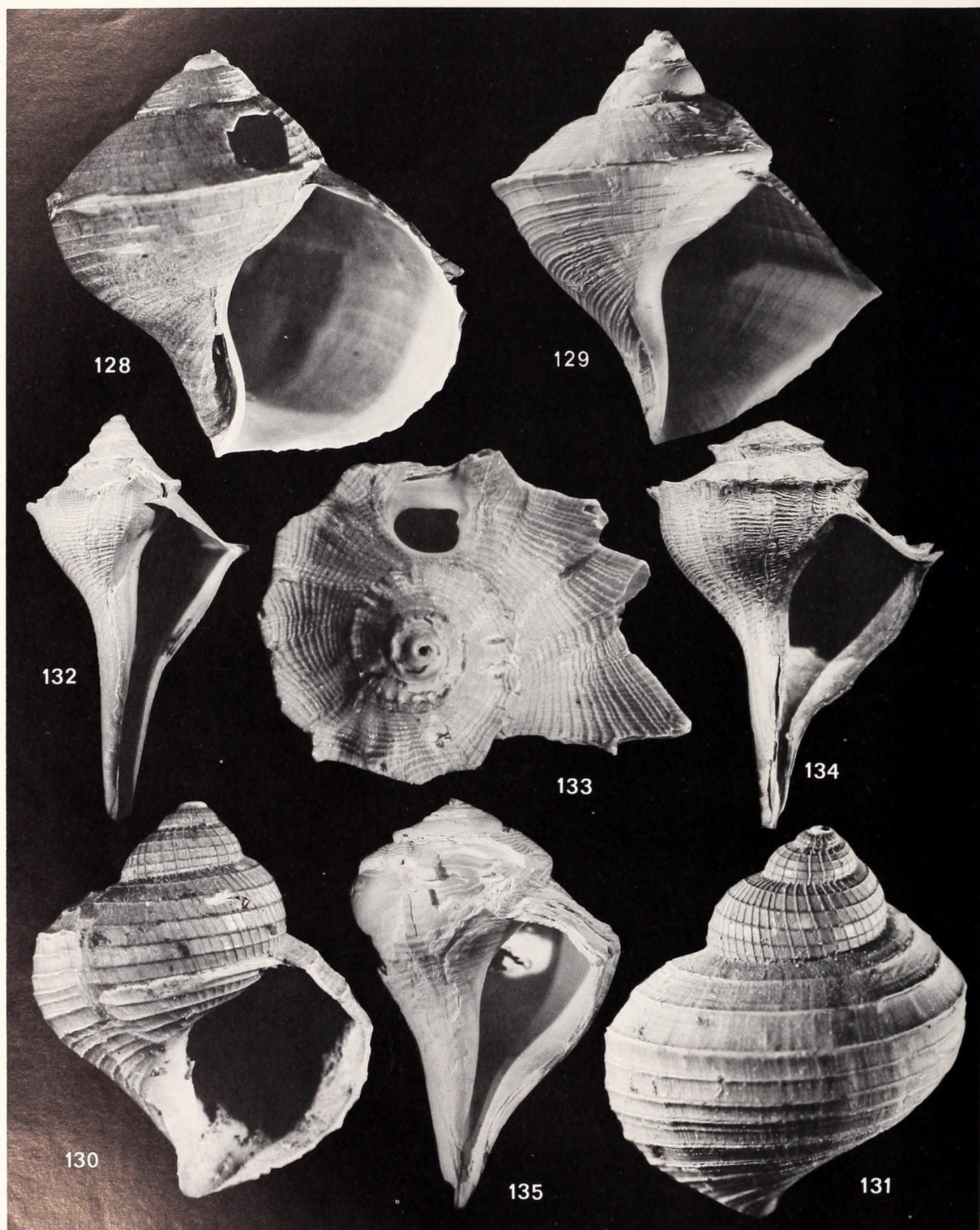
Figures 137 and 138. *A. orientalis,* holotype, diameter 15 mm.

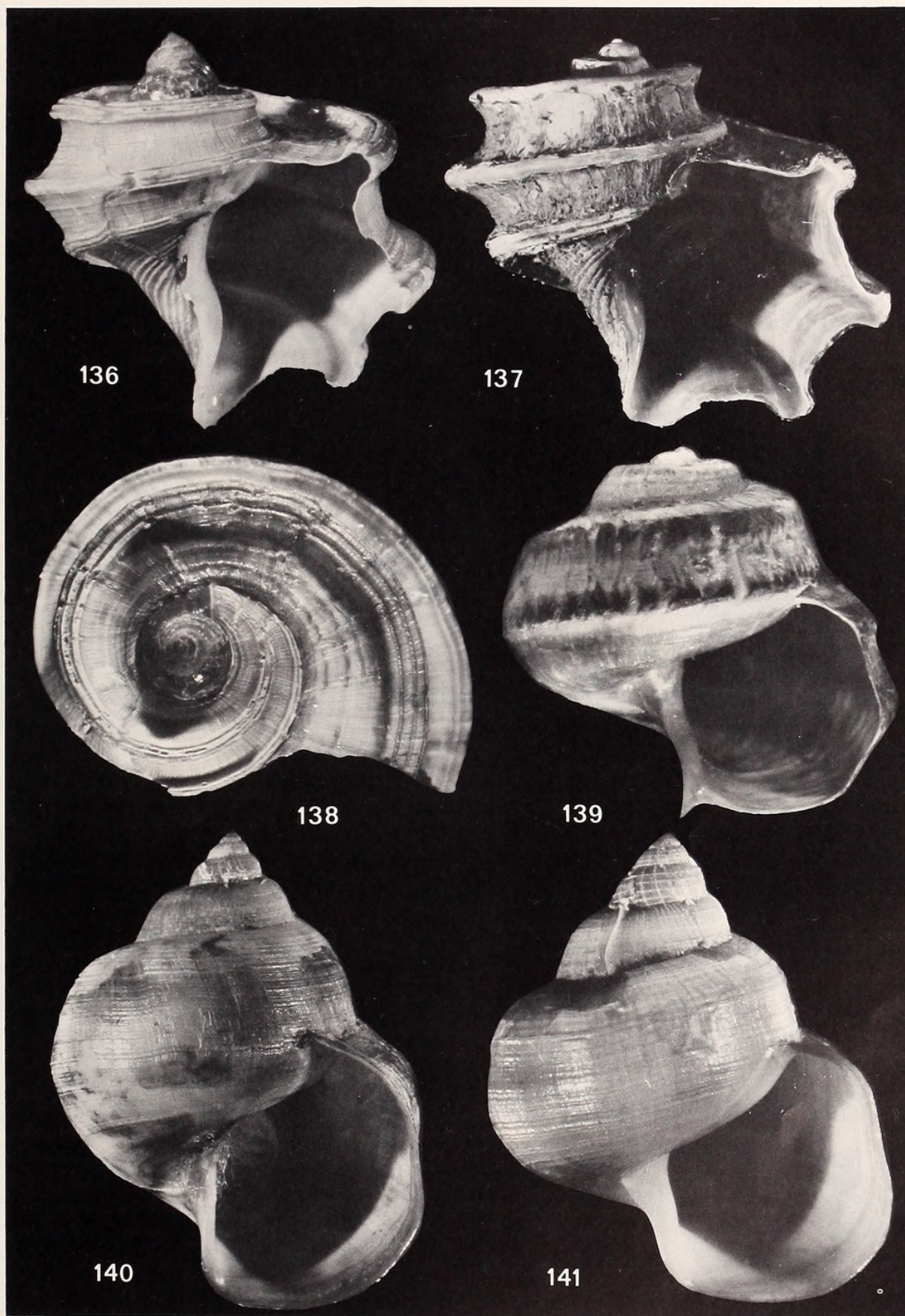Figure 139. *A. schepmani,* holotype, diameter 5.9 mm.

Figure 140. *A. flexibilis,* holotype, diameter 18.0 mm.

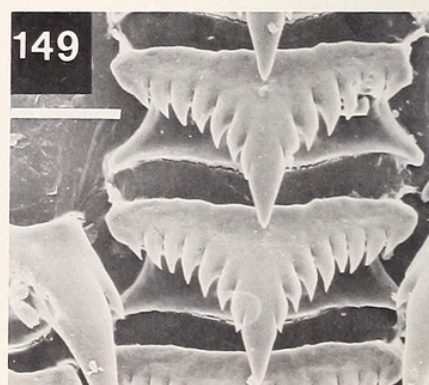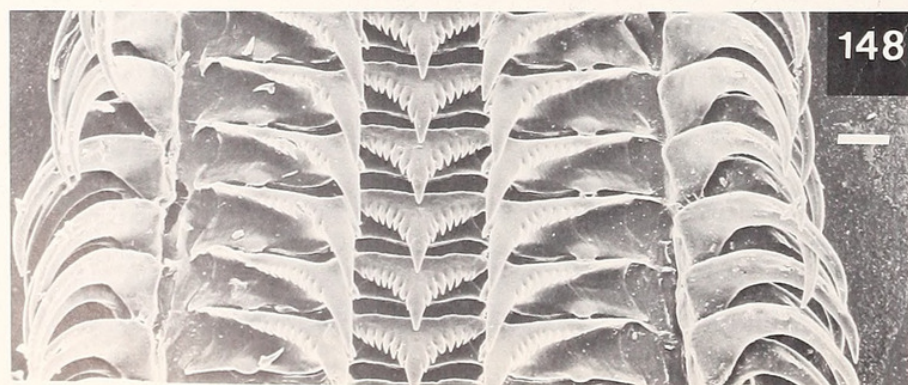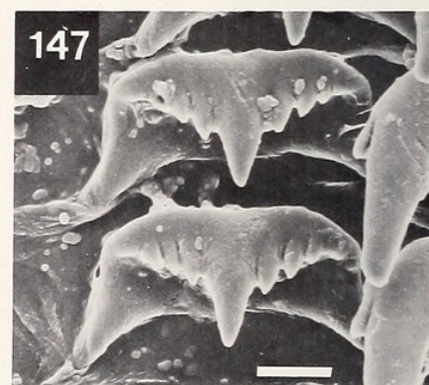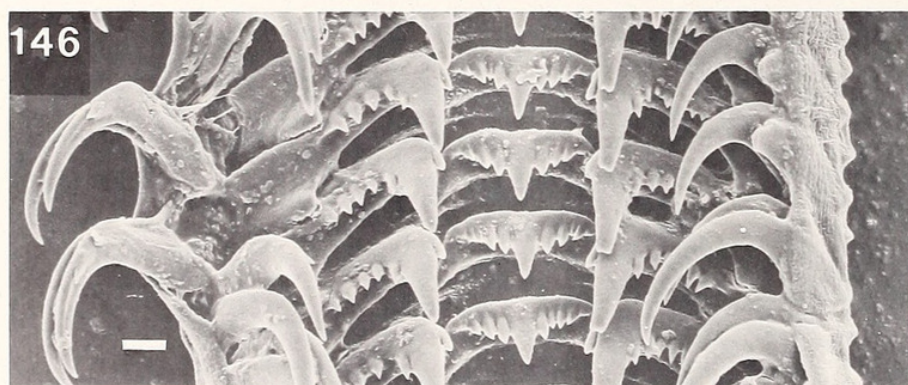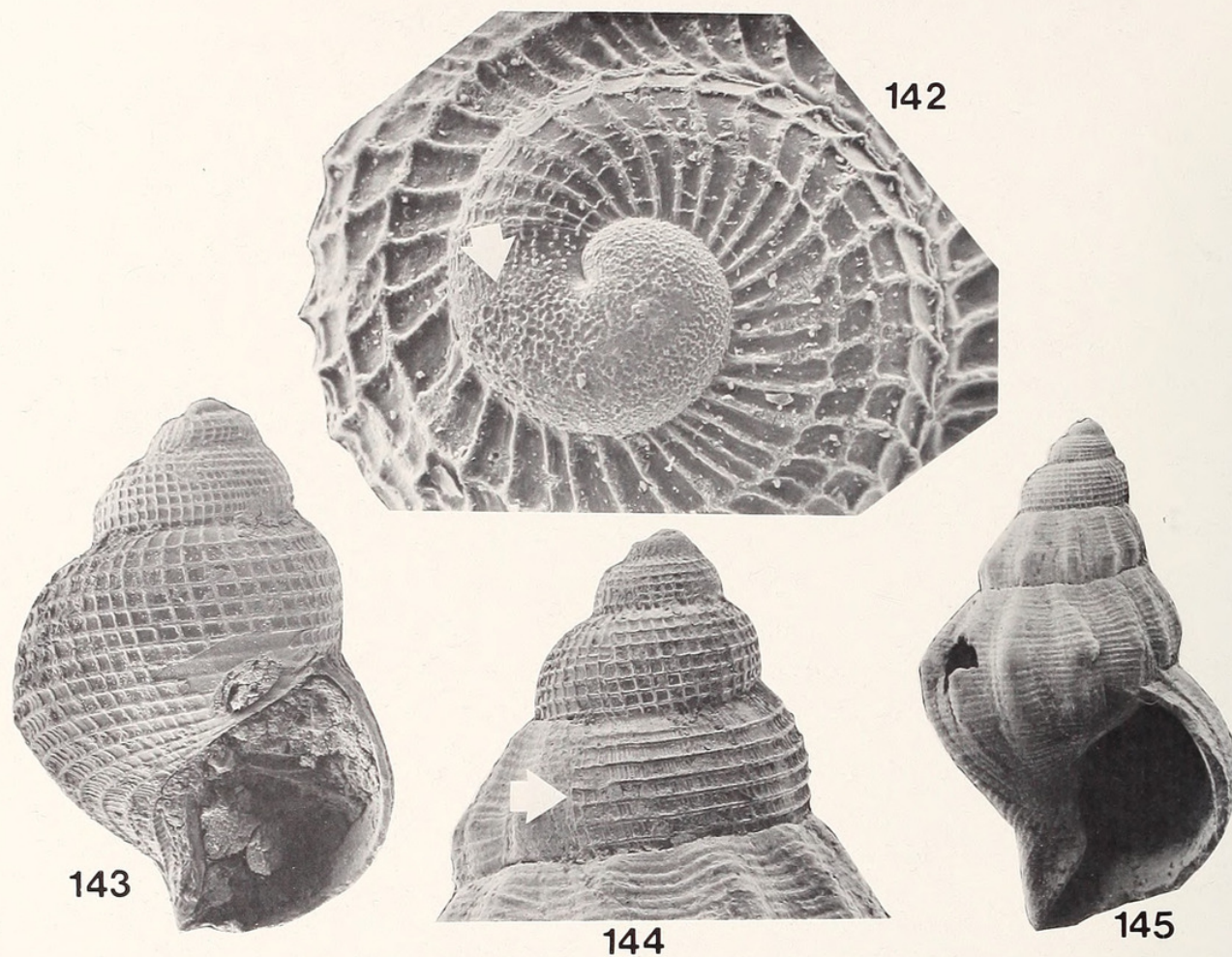Figure 141. *A. flexibilis* (S of Zanzibar, USNM), height 15 mm.

