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A review of the Genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea)

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ABSTRACT. The family Rissoidae is defined, and a detailed diagnosis of the family is given. The characters of the shell (and protoconch), radula, operculum, head-foot and anatomy are described and discussed for the family and for each genus (where they are known). The Rissoidae is contrasted with other Rissoacea, and the relevance of genital characters in higher classification is discussed. The genera are reviewed in the light of new information on the anatomical, radular, opercular and head-foot characters as well as shell microsculpture and other aspects of shell morphology. Thirty one genera and 24 subgenera are recognized in the family. Four of the subgenera are described as new, and one new genus and species are also described. A further 106 genus-group taxa are listed as synonyms. Eleven family-group taxa are included in the synonymy of the Rissoidae, and two subfamilies (Rissoinae and Rissoininae) are recognized. Of the remaining 119 genus-group taxa referred to the Rissoidae by previous reviewers, four Jurassic genera are tentatively included in the family and the remaining 115 are included in other families. A phenetic classification of the genera is developed using a summary of unweighted characters. The Falsicingulidae is diagnosed and it is suggested that it is closely allied to the Pomatiopsidae. A new family is created for *Epigrus* Hedley.

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CONTENTS

The rissoids are a group of small to minute epifaunal prosobranchs that are abundant in seas throughout the world. Almost all are marine although a few species live in brackish water. Some closely related families are adapted to live in fresh and brackish water, and four of these are, at least in part, terrestrial.

Rissoids occur in considerable numbers in the north-eastern Atlantic and the Mediterranean Sea, and some species achieve a high biomass in intertidal and shallow sublittoral habitats (Fretter & Graham, 1962). The larvae of some have been shown (Lebour, 1934) to be important as food for larval herrings.

The Rissoidae have proved to be very difficult to classify at all levels because of their small size, diverse form and the confusion caused by convergence, especially in shell characters. Although there have been attempts to revise the genera and subfamilies contained within the Rissoidae (*sensu lato*) no previous author has had access to the quantity of material examined during this revision. The reviews of Thiele (1929) and Wenz (1939) were but small parts of major treatises and were based, in the main, on the general similarity of shells, as was the compilation of generic units by Coan (1964). I revised the subfamilial classification of the Rissoidae, and some of the genera it contains, on the basis of observations and anatomical work on New Zealand species (Ponder, 1967). This work refined the fundamentally sound work of Thiele (1929), and substantially modified Coan's (1964) listing of subfamilies and genera, but was limited because of lack of specimens of many genera. Nordsieck (1972) revised the European species and introduced many changes, especially at the generic level. The classification of prosobranchs by Golikov & Starobogatov (1975) placed members of what I considered (1967) a single family in ten families assigned to five superfamilies. Slavoshevskaya (1975a) recognized seven families amongst the rissoids (*sensu lato*) on the basis of differences in their genitalia, and later (1983) raised the Rissoacea to the level of suborder. I (Ponder, 1967) recognized four subfamilies of which two are now included in a separate family, Barleeidae (Ponder, 1983a), and several genera that were previously included in the Rissoidae have now been placed in the Iravadiidae (Ponder, 1984) and Cingulopsidae (Ponder & Yoo, 1980).

This paper assesses the taxonomic position of genera previously assigned to the Rissoidae, and reviews genera now included in the family. Type-species of genera have been examined whenever possible. The classification adopted is based on a combination of characters found in the shell, radula, operculum and, where possible, from the details of the head-foot and internal anatomy of living specimens. The assessment of the significance of these characters and the relationships of the genera is primarily subjective. A large number of characters are tabulated to facilitate comparison and these are analysed using data processing methods (Appendix 3) to give a somewhat more objective assessment of intergeneric relationships.

The classification presented is still at a somewhat tentative stage, largely because of lack of information regarding living animals and anatomical features of some type-species of genera. It is, however, unlikely that even with further delay in publication, the amount of information available will alter substantially.

Biology

Ecology and habits. Rissoids are found generally in the shallow seas of the world and in the mid to lower littoral zone. A few species live on the continental slopes and in abyssal depths. The greatest diversity of species is found in the lowest littoral and shallow sublittoral where the majority occur on algae, beneath stones, slabs of coral or other objects that provide shelter. Habitat may be associated with presence or absence of pigmentation and a posterior pedal mucous gland. In general the species living on algae are highly mobile, usually have a well developed posterior pedal mucous gland and are often pigmented. Species living beneath stones usually lack a posterior pedal gland and have a translucent-white head-foot. Species with a posterior mucous gland generally have the ability to secrete threads of mucus and suspend themselves from the surface film. The usual mode of locomotion is by the action of pedal cilia in a mucous film. The behaviour and locomotion of *Rissoa parva* (Da Costa) has been described by Delphy & Magne (1938).

It is assumed that most rissoids are annuals (Fretter & Graham, 1978) but there is very little data available to support this view. Wigham (1975) has shown that *Rissoa parva* has a life span of 8–9 months or only 3–4 months depending on the time of settlement.

Feeding. Most algal-living species appear to feed on the diatomaceous or micro-algal film covering the macro-algae they inhabit, rather than the macro-alga itself. Some species that shelter beneath stones or in crevices, feed on Foraminifera (e.g. *Rissoina*: Kosuge, 1965; Ponder, 1968) but these species have particles of other food in their stomachs. Presumably some deep-sea species, and possibly some shallow-water forms, are selective deposit feeders. *Alvania jeffreysi* (Waller), and *Cingula* (= *Setia (Pseudosetia)*) *turgida* (Jeffreys) are said to feed selectively on Foraminifera (Warén in Fretter & Manly, 1979), but I have observed that these species have considerable quantities of fine detrital material in their stomachs, and forams do not appear to be a major food item.

Fretter & Manly (1979) have shown that *Alvania punctura* (Montagu) feeds selectively on diatoms and dinoflagellates to the exclusion of detrital particles, whereas *Rissoa* (= *Pusillina*) *inconspicua* Alder differed in that the stomach contained fragmented plant tissue in addition to unicellular algae and detritus. *Rissoa parva* is even less selective, including much detritus in its diet. Fretter & Graham (1978) give additional details for several European species.

Distribution

Rissoids inhabit all seas of the world ranging from the Arctic and Antarctic to the tropics. Some genera, particularly those containing species with planktotrophic larvae, have widely distributed species and are either world-wide in distribution (e.g. *Alvania*, *Rissoina*) or are distributed throughout the Indo-Pacific region (e.g. *Lucidestea*). Other genera are confined to relatively small geographic areas, and these are usually genera whose species undergo direct development (e.g. *Attenuata*, *Lironoba*, *Cingula*). A few genera (in particular *Onoba*) have world-wide distributions, and contain mostly species that have direct development as their reproductive mode. *Onoba* has a distribution in the temperate and cold regions of both hemispheres. The genus *Rissoa* (in the narrow sense used herein) has pelagic larvae but is restricted to the north-eastern Atlantic and the Mediterranean area. This genus probably arose in the early Tertiary after the establishment of the present Atlantic oceanic circulation pattern which limits westward dispersal opportunities.

Stratigraphic range. The first known rissoids occur in the Middle Jurassic (Great Oolite) of Europe (see under *Rissoina* and *Zebina* below). These may have evolved from the Pseudomelaniidae, a diverse, extinct group which may have also given rise to several other mesogastropod families. Few rissoids are recorded from Cretaceous rocks, but many are known through the Tertiary. The Eocene faunas, particularly of Europe, contain a wide variety of species and many of the living genera extend back to the Eocene.

The fossil record is poor, probably because most rissoids inhabit shallow-water, hard-shore environments which do not generally provide good conditions for fossilization. Moreover, in many deposits, small fossils are leached from the rocks leaving only the relatively massive macrofossils. Potentially useful fossil faunas have been either ignored or treated superficially owing to considerable neglect of small molluscs by palaeontologists.

The Anglo-Parisian Basin, whose very extensive faunas from early Tertiary times are well known, has provided most of the useful material, and represents a wide range of environments. New Zealand has a reasonably well studied Tertiary fauna of small gastropods, and there are some, mostly deeper water species known (but undescribed) from southern Australia. Very few species have been described from North and Central America but many are known from the middle and late Tertiary rocks of Europe. Middle and late Tertiary faunas containing rissoids have also been described from Indonesia, Japan and various Pacific islands.

There are very few Mesozoic records attributable to the Rissoidae although this situation may change when more work has been done on the smaller fauna. The only material I have been able to verify comes from Europe and North America.

Egg capsules, Larval development and Protoconchs

Almost all information about eggs and larvae of rissoids is based on European species. Those investigated have egg capsules that are lens-shaped, ovoid or spherical and contain from one to about 100 eggs (Lebour, 1934; Thorson 1946; Fretter & Graham, 1962, 1978). The egg capsules are laid on various surfaces including rock, algae, sea grasses etc. As is the case with most marine invertebrates, species with free-swimming (planktotrophic) veliger larvae have smaller and more numerous eggs than those having direct development. Species such as *Onoba aculeus* (Gould) and *Cingula trifasciata* (J. Adams) have one to four eggs and undergo direct development. In the various species of *Alvania* and *Rissoa* (including *Pusillina*) investigated, the capsules contained 6–100 eggs, and most had a planktonic larval stage.

As a general rule, the smaller and more numerous the eggs, the smaller the initial whorl of the protoconch. In addition, the outer lip of the larval shell of planktotrophic species is bisinuate to accommodate the velar lobes where they emerge from the shell. In species with direct development, the eggs are larger owing to yolk reserves, and consequently the initial whorl of the protoconch is usually large. Because there is no free-swimming veliger, there is no indentation in the outer lip of the larval shell. These features are readily observed in the protoconch, allowing determination of the type of larval development of a given species (for a review of the literature see Jablonski & Lutz, 1980).It is usually assumed that indirect development with a free-swimming larval stage is primitive and once lost cannot be resumed. However, species with lecithotrophic development, or direct development where a functional velum is retained by the embryo, may be able to revert to a planktotrophic larval mode given a relatively small change in the amount of yolk in the eggs.

Protoconch microsculpture. The initial whorl (or protoconch 1) of the protoconch of species having pelagic larval development is formed in the egg capsule. It is usually sculptured with a few spiral lirae with granules between them in, for example, species of *Rissoa*, *Alvania* and *Benthonella* (Figs 77D; 79B; 86C;

87B; 90B, F; 91F; 119B). The sculpture (if present) on the larval shell secreted by the veliger is variable. In species with direct development the protoconch is equivalent to the initial or prelarval part of the protoconch of indirect developers (protoconch 1). A basic pattern of smooth-topped, spiral ridges with granules between is exaggerated in two groups that appear to have exclusively direct development: *Onoba* (*Subestea*) (Fig. 115B, G) and *Attenuata* (Fig. 127B, E); and in some of the direct developers in the genera *Alvania* (Fig. 93A, D) and *Manzonia* (Fig. 101B, C). The reduction or loss of sculpture on the initial whorl of the protoconch of species of *Rissoa* and *Pusillina* may explain why the direct developers in *Pusillina* have relatively weak microsculpture on the protoconch, although some species in the apparently primitive group *Pusillina* (*Haurakia*) (Figs 81B, 82G) have more strongly sculptured protoconchs. Other species in genera showing similarities to *Rissoa* in the external features of the animal (e.g. *Powellisetia*, Fig. 116B, E; *Obtusella*, Fig. 118B; *Lucidestea*, Fig. 121B, H) have weakly sculptured protoconchs. These have either the basic pattern of threads or lirae with granules between, or can be derived from such a pattern.

Several modifications of the 'basic' pattern are found. The granules may become enlarged and lined up in spiral rows of beads as seen in *Merelina* (Figs 123 B, F, D; 124 B, F). An intermediate stage occurs in *Pusillina* (*Haurakia*) *hamiltoni* (Suter) (Fig. 81B) and in *Setia fusca* (Monterosato) (Fig. 85B) in which the spiral threads are reduced or absent and the granules are enlarged and approximately spirally arranged. In some species of *Pusillina* (*Haurakia*) spiral lines predominate, in another the granules are large and irregular and there are no spiral lirae, while another is almost smooth. Some species of *Setia* (Fig. 85 G, F) have either lost the granules, and the spiral lirae are retained and strengthened, or alternatively, the granules have become fused into spiral ridges. A few species of *Alvania* have a zig-zag protoconch sculpture (Fig. 94F). Two species of '*Turboella*' described from the Upper Cretaceous of North America (Ripley Formation) have very similar shells but very different protoconch microsculpture. '*Turboella*' *crebricostata* Sohl (Fig. 92H) has a protoconch on which the spiral and axial elements appear to have fused to give a rather irregularly-pitted surface. The other species, *T. tallahatchiensis* Sohl (Fig. 92E), has low, smooth, broad spiral ridges with narrow, simple grooves between. Both of these species were probably direct developers. Unfortunately no Cretaceous rissoid possessing a multispiral protoconch has been available for study. Clearly, the diversification of microsculpture in protoconchs of the Rissoidae, especially in those of direct developers, is considerable and commenced at a very early stage in the evolution of the group. The pattern of spiral ridges with granules between may be a basic pattern which could evolve in most genera of Rissoidae following the loss of a free swimming larval stage. The meagre fossil evidence, however, does not substantiate the view that this pattern may be primitive because it is not found in either of the two Upper Cretaceous species investigated.

The other important protoconch microsculpture is the pitted type. This consists of either minute, circular, steep-sided pits or shallow craters with curved sides and base. Pitted microsculpture is found in a few species of *Rissoina* (Figs 129C; 130F) which is an anatomically primitive group, and one that extends back to the Jurassic. It is also seen in species of *Boreocingula* (Fig. 120A, B, G). Two families belonging to the Rissoacea, the Barleeidae and the Hydrobiidae, include many species with a pitted protoconch microsculpture. In the latter it is of the shallow crater type and, in Barleeidae, both types are found (Ponder, 1983a).

Relationships to other Families in the Rissoacea

The first members of the superfamily may possibly have arisen in the Permian but the first fossils that can be attributed to the Rissoidae are known from the Middle Jurassic. Hydrobiid-like snails in the Permian (Davis, 1979) may be based on an erroneous identification. The Micromelaniidae, a freshwater family, has a possible fossil record from the Jurassic (Wenz, 1938, 1939). The non-marine Pomatiopsidae have a fossil record reaching back to the Cretaceous (Davis, 1979).

According to Wenz (1938), only the Rissoidae, Hydrobiidae, Stenothyridae and Bythiniidae (= Bulimidae) have definite records back to the Paleocene. Certainly by the Eocene a considerable radiation had taken place in both the Hyrobiidae and the Rissoidae. It is logical to assume that marine rissoaceans gave rise to the freshwater groups.

The initial radiation of most of the rissoacean families probably took place in the Cretaceous but there is little fossil evidence for this. Even if fossil material were readily available, accurate familial determination would be extremely difficult, if not impossible.

It can be postulated that the rissoacean families arose from a mesogastropod ancestor that had open male and female pallial genital ducts and lacked a penis (Ponder, 1983a). It also had a thick, horny operculum with a peg arising from the nucleus similar to that found in *Rissoina* (Rissoidae), *Barleeia* (Barleeidae) (Ponder, 1967, 1983a), the Cingulopsidae (Ponder & Yoo, 1980) and Rastodentidae (Ponder, 1966b). The ancestral rissoacean would also have had an oesophageal gland, a style sac with the potential to develop a crystalline style, and an inner chitinous shell layer (Ponder, 1983a). Most of these features are found in the primitive littorinacean family Eatoniellidae (Ponder, 1968). It is assumed that the pallial and metapodial tentacles were developed early in the evolution of the 'archi-rissoid'. In addition the inner chitinous shell layer and the oesophageal gland were lost and the crystalline style formed. The Rastodentidae and Cingulopsidae probably diverged from the same stock before the development of a penis. The Bythiniidae presumably also diverged at an early stage because it appears to have developed the penis independently. In the Bythiniidae the penis is of pallial origin but in some other rissoacean families it appears to be of pedal origin (Davis, 1979). The calcareous material in the operculum of the Stenothyridae, Bythiniidae and a few genera of the Hydrobiidae may suggest that these families are more closely related to one another than to the Rissoidae but this is unlikely when other differences are considered. The Barleeidae and a few rissoid genera retain the primitive opercular peg but the majority have lost it to develop a simple, paucispiral operculum. Rudimentary opercular pegs are found in some species of Anabathrinae (Barleeidae) (Ponder, 1983a) and in *Lironoba australis* (T. Woods) (Rissoidae) (Fig. 125B,C).

The multispiral, circular operculum and depressed shell of the Vitrinellidae are probably secondary developments, the former being correlated with the circular aperture found in that family. This same correlation is seen in the Hydrobiidae in which genera with flat or depressed shells usually have a circular operculum.

The invasion of freshwater was undertaken by several different groups. The brackish-water and freshwater Stenothyridae, and the brackish-water Hydrococcidae, are similar to the rissoids in having a metapodial tentacle. *Hydrococcus* has a posterior pallial tentacle (Ponder, 1982), and some species of the partly estuarine group Iravadiidae (Ponder, 1984) have a reduced pallial tentacle or metapodial tentacle. Some species of the brackish-water genus *Hydrobia* (Hydrobiidae) have a pallial tentacle (Hershler & Davis, 1980).

The hydrobiids and related groups, including the Micromelaniidae, underwent an enormous radiation which probably commenced during the early Cretaceous. They probably arose from a rissoid stock but lost (except in the case of *Hydrobia*) any accessory tentacles. The hydrobiids possibly evolved independently from the superficially similar Pomatiopsidae (Davis, 1979), the main evidence for this being differences in the female genitalia. The female genital system of the Stenothyridae is similar to that of the Pomatiopsidae, and consequently these families may possibly have had a common ancestry.

The Assimineidae and Truncatellidae range from estuarine to marine conditions, are generally supralittoral in habit and, particularly in the case of the Assimineidae, have also become terrestrial. They probably both evolved from a common stock along with the Pomatiopsidae as discussed below. The Aciculidae, which are sometimes included in the Littorinacea, have become completely terrestrial.

The reproductive system and higher classification. The reproductive system, and in particular the female genital system, has been used by several authors as a basis for higher groupings within the Rissoacea as here recognized (e.g. Golikov & Starobogatov, 1975; Slavoshevskaya, 1975a). Within what I consider to be the Rissoidae, Golikov & Starobogatov (1975) recognized the Alvaniidae (Alvanioidea), four families in the Rissooidea, and the Lironobidae in the Rastodentoidea. Slavoshevskaya (1975a) recognized Rissoidae, Alvaniidae, Onobidae and Haurakiidae. Except for the Lironobidae, which was erected on radular characters, all the other families recognized by these three workers were based on differences in their genital systems. Golikov & Starobogatov (1975) also recognized the Barleeidae and the Anabathridae as separate families. The Falsicingulidae (Slavoshevskaya, 1975b) is provisionally placed herein near the Pomatiopsidae (see below).