planktotrophic development. We also figure the apical whorls of *Ficus subintermedia,* which has a multispiral protoconch and may indicate planktotrophic larval development.

Thalassocyon Barnard, 1960

Thalassocyon BARNARD, 1960:440.

Type species: By original designation, *Thalassocyon bonus* Barnard, 1960, recent, deep water off South Africa.

Remarks: The Ficidae contains mainly shallow-water species, but *Thalassocyon* Barnard, 1960, of which two nominal species have been described, is only known from depths below 1000 m. BEU (1969) transferred the genus from Cymatiidae where Barnard described it to the Ficidae because of shell and radular morphology.

Recently we became aware that J. Knudsen (unpublished) had started, long ago, a treatment of the specimens of *Thalassocyon* taken by the Galathea Expedition in the Kermadec Trench (BEU, 1969), with the intention to describe their morphologies and to synonymize *T. tui* Dell, 1967, with *T. bonus.* This work had never been finished and when he learned of our intentions to do the same, he made his notes and material available to us.

One half-grown shell of *Thalassocyon* (NMNZ M 35293), from off East Cape, New Zealand, 1000 m, with a badly corroded apex, had brownish fragments remaining from the larval shell. The species possibly has planktotrophic larval development.

Anatomy of *Thalassocyon*

The foot is small, with wrinkled sides and a distinct propodium. It lacks a posterior pedal gland and the drawn out anterior corners that are present in *Ficus.* The operculum is small, black, and circular, with a lateral, corroded nucleus (similar to that of *Distorsio*) and does not fill the aperture. The head is large and broad compared with *Ficus* and does not have a long slender neck. The tentacles are short and conical and lack eyes.

The pallial cavity is large and spacious, with a simple, muscular margin that does not cover the outside of the shell (which is indicated by the thick, bristly periostracum). The inhalant siphon is thick and muscular, strongly contracted. An exhalant siphon is indicated by a triangular lobe at the right extremity of the pallial edge.

The male has a long, slender, simple, finger-shaped penis, to which the sperm is transported via a simple, narrow, open furrow that crosses over to the side of the pallial cavity and backwards. The rectum is simple and opens far back in the pallial roof; in the female it runs between the pallial oviduct and the pallial skirt. The rectum of three specimens contained numerous, large fecal pellets, neatly aligned and connected by mucus strings. Identifiable contents were sand, numerous pieces of cuticle, and large quantities of broken polychaete bristles, somewhat similar to the large bristles of the families Aphroditidae and Amphinomidae.

The gill occupies almost the whole distance from the bottom to the opening of the pallial cavity and consists of about 60 triangular leaflets, which are 1.6 mm wide and 2.0 mm high in the central part of the gill. The osphradium is regularly bipectinate with about 40 pairs of high leaflets.

The proboscis is simple and can probably be extended to a length approaching the length of the shell (partly everted in one specimen). In the retracted state it occupies the anterior, dorsal $\frac{1}{6}$ of the volume of the cephalo-pedal haemocoel. The buccal mass is small and slender, with a pair of jaws similar to those of *Ficus.* The anterior oesophagus is slender and fused with the thick-walled salivary ducts, which pass through the nerve ring on their way to the two large, simple salivary glands that lie in the anterior part of the cephalo-pedal haemocoel. The salivary glands abut the cerebral ganglia and are pushed forwards by the huge oesophageal gland, which fills $\frac{5}{6}$ of the cavity. The gland is solid and consists of numerous thick, spongy, transversal folds.

Radula. See Figures 1 and 2. The size is remarkably only $\frac{1}{4}$–$\frac{1}{5}$ that of a specimen of *Ficus subintermedia* of the same size.

The nervous system was not examined.

Thalassocyon bonus Barnard, 1960

(Figures 1, 2, 132–135)

Thalassocyon bonus BARNARD, 1960:440.
Thalassocyon tui DELL, 1967:309. (New synonym.)

←

Explanation of Figures 142 to 149

Kaiparanura, shells; *Ficus* and *Distorsio,* radulae.

Figures 142 and 143. *Kaiparanura spiralis,* larval shell (NMNZ), diameter of protoconch I, 225 µm (border to teleoconch indicated by arrow); height of larval shell (Figure 143), 2.75 mm.

Figures 144 and 145. *K. spiralis,* complete shell (Figure 145) and apex (Figure 144) (NZGS). The white arrow indicates border between larval shell and teleoconch. Height of larval shell (Figure 144), 2.0 mm; height of shell (Figure 145), 7.5 mm.

Figures 146 and 147. *Distorsio clathrata* (SMNH), radula. Scale lines 10 µm.

Figures 148 and 149. *Ficus subintermedia* (New Caledonia, MNHN), radula. Scale lines 50 µm.
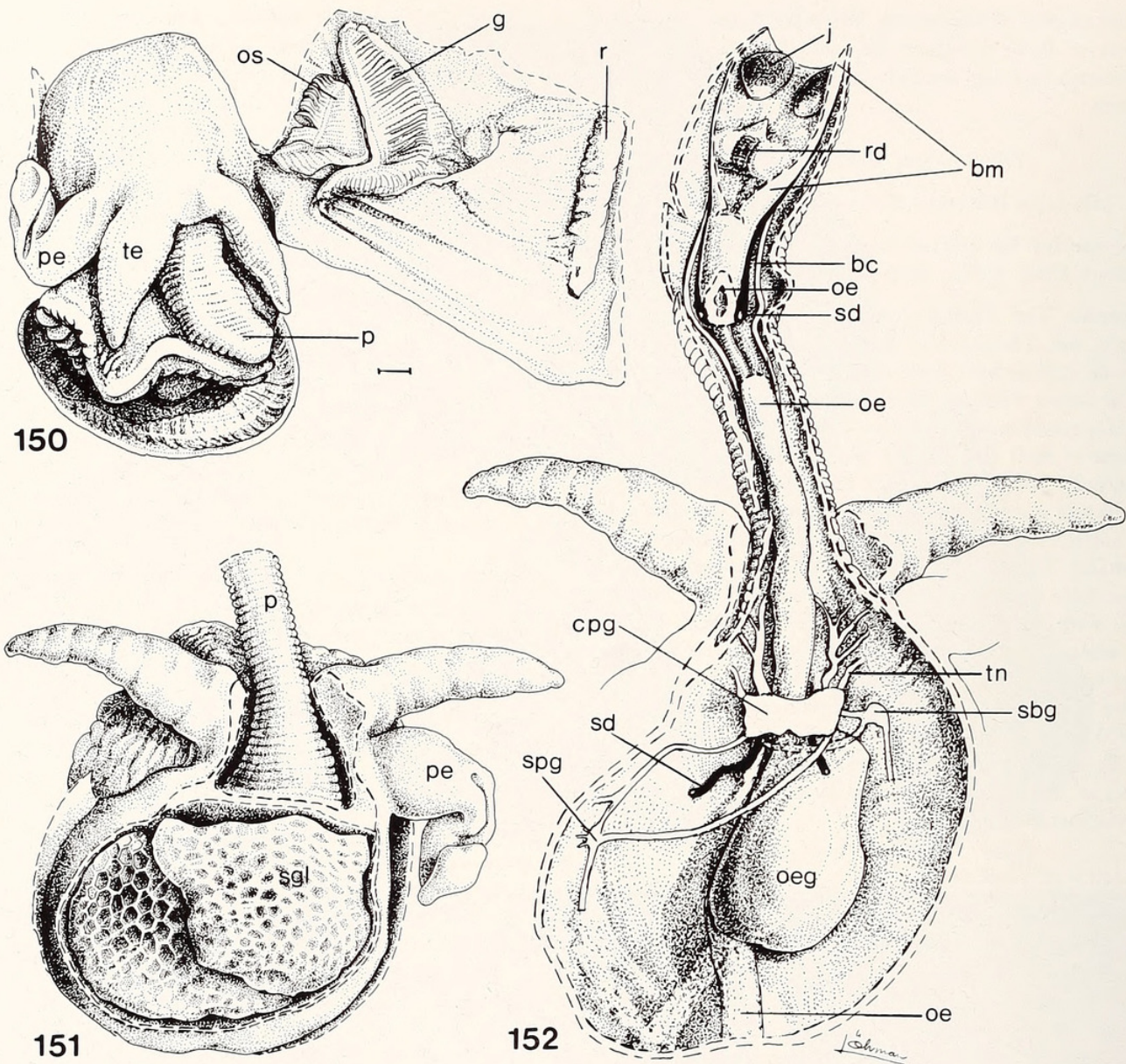
Explanation of Figures 150 to 152

Anatomy of *Oocorys sulcata* (off Portugal, MNHN). Scale line 1 mm.

Figure 150. Head-foot, pallial skirt. External features.

Figure 151. Body cavity opened to show salivary glands.

Figure 152. Body cavity and proboscis opened, salivary glands removed.

Key: bc, buccal cavity; bm, buccal mass; cpg, cerebro-pleural ganglion; g, gill; j, jaw; oe, oesophagus; oeg, oesophageal gland; os, osphradium; p, proboscis; pe, penis; r, rectum; rd, radula; sbg, suboesophageal ganglion; sd, salivary duct (marked black); sgl, salivary gland; spg, supraoesophageal ganglion; tn, tentacle nerve.

Type material: *Thalassocyon bonus,* holotype SAM A 9714; *T. tui,* holotype NMNZ M 21299.

Type localities: *Thalassocyon bonus,* 33°26′S, 16°33′E, 2280–2400 m, off western South Africa; *T. tui,* 30°11′S, 179°52′W, 1152–1205 m, W of Kermadec Islands.

Material examined: The type material; off South Africa,

33°49′S, 16°30′E, 2760 m, paratype, SAM A 9756; 34°37′S, 17°03′E, 2900–2980 m, paratype, SAM A 9759; 33°50′S, 16°30′E, 2720–2945 m, paratype, SAM A 9810; New Zealand, NE of Chatham Id., 42°56.3′S, 175°05′W, 1004–1011 m, 1 shell, NMNZ 75253; Lord Howe Rise, NZOI sta. P120, 35°45.7′S, 165°04.1′E, 950 m, 1 shell, NZOI; 30°11.5′S, 179°52′W, 965–975 m, holotype, NMNZ M 21299; NZOI sta. J41, 36°50′S, 170°13′E, 2060 m, 1 spec-
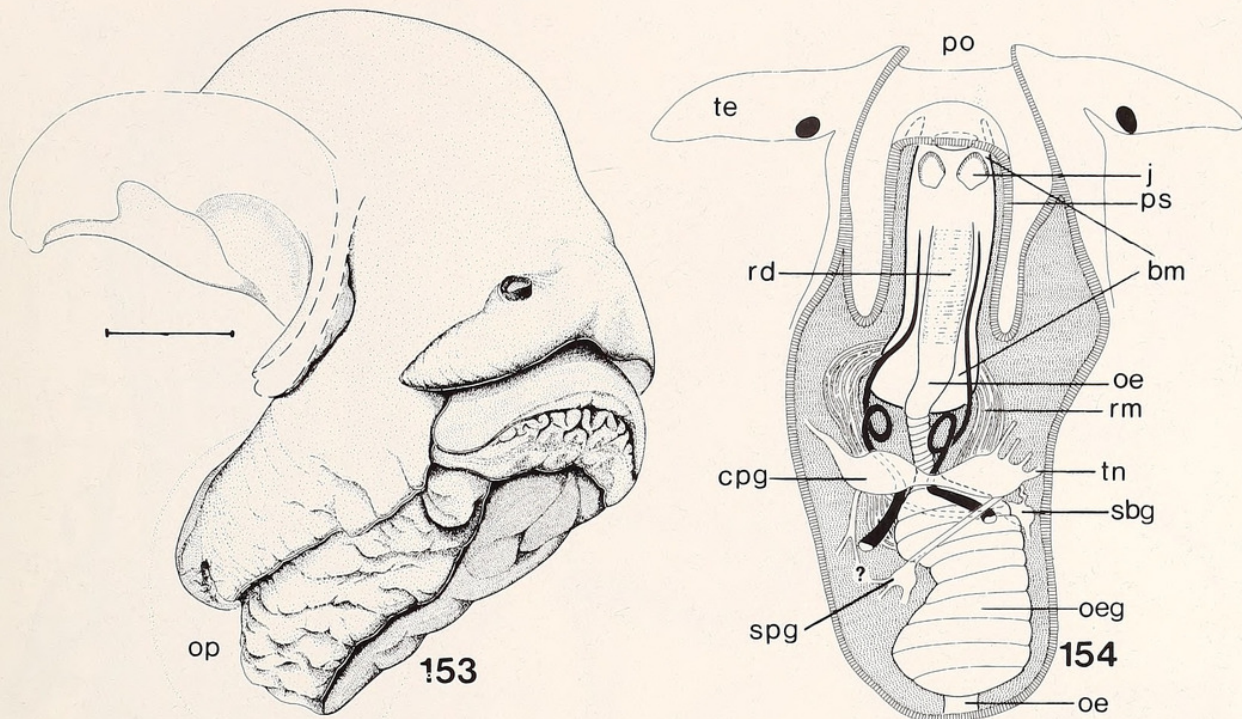
Explanation of Figures 153 and 154

Anatomy of *Pisanianura breviaxe*.

Figure 153. Head-foot, pallial skirt removed. Scale line 2 mm.

Figure 154. Schematic plan over body cavity, salivary glands removed.

Key: bm, buccal mass; cpg, cerebro-pleural ganglion; j, jaw; oe, oesophagus; oeg, oesophageal gland; po, proboscis opening; ps, proboscis skirt; rd, radula (seen by transparency); rm, retractor muscles; sbg, suboesophageal ganglion; spg, supraoesophageal ganglion; te, tentacle; tn, tentacle nerve; ?, zygoneury not verified.

imen, NZOI; NZOI sta. P940, 41°22.7'S, 166°44.4'E, 2092–2154 m, 1 shell, 1 specimen, NZOI; 36°40.1'S, 172°44.7'E, 1622–1634 m, 1 specimen, NMNZ M 74630; NZOI sta. P941, 41°15.2'S, 167°07.2'E, 1457–1463 m, 1 specimen, NZOI; off East Cape, 37°30'S, 179°22'E, 1140–1215 m, 1 young shell, diam. 12.9 mm, NMNZ 35293; S of Amsterdam Id., R/V *Marion Dufresne* cruise MD50 sta. DC167, 38°24'S, 77°29'E, 1430–1600 m, 1 worn shell, MNHN; off Queensland, ca. 2000 m, 1 specimen, AMS (uncatalogued); Galathea Expedition sta. 665, Kermadec Trench, 36°38'S, 178°21'E, 2470 m, 2 specimens, ZMC; Galathea Expedition sta. 668, Kermadec Trench, 36°23'S, 177°41'E, 2640 m, 4 specimens, 1 shell, ZMC.

Distribution: From South Africa, west to the Kermadec Islands, abyssal.

Remarks: During our search for larval shells of *Thalassocyon* we examined all specimens of the genus in AMS, NMNZ, SAM, and MNHN. When the two nominal species were described they were known only from a very few specimens from South Africa and New Zealand. The richer material now available, including specimens from Queensland (*Thalassocyon* was also recently recorded from off New South Wales, 570–950 m, by COLMAN, 1987) and Amsterdam Island, indicates that the specimens from South Africa and New Zealand can hardly be distinguished, al-

though specimens from South Africa usually have a taller spire than those from New Zealand. Specimens from Amsterdam Island, which are geographically intermediate, however, are intermediate in this character and we suppose there is a cline in the height of the spire (Figures 132–135).

Family TONNIDAE Suter, 1913

(Figures 9–14, 49, 61, 62, 73–79)

The Tonnidae is mainly restricted to shallow water, above 100 m. We figure radulae and jaws, as well as the shell, operculum, and the radula of a larva for comparison with other families. The only genus that occurs in deep water is *Eudolium* Dall, 1889. The type species, *E. crosseanum*, was discussed and several shells figured by PIANI (1977). The species of the genus were reviewed by CERNOHORSKY (1976). We illustrate a young specimen from the Azores with an intact larval shell (Figures 78, 79) and the radula (Figure 11).

The larva of *Tonna* has been figured and described several times (*e.g.*, MACDONALD, 1855; FISCHER, 1863; DAWYDOFF, 1940; LAURSEN, 1981).

The competent larva has an uncalcified shell (Figures 73, 74) of about 5 mm in diameter. Immediately after
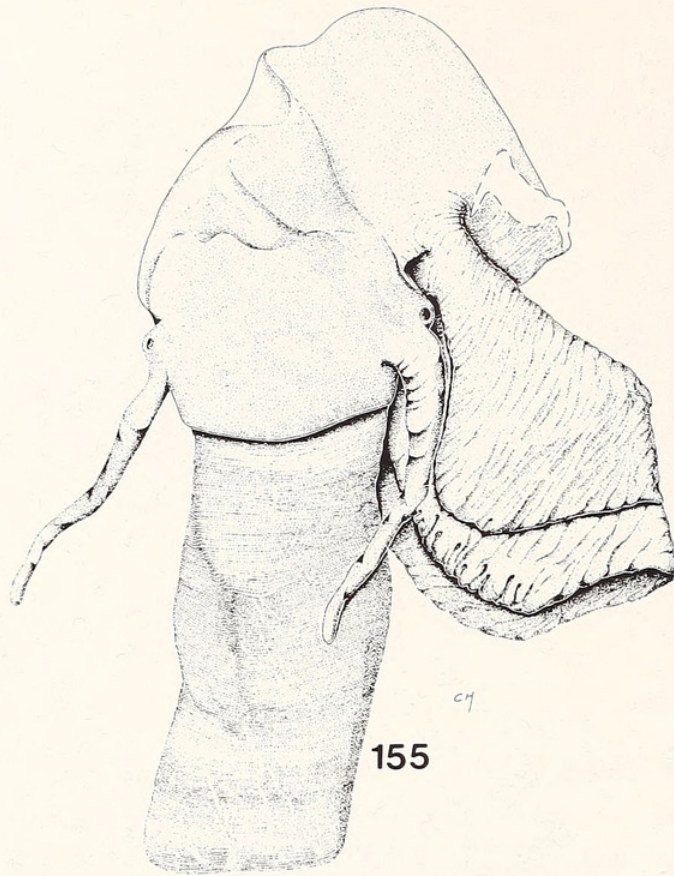
155
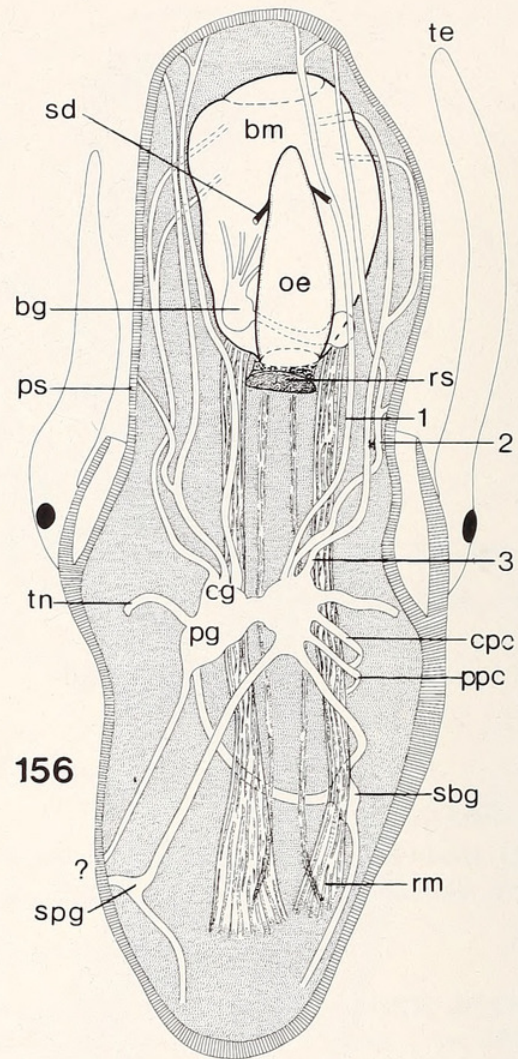
156
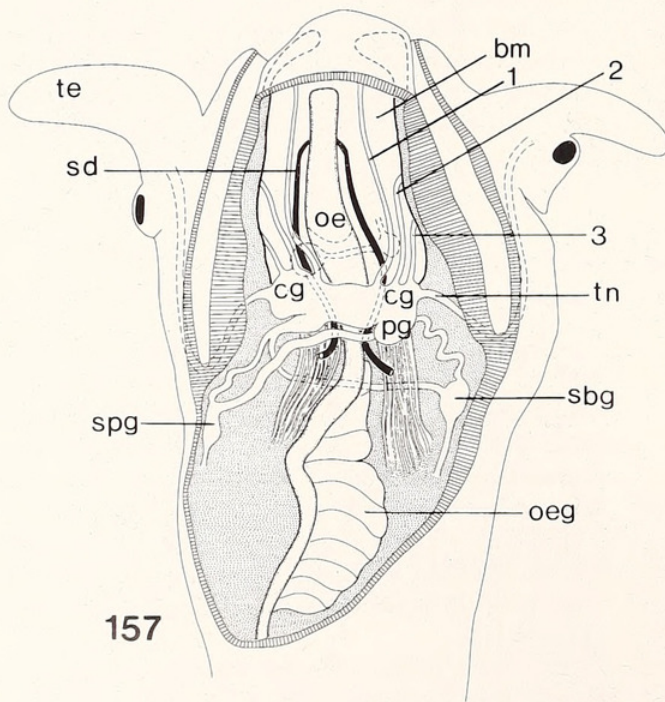
157
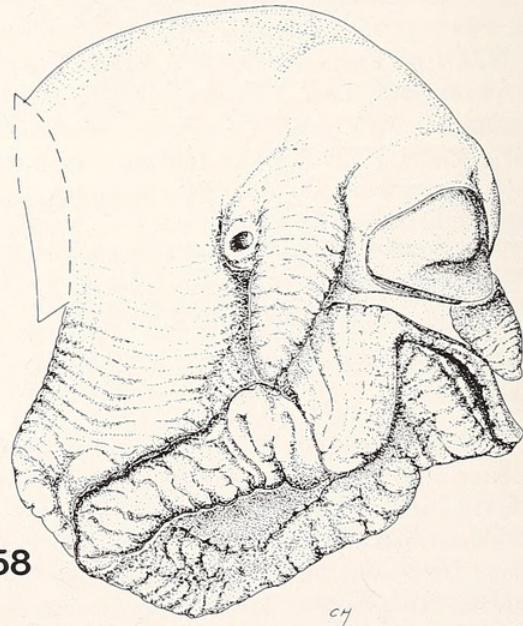
158
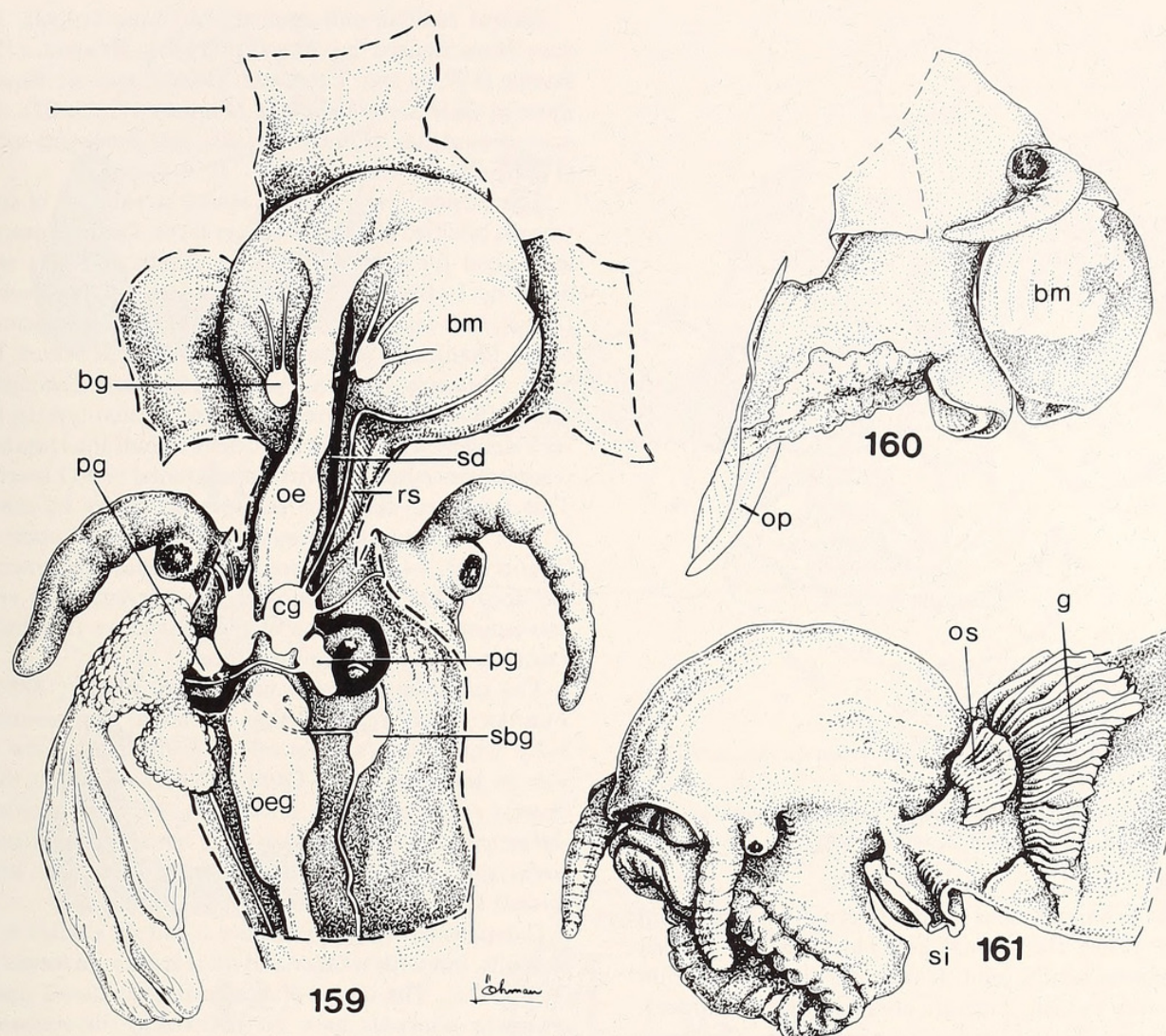
Explanation of Figures 159 to 161