The various types of female genital systems seen in the Rissoidae (as here defined) can be derived from a hypothetical ancestral form somewhat similar to that seen in the littorinacean *Pomatias elegans* (Müller) (Creek, 1951) with a posterior sperm-receiving structure, a ventral slit along the pallial (or lower) oviduct gland and an albumen gland continuous with the lower oviduct gland and embedded in the visceral wall. There probably was a small seminal receptacle, an outgrowth from the 'renal' oviduct, placed immediately posterior to the bursa copulatrix. The only rissoacean genus that is known to have a structure similar to this hypothetical form is *Merelina* (see below), although *Obtusella intersecta* (Wood) and *Lucidestea atkinsoni* (T. Woods) also appear to have ventrally open lower oviduct glands. Johansson (1953) postulated a similar ancestral form in which the ventral groove had closed over along its middle section leaving short, slit-like posterior and anterior openings. Slavoshevskaya (1975a) suggested that the primitive bursa is a pallial structure opening close to a posterior genital opening, but separate from it. In *Pomatias* the bursa is formed from the expanded distal end of the upper oviduct and has a broad, ventral opening to the posterior end of the mantle cavity. A groove passing through the bursa conducts the eggs to the pallial oviduct. The proximal portion of the expanded upper oviduct acts as a sperm storage area. It is probable that the seminal receptacle arose as a diverticulum from this part of the oviduct to store larger quantities of sperm. The posterior opening of the bursa in this hypothetical ancestor is, as in *Pomatias*, at least partially separated from the egg conducting groove which transported the ova into the open glandular genital duct.

Evolution from a primitive condition, such as that described above, involved the ventral closure of the pallial oviduct gland and the loss of the posterior bursal opening by moving the point of sperm reception anteriorly by way of a ciliated sperm gutter running along one edge of the open pallial oviduct gland. In *Merelina elegans* (Angas) the pallial oviduct gland is open throughout its length, and an open sperm groove runs along its left edge in its anterior half. This sperm groove closes over in the posterior half of the oviduct gland to expand into a broad posterior sac containing sperm. This in turn opens to a bursa copulatrix by a short duct. A narrow seminal receptacle arises from the expanded upper oviduct (= coiled oviduct of Hydrobiidae and upper oviduct gland of Rissoidae). Johansson (1948, 1950, 1956) has hypothesized that closure of the lower oviduct gland took place in at least two different ways. In the Hydrobiidae the closing of the pallial oviduct proceeded in a forward direction enclosing the ciliated sperm groove in the ventral channel of the gland, as shown by a longitudinal ciliated fold in the ventral channel. In *Rissoa* the closure may have started at the anterior end and moved backwards, and the ciliated sperm groove remained partly external (Johansson, 1948, 1956). It has been suggested that genera such as *Alvania* which lack this external fold are part of a separate radiation from genera such as *Rissoa* (Johansson, 1948, Davis, 1979). There is, however, insufficient evidence to support this view. Fretter & Graham (1962, p. 359) state that no external fold has been found in any of the British species investigated by them, nor was one found in the two *Alvania* species examined by Johansson (1956). Most species of Rissoidae (as here recognized) have a well developed, thin-walled ventral channel and, with the exception of species of *Rissoa*, have no trace of an external groove or fold which has, presumably, been lost (Johansson, 1939, 1948, 1956; Fretter & Patil, 1961; Fretter & Graham, 1962; Ponder, 1968; observations herein). It is difficult to see why species of *Rissoa* have retained this fold when species of *Pusillina* and other genera, such as *Onoba* and *Alvania*, which appear to have less derived reproductive systems, have apparently lost it. This assumed loss may be partly due to the small size of the majority of rissoids, *Rissoa* species being relatively large. Two genera (*Lucidestea* and *Obtusella*) containing species of very small size, have a ventral slit in the lower oviduct gland. Further work on these species is required to establish whether or not this ventral opening is primitive.

Closure of the sperm groove and ventral capsule gland in *Rissoina* and related genera (*Zebina*, *Schwartziella*, *Stosicia*) has apparently occurred in a manner similar to that in the Hydrobiidae (Johansson, 1948) and the Iravadiidae (Ponder, 1984) where the sperm groove is enclosed within the ventral channel and separated from the remainder of the channel by a muscular fold. The sperm groove is closed over, in at least the posterior part of the lower oviduct gland, to form a separate sperm duct (bursal duct), whereas the seminal receptacle opens into the ventral channel. In other rissoids the seminal receptacle and the bursal duct both open to the ventral channel. Convergence with the 'normal' rissoid condition could be obtained by the loss of this fold, resulting in a simple, thin-walled ventral channel. In juvenile *Onoba 'striata'* (? = *aculea* (Gould)), Johansson (1948) has reported a weak fold that separates the vaginal lumen (= sperm groove), which suggests that the simple ventral channel, in this genus at least, may be derived by loss of an internal muscular fold.

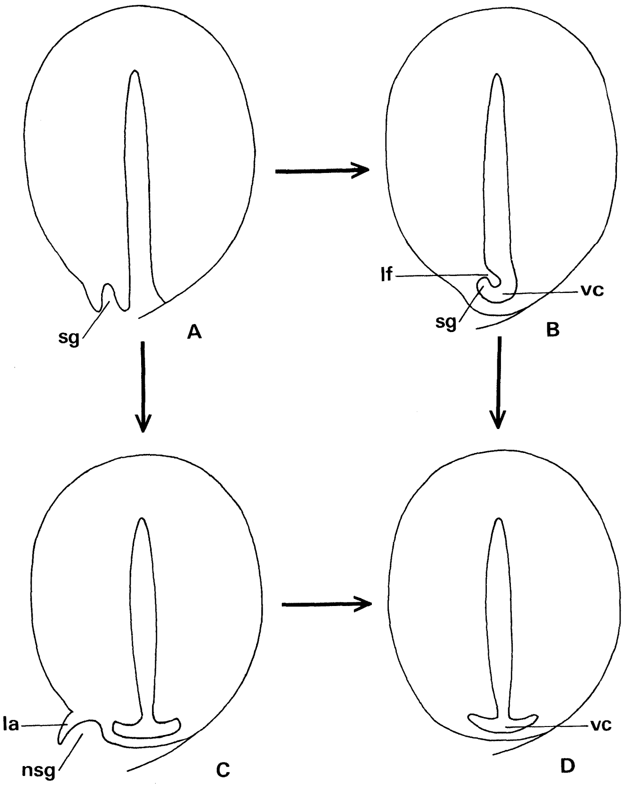

Fig. 1. Hypothetical evolution of the ventral channel in the capsule gland of the Rissoidae. The figures are all diagrammatic transverse sections of the middle part of the capsule gland. **A**, ancestral condition, open ventrally with sperm groove (e.g. *Merelina*); **B**, closed ventrally with sperm groove enclosed (e.g. *Rissoina*); **C**, closed ventrally with sperm groove external (e.g. *Rissoa*); **D**, closed ventrally and all trace of sperm groove lost. Derived from either B or C (for further explanation see text). *la*-external lateral fold; *lf*-lateral fold in ventral channel; *nsg*-non-functional sperm groove; *sg*-sperm groove; *vc*-ventral channel.

The hypothetical closure of the lower oviduct gland in the Rissoidae can be summarized as follows (see Fig. 1). Firstly the open duct (Fig. 1A) with its seminal groove (as in *Merelina*) closes posteriorly, this being seen in *Lironoba australis* (T. Woods). The sperm groove is enclosed within the ventral channel (Fig. 1B), as in *Rissoina* and its allies, or is left external and functionless (Fig. 1C), as in *Rissoa*. The simple ventral channel of the majority of species of the Rissoidae could be derived from either of these types of closure by loss of the internal or external fold (Fig. 1D).

The separation of the sperm groove as a separate duct in the posterior part of the lower oviduct gland of *Rissoina* and some related genera is paralleled by a similar (but not homologous) separation of the ventral channel (not just the sperm duct) in some rissoids, for example, *Alvania subsoluta* (Aradas) (Johansson, 1956) and *Rissoa* (= *Pusillina* herein) (*Haurakia*) *hamiltoni* (Ponder, 1968).

The oviduct gland consists of two parts in the Rissoidae, an upper and a lower gland. In all other rissoaceans the oviduct gland retains its presumably primitive state with only a single glandular mass

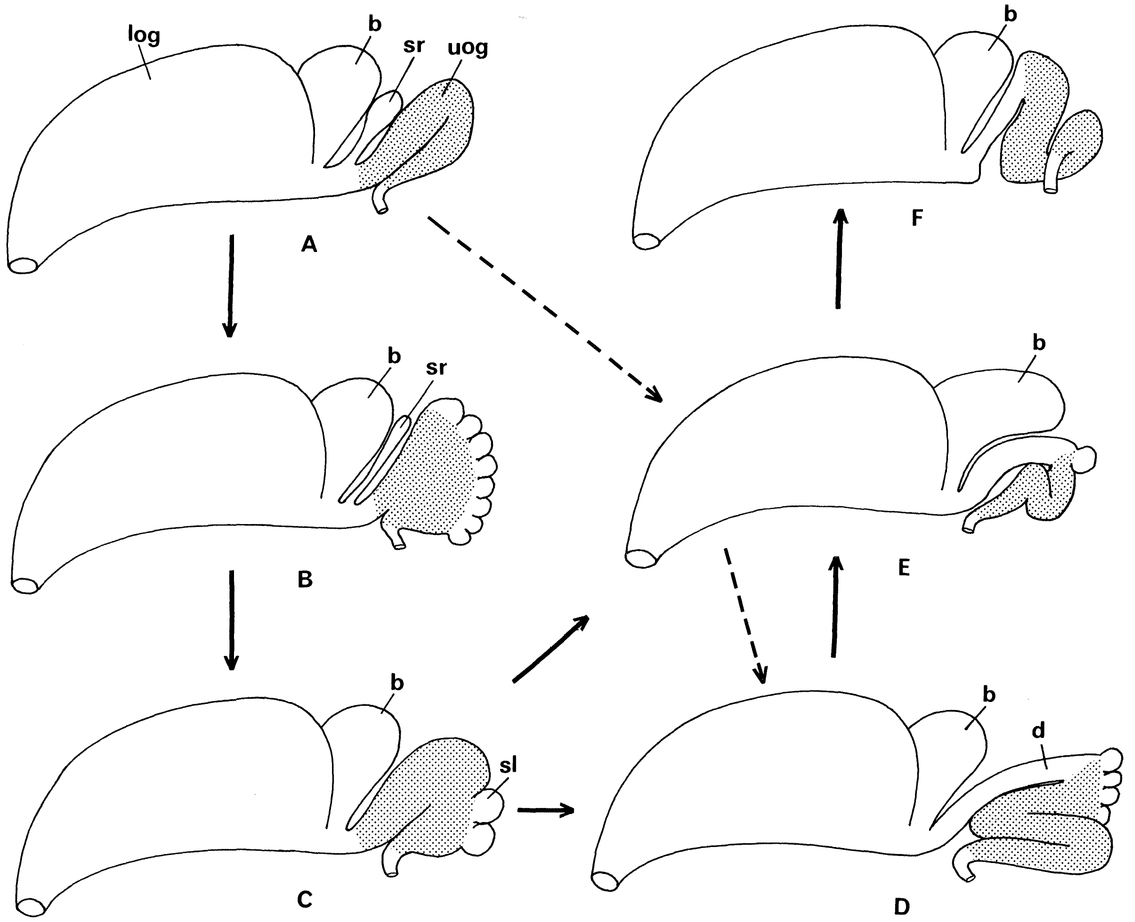

Fig. 2. Hypothetical evolution of the upper oviduct gland and associated sperm sacs. The solid arrows show the development (and loss) of the multiple sperm sacs from the sperm-storing lobes of the upper oviduct gland. The broken arrows show an alternative direction of evolution. **A**, *Onoba*; **B**, *Rissoa*; **C**, *Pusillina* (*Haurakia*); **D**, *Alvania*; **E**, *Alvania* and *Cingula*; **F**, *Frigidoalvania*. For further explanation see text. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *log*-lower oviduct gland; *sl*-sperm-storing lobe; *sr*-seminal receptacle; *uog*-upper oviduct gland.

consisting of albumen and capsule gland. The albumen gland of most rissoacean families stains almost identically to the upper oviduct gland of the Rissoidae, suggesting that they may produce similar secretions. The albumen gland of the other families, however, is presumably homologous with the posterior part of the lower oviduct gland in the Rissoidae.

The bursa copulatrix and the seminal receptacle lie on the right side between the upper and lower oviduct glands in many rissoids, and this is probably the primitive state. Fretter & Patil (1961) reported a posterior seminal receptacle in *Cingula cingillus* (= *trifasciata*). This condition is paralleled in species of *Alvania* but, as suggested below, the sperm sacs in *Cingula* and *Alvania* may not be homologous with those in other rissoids.

Some species of *Alvania* have the upper oviduct gland reduced to a short, coiled, expanded glandular tube whereas others have a well developed upper oviduct gland (Johansson, 1956; Fretter & Patil, 1961). The upper oviduct gland is probably homologous with the narrow, coiled muscular tube (= 'renal oviduct' of some authors) in the Hydrobiidae. The condition in some *Alvania* species is superficially similar, and has been regarded as an intermediate one between the Rissoidae and the Hydrobiidae (Johansson, 1956; Davis, 1979, 1980). It is, however, extremely unlikely that *Alvania* is ancestral to the Hydrobiidae, judging from the dissimilarity of many other characters.

The seminal receptacle is lost in some species of *Pusillina*, for example, *Pusillina (Haurakia) hamiltoni* (Ponder, 1968). *Alvania* and *Cingula* have 1-5 sperm pouches that function as seminal receptacles. These may not be homologous with the seminal receptacle of other rissoids since they may have been derived from posterodorsal sperm-storing lobes of the upper oviduct gland, similar to those in species of *Rissoa* and in some species of *Pusillina*. The possible evolution of the upper part of the glandular oviduct and its associated sperm sacs is summarized in Fig. 2. A simple, coiled or U-shaped upper oviduct gland is taken to be primitive (Fig. 2A), and is associated with a seminal receptacle. Such glands have no external modification and are known to contain stored sperm in some species, for example, *Pusillina* (*Haurakia*) *hamiltoni* (Ponder, 1968) and *Alvania subsoluta* (Johansson, 1956). The posterodorsal sperm-storing lobes seen in ***Rissoa*** and species of ***Pusillina*** **(s.s.) (Fig. 2B) are confined to two posterior blisters in**

Pusillina (*Haurakia*) *marmorata* (Hedley) (herein), and this species has also lost the seminal receptacle (Fig. 2C). Reduction of the glandular tissue in the distal part of the upper oviduct gland to form a thin-walled duct opening directly into the base of the region of the upper oviduct glands that has sperm-containing lobes would result in a condition similar to that seen in some species of *Alvania* (Fig. 2D). A similar result would be obtained by the elongation of the oviduct between the upper and lower oviduct glands carrying the seminal receptacle with it. The structure and orientation of the multiple sperm sacs in the larger species of *Alvania* examined, supports the hypothesis that these are derived from sperm storing lobes on the upper oviduct gland but there is no firm evidence to prove this. Two other genera, *Cingula* and *Frigidoalvania,* have an elongate, non-glandular tube separating the upper and lower oviduct glands (Fig. 2E,F). It is the sperm sac at the posterior end of this tube that was referred to as a posterior seminal receptacle in *Cingula* by Fretter and Patil (1961). Some species of *Alvania* also have only a single sperm sac (Fig. 2E).

In some groups the vestibule has become swollen anteriorly and functions as an anterior sperm storage structure (Fig. 3, *asp*), or 'pseudo-bursa'. This is seen in some species of *Pusillina* (Johansson, 1939, 1956; Ponder, 1968 and Figs 3B; 13) with modifications seen in *Lucidestea* (Figs 3D; 44A), *Obtusella* (Fig. 44D,E) and *Voorwindia* n. gen. (herein) (Figs 3C; 46) as well as in *Rissoina* (Ponder, 1968 and Figs 3A; 52) and *Schwartziella* (Marcus & Marcus, 1964). The presence of this structure in *Rissoina*, as well as in *Pusillina* and several other groups, suggests that sperm storage in the vestibule may be an early modification that arose with the closure of the capsule gland. The anterior bursa copulatrix seen in some other rissoacean families may possibly be homologous with this structure.

Hyala vitrea (Montagu) (Johansson, 1950) and some *Iravadia* spp. (Ponder, 1984) have a somewhat posteriorly placed, long, slit-like opening to the pallial oviduct that perhaps represents a primitive condition in which only partial closure of the originally open pallial oviduct has taken place. In most of these species the bursa is pallial and lies on the left side of the glandular oviduct. It may be a new structure derived from an analogue of the 'pseudo-bursa' in the Rissoidae. A large seminal receptacle lies alongside the posterior portion of the single oviduct gland. Golikov & Starobogatov (1975) have created the Hyalidae on the basis of these differences in the female reproductive systems. I have shown elsewhere (Ponder, 1984) that *Hyala* and *Iravadia* are related and can be grouped together in the Iravadiidae.

In *Barleeia* the pallial gland is divorced from sperm collecting as there is a separate, posteriorly placed, spermathecal opening. The duct of the oviduct gland is completely surrounded by glandular tissue; not thin-walled ventrally as in the rissoids (Fretter & Patil, 1961; Slavoshevskaya, 1975a; Ponder, 1983a). *Barleeia* has a single seminal receptacle that opens to the spermatheca and lies on the left side of the albumen gland. There is no bursa copulatrix. Some other genera in the Barleeidae have a thin-walled ventral channel in the capsule gland but the seminal receptacle (and the bursa when it is present) lies on the left side of the oviduct gland, not the right as in the Rissoidae. The Pomatiopsidae (Davis, 1979), the Stenothyridae (Kosuge, 1969), the Hydrococcidae (Ponder, 1982) and the Cingulopsidae (Fretter & Patil, 1958) all have diaulic female reproductive systems, at least in some species.

Obtusella intersecta has an anterior opening leading to an anterior sperm sac and a separate, ventral, slit-like opening to the lower oviduct gland. *Lucidestea atkinsoni* has a similar reproductive system but there is a single, ventral opening. The diaulic condition in *Obtusella* appears to be only a modification of the basic rissoid pattern, and not a major departure from it.

Species of *Falsicingula*, like those of the Assimineidae, Pomatiopsidae, Truncatellidae and some belonging to the Barleeidae, have the duct through the oviduct gland completely surrounded by glandular tissue. *Falsicingula* differs from species of the Pomatiopsidae and some barleeids in lacking a separate bursal opening (Lazareva, 1971; Slavoshevskaya, 1975b). Consequently, the duct of the oviduct gland might be assumed to be used for copulation, as it is in the similar Assimineidae (Fretter & Patil, 1961; Marcus and Marcus, 1965). My examination of the anatomy of *Falsicingula aleutica* (Dall) has indicated that copulation probably occurs through the renal opening, as in some Pomatiopsidae (Davis, 1979). I have examined the anatomy of a species of *Truncatella*, and renal copulation is almost certainly occurring in that genus as well. This suggests that, given the lack of major additional morphological differences, the Pomatiopsidae, Falsicingulidae and Truncatellidae may be much more closely related than suspected by recent workers. The Assimineidae may represent a stage in the evolution of the same group that has dispensed with renal copulation to allow copulation through the terminal genital opening of the oviduct. *Falsicingula*, like *Barleeia*, has a single oviduct gland, and the two sperm sacs lie just behind the glandular oviduct. In *Falsicingula* the reno-gonadial duct is used for transporting sperm from a special pocket in the kidney that functions as an accessory storage area. Sperm storage in the pericardium was not observed in *F. aleutica* but was reported by Lazareva (1971) and Slavoshevskaya (1975b) in *Falsicingula* spp.

Davis (1979) has adopted the view that the Hydrobiidae and Pomatiopsidae do not have an immediate common ancestor because of differences in the female genitalia. It is possible, however, that the separate sperm tube (spermatheca) seen in the Pomatiopsidae is not, as suggested by Davis, independantly derived from the ventral channel of the Hydrobiidae. It could be a ventral channel that has become separated from the capsule gland and closed to form a spermathecal duct lying beneath the capsule gland (as in the Pomatiopsinae of the Pomatiopsidae).