Anatomy of **Laubierina peregrinator**.

Figure 159. Dissection of body cavity.

Figure 160. Head-foot, right side, buccal mass partly everted, pallial skirt removed.

Figure 161. Head-foot, right side.

Key: bg, buccal ganglion; bm, buccal mass; cg, cerebral ganglion; g, gill; oe, oesophagus; oeg, oesophageal gland; op, operculum; os, osphradium; pg, pleural ganglion; rs, radular sac; sbg, sub-oesophageal ganglion; sd, salivary duct; si, siphon.

←

Explanation of Figures 155 to 158

Anatomy of *Akibumia* sp.

Figures 155 and 156. *A schepmani,* head-foot (Figure 155) and organization of body cavity; salivary glands and most of oesophagus removed (Figure 156).

Figures 157 and 158. *A orientalis,* organization of body cavity; salivary glands removed (Figure 157) and head-foot without pallial skirt (Figure 158).

Key: bm, buccal mass; bg, buccal ganglion; cg, cerebral ganglion; cpc, cerebro-pedal connective; oe, oesophagus; oeg, oesophageal gland; pg, pleural ganglion; ppc, pleuro-pedal connective; ps, proboscis sheath; rm, retractor muscles; rs, radular sac; sd, salivary duct (marked black); spg, supraoesophageal ganglion; te, tentacle; tn, tentacle nerve; 1, nerve to mouth; 2, nerve to lips and proboscis sheath; 3, nerve to lips and buccal mass; ?, zygoneury not verified.
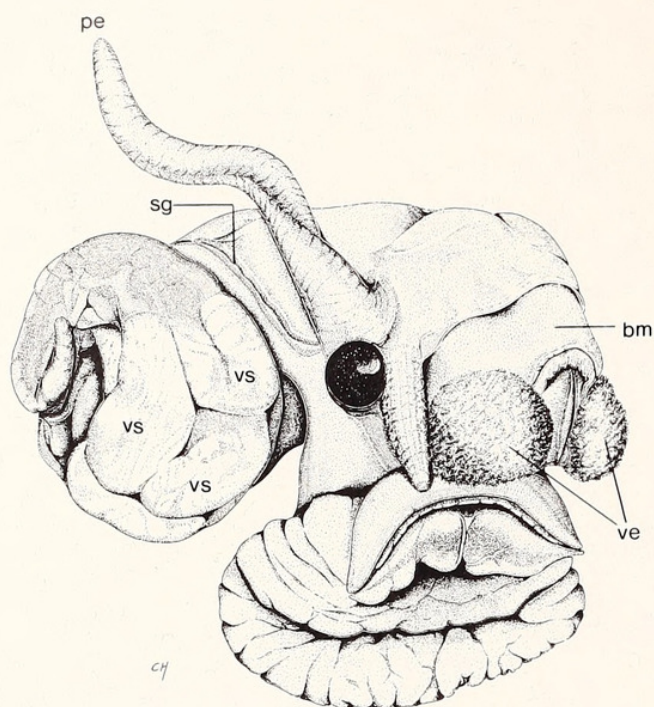
Figure 162

Recently metamorphosed young of **Laubierina** sp. (Mozambique Channel).

Key: bm, partly everted buccal mass; pe, penis; sg, seminal groove; ve, remains of velum; vs, vesicula seminalis.

settlement the animal starts to fill it internally with calcium carbonate. When the animal gets older the larval shell finally becomes totally solid. If then the old periostracum starts to decay (which evidently does not always happen), only the internal mould remains (Figure 76). The same development of the larval shell occurs in *Eudolium*. The internal mould shown in Figure 76 was obtained from the shell in Figure 75 by dissolving the periostracum in bleach.

The competent veliger larva of *Tonna* has a radula similar to that of the adult (Figures 9, 10).

Family CASSIDAE Latreille, 1825

(Figures 15–24, 50, 51, 63–66, 115–120, 150–152)

Since ABBOTT's (1968) and BEU's (1976, 1981) treatments of members and classification of the family, *Morum* Röding, 1798, has been shown to belong to the Harpidae (HUGHES, 1986b); subgenera and synonyms of *Morum* are reviewed by BEU (1976).

Several radulae and opercula of *Cassis* Scopoli, 1777, have been figured by ABBOTT (1968), BANDEL (1984), BAYER (1971), and TROSCHEL (1863), and we illustrate those of *Galeodea echinophora* (Figures 17, 18, 22), *Semicassis granulatum* (Figures 19, 20), and *Semicassis saburon* (Figure 21) for comparison.

The cassids have a smooth, round larval shell of several whorls, calcified also in the veliger larva, that was described in general for several species by ABBOTT (1968) and in detail by LAURSEN (1981) for *Semicassis granulatum* and *Cypraecassis testiculus* (Figures 115–117). The operculum of the Phaliinae (*Semicassis* Mörch, 1852, *Phalium* Link, 1807, *Casmaria* H. & A. Adams, 1853, and *Echinophoria* Sacco, 1890, among others) is of an unusual type in being very slender, with a lateral nucleus at half the length, and is sometimes equipped with strong radial ribs (Figure 65). This has been described for several species by ABBOTT (1968). In *Semicassis granulatum* the larval operculum (Figures 63, 64) can be seen also in adult specimens. In the deep-water genus *Oocorys*, the operculum is simply paucispiral, which is one of the characters that induced FISCHER (1883) to erect the genus.

The larva of *Oocorys* is not known. DALL (1889) and TURNER (1948) reported that the larval shell consists of 2–2.5 whorls that are smooth or sculptured in the same way as the teleoconch. QUINN (1980) described that of *Oocorys caribbea* Clench & Aguayo, 1939, as multispiral and reticulated. We have seen some remains of a reticulated larval shell on specimens of *Oocorys umbilicata* and *O. bartschi* (Figures 118, 119).

Competent cassid larvae have a radula similar to that of adults, but with weaker and more membranaceous teeth (Figure 23). The larvae of *Semicassis granulatum* and *Cypraecassis testiculus* have an indistinctly bipectinate osphradium, with those leaflets facing away from the gill being much smaller.

Position of Oocorythidae Fischer, 1885

The "family" Oocorythidae has usually been regarded as a subfamily of the Tonnidae (THIELE, 1929; WENZ, 1941; BOSS, 1982). DALL (1909) concluded that the Oocorythidae could not be distinguished from the Cassidae, a conclusion disputed by QUINN (1980). Quinn discussed the systematic position and status of the family and concluded that it was distinct from the Tonnidae and contained the genera *Oocorys* Fischer, 1883, *Hadroocorys* Quinn, 1984, *Dalium* Dall, 1889, *Galeoocorys* Kuroda & Habe, 1957, and perhaps also *Galeodea* Link, 1807. PONDER (1984) agreed with BEU (1981) who placed Oocorythidae as a

→

Figure 163

Principles and possible pathways of the evolution of the larval shell of the Tonnoidea.

1. This is considered the ancestral type of planktotrophic larval shell.
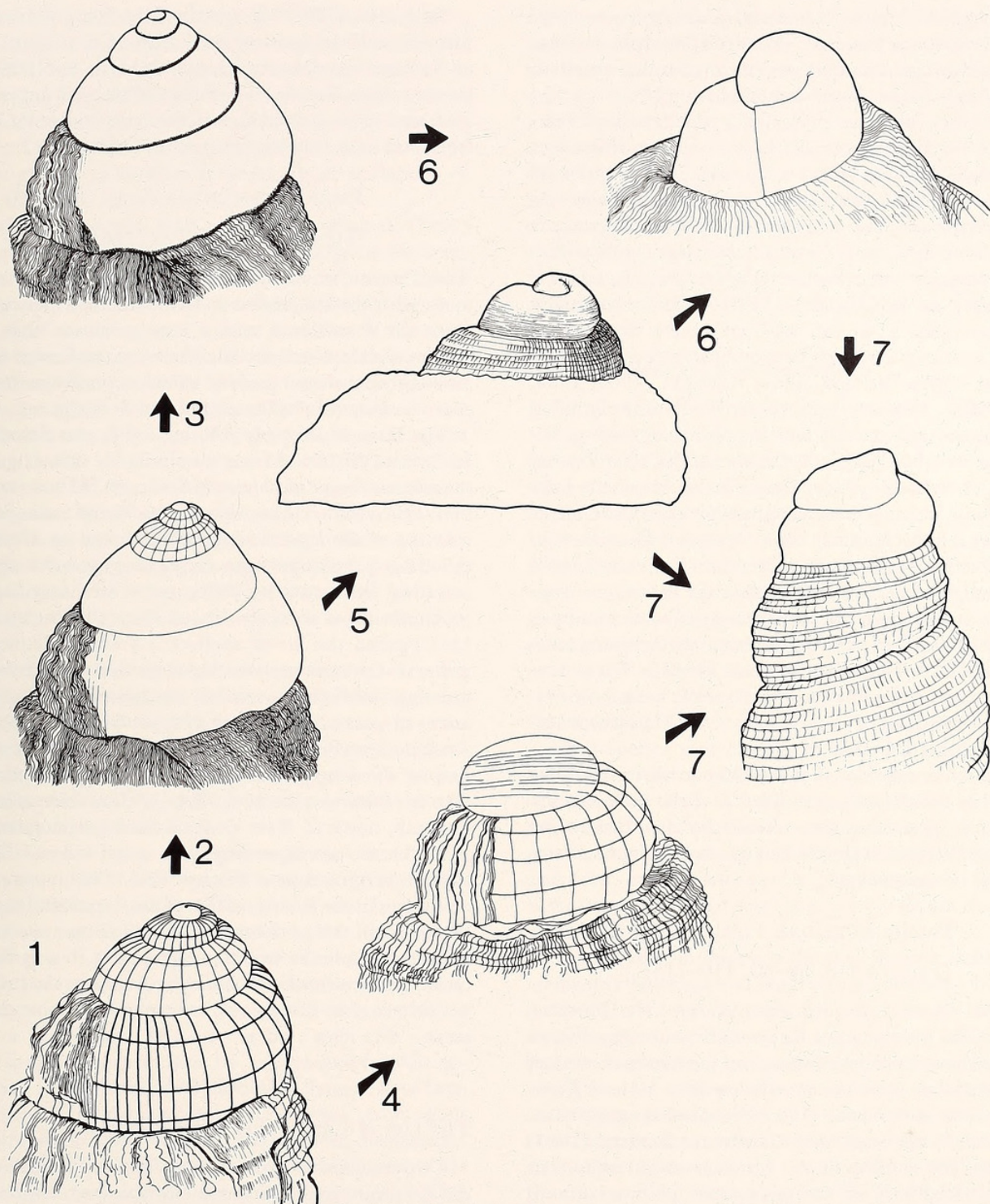
2. Changes in the protoconch II primarily affect the later part of the shell, and usually consist of loss of sculpture.