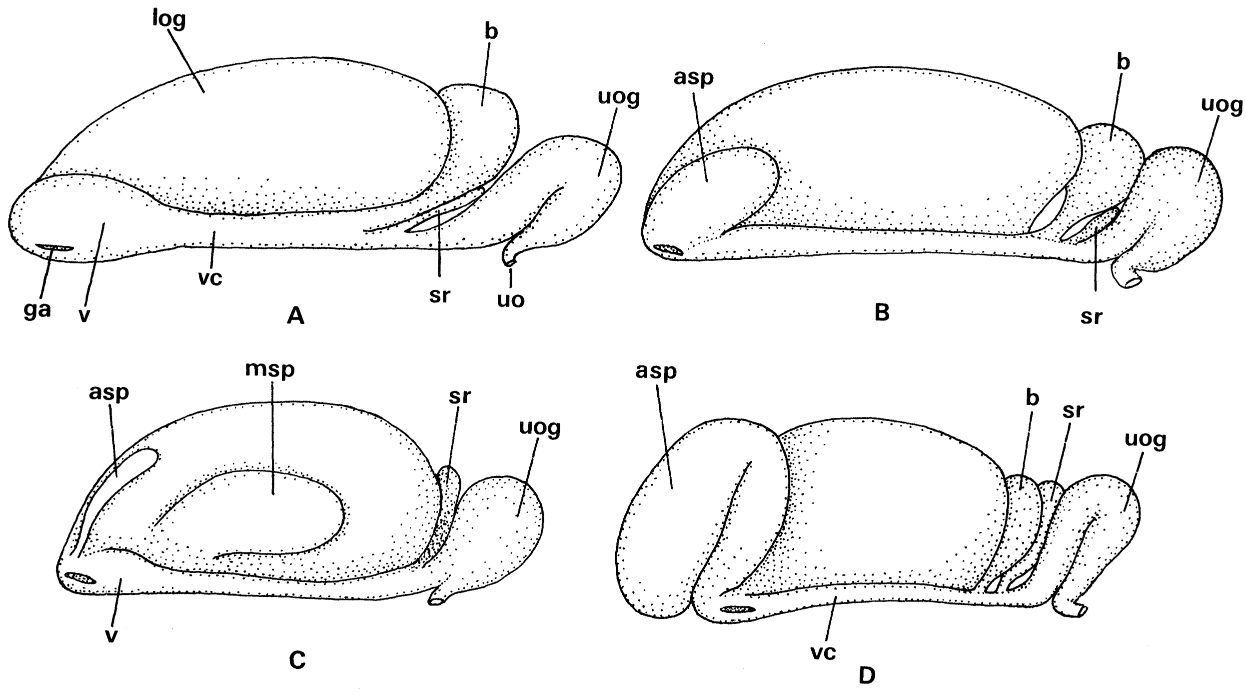

Fig. 3. Examples of anterior sperm sacs in the Rissoidae. **A**, *Rissoina*, *Schwartziella* and *Zebina*; **B**, *Pusillina*; **C**, *Voorwindia* n.gen.; **D**, *Lucidestea*. *asp*-anterior sperm pouch; *b*-bursa copulatrix; *ga*-genital aperture; *log*-lower oviduct gland; *msp*-median (or lateral) sperm pouch; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel.

Various degrees of an analogous separation are seen in the genera related to *Rissoina*, in several species in the Anabathrinae (Barleeidae) (Ponder, 1983a) as well as the Hydrobiidae, for example, *Littoridina australis nana* (Marcus & Marcus, 1963) and *Spurwinkia* (Davis, 1982). Once free of the oviduct gland the spermathecal duct can be shortened, as in *Barleeia* and most Triculinae (Pomatiopsidae) (Davis, 1979), or lost, as in *Lacunopsis* (Triculinae) (Davis, 1979) and (probably) *Truncatella, Falsicingula* and *Assiminea*. Davis (1979) gives as the major evidence for assuming an independant origin of the ventral channel and spermathecal duct the different ontogenetic derivations of these structures. In immature *Hydrobia ulvae* (Pennant) (Johansson, 1948) there is a ciliated groove along the median lip of the open pallial oviduct but in the Pomatiopsidae (Davis *et. al.,* 1976) the pallial oviduct is a solid core of tissue that later cavitates, and the spermathecal duct is derived from a bud from the bursa copulatrix. These seemingly different origins may, perhaps, be expected because the separated oviduct gland and spermathecal duct will probably have a different ontogenetic development from the connected gland and ventral channel. The ciliated gutter on the capsule gland in immature *Hydrobia* is later incorporated into the ventral channel (Johansson, 1948) and, as this is continuous with the bursa copulatrix, it might be homologous with the spermathecal duct.

The presence and absence of a pallial prostate gland does not appear to have major taxonomic significance. Prostatic tissue apparently develops in either the pallial duct or in the penis. The different location of the prostatic tissue has been used by some authors to support the creation of new families. The presence of a pallial prostate gland in *Pusillina inconspicua* and in *Pusillina* (*Haurakia*) *hamiltoni*, and a penial prostate in species of *Rissoa* has been used as evidence to separate two families (Slavoshevskaya, 1975a). I do not concur with this argument because in most other respects species of *Rissoa* and *Pusillina* are so similar that most authors have considered them to be congeneric.

Golikov & Starobogatov (1975) include *Rissoina chathamensis* (Hutton) in their Merelinidae because it has an open (pallial) prostate and therefore, according to them, cannot belong in the Rissoinidae. The variation in the prostate of species of *Rissoina* is considerable, being open, closed, present or absent depending on the species. Clearly the details of the male genitalia are of little taxonomic significance except perhaps, in some cases, at the subgeneric or generic level.

Golikov & Starobogatov (1975) state, as the main reasons for distinguishing the "new" family Onobidae, that it "differs from Rissoidae by the presence of a prostate and a connection between the vas deferens and anterior (not posterior as in Rissoidae) part of the mantle cavity". The male genital system of *Onoba semicostata*, the type-species of *Onoba*, has a posterior, narrow tubular opening (Fretter & Patil, 1961; Fig. 1C) like that seen in several rissoids, and there is no indication of an anterior opening. Different types of male genital systems found in the Rissoidae are summarized in Fig. 8.

Characters Used in Classification

Character states in the Rissoidae that are assumed to have been possessed by an ancestral rissoacean (see above) and, therefore, can be taken to be primitive (see Tables 1, 2), include an open prostate gland and an open penial groove (e.g. in *Rissoina* and *Merelina*), a pegged operculum (e.g. in *Rissoina* and *Lucidestea*) and the presence of pallial and metapodial tentacles (in several genera).

The primitive female genital system presumably has a coiled upper oviduct gland with the bursa copulatrix and seminal receptacle lying on the right side between the upper and lower glands and opening directly below to the ventral channel. The ventral part of the glandular pallial oviduct is probably open in the most primitive state (Fig. 1), and the evolution of this part of the reproductive system is discussed above in detail.

The alimentary canal lacks primitive features such as an oesophageal gland and oesophageal pouches. A crystalline style is usually present, and jaws are probably present in all species.

The inner chitinous layer (Ponder & Yoo, 1976), seen on the inner surface of the shell of barleeids and eatoniellids, is absent in the Rissoidae and in most other Rissoacea. In other shell characters the simple peristome is taken to be primitive whereas a duplicate peristome is derived. Sculptural characters are difficult to assess and no one character state is seen as clearly primitive. The aperture may have anterior and/or posterior channels that are largely developed in response to the extrusion of either pallial or cephalic tentacles. These occur in a number of genera, in particular *Rissoina*, and may be primitive, at least in that genus.

Whereas some character states can, with reasonable confidence, be regarded as primitive or derived, a considerable number cannot be so categorized. Most genera share a combination of primitive and derived character states and, because of this, as well as the patchy nature of the data base, a cladistic analysis is not attempted.

Tables 3 and 4 summarize the shell, opercular and radular characters used in separating the genera. The following characters have been tabulated:

Shell: **protoconch**. The number of protoconch whorls and the relative size of the initial whorl are a guide to the type of larval development (see above). A 'multispiral' protoconch is here defined as one with two or more whorls, whereas a paucispiral protoconch usually has about 1½ whorls. The sculpture of the protoconch varies considerably and is discussed in detail above.

Teleoconch. The shape of the teleoconch is defined in standard terms such as ovate, ovate-conic etc. Sculpture can be either axial, spiral or both. If both types of sculpture occur in approximately equal strength it is termed clathrate. Basal sculpture may be weaker or different from that of the rest of the shell. The size of the umbilicus is variable. When absent or only a slit is present, the shell is regarded as being non-umbilicate. The aperture may have a posterior angulation and, in some genera, a posterior channel or sinus when viewed from the side. A deep posterior notch occurs in one genus (*Folinia*). An anterior apertural channel occurs in some genera, in others the aperture is entire (simple) anteriorly. The peristome can be either simple or duplicated. A peristome is regarded as duplicated when the shell surface immediately within the outer lip is raised in a second rim. A weak to very strong varix may be present on the outer surface of the outer lip just behind its edge. This lip may be either opisthocline, prosocline or orthocline and, rarely, curved outwards (reflected). The degree of periostracal development was also examined.

Shell size, as used in the diagnoses, is based on length and is as follows: large (1 cm or more), medium (5 mm–9 mm), small (5 mm–2 mm) and minute (less than 2 mm).

Operculum. The primitive state is assumed to be thick, with a peg arising from the nucleus on the inner side (as in *Rissoina*). The thin operculum seen in most rissoids has presumably lost the peg but in *Lironoba australis* a rudimentary peg is found and in *Lucidestea* spp. a small peg is present. Genera such as *Merelina*, with a subcircular aperture, have the nucleus subcentrally placed whereas in other genera the nucleus is closer to the margin (eccentric).

Radula. The radula of the majority of Rissoidae is very similar but some characters have proved to be useful in separating genera. The central teeth (Fig. 4) are the most useful and are usually most readily observed in SEM photos. They have one or more pairs of cusps (here referred to as basal denticles) arising from the face of the teeth. A single pair of basal denticles is found in the majority of genera and is assumed to be the primitive state. The lateral margins of each central tooth slope at an angle to the dorsoventral axis of the tooth and this angle has been measured to indicate the degree of slope.

The lateral margins are thickened and sometimes give off denticle-like, ventrally directed structures developed from them. The cutting edge of the central teeth is curved forward and down causing the cusps it bears to point ventrally. These cusps are often somewhat variable in number, even within a single radula. The median cusp is usually larger and longer than the lateral cusps which usually decrease in size laterally.

The lateral teeth are similar in shape throughout the family, having the cutting edge on the inner portion, the outer portion being narrow and attached to the radular membrane. The cutting edge bears a number of cusps and one of these (the primary cusp) is larger than the others.

Cusp formulae are given for the central and lateral teeth. A '+' is used to separate each group of cusps and a '–' to indicate the range of cusp numbers within

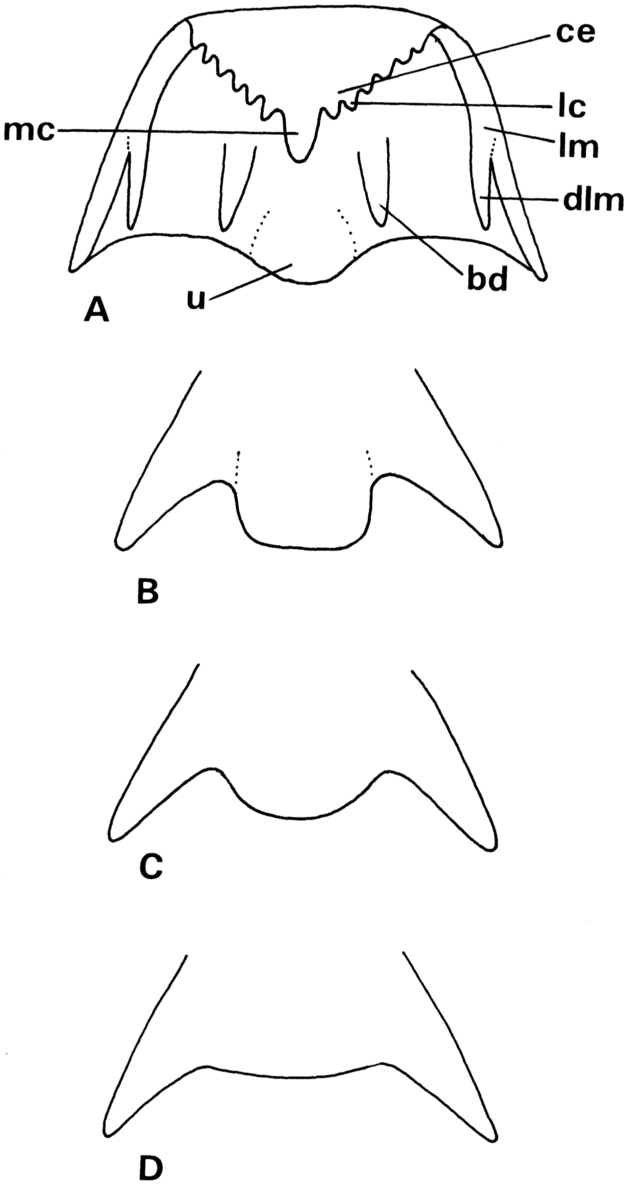

Fig. 4. Central radular tooth, identifying the structures referred to in descriptions **(A)**, and outlines of the ventral margin showing different degrees of development of the 'U-shaped' ventral extension **(B-D)**: **B**, well developed; **C**, moderately developed; **D**, not developed. *bd*-basal denticle; *ce*-cutting edge; *dlm*-denticle derived from lateral margin; *lc*-lateral cusp; *lm*-lateral margin; *mc*-median cusp; *u*-U-shaped ventral extension.

each group. Brackets indicate very weak cusps.

The inner marginal teeth are long and narrow, with small cusps on the curved distal ends and on the upper part of the outer edge. The outer marginal teeth are similar in shape and size to the inner marginal teeth, and have small cusps distally and along the distal ½-⅓ of the inner side of the tooth. In *Rissoina*, and in at least one species of *Zebina*, the cusps are also present on the outer edge.

Head-foot. The main head-foot characters used are identified in Figure 5. The snout is generally bilobed distally and is, in some species, capable of extending 2-3 times its resting length.

The cephalic tentacles are longer than the snout, and the eyes are situated in swellings at their outer bases. The eyes are, apparently, lost in some deep-water groups (e.g. *Benthonella*, *Frigidoalvania*), or at least all trace of pigment has gone. The cephalic tentacles have more or less parallel sides in all Rissoidae, although slight tapering towards the distal end can occur or, in some species, the distal end is slightly expanded. Ciliary tracts on the dorsal and ventral surface drive particles away from the head (i.e. across the tentacles away from the snout). These cilia become fused into stationary 'setae' in some genera, especially in those whose species are small in size. The foot is usually slightly expanded in front with angled or pointed anterolateral corners. The anterior pedal gland opens to the anterior edge of the foot and is overlain by the propodium. The middle part of the foot is constricted to a greater or lesser extent, this being particularly marked in species of *Rissoa* and in at least some species of *Pusillina*. The sole of the posterior portion of the foot (metapodium) is, in the primitive state, supplied with abundant epithelial glands. These have invaginated to form a posterior pedal gland in some genera. This gland has a short, slit-like opening which does not reach to the posterior end of the foot as it does in some families (e.g. Barleeidae and Eatoniellidae).

The opercular lobe is simple in all genera. Dorsally, the posterior end of the foot has a short, triangular tentacle emerging from beneath the opercular lobe. This tentacle is lost in some species or has become modified in two main ways (Fig. 6): in *Alvania* it has broken up to form several short tentacles (Fig. 6D), or, as in *Manzonia costata*, the apex of the triangular tentacle has been produced into a slender tentacle (Fig. 6B). In some species of *Rissoa* the triangular part is fused to the dorsal surface of the foot and the slender tentacle projects from its apex some distance behind the operculum. In several genera the triangular part is lost and the single, slender tentacle rises from the mid-dorsal part of the foot well behind the opercular lobe (Fig. 6C). Figure 6 shows how this state could evolve from more than one ancestral state.

The pallial tentacles arise from the edge of the mantle in the anterior (left) and posterior (right) corners of the aperture. These are usually short, rather inconspicuous and ciliated. One or both of these tentacles can be lost and, in *Rissoina*, one (the left) is often bifid. The presence of two pallial tentacles is assumed to be a primitive character state within the family.

Tables 5 and 6 summarize the anatomical characters used in this work. The male and female genitalia, stomach, ctenidium and osphradium have been used as these systems are usually more easily examined even in minute species for which small amounts of material are available. The following characters and character-states have been tabulated:

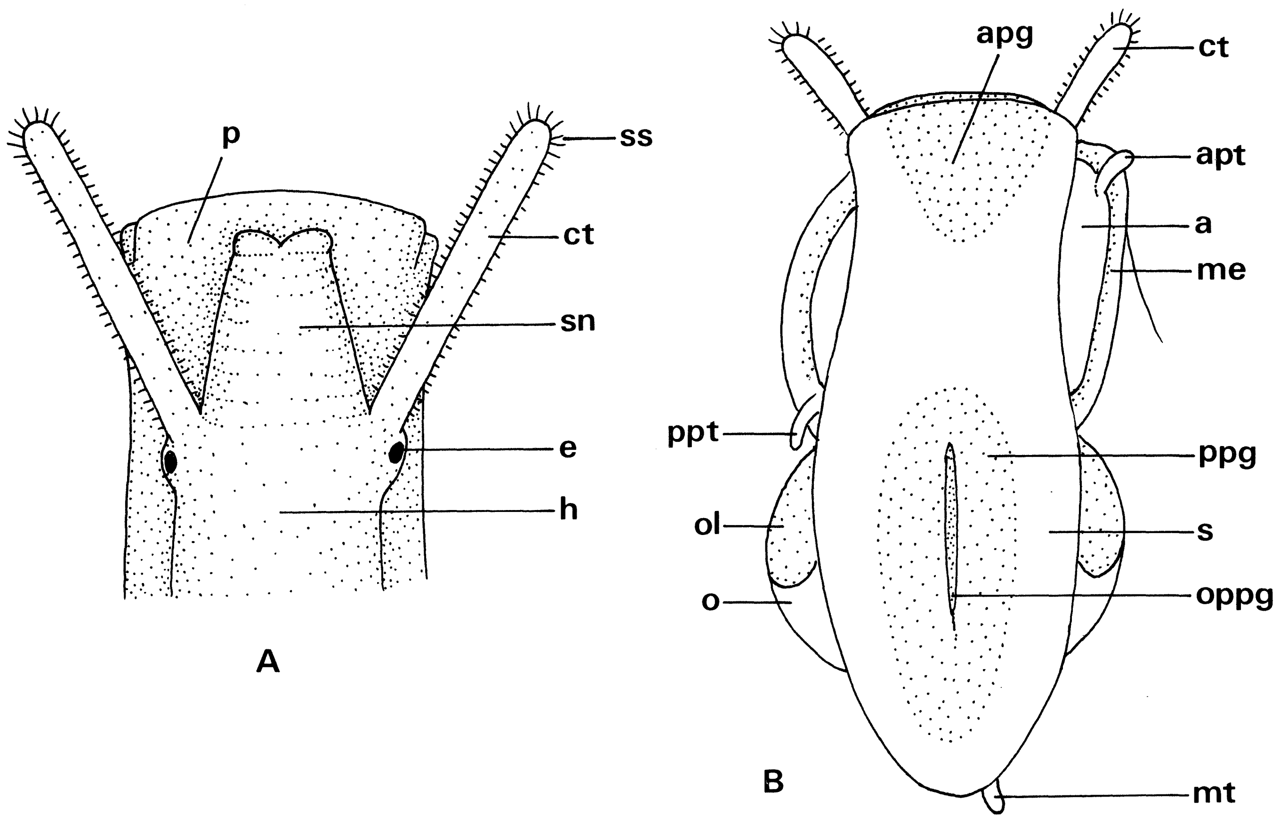

Fig. 5. The head and foot identifying the main characters used in descriptions: **A**, dorsal view of head and anterior foot; **B**, ventral view of foot and mantle edge. *a*-aperture and opening to pallial cavity; *apg*-anterior pedal gland; *apt*-anterior (left) pallial tentacle; *ct*-cephalic tentacle; *e*-eye; *h*-head; *me*-mantle edge; *mt*-metapodial tentacle; *o*-operculum; *ol*-opercular lobe; *oppg*-opening of posterior pedal gland; *p*-propodium; *ppg*-posterior pedal gland; *ppt*-posterior pallial tentacle; *s*-sole; *sn*-snout; *ss*-stationary setae.