3. Loss of calcification can also happen independently of stage in development, but because it seems to be an adaptation to long-lasting planktotrophic life, it normally happens only in such species.

4–6. Loss of planktotrophy can take place from any stage in the evolution of the planktotrophic larval shell. This leads to a paucispiral larval shell, where the original sculpture may remain or finally may be lost, as in Figure 6.

7. Calcification of the aperture before the initial whorl (as in *Sassia* [*Austrosassia*] spp., see BEU, 1988a) is still another modification of the intracapsular development (well known from the Buccinidae).

This scheme is not supposed to show the actual evolution within the superfamily, but only to give examples of the direction of the evolution.

subfamily of Tonnidae, but placed *Galeodea maccamleyi* Ponder, 1984 in the Cassinae. (Ponder's description of that species contains good anatomical information and excellent figures of the radula, jaws, and operculum.)

We find the placement of the Oocorythidae as a subfamily of the Tonnidae untenable because of the differences in the radula (Figures 9–14 vs. 15–24), jaws (Figures 49 vs. 50 and 51) and operculum (Figures 61 and 62 vs. 63–66). On the other hand, we can see no strong arguments against the association of Oocorythidae with the Cassidae. The radulae are quite similar (Figures 15, 16, and 24, and pointed out by BANDEL, 1984). Also, the soft parts are similar as far as we can see from the few descriptions of cassid anatomy that have been published (*e.g.,* QUOY & GAIMARD, 1835; PANCERI, 1869; REYNELL, 1905, 1906; WEBER, 1927; HUGHES & HUGHES, 1981), from QUINN's (1980) description and our own dissections of *Oocorys sulcata* (Figures 150–152), and from HALLER's (1893) description of *Galeodea echinophora*. Finally, the shells form a continuous series of increasing complexity of the incremental scars and siphonal canal (*Oocorys–Galeodea–Cypraecassis–Cassis*). The only difference from the cassids pointed out by QUINN (1980) is that the cassids are supposed to have the tip of the inner marginal tooth equipped with denticles (sometimes also present on the outer marginal, *cf.* ABBOTT [1968] and BANDEL [1984]). These denticles were said to be absent in *Oocorys*. We have, however, found such denticles in *Oocorys sulcata* and *Galeodea echinophora* (Figures 22, 24).

We therefore consider that the Oocorythidae should be included in the Cassidae (as does A. Beu, pers. comm., who also suggests that they should be classified in the Cassinae). Whether it should be kept as a distinct subfamily or not, we cannot say.

Family BURSIDAE Thiele, 1925

(Figures 5–8, 58–60, 110–114)

BEU (1981) gave a detailed description of the Bursidae and described the soft parts for several species, in addition to summarizing earlier knowledge on the family. LAURSEN (1981) described the larva of some western Atlantic *Bursa* Röding, 1798, and RISBEC (1955) described the gross morphology of *Bursa* from New Caledonia. BANDEL (1984) questioned the validity of the Bursidae as a family, but this was based only on the comparison of radulae with those of the Cymatiidae.

We find the Bursidae a well-defined unit, characterized by several independent characters (*i.e.,* posterior canal, reduced jaws, 3 accessory salivary glands [Beu, pers. comm.], globular, calcified larval shell, and similar teleoconchs) and support Beu's view. We figure the larval shell, operculum, and radula (which shows a remarkable similarity to the Tonnidae) for comparison (Figures 5–8, 58–60, 110–114) with other Tonnoidea. We examined several larvae but did not succeed in finding a radula.

DE FOLIN (1884:212) described the larva of an unidentified *Bursa* from southwestern Europe or western Africa as *Talisman parfaiti* (types examined in MNHN). The generic name *Talisman* de Folin, 1884, will not interfere with any of the generic names normally in use for bursids from that area because those all are older.

Family PERSONIDAE Gray, 1854

(Figures 84, 121, 122, 146, 147)

The Personidae is characterized by the central radular tooth with distinct, down-curved corners, a periostracum as in the Ranellinae, and a long proboscis that in the retracted state is coiled. The shell has (in Recent species) a strongly developed parietal shield, a small aperture, and characteristic columellar ridges and denticles.

The larva of *Distorsio* Röding, 1798, was described by LAURSEN (1981) and from the similarity of his figure and the original figure of *Calcarella* Souleyet, 1850, we conclude that they refer to closely related species. We also conclude that one of the "giant veligers" described by DAWYDOFF (1940:fig. 2) belongs to the same group, and that the larva described by SIMROTH (1911) under the name *Calcarella spinosa* Souleyet is closely related. BEU (1987:figs. 133, 137 139) figured the larval shell of a young specimen with parts of the strongly developed periostracal fringes remaining. We figure a recently metamorphosed larva with traces of post-larval growth (Figure 84) and the apex of *Distorsio* sp. (Figure 122). The larval shell is similar to that of *Bursa* spp., but differs by having smooth initial whorls. *Distorsionella lewisi* Beu, 1978a, from about 600 m depth, north of New Zealand, has a reticulated larval shell, but the corresponding larva is not known. The protoconch is figured here (Figure 121). This larva presents a problem in the determination of developmental type. The sculpture on the protoconch certainly is the type found in species with planktotrophic development, but at the same time it has fewer whorls than what is normal in those, and we believe that it does not have planktotrophic development.

DISCUSSION

The Use of Larval Shells in Classification

Two contrary views on the phylogenetic significance of the different types of protoconchs have been expressed for several decades. One point of view was expressed by DALL (1924): "In common with most students of the Mollusca for some years I have regarded the nucleus characters as more or less indicative of genetic affinity, but recently having had to work over large numbers of deep water species, especially toxoglossate forms, and to utilize Hedley's fine monograph of the Australian Turridae, I have found this view to involve so many apparently preposterous combinations of unlike things and separation of similar things, that I have come to the conclusion that this view

cannot be maintained." And further: "When two marine forms of similar anatomical structure exhibit different nuclei, I conclude that the adaptive modification is not of serious value in classification, and in most cases should not be considered as of more than sectional or subgeneric importance. The parallel occurrence of similar nuclei in widely different groups of families is obviously no indication of genetic affinity."

Exactly the opposite view was held by FINLAY (1931) who emphasized that the protoconch was a good character for classifying Tonnoidea: "I think the only satisfactory basis for the classification of the Cymatiidae is the protoconch, and would reject a species from any of the shell groups if it does not agree with the other members in apex." And further: "After a number of years careful examination of gastropod apices, I am fully satisfied, in spite of what several authors have written, that the protoconch is one of the most valuable criteria for systematic classification. Not only have I never found it to vary from type in a homogeneous genus, but I have also found it so generally constant that in my opinion considerable importance must be placed on it in determining lineage relationships. To the palaeontologist it is as important as the radula is to the malacologist, and should be given just as much consideration."

After scientists had noticed the occurrence of very different types of larval shells within a well-defined genus, the larval shell has obtained a bad reputation as a systematic character among many malacologists, while others have uncritically used this to separate genera. To understand these discrepancies it is necessary to consider the evolutionary background.

Planktotrophic larval development is considered to be the ancestral mode of development in marine invertebrates in general (STRATHMANN, 1978, 1985), and in marine gastropods in particular (JABLONSKI & LUTZ, 1983). Non-planktotrophy is a derived condition that has appeared, obviously independently, in different families and genera. Each time such a change takes place, it affects only a single species or population. This species may then give rise to a new lineage, characterized by non-planktotrophic development, or may become extinct. Such changes have been documented by paleontologists. A reversal, from non-planktotrophy to planktotrophy, has not been documented and seems less likely, at least if the larval development has been modified so much that the larva has lost the ability to swim or feed on plankton.

When a species changes from planktotrophic to lecithotrophic development, the larval shell, too, is affected, and must therefore be regarded as a new, acquired character.

With this background knowledge, we assume that the two views on the systematic value of the larval shell are the result of lack of discrimination between larval shells of different developmental types, and we can see (as did MARSHALL, 1978) no reason why species with different types of development necessarily have to be classified in different subgenera or genera, as often has been emphasized. (BOUCHET [1989] has reviewed a number of cases of closely related prosobranch species that differ almost only by having plankto- and lecithotrophy, respectively, and correspondingly different types of larval shells.)

We also assume that as long as larval shells of planktotrophic larvae are compared, they are good indicators of relationship and have the same taxonomic value as teleoconchs. Among those sharing the view of FINLAY (1931) on the other hand, the protoconch has been overestimated in value, and used in the wrong way, by comparisons made among protoconchs with different biological origins.

Larval Development of Tonnoidea

Detailed descriptions of the spawn (AMIO, 1963; LAMY, 1928; PENCHASZADEH, 1981; PETIT & RISBEC, 1929; RISBEC, 1931, 1936; THORSON, 1940) and early development of tonnoid larvae exist, covering the time until hatching (ANDERSON, 1959, 1966; BANDEL, 1975; D'ASARO, 1969; GOHAR & EISAWY, 1967; HUGHES, 1986a; LAXTON, 1969; PHILPOTT, 1925). The development of the later larva, however, has attracted less attention and little detailed information exists; but as in most caenogastropod taxa, planktotrophy and lecithotrophy are reflected in the morphology of the larval shell, in accordance with THORSON's (1950) "apex theory" and other references cited by ROBERTSON (1976).

Most species that have been described in detail leave the egg capsule as planktonic veliger larvae with a shell of a diameter of up to 0.4 mm and consisting of less than one whorl, which constitutes protoconch I. (Reports on presumed adelphophagy in *Tonna* [PENCHASZADEH, 1981] discussed by HOAGLAND & ROBERTSON [1988] and BOUCHET [1989] need confirmation, but do not change our discussions.)

The first discontinuity in the shell surface indicates the moment of hatching and separates protoconch I from protoconch II, which is formed during the time the larva feeds on phytoplankton. Protoconch II consists of 2.5–4 whorls, and its diameter is 1–5 mm. After metamorphosis, the young benthic snail secretes the teleoconch, which is separated from protoconch II by a second discontinuity. The two discontinuities, reflecting hatching and metamorphosis, can be observed on the apical parts of well-preserved Recent and fossil shells (Figures 73–79, 87, 88, 101–103, 106–109). Without consideration of the mode of the development, a protoconch is always present and statements indicating the absence of protoconch in some tonnoid taxa (BEU, 1988a:1) are erroneous, although in some species it is not clearly demarcated, or in certain species with lecithotrophic development it may be only partly calcified or in other ways changed because of the specific ontogeny.

Of the tonnoids with detailed information on the mode of development, *Galeodea echinophora* hatches as a crawling juvenile; its larval shell has a diameter of 1.1–1.6 mm

(HUGHES, 1986a) and a single discontinuity is present on the apical part of the shell, demarcating the protoconch from the teleoconch (Figure 120).

BEU (1988a) described the development of *Sassia* (*Austrotriton*) *subdistorta* (Lamarck, 1822), which never forms a normal protoconch I. This species has lecithotrophic development, and the initial whorl is not calcified until late and has the appearance of being incomplete or broken.

Occurrence of non-planktotrophic development is also known, from indirect (protoconch) evidence, in other Cassidae and Ranellidae (examples: species of *Sassia*, see KESTEVEN, 1902:figs. 1–6, BEU, 1987:figs. 127, 130, and this paper, Figure 91; *Sassia* [*Cymatiella*], see BEU, 1988a: figs. 18–21; *Eocymatium pyraster* (Lamarck, 1803), see BEU, 1988b:text-fig. 1G).