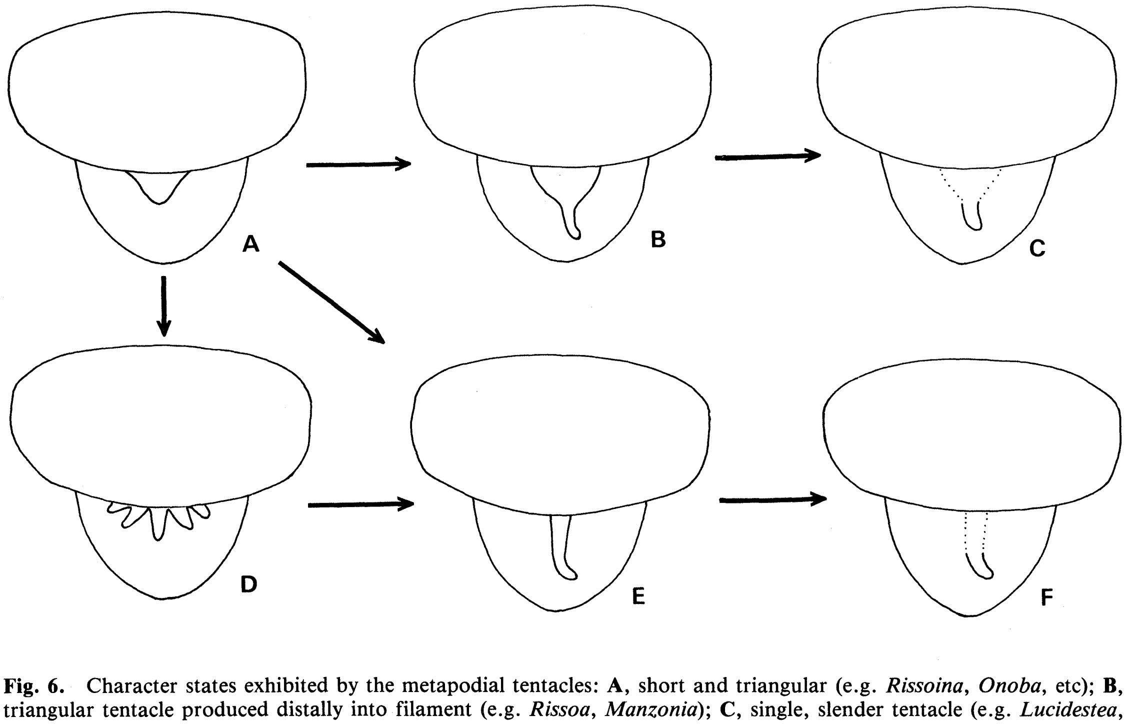

Fig. 6. Character states exhibited by the metapodial tentacles: **A**, short and triangular (e.g. *Rissoina*, *Onoba*, etc); **B**, triangular tentacle produced distally into filament (e.g. *Rissoa*, *Manzonia*); **C**, single, slender tentacle (e.g. *Lucidestea*, *Pusillina*); **D**, multiple tentacles (*Alvania*); **E**, hypothetical reduction of multiple tentacles; **F**, convergent character state to C.

Ctenidium and Osphradium. The filaments vary from triangular (width of base (i.e. length of attachment) equal to, or more than, half the length) to finger-like (width of base less than half the length), and from well developed to absent. The vestigial state is that in which only a few rudimentary posterior filaments remain. In most species the osphradium is nearly as long as the ctenidium and is usually wider than the filament bases.

Stomach. The stomach was observed from its inner (i.e. ventral or columellar) side after removing the posterior genitalia and digestive gland. The stomach-style sac ratio is the length of the stomach plus the style sac divided by the length of the style sac. The stomach length-width ratio is the length of the stomach (including the style sac) divided by its maximum width (see Fig. 7).

Intestine. In some species the intestine is thrown into folds close to the posterior pallial wall whereas in others it follows a more or less straight course.

Male genitalia. The penis lies behind the right eye in all the species observed. It is usually large, generally lies more or less straight within the pallial cavity and extends to about the posterior end of the cavity in mature individuals. Distally there may be a filament that emerges abruptly from a rounded end. In other species the distal end tapers rapidly to a point that is sometimes filament-like. Only the former type, however, is here regarded as a penial filament. In other species the distal end is blunt, or pointed, with a simple terminal pore. The distal end of the penis is often expanded and complex in species of the Rissoininae.

The penial duct is usually closed and typically runs along the right side near the edge (i.e. is lateral) but has migrated towards the centre of the penis in a few species. In the presumed primitive state (Fig. 8A) the penial duct is an open groove, for example, in some species of *Rissoina* and in *Merelina.* A few species have a closed penial duct with the line of fusion still visible,for example, in *Cingula trifasciata* (Fretter & Patil, 1961) and in *Alvania jeffreysi.*

The prostate (Fig. 8) may be entirely within the roof of the posterior part of the pallial cavity (Fig. 8A–C) or in some genera it partly extends back into the kidney (i.e. is visceral) (Fig. 8D). In one genus it is entirely visceral (Fig. 8E). Species of *Rissoa* lack a pallial prostate gland and have developed prostatic tissue in the penis (Fig. 8F). The prostate usually maintains a small posterior opening to the pallial cavity but is completely open in a few genera (Fig. 8A). A peculiar muscular papilla is developed inside the prostate gland in *Cingula* (Fig. 8C). The seminal vesicle is similar in all genera, being a thickened, coiled part of the visceral vas deferens. It lies over the posterior part of the inner wall of the stomach or immediately behind the stomach and beneath the testis. The pallial vas deferens is a narrow, straight to slightly undulating tube lying just beneath the epithelium at the junction of the pallial roof and the right side of the 'neck'. It does not become invaginated or markedly muscular to form an ejaculatory duct (*sensu* Davis, 1980). In a few species the pallial vas deferens is an open groove (Fig. 8A).

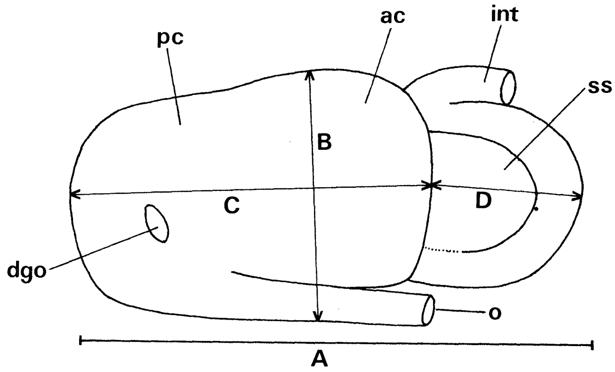

Fig. 7. Stomach viewed from its inner side showing the main structures. The lines A-D indicate the parts measured to obtain the length/width ratio (A/B) and the stomach/style sac ratio (C + D/D). *ac*–anterior chamber; *dgo*–digestive gland opening; *int*–intestine; *o*–oesophagus; *pc*–posterior chamber; *ss*–style sac.

Female genitalia. The pallial opening is usually small, terminal or subterminal but other states include the lower oviduct gland being open ventrally or with a slit-like opening. A sac-like vestibule lies anteriorly and is sometimes used for sperm storage. In some species this structure is very prominent whereas in others it is barely distinguishable in dissection. This same situation applies to the ventral channel, which may be a distinct, muscular strip or duct or, in others, almost indistinguishable from the gland. In some species the ventral channel is stripped free of the posterior portion of the lower oviduct gland whereas in others it is firmly attached and is open to the gland throughout. Species of one genus (*Rissoa*) have a simple flap or fold on the inner side of the lower oviduct gland. This gland may terminate at the posterior wall of the pallial cavity, or may extend behind it, bulging into the kidney. It can usually be divided into an anterior capsule gland and a short, posterior albumen gland. The bursa copulatrix is a large to small sac (relative to the upper oviduct gland) and is absent in a few species. The seminal receptacle is usually small and sometimes absent. Sperm pouches, probably not homologous with the seminal receptacle, are found in *Alvania* and *Cingula* and, for the purposes of comparison, are not treated as seminal receptacles in Table 5. The upper oviduct gland is closely joined to the lower oviduct gland by a very short duct (in most genera) or a long duct. The gland itself may be a single glandular mass or have finger-like lobes in which can be seen silvery pockets of sperm. This gland may be either tightly coiled or a simple, compact body.

Some female specimens, in several genera, possess a non-functional penis. It is smaller than the penis of a mature male and the female system in these specimens is well developed, usually with a mature ovary and sperm in the sperm sacs. For the purposes of the descriptions of female genitalia these specimens are ignored or treated as females.

Nervous system. This was investigated in only a few species. The relative positions of the supra and suboesophageal ganglia, and the degree of separation of the cerebral ganglia, were the main characters noted.

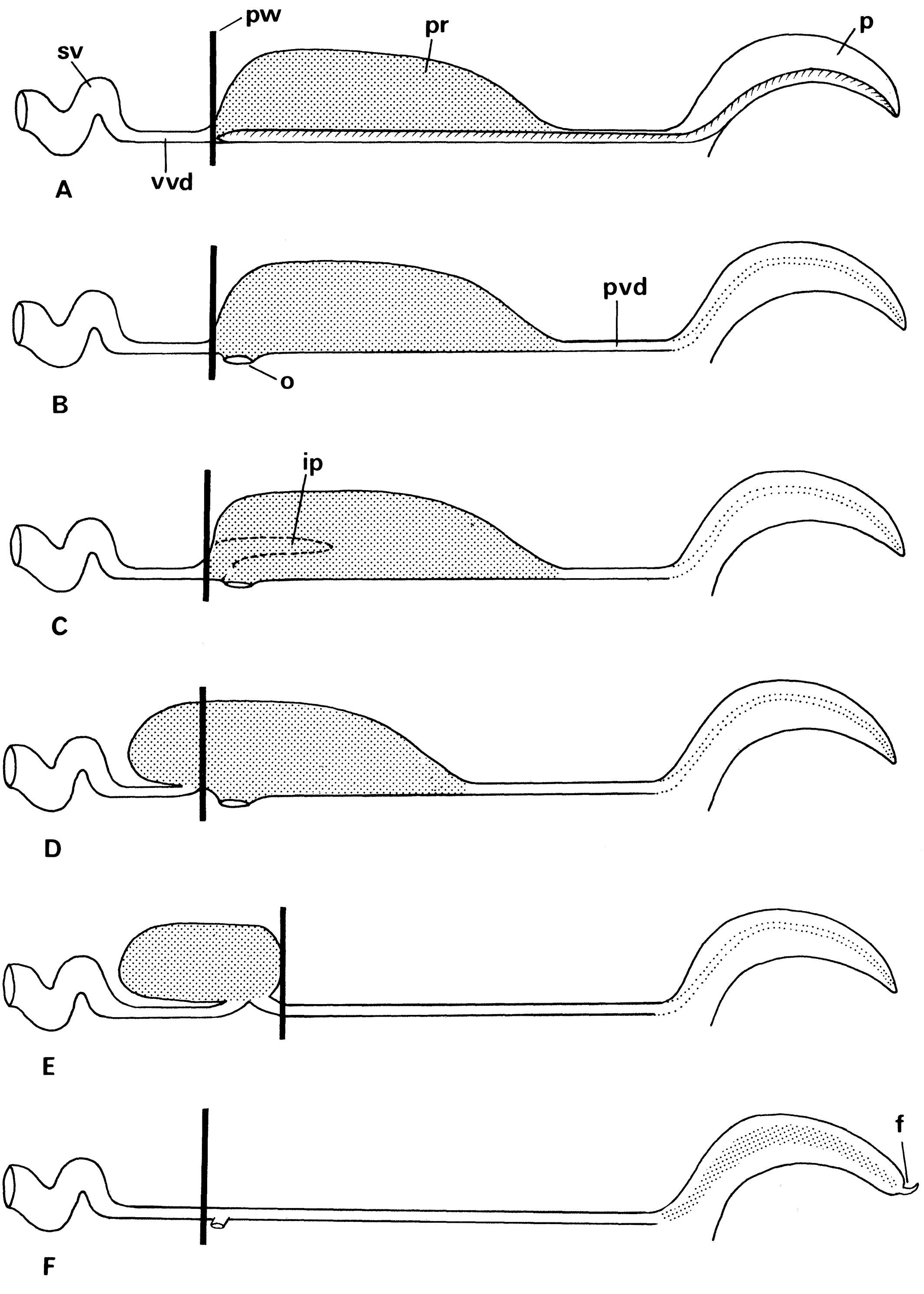

Fig. 8. Male genitalia of Rissoidae showing the main character states of the prostate gland: **A**, open prostate gland and open penial groove (e.g. *Rissoina*, *Merelina*); **B**, closed prostate gland (except for small posterior opening) and closed penial duct, prostate gland entirely pallial (e.g. *Pusillina*); **C**, closed prostate gland with internal papilla (*Cingula*); **D**, closed prostate gland, partly embedded in kidney wall (e.g. *Onoba*); **E**, closed prostate gland, entirely embedded in kidney wall (*Voorwindia* n. gen.) **F**, prostate gland absent in pallial region; prostatic tissue in penial duct (*Rissoa*). *f*-filament; *ip*-internal pappilla; *o*-pallial opening of prostate; *p*-penis; *pr*-prostate gland; *pvd*-pallial vas deferens; *pw*-posterior pallial wall; *sv*-seminal vesicle; *vvd*-visceral vas deferens.

Taxonomy

Class Gastropoda
Subclass Prosobranchia
Order Caenogastropoda Cox, 1959
Suborder Mesogastropoda Thiele, 1929
Superfamily Rissoacea Gray, 1847

Includes: Truncatellacea Gray, 1840 (submission to be made to ICZN to suppress this name); ? Aciculacea Gray, 1850; Barleeiacea Gray, 1857; Caecacea Gray, 1857; Assimineacea Fischer, 1885; Tornacea Sacco, 1896; Skeneopsacea Iredale, 1915; Rastodentacea Ponder, 1966; Alvaniacea Nordsieck, 1972. All of the above except Rissoacea and Truncatellacea were elevated to superfamily rank by Golikov & Starobogatov, 1975. Rissoinacea Stimpson, 1865 as recognized by Nordsieck, 1972.

Family RISSOIDAE

Gray, 1847b: 152 (as Rissoaina)

Diagnosis. *Shell*: small to minute, ovate to elongate-conic, thin to solid, without inner chitinous shell layer. Protoconch 1½ whorls to several, smooth or variously sculptured with a spiral, zig-zag, reticulate or dotted pattern of raised or pitted sculpture; never predominantly axial. Teleoconch with sculpture lacking, or of axial or spiral elements, or reticulate; weak to strong. Whorls flat to moderately convex, rounded to strongly angled, rarely sharply angled. Suture usually distinct, sometimes indistinct. Umbilicus usually small or closed. Aperture oval to D-shaped, with simple or duplicate peristome; outer lip with or without external varix; with or without a weak sinus posteriorly; with or without a channel anteriorly. Columella simple, usually slightly concave or straight, rarely slightly convex.

Operculum: oval to subcircular, composed of a single layer, horny, thin to thick, of few whorls; nucleus eccentric; last whorl by far the largest. If thin, rarely with a peg, if thick, with a peg.

Head-foot: with short to rather long snout, usually bilobed, with a pair of small jaws composed of simple rodlets. Cephalic tentacles long to rather short, slender, ciliated in most species and often with group of long, stationary cilia distally. Eyes in bulges at outer bases of cephalic tentacles. Foot short to long, always with an anterior pedal mucous gland and, in some species, with posterior pedal mucous gland with short, slit-like opening in middle of metapodium not extending to posterior end of foot. Opercular lobe usually conspicuous, lacking tentacles. Foot sometimes with short to long, broad to narrow metapodial tentacle, 3–7 narrow metapodial tentacles in species of *Alvania*. Mantle edge sometimes with an anterior (left) and/or a posterior (right) pallial tentacle.

Radula: taenioglossate, with small to moderate central teeth, usually more or less rectangular to triangular in shape, with several cusps; median one longest, and 1–2 pairs of processes (basal denticles) emerging from face of teeth (if 2 pairs inner-most shortest); sometimes an additional pair of denticles produced from thickened lateral margins. Lateral teeth elongate, with several cusps on either side of larger primary cusp; all cusps confined to about inner half of each tooth. Marginal teeth elongate, approximately sickle-shaped, with small cusps on approximately upper ⅓ of outer edge of each inner marginal tooth, and on approximately upper ¼ of each outer marginal tooth; usually not developed on outer edge of outer marginal teeth.

Anatomy: ctenidium with triangular to finger-shaped filaments, or rudimentary or absent. Osphradium well developed, nearly as long as ctenidium and usually wider than bases of ctenidial filaments, with broad central area bordered by pair of ciliated ridges. Oesophageal gland absent; a single pair of simple, tubular salivary glands lie above circum-oesophageal nerve ring. Crystalline style present in most species; stomach with short to very long posterior chamber, single digestive gland opening and gastric shield. Intestine and rectum simple; intestine looping around perimeter of style sac and continuing as simple loop over kidney. Some folding of intestine may occur adjacent to posterior pallial wall but otherwise straight. Kidney simple, not markedly expanded amongst viscera, usually with thickened outer wall (nephridial gland). Circum-oesophageal ganglia with suboesophageal ganglion separated from right pleural ganglion by rather short connectives or abutting, supra-oesophageal ganglion separated from left pleural ganglion by short to long connective. Cerebral ganglia abutting or separated by short commissure. Pleural and cerebral ganglia fused. Pedal ganglia separated from cerebro-pleural complex by connectives.

Male genital system variable; with or, sometimes, without pallial or visceral prostate gland but, when absent, prostatic tissue present in penis. Prostate gland open or closed, usually, if closed, with small posterior opening. Penis small to large, typically simple, with complex distal portion in some genera; with or without terminal filament; with enclosed duct or open penial groove. Pallial vas deferens straight; passes along junction of pallial wall and neck; slightly undulating to straight on neck before entering penis; closed (or open in a few genera) on surface; not markedly muscular. Seminal vesicle an expanded, coiled tube folded over inner wall of stomach and/or immediately behind stomach. Testis lies above digestive gland on most whorls of visceral coil.

Female genital system with upper and lower oviduct glands separate. Seminal receptacle and bursa copulatrix usually present, at right side of posterior end of lower oviduct gland. Accessory sperm pouches developed, in several genera, in upper oviduct gland. Vaginal opening terminal to subterminal in relation to lower oviduct gland, or gland open ventrally. Glandular oviduct with thin-walled, simple ventral channel, or open sperm groove contained within ventral channel. Sperm groove, in some species, closes to form a separate duct from ventral channel. Upper oviduct gland simple or coiled, rarely reduced to non-glandular coiled tube. Ovary lies above digestive gland over at least half of visceral coil.

Egg capsules: single, lens-shaped to spherical, with thin, horny outer covering; 1 to many eggs. Development direct or with a planktonic larval stage.

Subfamily classification. The group of genera related to *Rissoina* appear to be sufficiently distinct to allow them subfamilial status. Phenetic classifications using various combinations of characters consistently separate out this group from the majority of the remainder of the genera (see Appendix 3) even though there is only one significant character that is unique to this group and is possessed by all its members. This character, judged to be an important one, is the separation of the sperm tube along at least part of the lower oviduct gland.

The two subfamilies are briefly diagnosed below.

Subfamily Rissoinae

?Mohrensterniinae Pchelintsev, *et al.*, 1960: 147.
Cingulinae Coan, 1964: 165.
Lironobinae Ponder, 1967: 219.
Onobidae Golikov & Scarlato, 1967: 33.
Alvaniinae Nordsieck, 1972: 178; Golikov & Starobogatov, in Golikov & Scarlato, 1972: 95*.
Merelinidae Golikov & Starobogatov 1975: 211.
Haurakiidae Slavoshevskaya, 1975a: 120.

Diagnosis. *Shell*: as for family.

Operculum: as for family; thin if peg present.

Head-foot: as for family; pigmentation present or lacking, metapodial tentacle(s) triangular or finger-shaped. Pallial tentacles often present, always simple.

Radula: as for family.

Anatomy: as for family; male typically with prostate gland closed; penis usually simple and with closed penial duct. Female with simple ventral channel in lower oviduct gland or, rarely, gland open ventrally; no separate sperm duct.

Subfamily Rissoininae Stimpson, 1865: 4.

Zebininae Coan, 1964: 165.
Phosinellinae Coan, 1964: 165.
Rissolinidae Voorwinde, 1966: 42.
Foliniinae Nordsieck, 1972: 172.

Diagnosis. *Shell*: as for family; typically elongate-conic with well developed posterior angulation in aperture and, sometimes, with anterior apertural channel.

Operculum: as for family; thick if peg present.

Head-foot: as for family, pigmentation lacking; metapodial tentacle triangular. One to two pallial tentacles usually present, one sometimes bifid.

Radula: as for family.

Anatomy: as for family; male typically with prostate gland open along at least part of its length; penis usually expanded distally, often complex in structure, typically with open penial groove. Female with sperm duct usually expanded and internally folded anteriorly and forming a separate duct for most or part of the length of the upper oviduct gland.

Remarks. The family-group names included in the synonymies of the two subfamilies of Rissoidae have mostly been erected in recent years. Coan (1964) recognized as separate families the Rissoidae and Rissoinidae and erected, within the Rissoinidae, three new subfamilies (see synonymy above). *Rissoina* and *Phosinella* were shown to be congeneric by Kosuge (1965) and Ponder (1967). Coan (1964) based his subfamily Zebininae on "smooth genera or genera with confined axial sculpture". However, some smooth and variously axially ribbed species are congeneric with *Rissoina*. Because shell sculpture is often extremely misleading in rissoid genera, this is not a sufficient reason for separating subfamilies. The most obvious difference between *Rissoina* and *Zebina* is the thin, smooth operculum of the latter in contrast to the thick, pegged operculum of *Rissoina*. *Schwartziella* also has a thin, smooth operculum and is virtually identical to *Rissoina* species in shell features (Kosuge, 1965; Ponder, 1968 and herein) and anatomically (Marcus and Marcus, 1964). *Schwartziella* was regarded as a subgenus of *Rissoina* by Coan (1964). It would thus appear that members of the *Rissoina* group are probably all closely related and not divisible into categories above genus level. A fourth subfamily recognized by Coan (1964) in the Rissoinidae, the Barleeinae, is not related to *Rissoina* and can be recognized as a separate family (Ponder, 1983a).

Cossmann (1921) considered the *Rissoina* group to have a different origin from the *Rissoa* group, *Rissoina* having been derived from near the Loxonematacea and *Rissoa* from the Palaeozoic Littorinacea. His conclusions were based on certain shell characters which, although important at the generic level, seem not to be relevant in defining higher categories.

Ponder (1967) upheld the *Rissoina* group as a subfamily within the Rissoidae separated chiefly on the stomach morphology and features of the head-foot. It is now known that intermediate situations in both the stomach and external appearance of the animal are found and there is only one significant additional character (the separation of the sperm duct in the female) that would consistently enable separation of the two subfamilies (see Tables 3–6). However, when a combination of characters is considered, there does appear to be sufficient grounds for recognising the *Rissoina* group as a distinct subfamily. When the characters listed in Tables 3–6 are analysed phenetically the genera fall into two distinct groups (see Appendix 3). Genera intermediate in various aspects between these groups include *Onoba* and *Merelina*, both being the type genera of two family names. Much of the evidence used by Golikov & Starobogatov (1975) for recognizing

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* I have been unable to determine which has priority.

these families was based on differences in the genital system, and, as discussed above, this appears to be insufficient to allow even subfamily recognition (see also Appendix 3).

Coan (1964) erected the Cingulinae "around the European *Cingula*". The genera he included have mostly smooth or weakly spirally sculptured shells but otherwise are very heterogeneous, so it was presumably on sculptural grounds that the subfamily was introduced. The type species of *Cingula* is very similar to *Alvania* in the anatomy of the female reproductive system although it has a rather unusual prostate structure. In other respects it is typical of other Rissoidae. Thus there appear to be no important anatomical or conchological grounds for separating *Cingula* from the remainder of the Rissoidae.

The Mohrensterniinae was intended to include rissoids lacking a varix on the outer lip, and included *Barleeia* as well as *Mohrensternia*. *Mohrensternia* is based on a European fossil species which may be related to *Rissoa* or may possibly belong in the Hydrobiidae. Unfortunately no Recent species are known (although *Rissoa parva* is sometimes included in this genus). The lack of a varix is a feature which occurs in many unrelated genera and, by itself, is quite inadequate to define a subfamily. The Lironobinae was introduced to cover species with strong spiral cords, a wide, but vertically narrow, central tooth of the radula and single cusped lateral teeth. In the one species examined the animal appeared to be blind. This species belonged to what Ponder (1967) believed to be a subgenus, *Nobolira*. Unfortunately no information is available about the radula of the type species of *Lironoba*, and the radula of only two species of *Nobolira* (= *Attenuata*) have been available for examination in this study. A few Australian species that appear to be related to *Lironoba* have been examined and they have a radula typical of the majority of genera in the Rissoidae. The sculptural differences in the protoconch are here given more weight and *Attenuata* and *Lironoba* are considered to be distinct genera. While it is possible *Attenuata* represents a very distinctive group (although this needs to be confirmed with anatomical data), *Lironoba* is probably a typical member of the Rissoidae. The anatomy of one species of *Lironoba* (*s.l.*) is similar to that of *Merelina* so that the relationships of *Lironoba* may be with *Merelina* rather than *Onoba* and other (superficially?) similar genera. The Haurakiidae and Alvaniidae are separated from *Rissoa* mostly by differences in their genitalia. The rationale for this is discussed in detail above, and grounds for separation at the family or subfamily level are insufficient.

Key to the Genera of the Rissoidae

The following key uses shell characters wherever possible. However, because of the considerable convergence in the shells in the Rissoidae, it is not possible to construct a key using shell features alone. For this reason some use is made of radular, opercular and head-foot characters, but additional anatomical characters are not used except in one couplet. It is appreciated that the use of non-shell characters will reduce the practical usefulness of the key. An added problem is that the protoconch sculptural characters, on the whole, are only detectable with an SEM.

Because many of the generic differences in the shells are somewhat subtle and difficult to key out in a dichotomous key the plates should be referred to while using it.

1. Shell with distinct anterior canal in aperture, non-umbilicate 2

——Shell without distinct anterior canal in aperture, umbilicate or non-umbilicate 7

2. Anterior canal hooked by bend in columella .... *Stosicia*

——Anterior canal simple 3

3. Sculpture of spiral cords; surface dull, minutely pitted, with one or more additional varices formed on body whorl or, rarely, spire .... *Pseudotaphrus*

——Sculpture absent or with weak to strong axial ribs and/or spiral cords or threads; surface glossy or dull, minutely pitted or smooth, with terminal varix only 4

4. Deep posterior notch in aperture .... *Folinia* (in part)

——No deep posterior notch in aperture 5

5. Surface glossy, rendered punctate by weak axials and spirals .... *Cossmannia*

——Surface dull to shining (axial and spiral sculpture does not render surface punctate) or smooth 6

6\. Shell with heavy varix on heavy outer lip; distinct anterior and posterior channels in aperture; opercular peg present .... *Rissoina*

——Shell with weak to moderate varix on thin outer lip; anterior channel rather shallow, not well defined, posterior channel present; operculum unknown .... *Microstelma* (in part)

7\. Aperture with distinct anterior angulation 8

——Aperture without distinct anterior angulation 9

8\. Shell with strong to subobsolete axial ribs, spiral sculpture weak if present; aperture with shallow posterior channel .... *Microstelma* (in part)

——Shell with strong to weak axial ribs, or smooth and glossy with punctate microsculpture; spiral sculpture weak relative to axial sculpture but distinct; aperture with deep posterior notch .... *Folinia* (in part)

9\. Aperture with duplicated peristome 10

——Aperture with simple peristome 17

10\. Shell with predominantly strong spiral cords 11

——Shell with axial and spiral sculpture or with spiral striae 14

11\. Protoconch with distinct spiral ridges with axial striae between or with raised zig-zag spiral lines or with gemmate spirals 12

——Protoconch with a single spiral ridge or angulation; microsculpture of minute pits .... *Lironoba*

12\. Protoconch with gemmate spiral ridges .... *Manzonia* (in part)

——Protoconch with smooth spiral (or zig-zag) ridges 13

13\. Protoconch microsculpture between spiral ridges consisting of raised dots ... *Attenuata*

——Protoconch microsculpture between spiral ridges consisting of axial striae. Primary ridges zig-zag in some species .... *Cingula* (in part)

14\. Shell ovate-conic, with fine spiral threads .... *Amphirissoa*

——Shell ovate-conic to elongate-conic, smooth or with both axial and spiral sculpture, both or one or the other well-developed 15

15\. Protoconch paucispiral, with gemmate spiral ridges; central teeth of radula with 2 pairs of basal cusps .... *Merelina*

——Protoconch (if paucispiral) with smooth or gemmate spiral ridges or (if multispiral) with weak spiral thread (otherwise smooth) or netted sculpture; central teeth of radula with single pair of basal cusps 16

16\. Shell minute (less than 2 mm in length), ovate-conic, with axial ribs and 1 or a few strong spiral cords; axial ribs strong over base of shell; protoconch (if multispiral) smooth except for weak spiral thread or (if paucispiral) with irregular spiral ridges .... *Parashiela*

——Shell small (usually greater than 2 mm in length), ovate-conic to elongate-conic, with axial and spiral sculpture clathrate or with axials predominant and with numerous, fine spiral threads; axial ribs weak to absent over base of shell; protoconch variously sculptured .... *Manzonia* (in part)

17\. Central teeth of radula with 2 pairs of basal processes independant of lateral margins 18

——Central teeth of radula with 1 pair of basal processes (1–2 pairs of secondary processes may emerge from lateral margins) 19

18. Operculum simple .... *Obtusella*

—— Operculum with peg .... *Lucidestea*

19. Shell with axial and spiral sculpture well developed or spiral sculpture well developed and predominant 20

—— Shell with axial sculpture predominant, or smooth (spirals, if present, weak threads only) 26

20. Shell without distinct varix on outer lip; outer lip prosocline 21

—— Shell with distinct varix on outer lip; outer lip prosocline to opisthocline 22

21. Protoconch with spiral cords or threads .... *Cingula* (in part)

—— Protoconch with spiral rows of pits .... *Boreocingula*

22. Periostracum well developed; shell ovate with angled whorls and few spirals; protoconch paucispiral .... *Frigidoalvania*

—— Periostracum poorly developed; shell ovate-conic to elongate-conic, usually with convex whorls, spirals usually numerous; protoconch multispiral or paucispiral . 23

23. Shell elongate-conic; aperture pyriform .... *Lapsigyrus*

—— Shell ovate-conic to elongate-conic; aperture oval to sub-circular 24

24. Protoconch paucispiral, with spiral cords or spiral rows of gemmae; teleoconch ovate-conic, with strong spiral cords .... *Alvania* (in part)

—— Protoconch multispiral or paucispiral, variously sculptured; teleoconch ovate-conic to elongate-conic, with clathrate sculpture or spiral sculpture; if with spiral cords shape elongate-conic 25

25. Sculpture typically clathrate; 3–7 metapodial tentacles .... *Alvania* (in part)

—— Sculpture typically spiral, or with axial ribs and spiral threads; 1 metapodial tentacle .... *Onoba* (in part)

26. Shell thick and solid, elongate-conic; aperture pyriform, usually with heavy varix; head-foot unpigmented 27

—— Shell sturdy (but not thick) to thin; aperture pyriform to sub-circular, with well-developed varix to no varix; head-foot pigmented or unpigmented 28

27. Shell glossy, with or without axial ribs on early spire whorls and/or spiral threads; usually smooth .... *Zebina* (in part)

—— Shell with axial ribs over whole surface; no spiral sculpture .... *Schwartziella*

28. Protoconch spirally ridged 29

—— Protoconch smooth or weakly sculptured 31

29. Teleoconch finely spirally-striate or smooth; protoconch paucispiral, with large initial whorl 30

—— Teleoconch axially-costate or smooth; protoconch multispiral, with small initial whorl .... *Benthonella*

30. Shell ovate-conic, with very weak (or absent) varix .... *Setia*

—— Shell elongate-conic, with varix .... *Onoba* (in part)

31. Protoconch with dome-shaped apex; teleoconch smooth or variously sculptured 32

—— Protoconch with pointed apex; teleoconch smooth except for spiral cords on base .... *Striatestea*

32. Shell with axial ribs predominating; outer lip with sinuate edge 33

—— Shell with fine spiral striae or smooth; outer lip with only a very slight indication of a posterior indentation 34

33. Pallial prostate gland present, penial duct simple .... *Pusillina*

—— Pallial prostate gland absent, penial duct with prostatic tissue .... *Rissoa*
(Note: *Mohrensternia* also keys out here; it can be separated from *Rissoa* by the lack of a labial varix and from *Pusillina* by its larger size).

34. Shell ovate to ovate-conic 35

—— Shell elongate-conic 36

35. Protoconch with large initial whorl .... *Powellisetia*

—— Protoconch with small initial whorl .... *Voorwindia*

36. Outer lip orthocline; shell surface smooth; outer lip dentate within in some species .... *Peringiella*

—— Outer lip prosocline to opisthocline; shell surface smooth (outer lip opisthocline if smooth) or spirally sculptured or with axial and spiral sculpture; outer lip smooth within .... *Onoba* (in part)

Review of Genera

The 31 rissoid genera recognized as being valid are arranged in two subfamilies and, within the Rissoinae, in convenient groups which reflect their general similarity, but not necessarily their phyletic relationship. A list of the recognized genera and subgenera (included in parentheses), in the order in which they appear in the text, follows.

Subfamily Rissoinae

Rissoa group

Alvania group

Onoba group

Merelina group

Attenuata group

Subfamily Rissoininae

Genus *Rissoa* Desmarest, 1814

Rissoa (Fréminville ms) Desmarest, 1814: 7. Type-species *Rissoa ventricosa* Desmarest, 1814; subsequent designation Bucquoy, Dautzenberg & Dollfus, 1884: 262. Recent, Mediterranean Sea (Figs 10C; 76A–D).

Rissoia invalid emend.

Loxostoma Bivona-Bernardi, 1838: 4 (= *Loxotoma*, error). Type-species *Loxostoma denticulus* Bivona-Bernardi, 1838, = *Rissoa monodonta* Philippi, 1836; subsequent designation Verduin, 1983: 61. Recent, Mediterranean Sea (Fig. 78A, B).

Goniostoma (Megerle ms) Villa, 1841: 29 (not preocc. by *Gonyostoma* Swainson, 1840). Type-species *Turbo auriscalpium* Linné, 1758; subsequent designation Coan, 1964: 166. Recent, Mediterranean Sea (Fig. 77E, F).

Zippora Leach in Gray, 1847a: 270, *nomen nudum*; Leach, 1852: 169. Type-species *Zippora drummondi* Leach, 1852, = *Turbo auriscalpium* Linné, 1758; monotypy. Recent, Mediterranean Sea (Fig. 77E, F).

Turboella (Leach ms) Gray, 1847b: 152 (= *Turbella*, error), not *Turboella* Leach in Gray, 1847a, *nomen nudum*. Type-species *Turbo parvus* Montagu, = *Turbo parvus* da Costa, 1778; original designation (see Verduin, 1976: 22 for discussion on type selection and validity of name). Recent, Europe (Figs 10B; 79A–C).

Anatasia Gistel, 1848: 169, *nomen nudum*.

Apanthausa Gistel, 1848: X, *nomen nudum*.

Persephona Leach, 1852: 189, not Leach, 1817. Type-species *Persephona rufilabris* Leach, 1852, = *Rissoa rufilabrum* Alder, 1844; subsequent designation, Bucquoy *et. al.*, 1884:280. Recent, Europe (N.B. Nordsieck, 1972 cites *R. violacea* Desmarest (Fig. 76E–H) as the type of his replacement name *Lilacinia* but that species name was not included in the species originally listed by Leach). Recent, western Europe.

Lamarckia Leach, 1852: 195, not Olivi, 1792. Type-species ***Buccinum costatum*** 'da Costa', = ***Turbo costatus*** ***Pultney, 1813,*** not von Salis, 1793, = ***Helix labiosa*** Montagu, 1803; monotypy. Recent, Europe.

Rissostomia Sars, 1878: 448. Type-species *Turbo membranaceus* J. Adams, 1800; monotypy. Recent, N.W. Europe (Fig. 77A–D).

Apicularia Monterosato, 1884a: 139, 1884b: 56. Type-species *Rissoa similis* Scacchi, 1836; subsequent designation Crosse, 1885: 140. Recent, Mediterranean Sea (Fig. 78C–F).

Sabanea (Leach ms) Monterosato, 1884a: 138 (not Leach in Gray, 1847a). Type-species *Rissoa parva* da Costa, = *Turbo parvus* da Costa, 1778. Recent, Europe (Figs 10B; 79A-C).

Schwartzia Bucquoy, Dautzenberg & Dollfus, 1884: 278. Type-species *Rissoa monodonta* 'Bivona, 1832' (= Philippi, 1836 *ex* Bivona-Bernardi ms). Recent southern Europe and Mediterranean Sea (Fig. 78A, B).

?*Nititurboella* Nordsieck, 1972: 202. Type-species *Turboella* (*Nititurboella*) *allermonti* Nordsieck, 1972, unnecessary replacement name for *Apicularia nitens* Monterosato, 1884, not *Rissoa nitens* Frauenfeld, 1867, a species of *Lucidesta* (*A. nitens* = sculptureless form of *Rissia similis* Sachi, 1836, *fide* Verduin, *in lit.*, 1982); original designation. Recent, Mediterranean Sea.

Sfaxiella Nordsieck, 1972: 207. Type-species (*Rissoa* (*Zippora*)) *nina* Nordsieck, 1968; original designation. Recent, Mediterranean Sea.

Liavenustia Nordsieck, 1972: 208. Type-species (*Apicularia*) *lia* (Benoit ms) Monterosato, 1884; original designation. Recent, Mediterranean Sea.

Gueriniana Nordsieck, 1972: 212. Type-species (*Rissoa*) *guerinii* Récluz, 1843; original designation. Recent, Europe and Mediterranean Sea (Figs 9; 10A; 11A, B).