LAURSEN (1981) described and figured a larva as "unidentified larva A." Judging from his figures and description, and considering the genera known or presumed to occur in the area where this larva was taken, this may be the larva of a species of *Pisanianura, Oocorys,* or possibly *Gyrineum* Link, 1807. The shape and the sculpture agree and the size range given by Laursen (2.5–3.5 mm) covers all our measurements from preserved apices. His drawings were prepared from specimens close to metamorphosis as is indicated by the ribs being more crowded towards the outer lip. According to Laursen, as many as 2782 specimens were caught between 5° and 35°N in the Atlantic and it was said to be the fifth most common species in his material of 38,000 prosobranch larvae. We have tried to examine Laursen's figured specimens for direct comparison, but it proved impossible to find them in the Zoological Museum in Copenhagen, where this material is kept. Several samples labelled "A" contained mixtures of typical *Cymatium* larvae (*e.g.,* our Figure 98).

Systematical Implications of the Larval Shell Morphology in Tonnoidea

The first result of our discussions above is that we agree with SMITH (1945), who advocated *Ficus* to be a monophyletic genus despite the occurrence of multispiral and paucispiral larval shells in the genus. We do, however, exclude the Ficidae from further comparisons with other Tonnoidea because of the very different larval shell.

Our view on the controversy about larval shells does not imply that genera or subgenera comprising only species with non-planktotrophic development are necessarily polyphyletic. For instance, *Sassia* (*Austrotriton*) is defined by BEU (1988a, b) as a subgenus containing "fossil and living species with caricelloid apices (. . .), reflecting direct development." This shared apical morphology (and mode of development) may be the result of convergence (with *Austrotriton* being polyphyletic) or may be derived from a common ancestor (with *Austrotriton* being monophyletic). Evidence for this is to be looked for in the other shell characters and history of the group, as BEU (1988a) also

did after, we think, overemphasizing the importance of the protoconch. Similarly, we find the erection of *Eocymatium* Beu, 1988b, for a species with a paucispiral protoconch indicating lecithotrophic larval development not justified on the basis of that character alone. Again here we do not mean that *Eocymatium* is not a valid genus, but certainly its mode of larval development by itself does not justify erection of a new genus and Beu (pers. comm.) has emphasized that these two genera also are based on other characters.

The planktotrophic larval shell of tonnoids exhibits great variation between different families, when genera such as **Laubierina**, *Cymatium*, and *Semicassis* are compared. On the other hand, one shell type is represented in several families and subfamilies—a globular shell with a distinct sculpture of thin axial and spiral cords, sharply set off from a smooth surface and intersecting at right angles. *Sassia remensa* (Figure 90) and *S. raulini* (Figure 94) can be taken as examples of this.

A similar sculpture is known from the Cypraeoidea (*e.g.,* RICHTER & THORSON, 1975), the Cancellariidae (Beu, pers. comm.), the Trichotropidae (Warén, unpublished), and the Elachisinidae (Warén, unpublished). In the Trichotropidae, however, this sculpture appears only at the last part of the larval shell and, in the other groups, the ribs are much broader and constitute most of the surface, so that there are no large, smooth interspaces. Therefore we consider the similarity of larval tonnoid shells to those of the other families to be due to convergence.

Reticulated larval shells, similar to those of *Sassia*, occur in the following families and subfamilies: Personidae, **Laubierinidae**, "Oocorythinae," Neptunellinae, and **Pisanianurinae**.

The groups that only have other types of planktotrophic larval shell are the Bursidae, some Cassidae, the Tonnidae, *Cymatium, Charonia,* and the Ranellinae. In the last four cases all species have a chitinous larval shell that has been interpreted as an adaptation to long planktonic life (PECHENIK *et al.,* 1984). Nevertheless, it shows the typical sculpture on the first part of protoconch II (Figures 77, 79, 103, 104).

In the Personidae we are not sure about the interpretation of the larval shell of *Distorsionella* (Figure 121), but it shows the typical reticulate sculpture.

In the Bursidae and Cassidae (Figures 110–117) only the first part of protoconch II has the typical reticulate sculpture, but still it is identical to that in *Sassia*.

In all of these taxa (except **Laubierinidae** and **Pisanianurinae**), there exist also larval shells without or with only very weak sculpture. This we consider a modification by loss of the net-sculpture, in the same way as it is lost on the later part of protoconch II in *Bursa* (Figure 110). There is no case in which an obviously different type of sculpture has evolved.

It is obvious and worth noting that the reticulate sculpture on planktotrophic larvae is better developed in the

deep-sea representatives of the different families. It is more pronounced in *Eudolium* (Figures 78, 79) than in *Tonna* (Figures 76, 77); it is present in *Distorsionella* (Beu, 1978a: fig. 5; this paper, Figure 121), a genus only known from moderately deep water, but absent in *Distorsio* (Figure 122), which is restricted to shallow water. It is strongly developed in many species of *Sassia* (Figures 90, 92), a genus of Ranellidae that had its distributional maximum in the early and mid-Tertiary, and is now restricted to deep water. It is also present in *Oocorys* (Figures 118, 119), but not in the shallow-water cassids. It is also the only type of larval shell known in the **Laubierinidae** and **Pisanianurinae**, both deep-water groups.

We therefore assume that this reticulate sculpture reflects the original condition in the Tonnoidea and that it has subsequently been modified in the more-advanced shallow-water and/or Recent representatives of the superfamily.

This conclusion has been summarized in Figure 163.

It is also obvious, from the discussions above, that the larvae of the Tonnoidea can be determined with good accuracy, at least to subfamily or genus, from existing knowledge. For specific determinations one still must rely on direct comparison of young specimens with preserved larval shells.

We have therefore compiled a key to the planktonic larvae of Tonnoidea.

Tentative Key to the Planktonic Larvae of Tonnoidea

A. Shell calcified, completely covered by reticulate sculpture .... **Laubierinidae**
　　　　　　　　　　　　　　　　　　　Pisanianurinae
　　　　　　　　　　　　Neptunellinae (some *Sassia*)
　　　　　　　　　　　　　　Cassidae (*Oocorys*)
　　　　　　　　　　　　Personidae (*Distorsionella*)
　　　　　　　　　　　　Ranellinae, *Gyrineum* sp.
A. Shell mostly smooth, sometimes with reticulate sculpture on apical whorls .... B
B. Shell calcified C
B. Shell not calcified .... E
C. Shell completely smooth .... D
C. Apical whorls with reticulate sculpture ... Bursidae
D. Operculum with internal ridge, radular teeth membranaceous .... Cassidae (excl. *Oocorys*)
D. Operculum without internal ridges, radular teeth normal .... Neptunellinae (some *Sassia*)
E. Shell with tall spire .... Neptunellinae
E. Shell globular .... F
F. Shell smooth .... Tonnidae
F. Shell with strongly developed periostracal fringes .... Personidae (excl. *Distorsionella*)
　　　　　　　　　　　　　　　　　　Ranellinae

Remarks: The family Ficidae is not included in the key because of incomplete knowledge. See remarks under that family. A complete larval shell of Oocorythinae has not been examined, but we know it to be reticulated (Figures 118, 119).

LITERATURE CITED

Abbott, R. T. 1968. The helmet shells of the world (Cassidae). Part 1. Indo-Pacific Mollusca 2(9):7–202.

Adams, H. & A. 1853–1858. The genera of Recent Mollusca. 1–2. J. van Voorst: London. xl + 484 + 661 pp., 138 pls.

Amadrut, A. 1898. La partie antérieure du tube digestif et la torsion chez les mollusques gastéropodes. Annales des Sciences Naturelles (Zoologie) (7)8:1–291.

Amio, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. Jour. Shimonoseki Univ. Fish. 12(2–3):15–144.

Anderson, D. T. 1959. The reproduction and early life history of the gastropod *Cymalitesta spengleri* (Perry). Proc. Linn. Soc. New South Wales 84:232–237.

Anderson, D. T. 1966. Further observations on the life histories of littoral gastropods in New South Wales. Proc. Linn. Soc. New South Wales 90:242–251, pl. 10.

Anonymous ("Members of Hanshin Shell Club"). 1986. Bibliography of Dr. Tokubei Kuroda. Nishinomiya. 102 pp., 33 pls.

Arakawa, K. Y. & S. Hayashi. 1972. On sexual dimorphism of fig shell, *Ficus subintermedia* (d'Orbigny). Venus 31:63–71.

Bandel, K. 1975. Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). Abhandlungen der Mathematishcen-Naturwissenschaftlichen Klasse der Akademie der Wissenschaften und Litteratur 1975(1):1–133, pls. 1–21.

Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandlungen 214:1–188, pls. 1–22.

Barnard, K. H. 1960. New species of South African marine gastropods. Jour. Conchol., London 24:438–442.

Bayer, F. M. 1971. New and unusual mollusks collected by R/V John Elliott Pillsbury and R/V Gerda in the tropical western Atlantic. Bull. Mar. Sci. 21(1):111–236.

Bellardi, L. 1873 ("1872"). I Molluschi dei terreni terziari del Piemonte e della Liguria. Parte I. Memorie della Reale

Accademia di Scienze, Torino (2)27:1–264, pls. 1–15. (For date of publication, see page 264.)

BEU, A. G. 1969. The gastropod genus *Thalassocyon* Barnard, 1960. N.Z. Jour. Mar. Freshwater Res. 3:445–452.

BEU, A. G. 1976. Revision of the southwest Pacific species of *Morum* (Oniscidia) (Gastropoda: Cassidae). Jour. Malacol. Soc. Australia 3:223–231.

BEU, A. G. 1978a. New records and species of Cymatiidae (Gastropoda: Prosobranchia) from the Kermadec Islands, Norfolk Ridge and New Zealand. Jour. Malacol. Soc. Australia 4:29–42.

BEU, A. G. 1978b. The marine fauna of New Zealand: the molluscan genera *Cymatona* and *Fusitriton* (Gastropoda, family Cymatiidae). Mem. N.Z. Oceanogr. Inst. 65:1–42.

BEU, A. G. 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. Australian Mus. 33(5):248–324.

BEU, A. G. 1985. A classification and catalogue of living world Ranellidae (=Cymatiidae) and Bursidae. Conchol. Amer. Bull. 13(4):55–66.

BEU, A. G. 1987 ("1986"). Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 2. Descriptions of 14 new modern Indo-West Pacific species with revisions of related taxa. N.Z. Jour. Zool. 13:273–355. (Published January 1987 *fide* Beu.)

BEU, A. G. 1988a. Two rare and bizarre species of *Sassia* Bellardi, 1872 (Gastropoda: Ranellidae) in southern Australia, with a new species and notes on the development of *Sassia* (*Austrotriton*). Jour. Malacol. Soc. Australia 9:1–9.

BEU, A. G. 1988b. Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 5. Early history of the families, with four new genera and recognition of the family Personidae. Saito Ho-on Kai Special Publication (Professor Kamio Kotaka Commemorative Volume) 2:69–96.

BEU, A. G. & W. O. CERNOHORSKY. 1986. Taxonomy of gastropods of the families Ranellidae (=Cymatiidae) and Bursidae. Part 1. Adoption of Ranellidae, and a review of *Linatella* Gray, 1857. N.Z. Jour. Zool. 13:241–266.

BOSS, K. 1982. Mollusca. *In:* Parker, S. P. (ed.), Synopsis and classification of living organisms 1:944–1166. McGraw-Hill Company.

BOUCHET, P. 1989. A review of poecilogony in Gastropoda. Jour. Moll. Stud. 55:67–78.

CAZENAVETTE, B. 1853. Note sur la coquille des jeunes *Dolium perdix*. Actes de la Société Linnéenne de Bordeaux 19:62–64.

CERNOHORSKY, W. O. 1976. Notes on the genus *Eudolium* Dall, 1889. Bull. Conchol. Sect. Auckland Mus. New Series 1(1):1–2.

CLENCH, W. J. & R. D. TURNER. 1957. The family Cymatiidae in the western Atlantic. Johnsonia 3(36):189–244.

COLMAN, P. 1987. A strange ficid new to the Australian fauna. Australian Shell News 59/60:1.

COSSMANN, M. 1901. Essais de paléoconchologie comparée, 4. Paris. 293 pp.

DALL, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer "Blake", Lieut.-commander C. D. Sigsbee, U.S.N, and commander J. R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part 2. Gastropoda and Scaphopoda. Bull. Mus. Comp. Zool. 18:1–492.

DALL, W. H. 1909. Contributions to the Tertiary paleontology of the Pacific coast. I. The Miocene of Astoria and Coos Bay, Oregon. U.S. Geol. Surv. Prof. Papers 59:1–278, pls. 1–23.

DALL, W. H. 1924. On the value of nuclear characters in the classification of marine gastropods. Jour. Wash. Acad. Sci. 14:177–180.

D'ASARO, C. N. 1969. The comparative embryogenesis and early organogenesis of *Bursa corrugata* Perry and *Distorsio clathrata* Lamarck (Gastropoda: Prosobranchia). Malacologia 9(2):349–389.

DAUTZENBERG, P. 1889. Contribution à la faune malacologique des îles Açores. Résultats des campagnes scientifiques.... Albert Ier 1:1–112.

DAUTZENBERG, P. & H. FISCHER. 1906. Mollusques provenant des dragages effectués à l'Ouest de l'Afrique. Résultats des campagnes scientifiques.... Albert Ier 32:1–125.

DAWYDOFF, C. 1940. Quelques véligères géantes de Prosobranches provenant de la mer de Chine. Bull. Biologique de France et de Belgique 74:497–508.

DAY, J. H. 1969. Feeding of the cymatid gastropod *Argobuccinum argus* in relation to the structure of the proboscis and secretions of the proboscis gland. Amer. Zool. 9:909–916.

DELL, R. K. 1956. The archibenthal Mollusca of New Zealand. Dominion Mus. Bull. 18:1–235.

DELL, R. K. 1967. Some Mollusca from deep water to the north of New Zealand collected by the Tui, 1962. Rec. Dominion Mus. Wellington 5(25):305–315.

DELL, R. K. & S. P. DANCE. 1963. The molluscan genus *Ranella* and the distribution of *Ranella olearium* (Linnaeus). Proc. Malacol. Soc. London 35:159–166.

FERRERO MORTARA, E., L. MONTEFAMEGLIO, G. PAVIA & R. TAMPIERI. 1981. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, parte I. Museo Regionale di Scienze Naturali: Torino. 327 pp.

FINLAY, H. J. 1931. On *Austrosassia, Austroharpa,* and *Austrolithes,* new genera; with some remarks on the gastropod protoconch. Trans. N.Z. Inst. 62:7–19.

FISCHER, P. 1863. Sur la coquille embryonnaire du *Dolium perdix*. Jour. Conchyl., Paris 11:147–149.

FISCHER, P. 1883. Diagnoses d'espèces nouvelles de mollusques recueillis dans le cours de l'expédition scientifique du Talisman (1883). Jour. Conchyl., Paris 31:391–394.

FOLIN, L., DE. 1884. Une série de mollusques des explorations de 1881–1883. Les Fonds de la Mer 4:201–212.

FORBES, E. 1852. On a new testacean discovered during the voyage of H.M.S. Rattlesnake. Rep. Brit. Assoc. Adv. Sci. 1851:77.

GOHAR, H. & A. M. EISAWY. 1967. The egg-masses and development of four taenioglossan prosobranchs from the Red Sea. Publ. Mar. Biol. Sta. Al-Ghadarqa, Egypt 14:109–147.

GOLIKOV, A. N. & Y. I. STAROBOGATOV. 1986. New gastropodan species *Conradia minuta* from temperate waters of north-western Pacific. Proc. Zool. Inst., Leningrad 148:90–92 [in Russian].

GRAY, J. E. 1854. On the division of the ctenobranchous gasteropodous Mollusca into larger groups and families. Proc. Zool. Soc. London 21:32–44.

HABE, T. 1961. Colored illustrations of the shells of Japan (II). Hoikusha: Osaka. xii + 183 pp., 66 pls. [in Japanese; English edition 1964].

HABE, T. 1962. Trichotropidae in Japan (Mollusca). Bull. Natl. Sci. Mus., Tokyo 6(2):67–77.

HALLER, B. 1893. Die Morphologie der Prosobranchier, ge-

sammelt auf einer Erdumsegelung durch die königl. italienische Korvette "Vettor Pisani." Morphologishe Jahrbücher 19:553–591, pls. 18–21.

HOAGLAND, K. E. & R. ROBERTSON. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or phantasy. Biol. Bull. 174:109–125.

HOUBRICK, J. R. & V. FRETTER. 1969. Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. Proc. Malacol. Soc. London 38:415–429.

HUGHES, R. N. 1986a. Laboratory observations on the feeding behaviour, reproduction and morphology of *Galeodea echinophora* (Gastropoda: Cassidae). Zool. Jour. Linn. Soc. London 86:355–365.

HUGHES, R. N. 1986b. Anatomy of the foregut of *Morum* Röding, 1798 (Gastropoda: Tonnacea) and the taxonomic misplacement of the genus. Veliger 29(1):91–110.

HUGHES, R. N. & H. P. HUGHES. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 20:385–402.

IREDALE, T. 1936. Australian molluscan notes. No. 2. Rec. Australian Mus. 19:267–340, pls. 20–24.

JABLONSKI, D. & R. LUTZ. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58:21–89.

KEEN, A. M. 1971. Sea shells of tropical west America. 2nd ed. Standford University Press: Standford, California. 1064 pp.

KESTEVEN, H. L. 1901. The protoconchs of certain Port Jackson Gasteropoda. Proc. Linn. Soc. New South Wales 1901(4): 709–720.

KESTEVEN, H. L. 1902. Notes on Prosobranchiata. No. 1. *Lotorium*. Proc. Linn. Soc. New South Wales 1902(3):443–485.

KURODA, T. 1958–1959. Descriptions of new species of marine shells from Japan. Venus 20(4):317–335, pls. 20–21 [pl. 20 published in the second issue of Vol. 20, Oct. 1958, and has the figures referred to, while the description was published in November, the year after].

LADD, H. S. 1977. Cenozoic fossil mollusks from western Pacific islands; gastropods (Eratoidae through Harpidae). U.S. Geol. Surv. Prof. Papers 533:1–84, pls. 1–23.

LAMY, E. 1928. La ponte chez les gastéropodes prosobranches. Jour. Conchyl., Paris 72:80–126.

LAURSEN, D. 1981. Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. Dana Report 89: 1–43.

LAWS, C. R. 1944. The molluscan faunule at Pakaurangi Point, Kaipara. No. 3. Trans. Royal Soc. N.Z. 73(4):297–312.

LAXTON, J. H. 1969. Reproduction in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). Zool. Jour. Linn. Soc. London 48:237–253.

LOCARD, A. 1897. Mollusques Testacés, 1. Expéditions scientifiques du Travailleur et du Talisman. Masson: Paris. 516 pp.

MACDONALD, J. D. 1855. Remarks on the anatomy of *Macgillivrayia pelagica* and *Chelotropis huxleyi* (Forbes); suggesting the establishment of a new order of Gasteropoda. Phil. Trans. Royal Soc. London 115(2):289–293.

MARSHALL, B. A. 1978. Cerithiopsidae (Mollusca: Gastropoda) of New Zealand, and a provisional classification of the family. N.Z. Jour. Zool. 5:47–120.

ÖRSTED, A. S. 1850. Forelöbig Underretning om Dyret af en Art af Slaegten *Pyrula* Lamk. 1801. Videnskablige Meddelelser fra Dansk Naturhistorisk Forening (1850):9–14, pl. 1.

PANCERI, P. 1869. Gli organi e la secrezione dell'acido solforico nei gasteropodi. Atti della Accademia delle Scienze Fisiche e Mathematiche, Napoli 4(10):1–56.

PECHENIK, J., R. SCHELTEMA & L. EYSTER. 1984. Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport. Science 224: 1097–1099.

PELSENEER, P. 1888. Report on the anatomy of the deep-sea Mollusca collected by H.M.S. Challenger in the years 1873–76. Reports on the Scientific Results of the Challenger Expedition. Zoology 74:1–40, pls. 1–4.

PELSENEER, P. 1906. Biscayan plankton. Part VII. Mollusca (excluding Cephalopoda). Proc. Linn. Soc. London (Zool.) 10:137–157, pls. 10–12.

PENCHASZADEH, P. 1981. A peculiar development pattern in *Tonna galea* from Venezuela. Internatl. Jour. Invert. Reprod. 4:209–212.

PETIT, E. & J. RISBEC. 1929. Sur la ponte de quelques gastéropodes prosobranches. Bull. Soc. Zool. France 54:564–570.

PHILPOTT, C. H. 1925. Observations on the early development of *Argobuccinum oregonense*. Publ. Puget Sound Mar. Biol. Stat. 3(74):369–380.

PIANI, P. 1977. Il genere *Eudolium* in Mediterraneo: alcuni problemi di sistematica generica e specifica. Conchiglie 13(1–2):27–40.

PILKINGTON, M. C. 1974. The eggs and hatching stages of some New Zealand prosobranch molluscs. Jour. Royal Soc. N.Z. 4:411–431.

PILKINGTON, M. C. 1976. Descriptions of veliger larvae of monotocardian gastropods occurring in Otago plankton hauls. Jour. Moll. Stud. 42:337–360.

PILSBRY, H. A. 1945. New Floridian marine molluscs. Nautilus 59:59–60.

PILSBRY, H. A. 1949. *Dissentoma*, the embryonic stage of *Cymatium martinianum* (Orb.). Nautilus 62:142.

PINNA, G. & L. SPEZIA. 1978. Catalogo dei tipi del Museo Civico di Storia Naturale di Milano. V. I tipi dei Gasteropodi fossili. Atti della Società Italiana di Scienze naturale e del Museo civico di Storia naturale, Milano 119:125–180.

PONDER, W. F. 1984. A new species of *Galeodea* (Cassidae, Gastropoda) from Queensland, Australia. Jour. Malacol. Soc. Australia 6(1–2):91–97.

QUINN, J. F. 1980. A new genus, species and subspecies of Oocorythidae (Gastropoda: Tonnacea) from the western Atlantic. Nautilus 94(4):149–158.

QUOY, J. J. C. & J. P. GAIMARD. 1835. Voyage des Découvertes de l'Astrolabe. Zoologie, 3. J. Tastu: Paris. 954 pp., atlas.

REYNELL, A. 1905. Some account of the anatomy of *Cassidaria rugosa* (Linn.). Proc. Malacol. Soc. London 6:292–299.

REYNELL, A. 1906. *Cassidaria rugosa*. Proc. Malacol. Soc. London 7:67.

RICHTER, G. 1984. Die Gehäuseentwicklung bei den Larven der Cymatiiden. Archiv für Molluskenkunde 115:125–141.

RICHTER, G. & G. THORSON. 1975. Pelagische Prosobranchier-Larven des Golfes von Neapel. Ophelia 13:109–185.

RISBEC, J. 1931. Notes sur la reproduction de quelques prosobranches néo-calédoniens. Annales de l'Institut Oceanographique 10(2):23–33.

RISBEC, J. 1936 ("1935"). Biologie et pontes de mollusques gastéropodes néo-calédoniens. Bull. Soc. Zool. France 60: 387–417.

RISBEC, J. 1955. Considerations sur l'anatomie comparée et la classification des gastéropodes prosobranches. Jour. Conchyl., Paris 95:45–82.

ROBERTSON, R. 1976 ("1974"). Marine prosobranch gastropods: larval studies and systematics. Thalassia Jugoslavica 10:213–238.

ROSSI RONCHETTI, C. 1955. I tipi della "Conchiologia fossile subapennine" di G. Brocchi, 7. Rivista italiana di Paleontologia 60(1):187–202.

ROVERETO, G. 1899. Prime ricerche sinonimiche sui generi dei gasteropodi. Atti della Societa ligustica di Scienze Naturale e Geografiche, Genova 10:101–110.

SCHELTEMA, R. 1966. Evidence for trans-Atlantic transport of gastropod larvae belonging to the genus Cymatium. Deep-Sea Res. 13:83–95.

SCHELTEMA, R. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water marine benthic gastropods. Biol. Bull. 140:284–322.

SCHELTEMA, R. 1972. Eastward and westward dispersal across the tropical Atlantic Ocean of larvae belonging to the genus Bursa (Prosobranchia). Internatl. Rev. Ges. Hydrobiol. 57:863–873.

SCHELTEMA, R. & I. WILLIAMS. 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and western Pacific mollusks. Bull. Mar. Sci. 33:545–565.

SCHEPMAN, M. M. 1909. The Prosobranchia of the Siboga Expedition. Part II. Taenioglossa and Ptenoglossa. Siboga-Expeditie 49b:107–231, pls. 10–16.

SIMROTH, H. 1896–1907. Bronn's Klassen und Ordnungen des Tier-Reichs. 3 (2). Mollusca: Gastropoda Prosobranchia. Leipzig. 1056 pp.

SIMROTH, H. 1911. Die Gastropoden des nordischen Planktons. Nordisches Plankton, Zoologie 5:1–36.

SMITH, B. 1907. A contribution to the morphology of Pyrula. Proc. Acad. Natur. Sci., Philadelphia 1907:208–220.

SMITH, B. 1945. Observations on gastropod protoconchs. Paleontologica Americana 3(19):1–48.

STRATHMANN, R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32:894–906.

STRATHMANN, R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16:339–361.

THIELE, J. 1929. Handbuch der Systematischen Weichtierkunde 1(1):1–376. G. Fischer: Stuttgart.

THORSON, G. 1940. Studies on the egg masses and larval development of Gastropoda from the Iranian Gulf. Pp. 159–238. In: Danish scientific investigations in Iran, part 2. Ejnar Munksgaard: Copenhagen.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25:1–45.