Lilacinia Nordsieck, 1972: 213, new name for *Persephona* Leach, 1852, not Leach, 1817.

Elatiella Nordsieck, 1972: 217. Type-species (*Rissoa*) *elata* Philippi, 1844, = *Helix labiosa* Montagu, 1803; original designation. Recent, Mediterranean Sea; Black Sea.

Diagnosis. *Shell*: of small to large size, elongate-conic, non-umbilicate; axial sculpture usually predominant, usually of prominent, broad ribs. Weak spiral threads often present, sometimes broad with spaces between them sunken to form shallow pits. Sculpture weak to moderately strong axial ribs; spiral cords weak, low, usually do not cross axial ribs; axials not terminated at periphery by a spiral cord but usually weak or absent on base; sometimes smooth. Aperture with shallow posterior sinus broadly rounded anteriorly; columella often thick, sometimes twisted. Outer lip opisthocline to prosocline, with weak to pronounced varix externally (Figs 76A, E; 77A, F; 78A, C; 79A). Protoconch narrowly conic, edge sinuate, usually more than two whorls. Prodissoconch usually small, slightly tilted, sometimes sculptured with a few, very weak spiral threads which disappear before commencement of second whorl; otherwise smooth (Figs 77C, D; 79B; see also Fretter & Graham, 1978; Thiriot-Quievreux & Babio, 1975).

Head-foot: cephalic tentacles long, sides slightly tapering to parallel, ciliated; anterior ⅓ of foot constricted, with posterior mucous gland. Mantle edge with only right (posterior) pallial tentacle. A single, slender metapodial tentacle usually emerges from triangular base. Exterior pigment patches usually present, often black or yellow (Clark, 1852; Jeffreys, 1869; Fretter & Graham, 1962; personal observations on several species) (Fig. 9).

Anatomy: based on *R. ventricosa*, Mar Chica, near Nador, Morocco (4 females), *R. guerinii*, Cala Rossa, Terrasini, Sicily (several males and females, and serial sections) and *R. parva*, Plymouth, England (several males and females and sections). Ctenidial filaments triangular; bases only slightly narrower than length (as in *R. ventricosa*) to finger-shaped or narrowly triangular with bases about half length or less. Osphradium about as long as ctenidium; about half width of gill bases in *R. ventricosa*, about equal to gill bases in *R. guerinii* and about ¾ of gill bases in *R. parva*. Stomach-style sac ratio 2.5–4.4 (2.5–2.9 in *R. ventricosa* and *R. parva*, 3.3–4.4 in *R. guerinii*); length-width ratio 1.6–3.3 (1.6–2 in *R. parva* and *R. ventricosa*, 2.8–3.3 in *R. guerinii*). Intestine-rectum convolute to slightly folded just behind and/or in front of posterior pallial wall.

Male (Fig. 11A, B) with penis long, parallel-sided, oval in section, with slender, subterminal filament (*f*) and submarginal duct containing prostatic tissue (Fig. 11A; *pt*). Pallial vas deferens (Fig. 11B; *pvd*) narrow, thin-walled, extending to posterior end of pallial cavity where it opens by way of a short duct (*po*) and receives visceral vas deferens (*vvd*). No pallial prostate gland. Seminal vesicle a convolute mass over inner wall of stomach.

Female (Fig. 10) with well developed vestibule (*v*), but with no evidence of sperm storage. A thin, narrow flap (*lf*) runs posteriorly from vestibule along left (inner) side of capsule gland just above ventral channel. Ventral channel (*vc*) conspicuous and forms a separate tube in posterior ⅓–½ of lower oviduct gland (*ot*). This tube gives off bursal duct immediately behind posterior pallial wall. Bursa copulatrix (*b*) about equal in size, or slightly larger than, upper oviduct gland and anterior two thirds lies within pallial roof in *R. ventricosa* (Fig. 10C) but, in *R. parva* (Fig. 10B), it protrudes only slightly into pallial roof in some specimens. In *R. guerinii* (Fig. 10A) bursa entirely behind pallial cavity. Seminal receptacle (*sr*) small relative to bursa, narrow to bulbous, on right side of upper oviduct gland at its anterior edge; opens ventrally to oviduct immediately behind bursal duct. Upper oviduct gland simple (i.e. not coiled), small (approximately ¼ of length of lower oviduct gland), divided dorsoposteriorly into finger-like lobes (*sl*) filled with sperm (not confirmed in *R. parva*).

Nervous system of *R. ventricosa* with cerebral commissure about half width of cerebral ganglia, and pleural ganglia fused to cerebrals. Supraoesophageal ganglion separated from right pleural ganglion by connective slightly longer than supraoesophageal ganglion. Suboesophageal connective about half length of suboesophageal ganglion.

A detailed account of the anatomy of *R. membranacea* and *R. lilacina* Récluz, 1843 has been given by Johansson (1948).

Operculum: simple, thin nucleus eccentric, last whorl large (Figs 76B, F, G; 78D, E).

Radula: central teeth, $\frac{1-3+1+1-3}{1+1 \qquad 1+1}$ with outer pair of basal denticles derived from lateral margins; ventral edge of each tooth with moderately developed U-shaped extension. Lateral teeth 0 − 4 + 1 + 2 − 7, marginal teeth with subequal cusps (Figs 76C, D, H; 77B, E; 78B, F; 79C).

Egg capsules: circular, lens-shaped, fixed to substrate (Lebour, 1934; Fretter & Graham, 1978).

Development: planktotrophic larval stage probably present in most species.

Distribution. North-eastern Atlantic (shores of Europe) and Mediterranean Sea (many species, see Smith, 1971; Nordsieck, 1972; Fretter & Graham, 1978; Verduin, 1982). Oligocene to Recent (Cossmann, 1921).

Material Examined.

+**R. ventricosa*. Several lots (BMNH, AMS).
+**R. monodonta*. Several lots (BMNH, AMS).
+**T. auriscalpium*. Several lots (BMNH, AMS).
+**T. parvus*. Many lots (BMNH, AMS).
+**T. membranaceus*. Several lots (BMNH, AMS).
+**R. similis*. A few lots (BMNH, AMS).
R. elata. 1 lot (ex Monterosato) (BMNH).
+ *R. guerinii*. Several lots (BMNH, AMS).
A. nitens. One lot ex Monterosato (BMNH).
A. lia. A few lots (BMNH, AMS).
A. nina. 2 paratypes (AMS).

Several other species were also examined in the course of this revision.

+ protoconch microsculpture has been examined.
* the radula and operculum have been examined.

Remarks. The large number of genus-group taxa listed as synonyms attests to the diversity in shell form of species in this genus. It is a group characteristic of shallow marine areas in the north-eastern Atlantic and Mediterranean Sea. Differences in shell shape and sculptural pattern do not appear to be correlated with any radular or protoconch features that might suggest a workable classification using narrower genus-group taxa than used here. Indeed the variability shown by some species (e.g. the '*Rissostomia*' group, Verduin, 1982) is very considerable, making genera or subgenera based on relatively minor shell characters even less tenable. When there is more anatomical information finer subdivisions may possibly become apparent but available evidence suggests that several species groups are present which cannot be readily grouped into subgenera based on anything more than minor, overlapping, shell characters.

Fretter & Patil (1961) and Fretter & Graham (1962) give some details of the anatomy of the reproductive systems of *R. parva* and *R. lilacina*, and Johansson (1939) has described the reproductive system of *R. violacea* (= *R. lilacina,*) and *R. membranacea*. Johansson (1948, 1956) discusses at length the significance of an external groove of the female pallial duct (of *Rissoa violacea*, = *R. lilacina*, and *R. membranacea*), which, he suggests, is due to a different method of closure of the duct from that of *Rissoa* (= *Pusillina* herein) *inconspicua*, which was also examined by Johansson (1939). Fretter & Graham (1962) state that both *R. lilacina* and *R. parva* have a thin-walled ventral channel in the lower oviduct gland (= capsule gland) but there is no reference to the presence or absence of an external groove or fold on the lower oviduct gland of *R. parva* in the accounts given by Fretter & Patil (1961) and Fretter & Graham (1962). This groove (or fold) is present in the three species of *Rissoa* I have examined, being readily observable in dissection (Fig. 10) as well as in sections.

The genus *Turboella* has been used with *Turbo parvus* as type by several authors, most recently Nordsieck

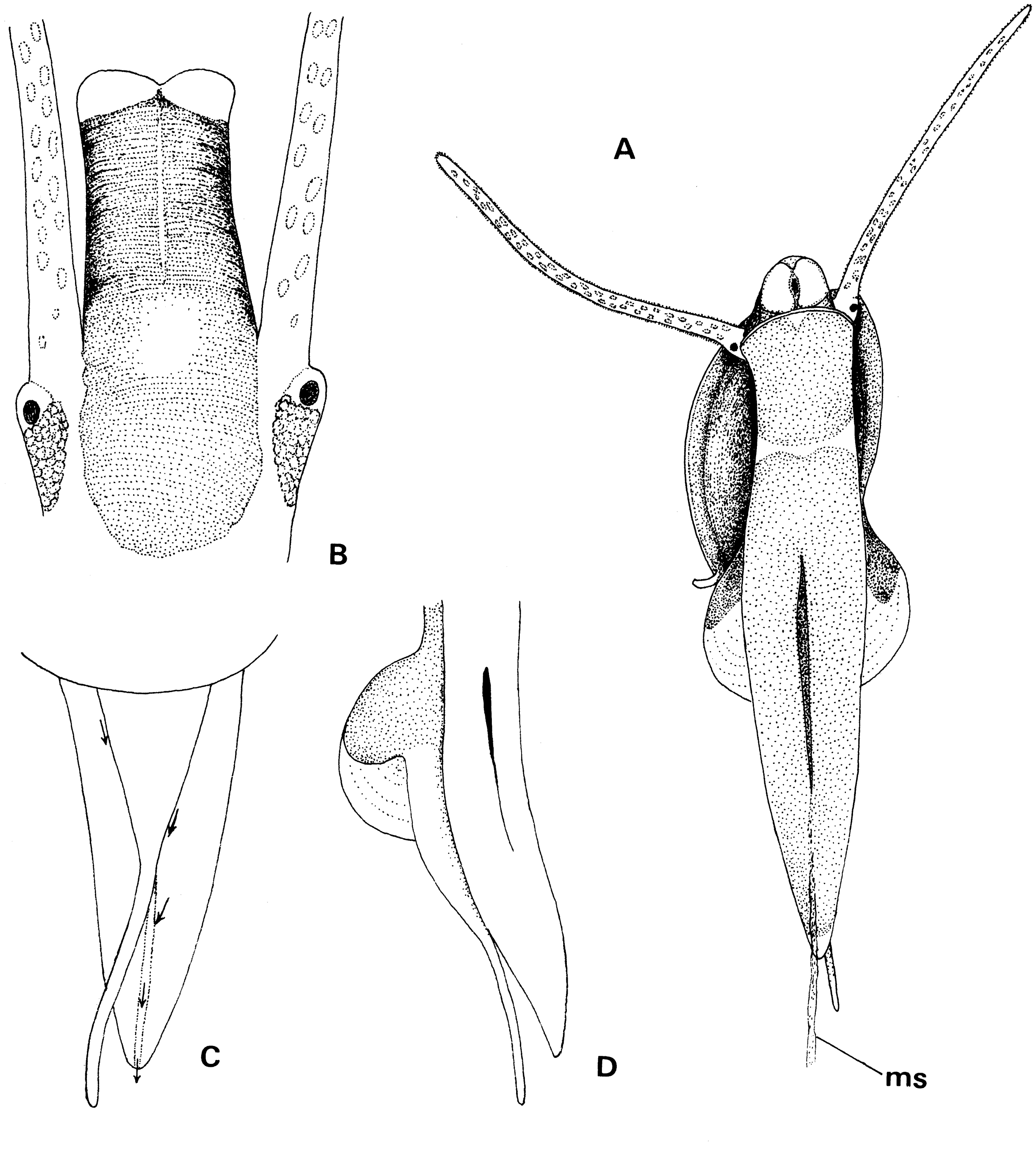

Fig. 9. Head-foot of *Rissoa guerinii* Récluz, Cala Rossa. Terrasini, Sicily: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of posterior foot showing metapodial tentacle, ciliation and median groove; **D**, lateral view of posterior end of foot showing metapodial tentacle. *ms*-mucous string. The arrows show the direction of ciliary currents.

(1972) and Verduin (1976). Verduin argues that *Turboella* Leach in Gray (1847a) is a *nomen nudum* and that *Turboella* Gray (1847b) is validly introduced. *Turboella* is introduced in Gray (1847b) as a synonym but is still available because it has been accepted in the literature as an available name (ICZN, article 11(d)). The 8 species names included in *Turboella* by Leach (1847a) were all listed as *nomina nuda* by Sherborn (1902-1913), but Coan (1964) argued that one is *Turbo calathiscus* Montagu, a possible synonym of *Alvania cimex* (Linné) type species of *Alvania*, which he designated as type. I have not followed Coan's (1964) interpretation because, as Verduin (1976) pointed out, Leach spelt the name *calathriscus*. In addition the difficulty of the correct identification of *T. calathiscus* has to be considered. Montagu based his species on a

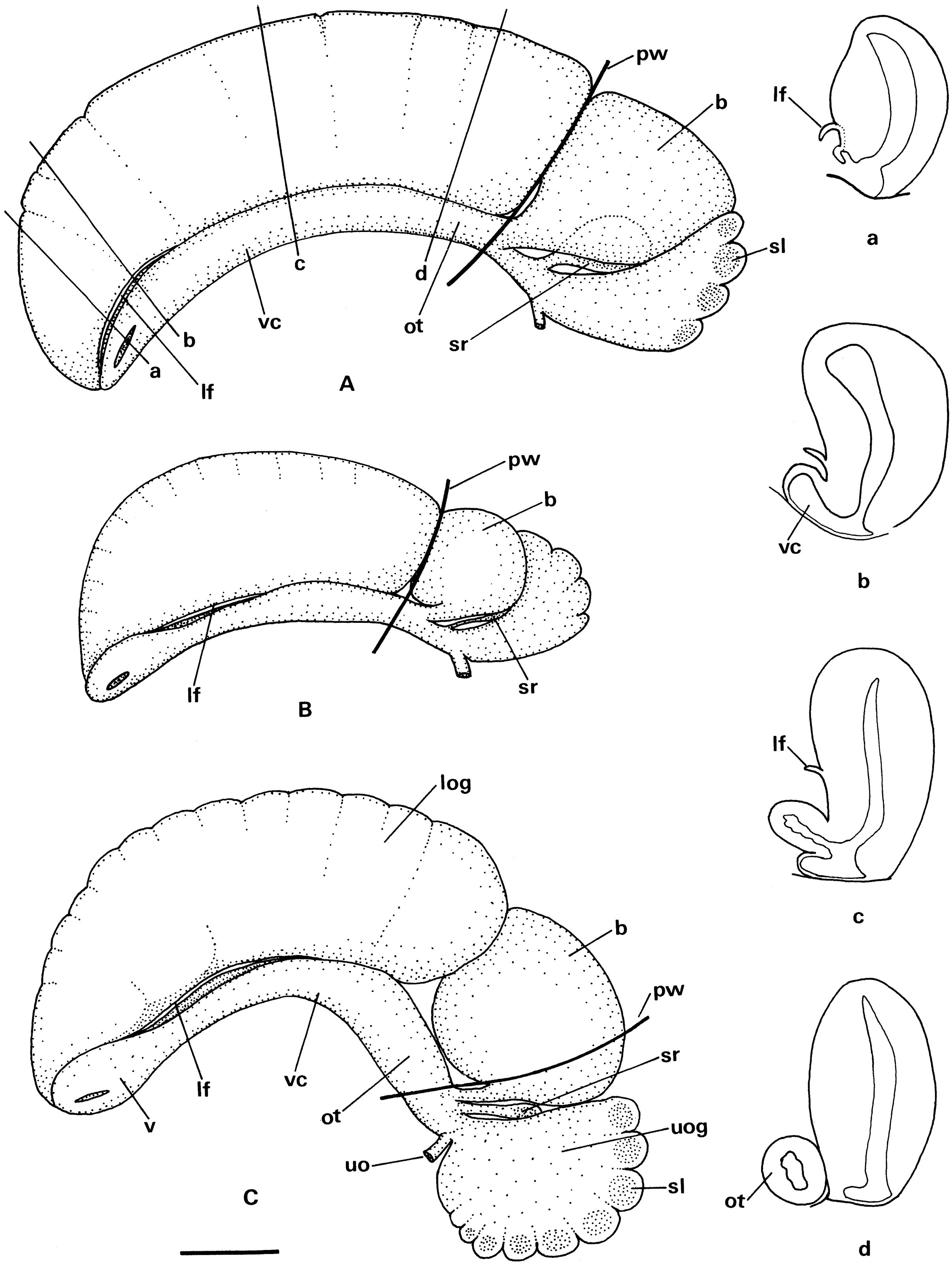

Fig. 10. Female genitalia of *Rissoa* species. **A,** *R. guerinii* Récluz, left side; **B,** *R. parva* (Da Costa), left side; **C,** R. ventricosa Desmarest, left side. Positions of sections a-d indicated. *b*-bursa copulatrix; *lf*-lateral fold; *log*-lower oviduct gland; *ot*-tubular part of oviduct; *pw*-posterior wall of pallial cavity; *sl*-sperm storing lobe; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel. **Scale:** 0.25 mm.

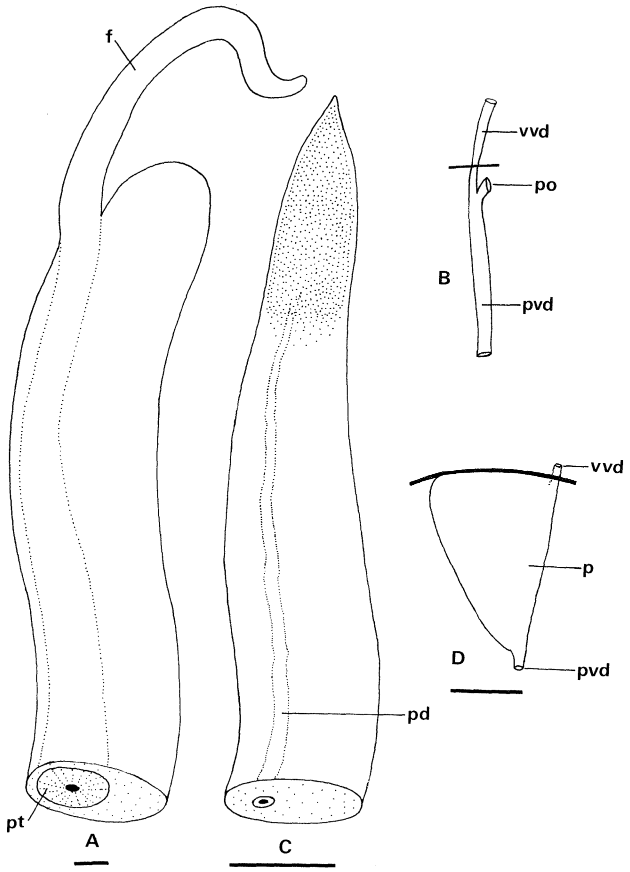

Fig. 11. Male genitalia of *Rissoa* and *Pusillina* species. **A-B**, *Rissoa guerinii* Récluz: **A**, distal half of penis; **B**, posterior end of pallial vas deferens. **C-D**, *Pusillina* (*Pusillina*) *inconspicua* (Alder): **C**, distal half of penis; **D**, prostate gland. *f*-filament; *p*-prostate gland; *pd*-penial duct; *po*-pallial opening; *pt*-prostatic tissue; *pvd*-pallial vas deferens; *vvd*-visceral vas deferens. **Scale:** 0.1 mm.

specimen from the island of Jura on the Scottish coast. *Alvania cimex* is unknown in N.W. Europe. Virtually all previous authors have regarded *Turbo parvus* as the type species of *Turboella*; consequently in the interest of stability I, like Verduin (1976), regard *Turboella* Gray, 1847a as a *nomen nudum*.