TROSCHEL, F. H. 1863. Das Gebiss der Schnecken 1(5):197–252, pls. 17–20. Berlin.

TURNER, R. 1948. The family Tonnidae in the western Atlantic. Johnsonia 2(26):165–192.

WATSON, R. B. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. 'Challenger' during the years 1873–76. Report on the Scientific Results of the Challenger Expedition, Zoology 42:1–756.

WEBER, H. 1927. Der Darm von Dolium galea L., eine vergleichend anatomische Untersuchung unter besonderer Berücksichtigung der Tritonium-arten. Zeitschrift für Morphologie und Ökologie der Tiere 8:663–801.

WENZ, W. 1941. Handbuch der Paläozoologie, Band 6. Gastropoda, Teil 5:pp. 961–1200. Berlin.

WILSON, B. R. & K. GILLETT. 1971. Australian shells. A. H. & A. W. Reed: Sydney. 168 pp.

WRIGLEY, A. 1929. Notes on English Eocene Mollusca, with descriptions of new species. III. Ficus. Proc. Malacol. Soc. London 18:235–251.

APPENDIX: LIST OF SPECIMENS FIGURED

FICIDAE

Thalassocyon bonus, NZOI sta. P941, Tasman Basin, 41°15.2'S, 167°07.2'E, 1452–1463 m (NZOI). Figures 1, 2.

Thalassocyon bonus, off East Cape, New Zealand, 37°30'S, 179°22'E, 1128–1200 m (NMNZ M 35293). Figure 133.

Thalassocyon bonus, NE of Chatham Id., New Zealand, 42°56'S, 175°05'W, 1004–1011 m (NMNZ M 75253). Figure 134.

Thalassocyon bonus, S of Amsterdam Id., MD50 sta. DC167, 38°24'S, 77°29'E, 1430–1600 m (MNHN). Figure 135.

Thalassocyon bonus, holotype (SAM A 9714). Figure 132.

Ficus communis Röding, 1798, Florida (SMNH). Figure 80.

Ficus sp., Seychelles, Reves 2 sta. 42, 04°31'S, 56°09'E, 52 m (MNHN). Figures 3, 4.

Ficus conditus (Brongniart, 1823), St. Paul les Dax, SW France, Burdigalien, lower Miocene, P. Lozouet coll. (MNHN). Figure 81.

Ficus sp., Philippines, Musorstom 3 sta. CP100, 14°00'N, 120°18'E, 189–199 m (MNHN). Figure 82.

Ficus subintermedia (d'Orbigny, 1852), New Caledonia, Musorstom 4 sta. CP148, 19°23'S, 163°32'E, 58 m (MNHN). Figures 148, 149.

BURSIDAE

Bufonaria marginata (Gmelin, 1791), Canaries, Gran Canaria, off La Luz, 100 m, coralline algae (SMNH 3271). Figures 7, 8.

Bufonaria marginata, off Mauretania, 18°54'N, 16°32'W, 60 m (MNHN). Figures 113, 114.

Bursa sp., Gilbert Id., Aranuka (SMNH 3853). Figures 5, 6, 59, 60.

Bursa sp., larva, Demeraby sta. DS02, 08°10'N, 49°05'W, 4430 m (MNHN). Figures 58, 110–112.

TONNIDAE

Tonna sp., larva, off SE South Africa, 33°34'S, 27°41'E, surface plankton, 10 Oct. 1902 (SMNH 2717). Figures 9, 10, 61, 62, 73, 74.

Tonna galea (L., 1758), Malta (SMNH). Figure 75.

Tonna galea, Macahé, Isla Santa Anna, off Rio de Janeiro, Brasil (SMNH). Figures 76, 77.

Tonna sp., Tamatave, Madagascar, young specimen (SMNH 2676). Figure 12.

Tonna allium (Dillwyn, 1817), Sumatra, Priaman (SMNH 474). Figures 13, 14, 49.

Eudolium crosseanum (Monterosato, 1869), Biacores sta. 161, the Azores, 37°40′N, 25°51′W, 590 m, young specimen, height 26.1 mm (MNHN). Figures 11, 78, 79.

CASSIDAE

Oocorys sulcata (Fischer, 1883), off S Portugal, Noratlante sta. B12, 36°22′N, 08°43′W, 2873 m (MNHN). Figures 15, 16, 24, 50, 150–152.

Oocorys abyssorum (Verrill & S. Smith, 1884), SE Atlantic, Vema sta. CP02, 11°00′N, 45°15′W, 5073 m (MNHN). Figure 66.

Oocorys bartschi Rehder, 1943, Pequegnat 68 A13 sta. 22, 27°38′N, 95°22′W, 476 m (MNHN). Figure 119.

Oocorys umbilicata Quinn, 1980, Gulf of Mexico, 21°30.3′N, 96°11.7′W, 2245 m (MNHN). Figure 118.

Galeodea echinophora (Linné, 1758), Mediterranean, Golfo di Genova, Sori, 35–55 m (SMNH 476). Figures 17, 18, 22, 51.

Galeodea echinophora, Mediterranean, Corsica, off Calvi, 50–70 m (SMNH). Figure 120.

Cypraecassis testiculus (Linné, 1758), larva, Dana sta. 1286: V, 15°17′N, 61°29′W, plankton (ZMC). Figures 23, 115–117.

Semicassis granulatum (Born, 1779), Mediterranean, Golfo di Genova, Sori, 20–30 m (SMNH 475). Figures 19, 20.

Semicassis sp. aff. *granulatum* (Born, 1778), Dana sta. 1353, 33°51′N, 66°43′W, plankton (ZMC). Figures 63, 64.

Semicassis granulatum, no loc. (SMNH). Figure 65.

Semicassis saburon (Bruguière, 1792), N'Diago sta. 5, 17°26′N, 16°39′W, 500 m (MNHN). Figure 21.

PISANIANURINAE

Pisanianura grimaldii, New Caledonia, Biocal sta. DW51, 23°05′S, 167°45′E, 680–700 m (MNHN). Figures 25, 26, 55, 68.

Pisanianura grimaldii, Biocal sta. DW51, 23°05′S, 167°45′E, 680–700 m (MNHN). Figure 95.

Pisanianura grimaldii, R/V *Vauban* sta. CH22, 12°27′S, 40°10′E, 680–700 m (MNHN). Figures 94, 127.

Pisanianura grimaldii, holotype, Azores (MOM), 27.6 mm. Figure 126.

Pisanianura breviaxe, Biocal sta. CP52, 23°06′S, 167°47′E, 540–600 m (MNHN). Figures 27, 123, 153, 154.

Pisanianura breviaxe, holotype, off Kochi Pref., Japan (NSMT Mo 38611). Figure 124.

Pisanianura inflata (Brocchi, 1814), Pradalbino, prov. Bologna, Italy, Pliocene, deep-water deposits (Coll. della Bella). Figures 93, 125.

Kaiparanura spiralis (Marshall, 1918), holotype (NZGS Tm 6921), Pakaurangi Point, Kaipara Harbour, New Zealand, Altonian or more probably Otaian age (Lower Miocene, A. Beu, pers. comm.). Figures 144, 145.

Kaiparanura spiralis, 1 mile NW of Pakaurangi Point, Kaipara Harbour, New Zealand (NMNZ M 81338). Figures 142, 143.

RANELLINAE

Argobuccinum pustulosum tumidum (Dunker, 1862), small specimen, 12 mm high, Waihau Bay, Cape Runaway (NMNZ 15045). Figures 52, 69, 86.

Fusitriton magellanicus (Röding, 1798), Patagonia, Puerto Pantalon, low tide (SMNH 663). Figure 53.

Fusitriton magellanicus, Portobello Canyon, ENE of Taiaroa Head, New Zealand, 540 m (NMNZ 9196). Figure 85.

Ranella olearia (Linné, 1758), Biacores sta. 41, 37°44′N, 29°04′W, 450–475 m (MNHN). Figures 31, 32.

Ranella olearia, Balgim sta. CP25, 36°41.5′N, 07°19.4′W, 544 m (MNHN). Figures 87, 88.

Ranella australasia (Perry, 1811), off Newcastle, NSW, Australia, 33°20′S, 152°17′E, surface plankton (AMS C 147218). Figures 30, 89.

NEPTUNELLINAE

Sassia kampyla (Watson, 1885), ENE of Taiaroa Head, 542 m, young specimen, height 6.9 mm (NMNZ 9196). Figure 28.

Sassia parkinsonia (Perry, 1811), Twofold Bay, NSW, height of shell 25 mm (AMS C 50074). Figure 29.

Sassia raulini (Cossmann & Peyrot, 1923), Chattian, Upper Oligocene of Bassin de l'Adour, coll. Lozouet (MNHN). Figure 90.

Sassia textilis (Tate, 1898), Muddy Creek, Hamilton, Victoria, Miocene (AMS C 146536). Figure 91.

Sassia remensa (Iredale, 1936), E of Lady Musgrave Id., Queensland, 23°52′S, 152°42′E, 296 m (AMS C 147348). Figure 92.

Charonia, larva, Dana sta. 1247:II, 17°57′N, 72°51′W, plankton (ZMC). Figures 37, 67, 99.

Charonia lampas (Linné, 1758), Conil, S Spain, from fishermen (SMNH). Figures 39, 40.

Cabestana cutacea (Linné, 1767), Messina, Sicily (SMNH 655). Figures 35, 54.

Cymatium, larva, Dana sta. 3940:Ia, 08°24′S, 42°54′E (ZMC). Figures 38, 70, 100.

Cymatium, larva, Dana sta. 3940:Ib, 08°24′S, 42°54′E (ZMC). Figure 34.

Cymatium, larva, Dana sta. 1253:V, 17°43′N, 64°56′W, plankton (ZMC). Figures 36, 98, 104.

Cymatium, young larva, Dana sta. 1337, 29°36′N, 64°01′W, plankton (ZMC). Figure 97.

Cymatium muricinum (Röding, 1798), Hawaii, coral reef at Honolulu (SMNH 649). Figure 33.

Cymatium problematicum Dautzenberg & Fischer, 1906, Gran Canaria, 15 m (SMNH). Figure 101.

Cymatium sp., Madeira, Eugenie Expedition (SMNH). Figures 102, 103.

PERSONIDAE

Distorsio reticularis (Linné, 1758), New Caledonia, 19°06'S, 163°10'E, 50 m (MNHN). Figure 122.

Distorsio clathrata (Linné, 1758), no data (SMNH). Figures 146, 147.

Distorsio sp., Philippines, Musorstom 3 sta. 117, 12°31'N, 120°39'E, 92–97 m (MNHN). Figure 84.

Distorsionella lewisi (Beu, 1978), New Caledonia, Biocal sta. DW66, 24°55'S, 168°22'E, 505–515 m (MNHN). Figure 121.

LAUBIERINIDAE

Laubierina sp., recently metamorphosed young, Mozambique Channel, Benthedi sta. 87, 11°44'S, 47°35'E, 3716 m (MNHN). Figures 41, 42, 56, 71, 162.

Laubierina sp., young, Caribbean, 21°35'N, 96°54.6'W, 937 m (MNHN). Figures 130, 131.

Laubierina peregrinator, Mozambique Channel, Benthedi sta. CH13, 12°13'S, 46°40'E, 2300–2500 m (MNHN). Figures 43, 44, 128, 129, 159–161.

Laubierina sp., the Azores, Biacores sta. 195, 37°56'N, 24°49.5'W, 1700–1776 m (MNHN). Figures 105, 107, 108.

Laubierina sp., Madeira sta. 13, 32°34'N, 17°07'W, 1970 m (MNHN). Figure 106.

Laubierina sp., New Caledonia, Biocal sta. DW48, 23°00'S, 167°29'E, 775 m (MNHN). Figure 96.

Akibumia orientalis, USBF sta. 4919, Kagoshima Gulf, Japan, 800 m (USNM 206835). Figures 45, 72, 136.

Akibumia orientalis, off Sydney, 33°36'S, 152°05'E, 1106–1143 m (AMS C 150223). Figures 46, 57, 157, 158.

Akibumia orientalis, holotype (ZMA 3.02.041). Figures 137, 138.

Akibumia schepmani, off S Queensland, 28°01'S, 153°59'E, 550 m (AMS C 150192). Figures 47, 48, 155, 156.

Akibumia flexibilis, Japan (ANSP). Figure 109.

Akibumia flexibilis, syntype (coll. Kuroda). Figure 140.

Akibumia schepmani, holotype (ZMA 3.62.001). Figure 139.

Akibumia flexibilis, Latham Id., S of Zanzibar, 06°52'S, 39°54'E (USNM 718939). Figure 141.

EPITONIIDAE

Akibumia reticulata Habe, 1962 (now Epitoniidae, provisionally *Epitonium*), holotype (NSMT M 39818). Figure 83.