Nordsieck (1972) used *Turboella* as a genus restricting it to species with relatively small, semitransparent, thin shells sculptured with ribs that (when present) are always discontinued below the periphery. He stressed that the most characteristic feature of the genus is that nearly all species possess ribbed and ribless forms. Nordsieck included 6 subgenera (including *Turboella* s.s.) in *Turboella* but Verduin (1976) dismissed this arrangement by stating that *Turboella* contains "at most 20 good species, which are so closely allied that it seems useless to arrange them in subgenera". Verduin revised the 9 eastern Atlantic and Mediterranean species of *Turboella* he considered to be valid and reduced *Turboella* to a subgenus of *Rissoa*, although no diagnosis of *Turboella* was given.

Verduin (1976) included the type-species of 5 of the subgenera recognized by Nordsieck (1972) (*Mutiturboella*, *Benzia*, *Turboella*, *Radiata* and *Pusillina*) in *Turboella* but did not mention the type species of *Nitituerboella* (*allermonti* Nordsieck = *nitens* Monterosato), although he stated that Nordsieck's *Turboella* (*Nitituerboella*) *allermonti crassa* is identical to *R. interrupta* (Adams) (? = *parva* da Costa). However, Verduin (*in lit.* 1982) has indicated that *T.* (N.) *allermonti* is a synonym of *Rissoa similis*. The majority of these species are tentatively placed in *Pusillina* below. The generic status of most of the small species grouped in '*Turboella*' by Nordsieck and Verdium must, however, remain in some doubt until more information is available about their anatomy.

Johansson (1939) showed that the anatomy of *Pusillina inconspicua* differs in a number of ways from that of the larger species of *Rissoa* that he examined, the most obvious being the presence of a pallial prostate gland in the male and a simple penis, whereas the male of *R. parva* (Fretter & Patil, 1961) and the two larger *Rissoa* species examined by Johansson (*R. lilacina* and *R. membranacea*) have a simple male pallial duct and the penis contains prostatic tissue. It is shown below that the type-species of *Pusillina*, *R. dolium* Nyst, has a similar anatomy to that of *R. inconspicua*.

In Nordsieck's (1972) diagnosis of *Turboella* the shell characters listed do not adequately separate his '*Turboella*' from *Rissoa*. For example, *R. parva* ranges from 1.8 mm to 5.0 mm in height, the upper range of which compares well with the normal length of several species included in *Rissoa* by Nordsieck. The shell of *R. parva* is not thinner than several *Rissoa* species and is certainly not more semitransparent. Several species of *Rissoa* also have the ribs discontinued at the periphery and several also show considerable sculptural variation, although generally not to the extent seen in some of the species of '*Turboella*'. The anatomical, protoconch and radular characters of *R. parva* do not exhibit any differences from those of species in *Rissoa*, and the general appearance of the shell is also extremely similar to species included in that genus.

With the exception of *R. parva* and *R. interrupta* (Adams, 1798) all the species included in '*Turboella*' by Verduin (1976) as well as *R. sarsi* Lovén, 1846 (= *R. albella* Lovén, 1846, not Alder, 1844) are probably best included in *Pusillina*, as they appear to be more similar to *Pusillina inconspicua* and *P. dolium* than to *Rissoa parva*.

As pointed out by Smith (1971), the name *Rissoa* was first introduced by Risso (1813a, b) and attributed to Fréminville, as were the 8 species in the list which accompanied it. As all of these species were *nomina nuda* at the time of publication, the authorship of *Rissoa* is attributed to Desmarest (1814), who was the first to validate the name.

The type designation of Bucquoy, Dautzenberg & Dollfus (1884) is cited by Coan (1964) as the earliest for *Rissoa* and I have failed to find an earlier valid designation. Gray (1847b) gives '*Helix labiosa*' Montagu, 1803 as the type of the genus. The species name *labiosa* is, however, not included in Desmarest's original list of species and is therefore not available for type designation.

The central teeth of the radula of *R. membranacea* (Fig. 77B) are somewhat atypical in having a wide, straight-edged median cusp which has probably been derived from the fusion of at least the two inner marginal cusps with the median cusp. This same fusion appears to have also occurred to a lesser extent with the cusps on the lateral teeth. In other features, however, this species is typical of *Rissoa*.

Species of *Rissoa* can be distinguished from those of *Alvania* by their usually more elongate shells, with spiral sculpture weak or lacking. The foot has a single metapodial tentacle and the external parts of the animal are usually heavily pigmented (Fig. 9). *Alvania* species have shorter shells with strong spiral sculpture. They have 3–7 metapodial tentacles and the exposed parts of the animal are less pigmented in most species.

Genus *Pusillina* Monterosato, 1884

Pusillina Monterosato, 1884b: 56. Type-species *Rissoa pusilla* Philippi, 1836, not Grateloup, 1828, = *R. dolium* Nyst, 1843; monotypy. Recent, Mediterranean Sea (Figs 13A; 79D, E).

Diagnosis. *Shell*: minute to small, ovate to conic, non-umbilicate to umbilicate, smooth or, typically, with axial ribs stronger than spiral sculpture; axial ribs usually obsolete on base. Aperture with simple peristome, inner lip narrow, attached to parietal wall, angled posteriorly, anterior end rounded, simple. Outer lip opisthocline to prosocline, with or without external varix. Protoconch of 1½ to 2¼ whorls, smooth or with spiral threads or spiral rows of minute, closely spaced pustules.

Head-foot: cephalic tentacles long, with parallel sides, ciliated; foot constricted in middle, with posterior mucous gland. Anterior (left) and posterior (right) pallial tentacles present, or only posterior. A single, slender metapodial tentacle present. Exterior pigment patches present in some species (often black and yellow).

Anatomy: ctenidium with bases of finger-shaped filaments narrower than width of osphradium; osphradium slightly shorter than ctenidium. Stomach-style sac ratio 2.2–3.7, length-width ratio 1.7–2.2

Male with straight, long penis, extending entire length of pallial cavity, with or without terminal filament. Penial duct marginal to subcentral, closed, lacking prostatic tissue. Prostate gland well developed, entirely pallial or partly embedded in kidney.

Female with well developed vestibule used for sperm storage in some species. Bursa copulatrix large (about equal to upper oviduct gland in size), to small (in relation to upper oviduct gland) or apparently absent in one species. Seminal receptacle small in relation to upper oviduct gland and immediately anterior to it (apparently absent in one species). Upper oviduct gland simple to U-shaped, smaller than lower oviduct gland, with or without posterodorsal lobes modified for sperm storage. Nervous system known only for subgenus *Haurakia*.

Operculum: simple, thin, nucleus eccentric, last whorl large.

Radula: central teeth $\frac{1-5+1+1-5}{1-0+1\quad 1+0-1}$; outer pair of basal denticles derived from lateral thickenings; marginal cusps usually 2–3; weak to well developed U-shaped ventral extension; lateral margins at about 20°–30°. Lateral teeth with formula $0-5+1+2-12$; marginal teeth with cusps on outer marginal confined to distal ¼ of inner face of tooth and distal end, usually subequal in length to those on inner marginal teeth, possibly absent in one subgenus.

Egg capsules: similiar to those of *Rissoa* (Lebour, 1934; Fretter & Graham, 1978).

Development: direct or with planktotrophic larval stage.

Distribution. North Atlantic and Mediterranean Sea, Japan, tropical western Pacific, South Africa and Australasia. Paleocene to Recent.

Remarks. Species of *Pusillina* and *Rissoa* are similar in many characters of the shell, radula, head-foot and anatomy. They are regarded as belonging to separate genera primarily because of important differences in their genitalia. Despite these differences the two groups are clearly very closely related as indicated by the large number of shared characters.

Lack of a pallial prostate gland and acquisition of penial prostatic tissue in *Rissoa* are modifications from what is here assumed to be the more primitive state seen in *Pusillina*—a pallial prostate gland and a simple penis. These differences were considered to be sufficiently important by Slavoshevskaya (1975a) to separate *Rissoa* and *Pusillina* (as *Haurakia*) into two separate families.

The lateral fold on the left side of the capsule gland found in *Rissoa* species is absent in the three species of *Pusillina* examined in this study and this was also demonstrated by Johansson (1939) in *Pusillina inconspicua*. Some species of *Pusillina* and *Rissoa* have posterodorsal lobes on the upper oviduct gland in which sperm is stored. In this feature, and in the overall plan of the female genitalia, *Pusillina* and *Rissoa* show considerable similarity.

The small, inconspicuous species of *Pusillina* are overshadowed by the abundant, larger species of *Rissoa* in the north-eastern Atlantic and Mediterranean. Some divergence in the ancestral *Pusillina*—*Rissoa* stock has occurred to produce four geographically separated groups which are here regarded as subgenera.

The hypothetical relationships of *Rissoa*, *Pusillina* and another apparently related genus, *Setia*, are summarised in Fig. 16.

Key to Subgenera of *Pusillina*

1. Penial filament present; distribution Indo-west Pacific .... *Haurakia*

——Penial filament absent; distribution Atlantic and Japan 2

2. Protoconch multispiral in most species; distribution eastern Atlantic and Mediterranean .... *Pusillina*

——Protoconch paucispiral, distribution western Atlantic 3

3. Shell with spiral sculpture; bursa and seminal receptacle present .... *Ameririssoa*

——Shell without spiral sculpture; bursa and seminal receptacle absent .... *Vicinirissoa*

Subgenus *Pusillina* s.s.

?*Varisetia* Nordsieck, 1972: 158. Type-species (*Rissoa* (*Setia*)) *quisquiliarum* Watson, 1886; original designation. Recent Azores.

Auriconoba Nordsieck, 1972: 170. Type-species (*Auriconoba*) *janusi* Nordsieck, 1972; original designation. Recent, Madeira, eastern Atlantic (Figs 15B; 78H).

Mutiturboella Nordsieck, 1972: 196. Type-species (*Rissoa*) *inconspicua* Alder, 1844; original designation. Recent, Europe (Figs 11C, D; 12; 13B; 80A–D).

?*Benzia* Nordsieck, 1972: 197. Type-species (*Paludina*) *benzi* Aradas & Maggiore, 1843; original designation. Recent, Mediterranean Sea (Fig. 78G).

Radiata Nordsieck, 1972: 201. Type-species (*Rissoa*) *radiata* Philippi, 1836; original designation. Recent, Mediterranean Sea.

?*Turgidina* Verduin, 1979: 47. Type-species *Rissoa* (*Turgidina*) *testudae* Verduin, 1979; original designation. Recent, Mediterranean Sea.

Diagnosis. *Shell*: ovate to ovate-conic or conic, umbilicate or non-umbilicate, sculpture (when present) of axial ribs terminating at periphery and, in some species, weak spiral threads. Aperture rounded to subpyriform, rarely with prominent posterior notch; varix strong to very weak (Figs 15B; 78G, H; 79E,F; 80A). Protoconch of about 1½–2¼ whorls, smooth or with weak spiral threads on first whorl (Figs 79G; 80C, D; see also Fretter & Graham, 1978, Fretter & Pilkington, 1971 and Thiriot-Quiévreux & Babio, 1975).

Head-foot: as for genus, based on *R. inconspicua* (Fig. 12) (Clark, 1852; Jeffreys, 1869; Fretter & Graham, 1978 and personal observation), *R. sarsi* Lovén (Jeffreys, 1869; Fretter & Graham, 1978) and *R. dolium* (preserved material).

Anatomy: based on *P.* (*Pusillina*) *dolium*, Cala Rossa, Terrasini, Sicily (5 females, 1 male); *P.* (*Pusillina*) *inconspicua*, Plymouth Sound, England, 9–18 m (3 females, 1 male); *P.* (*Pusillina*) *sarsi*, Sweden (sectioned material). Ctenidial filaments finger-shaped, ctenidium slightly longer than osphradium; only 3 filaments anterior to osphradium. Osphradium 2–3 times wider than gill bases. Stomach rather short (length/width ratio 1.7–2.2) with well developed style sac (stomach-style sac ratio 2.2–3.7). Rectum more or less straight within pallial roof; folded immediately behind posterior pallial wall.

Male with large, slightly tapering, strap-like penis (Fig. 11C). Distal portion of penis circular in section, apparently glandular and tapering rapidly to a point; penial duct (*pd*) sublateral to subcentral. Prostate gland (Fig. 11D; *p*) well developed, pallial (not confirmed in *P.* (*Pusillina*) *dolium*).

Female (Fig. 13) with large vestibule containing sperm in a pocket separate from capsule gland. No trace of flap on left side of capsule gland as seen in *Rissoa*. Ventral channel (*vc*) conspicuous, not separated from lower oviduct gland. Bursa copulatrix (*b*) and its duct lie opposite posterior pallial wall (as in *P. dolium*, Fig. 13A) or just behind (as in *P. inconspicua*, Fig. 13B). Bursa smaller than upper oviduct gland and about equal in size to seminal receptacle in *P. dolium*, relatively larger in *P. inconspicua*. Seminal receptacle (*sr*) elongate, lying between bursa and upper oviduct gland. Both bursa and seminal receptacle on outer (right) side of glandular oviduct and open to oviduct immediately below. Upper oviduct gland (*uog*) about ⅓ length of lower oviduct gland (*log*) and has, dorsoposteriorly, finger-like lobes filled with sperm (*sl*). It is apparently neither coiled nor folded.

See Johansson (1939) for additional information on *P. inconspicua*.

Operculum: as for genus.

Radula: very similar to *Rissoa*; central teeth $\frac{2-4+1+2-4}{1+1 \quad 1+1}$;lateral teeth 3–5 + 1 + 6–10 (Figs 79D; 80B).

Egg capsules: lens-shaped, circular, attached to substrate (*P. inconspicua*: Lebour, 1934; Fretter & Graham, 1978).

Development: planktotrophic larvae probably present in most species.

Distribution. West coast of Europe, Canary Islands, Mediterranean Sea (see Remarks under *Rissoa* above), Sea of Japan (? *Hydrobia plicosa* Smith, 1875).

Paleocene, France: *Turbella pachycolpa* Cossmann, 1928.

Eocene, France: *Bulimus nanus* Lamarck, 1804.

Material Examined.

+**R. dolium*. 1 lot, ex Monterosato (BMNH) and a few additional lots (AMS).

A. janusi. 3 paratypes, ex F. Nordsieck (AMS).

R. quisquiliarum. Syntypes (BMNH).

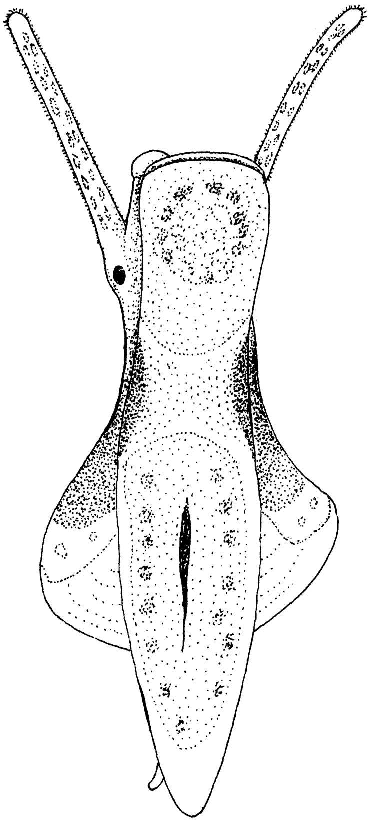

Fig. 12. Ventral view of head-foot of *Pusillina* (*Pusillina*) *inconspicua* (Alder), Plymouth, England.

+**R. inconspicua*. Many lots (BMNH, AMS).
  R. benzi. 1 lot (BMNH).
  Auriconoba watsoni Nordsieck, 1972 (= *Rissoa picta* Watson, 1873 not Jeffreys, 1867), one lot (MCZ).
+**Rissoa sarsi* Lovén, 1846. A few lots (BMNH, AMS).
+ *B. nanus*. A few lots (AMS).

Remarks. See also remarks above under *Rissoa*. The anatomy of the type-species of *Pusillina* and its shell characters agree with those of *Rissoa inconspicua*, the only difference being its somewhat more slender shell. It is possible that the subgenus *Pusillina*, as here recognized, comprises a group of species derived from more than one line, within the *Rissoa* group, by reduction in size. One of the earliest known species of *Pusillina* s.s. is *P. nana* (Lamarck) (Fig. 79F), a very abundant Eocene species in the Paris Basin. This species is not unlike *Pusillina dolium* and shows a wide range of variation including non-costate forms. From this it could be inferred that *Pusillina* has arisen earlier than *Rissoa*. Somewhat similar species included in '*Turboella*' (= *Pusillina* in part) by Cossmann (1921) and Sohl (1960) extend back to the upper Cretaceous, although these appear to have features in common with *Alvania*. The two species described by Sohl (1960) (Fig. 92E–H) are presumably not ancestral to *Pusillina* because they have sculptured, paucispiral protoconchs.

There is little doubt that *Pusillina* and *Mutiturboella* are consubgeneric but *Benzia*, *Radiata* and *Varisetia* are based on type-species for which only shells are available.

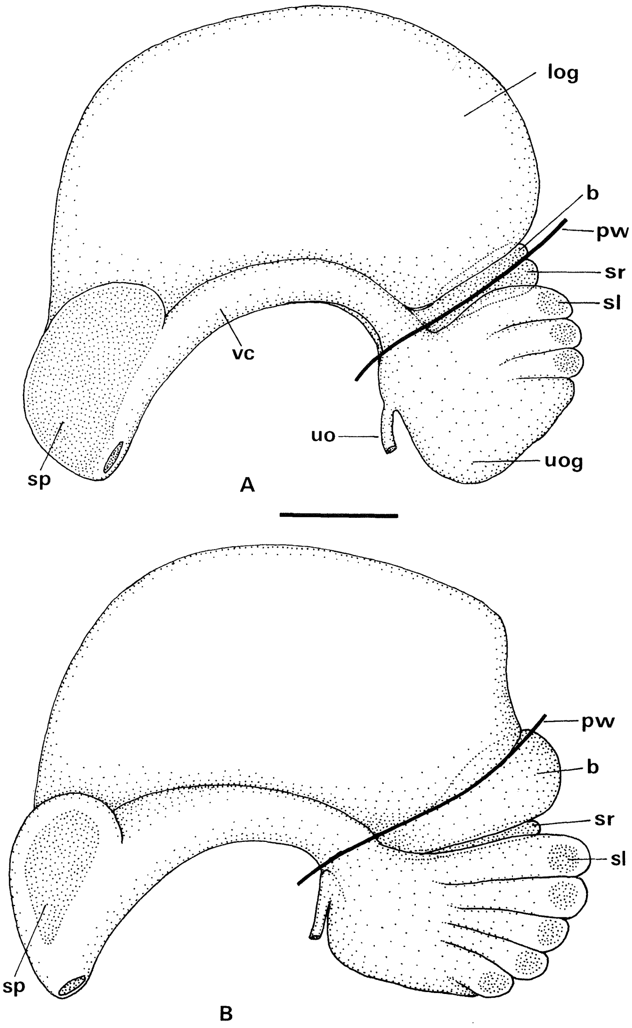

Fig. 13. Female genitalia of *Pusillina* (*Pusillina*) species. **A**, *P.(P.) dolium* (Nyst), left side; **B**, *P.(P.) inconspicua* (Alder), left side. *b*-bursa copulatrix; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sl*-sperm storage lobe; *sp*-sperm in vestibule; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

In these, only the gross teleoconch characters have been observed from typical material. They fall within *Pusillina* as here defined but, until animals have been examined, this synonymy cannot be firmly established. The type-species of *Turgidina* is also known only from the shell. It appears to differ in several shell characters from other species of *Pusillina*, as far as can be judged from the published illustrations and description, but until more evidence distinguishing this taxon from *Pusillina* is forthcoming it is tentatively included as a synonym.

Auriconoba janusi (Figs 15B; 78H) has a peculiar apertural development in which a broad, deep posterior channel is formed. A series of specimens of *Pusillina watsoni* (Nordsieck) from the Azores (MCZ) includes a few individuals with this type of aperture, the remainder being intermediate or having a normal *Pusillina* aperture. It appears that the apertural characteristics of *Auriconoba*, the genus in which *P. watsoni* was included by Nordsieck (1972), are not consistent and there are no additional characters to separate this small group of 'species' from *Pusillina*. It is possible that *A. janusi* is a synonym of *Rissoa guernei* Dautzenberg, 1889, some specimens of which also show a similar apertural development (van Aartsen, *in lit.*, 1982).

Sexual dimorphism has been reported in *Rissoa albella* Lovén (= *Pusillina sarsi* Lovén in which the shells of the males tend to be longer and more slender than those of the females (Rasmussen, 1973:247).

Slavoshevskaya (1979) has described the anatomy of '*Thapsiella*' *plicosa* (Smith) from the Sea of Japan. This species agrees in most respects with the three species of *Pusillina* (*Pusillina*) investigated anatomically but differs in having two pallial tentacles. It is tentatively placed here although its geographic location is widely separated from all other species attributed to this subgenus, these being confined to the north-eastern Atlantic and the Mediterranean Sea.

Subgenus *Haurakia* Iredale, 1915

Haurakia Iredale, 1915: 449. Type-species *Rissoa hamiltoni* Suter, 1898; original designation. Recent, New Zealand (Figs 14B; 81A-D).

Haurakiopsis Powell, 1937: 192. Type-species *H. pellucida* Powell, 1937; original designation. Recent, northern New Zealand (Fig. 82F, G).

Vitricithna Laseron, 1956: 452. Type-species *Cithna marmorata* Hedley, 1907; original designation. Recent, north-eastern Australia (Figs 14A; 82A-E).

Diagnosis. *Shell*: ovate-conic, with weak to moderately-strong axial ribs or smooth; ribs (if present) terminated at periphery by a spiral cord in some species. Anterior edge of aperture with shallow, broad excavation, posterior sinus broad, distinct (Figs 81A; 82A, F). Protoconch apparently smooth or with one or several spiral threads or rows of minute granules; of about 1½ whorls with large initial whorl or initial whorl small and of about 2½ whorls (Figs 81B; 82B, G).

Head-foot: as for genus, usually with an anterior as well as a posterior pallial tentacle. Based on *Pusillina* (*Haurakia*) *hamiltoni*, *P.* (*H.*) *mobilicosta* (Ponder, 1967, pl. 1, figs 2, 9); *P* (*H.*) *marmorata* (personal observation and Kay, 1979).

Anatomy: based on *P.* (*H.*) *hamiltoni*, Island Bay, Wellington, New Zealand (2 males and 2 females) and *P.* (*H.*) *marmorata*, Heron Island, Queensland (1 male, 2 females). Ctenidium with finger-like filaments, osphradium wider than filament bases and nearly as long as ctenidium. Stomach-style sac ratio 2.8, length-width ratio 2. Intestine-rectum looped immediately in front of posterior pallial wall, otherwise almost straight.

Penis long and parallel-sided in *P.* (*H.*) *marmorata*, with terminal filament about ⅓ length of penis; broad, tapering, with small, subterminal filament ⅐ length of penis) in *P.* (*H.*) *hamiltoni*. Penial duct submarginal and narrow in both species. Prostate gland well developed, bean-shaped, protruding behind posterior pallial wall for ¼-⅓ of length. Seminal vesicle coiled over inner side of posterior stomach.

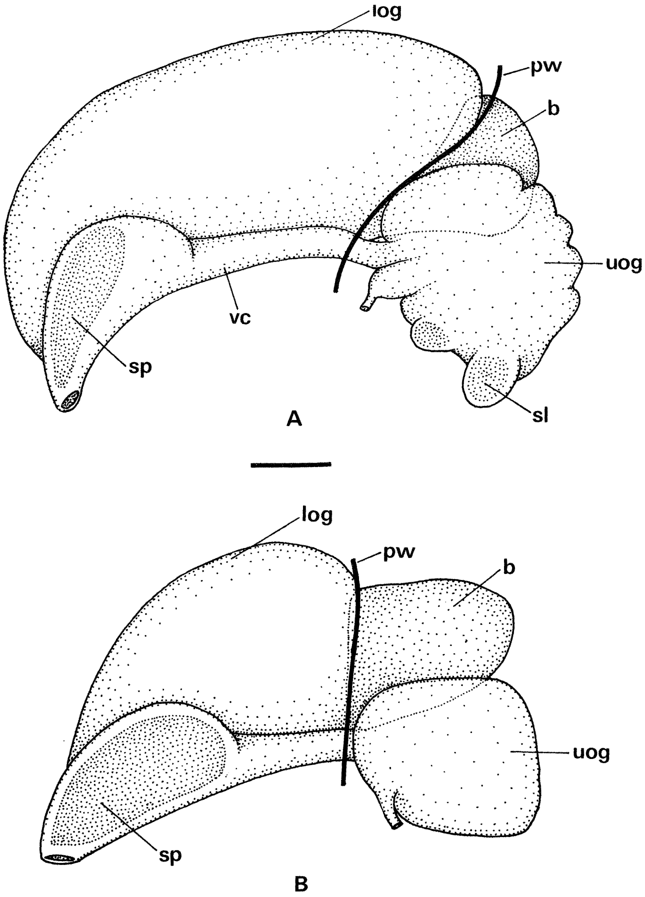

Fig. 14. Female genitalia of *Pusillina* (*Haurakia*) species. **A**, *P.(H.) marmorata* (Hedley), left side; **B**, *P.(H.) hamiltoni*, left side. *b*-bursa copulatrix; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sl*-sperm storage lobe; *sp*-sperm in vestibule; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm (both figures to same scale).

Female (Fig. 14) with vestibule modified as an anterior sperm sac (*sp*). Ventral channel (*vc*) well developed, with no evidence of an external lateral fold on left side of capsule gland. Lower oviduct gland (*log*) confined to pallial cavity. Bursa copulatrix (*b*) almost as large as upper oviduct gland, immediately behind posterior pallial wall on left side of oviduct glands. Upper oviduct gland about 1.5-2.0 times length of lower oviduct gland. Sperm storage in main lumen of lower oviduct gland in *P.* (*H.*) *hamiltoni* (Ponder, 1968) and in a few blister-like outgrowths around ventral and posterior edges (most conspicuously in one posteriorly) in *P.* (*H.*) *marmorata* (Fig. 14A, *sl*). Upper oviduct gland apparently not coiled but shows traces of fused U-shape, thickly glandular in *P.* (*H.*) *hamiltoni*, more flattened and *Rissoa* -like in *P.* (*H.*) *marmorata*. There is no seminal receptacle.

Nervous system (of *P.* (*H.*) *hamiltoni*) with cerebral ganglia joined by a short commissure (about ¼ width of cerebral ganglion). Supraoesophageal and suboesophageal ganglia joined by short connectives to the pleural ganglia, supraoesophageal connective $\frac{5}{7}$ length of supraoesophageal ganglion, suboesophageal connective about ½ length of suboesophageal ganglion. Pleural ganglia loosely fused to cerebral ganglia.

Ponder (1968) gives additional anatomical information on *P.* (*H.*) *hamiltoni*.

Operculum: as for genus (Figs 81C; 82C).

Radula: as for genus; but with one pair of basal denticles and a pronounced tongue-like ventral extension on central teeth. Central teeth $\dfrac{2-5+1+2-5}{1\qquad\quad 1}$, lateral teeth $2-4+1+4-12$ (Figs 81D; 82D, E).

Egg capsules: unknown.

Development: assumed to be direct or with planktotrophic larval stage.

Distribution. Tropical Indo-Pacific: *C. marmorata*.

Miocene, Eniwetok Atoll, Pacific: *Amphithalamus* (*Cerostraca*) *jeffcoati* Ladd, 1966.

Temperate Australia: *Rissoia* (*Pusillina*) *discrepans* Tate & May, 1900, = *Rissoa incompleta* Hedley, 1908; *Cithna angulata* Hedley, 1907.

New Zealand: *R. hamiltoni*, *H. pellucida* and several other species (Ponder, 1967, Powell, 1979).

South Africa: *Rissoa africana* Thiele, 1925, = *R. africana pluricostata* and *R. aequatorialis* both Thiele, 1925; *R. gilva* Turton, 1932; *Rissoa denseclathrata* Thiele, 1925; *Rissoa hertzogi* Thiele, 1925.

Oligocene-Miocene of Tasmania: *Rissoina tateana* T. Woods, 1871; *Haurakia crassicosta* May, 1921.

Miocene-Pleistocene of New Zealand: *Haurakia onerata* Laws, 1939; *Haurakia sodalis* Laws, 1939; *Haurakia chemnitzia* Laws, 1948; *Powellisetia marshalli* Grant-Mackie & Chapman-Smith, 1971.

Material examined.
+ * *R. hamiltoni*. Several lots (NMNZ, AMS).
+ *H. pellucida*. Holotype and paratypes (BMNH), paratypes (AMS, AIM).
+ * *C. marmorata*. Types (AMS) and many other lots.
* *R.* (*P.*) *discrepans*. Holotype (TM) and many other lots (AMS).
R. incompleta. Holotype (AMS).
+ * *S. angulata*. Holotype, paratypes and several other lots (AMS).
R. africana, *R. africana pluricostata* and *R. aequatorialis*. Types (HUM).
R. hertzogi and *R. denseclathrata*. Types (HUM).
R. gilva. Holotype and paratypes (OM) and paratypes (USNM).
R. tateana and *H. crassicosta*. Topotypes (AMS).
H. onerata, *H. sodalis* and *H. chemnitzia*. Paratypes (AUG).
P. marshalli. Holotype and paratypes (AUG).

Remarks. The species in this subgenus differ from *Pusillina* s.s. in having a more pronounced anterior excavation in the aperture of the shell, a tongue-like ventral edge on the central teeth of the radula and, in the type species, the presence of a pair of pallial tentacles (*P.* (*H.*) *marmorata* has 1-2 pallial tentacles). The teleoconch exhibits similar sculptural variation to that of *Pusillina* s.s. although several species of *P.* (*Haurakia*) have a distinct spiral cord at the upper margin of the base.

The species in this subgenus appear to have two different modes of development as exhibited in protoconch morphology. The majority, possessing paucispiral protoconchs, probably have direct development (Figs 81B; 82G) but a tropical species (*P.* (*H.*) *marmorata*) has a multispiral protoconch of the type associated with a planktotrophic larval stage (Fig. 82B). A multispiral protoconch is also known in a fossil species, *P.* (*H.*) *tateana*.

Ponder (1967) placed *Haurakiopsis* in the synonymy of *Haurakia* and reduced *Haurakia* to a subgenus of *Rissoa*. The inclusion of *Vitricithna* in the synonymy of *Haurakia* is, perhaps, less certain in view of the rather different protoconchs exhibited by 'typical' *Haurakia* species and *P.* (*Haurakia*) *marmorata*, the type species of *Vitricithna*. The general teleoconch shape, apertural features, anatomy, head-foot and radula are, however, very similar to the type-species of *Haurakia*. The lack of ornamentation of the teleoconch in *P.* (*H.*) *marmorata* is a feature also seen in some species of *Haurakia* from New Zealand. The anatomy of both *P.* (*H.*) *hamiltoni* and *P.* (*H.*) *marmorata* differs from species of *Pusillina* s.s. in that the male has a penial filament and the female lacks a seminal receptacle.

The subgenus *Haurakia* probably diverged from *Pusillina* very early in the Tertiary, possibly at the time of the closure of the Tethys Sea junction between the Indian Ocean and the Mediterranean Sea. The present distribution of *Pusillina* s.s. in the Mediterranean and eastern Atlantic and that of *Haurakia* in the Indo-Pacific supports this hypothesis. It is possible that *Pusillina plicosa* from the Sea of Japan (see above under *Pusillina* (*Pusillina*)) represents an isolated relic of the *Pusillina* s.s.—*Haurakia* stock that moved northwards after the closure of the Tethys Sea before the divergence of *Pusillina* s.s. and *Haurakia* commenced.

Subgenus *Ameririssoa* n.subgen.

Type-species: *Alvania pseudoareolata* Warén, 1974. Recent, north-western Atlantic (Figs 17; 83E, F; 84).

Diagnosis. *Shell*: ovate-conic, imperforate, with very weak to strong axial ribs, spiral threads and, in most specimens, weak spiral cords crossing axial ribs. Axial ribs do not extend over base; base with 2-3 spiral cords or smooth. Aperture ovate, simple, with thin, non-varicose, orthocline outer lip with weak posterior notch just below suture. No anterior excavation or channel (Figs 83E; 84A). Protoconch of about 1.5-1.7 whorls, finely spirally striate (Fig. 84F, G).

Head-foot: unpigmented; right and left pallial tentacles present; metapodial tentacle about as wide as long; tentacles short and broad, eyes well developed; snout bilobed and small relative to tentacle bases (about equal in width to one tentacle base) (preserved material, as below).

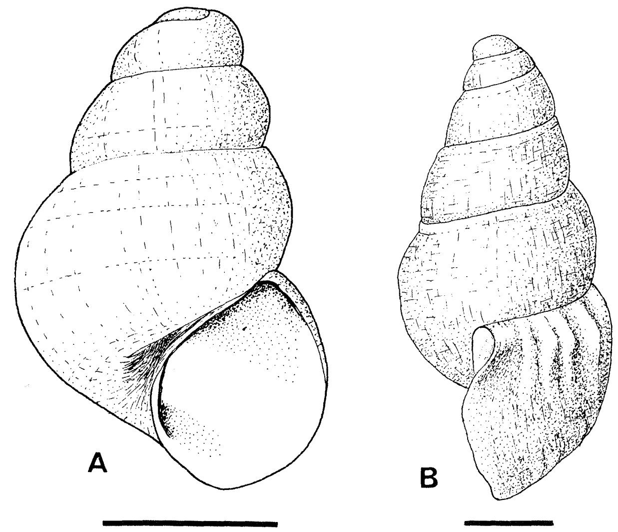

Fig. 15. **A**, *Setia* (*Setia*) *fusca* (Philippi), type-species of *Rudolphosetia* Monterosato, Palermo, Sicily (USNM, 332303); **B**, *Pusillina* (*Pusillina*) *janusi* (Nordsieck), type-species of *Auriconoba* Nordsieck, paratype (AMS, C.108981). **Scale:** 0.5 mm.

Anatomy: based on *P.* (*A.*) cf. *pseudoareolata*, off New York, 808 m (2 females, 1 male). Ctenidial filaments about twice as long as wide (relatively shorter than in most other species of *Pusillina*). Osphradium nearly as long as ctenidium; nearly 3 times wider than filament bases. Stomach-style sac ratio 2.3, length-width ratio 2.1. Intestine-rectum folded behind and in front of posterior pallial wall.

Penis evenly tapering, narrowly oval in section, with blunt, narrow termination. Penial duct marginal, closed. Prostate gland in male well developed, entirely within pallial roof.

Female (Fig. 17) has a well developed vestibule (*v*) but appears to lack a sperm pouch and shows no sign of sperm storage. Lower oviduct gland terminates at posterior pallial wall and a rather small bursa copulatrix (*b*) lies behind it on left side. Seminal receptacle (*sr*) about equal in size to bursa copulatrix and lies immediately behind it. Both bursa and seminal receptacle open ventrally into oviduct. Upper oviduct gland (*uog*) about half length of lower oviduct gland (*log*), outer (but not inner) surface pleated forming radiating lobes but these show no signs of sperm storage. Internal (left) surface of gland shows U-shaped loop.

Operculum: as for genus (Fig. 84C).

Radula: central teeth $\frac{3+1+3}{1+1\quad 1+1}$, ventral margin slightly convex. Lateral teeth $4+1+6-8$. Marginal teeth with small cusps; cusps on inner marginal teeth on distal ½ of outer edge and on inner distal ¼ of outer marginal teeth (Figs 83F; 84D, E).

Egg capsules: unknown.

Development: assumed to be direct.

Distribution. North-western Atlantic: *Cingula areolata* auct., = *A pseudoareolata* Waren, 1974.

Material examined.

+ **A. pseudoareolata*. A few lots, including paratypes (MCZ, AMS).

Remarks. The shell of *P.* (*A.*) *pseudoareolata* is similar to that of species of *Pusillina* s.s. except for the paucispiral protoconch and the well developed spiral sculpture seen in some specimens. The considerable variation in the sculpture of this species (cf. Figs 83E; 84A) is characteristic of many species of *Pusillina*. It is possible that more than one species will eventually be recognized.

The new subgenus differs from *Pusillina* s.s. in that the type-species apparently lacks sperm-storing capability in the lobes of the upper oviduct gland or in the vestibule. However, additional material is needed to confirm this. The presence of a left pallial tentacle, the lack of a distal glandular area on the penis, the marginal penial duct and the folding of the rectum in front as well as behind the posterior pallial wall, are other anatomical characters separating *Ameririssoa* from *Pusillina* s.s. In most other respects the two subgenera agree closely. The subgenus *Haurakia* is similar to *Ameririssoa* in having both right and left pallial tentacles and, in most species, a paucispiral protoconch. *Ameririssoa* differs from *Haurakia* in the same radular and apertural features which separate *Pusillina* s.s. and *Haurakia*.

The U-shaped upper oviduct gland, the retention of the left pallial tentacle, and sperm storage apparently being confined to the bursa copulatrix and seminal receptacle, are all assumed to be primitive features. They do not occur in either *Rissoa* or *Pusillina* s.s. This suggests that *P.* (*Ameririssoa*) may be a relictual early off-shoot from the ancestral *Pusillina—Rissoa* stock, possibly isolated in the western Atlantic after the break-up of the Tethys Sea (Fig. 16).

Subgenus *Vicinirissoa* n.subgen.

Type-species: *Rissoa harpa* Verrill, 1880. Recent, north-western Atlantic (Figs 18; 83A–D).

Diagnosis. *Shell*: ovate, narrowly umbilicate, with prominent, slender, axial ribs extending on to base. Spiral sculpture of weak, spiral threads. Aperture ovate, simple, with thin, non-varicose, weakly opisthocline outer lip. A weak sinus just below suture on outer lip, anterior edge of aperture not channelled or excavated (Fig. 83A). Protoconch of 1¾–2 whorls, sculptured with fine spiral lines (Fig. 83B).

Head-foot: unpigmented, metapodial tentacle narrow, short. Pallial tentacle present on right side only. Eyes small, snout short, bilobed (preserved material, as below).

Anatomy: based on *P.* (*V.*) *harpa*, off New York, 808 m (1 male and 2 females). Ctenidial filaments finger-shaped, about twice as high as wide; ctenidium nearly as long as osphradium and about 3 times wider than bases of filaments. Stomach-style sac ratio 2.4, length-width ratio 1.8. Rectum convoluted in front of posterior pallial wall.

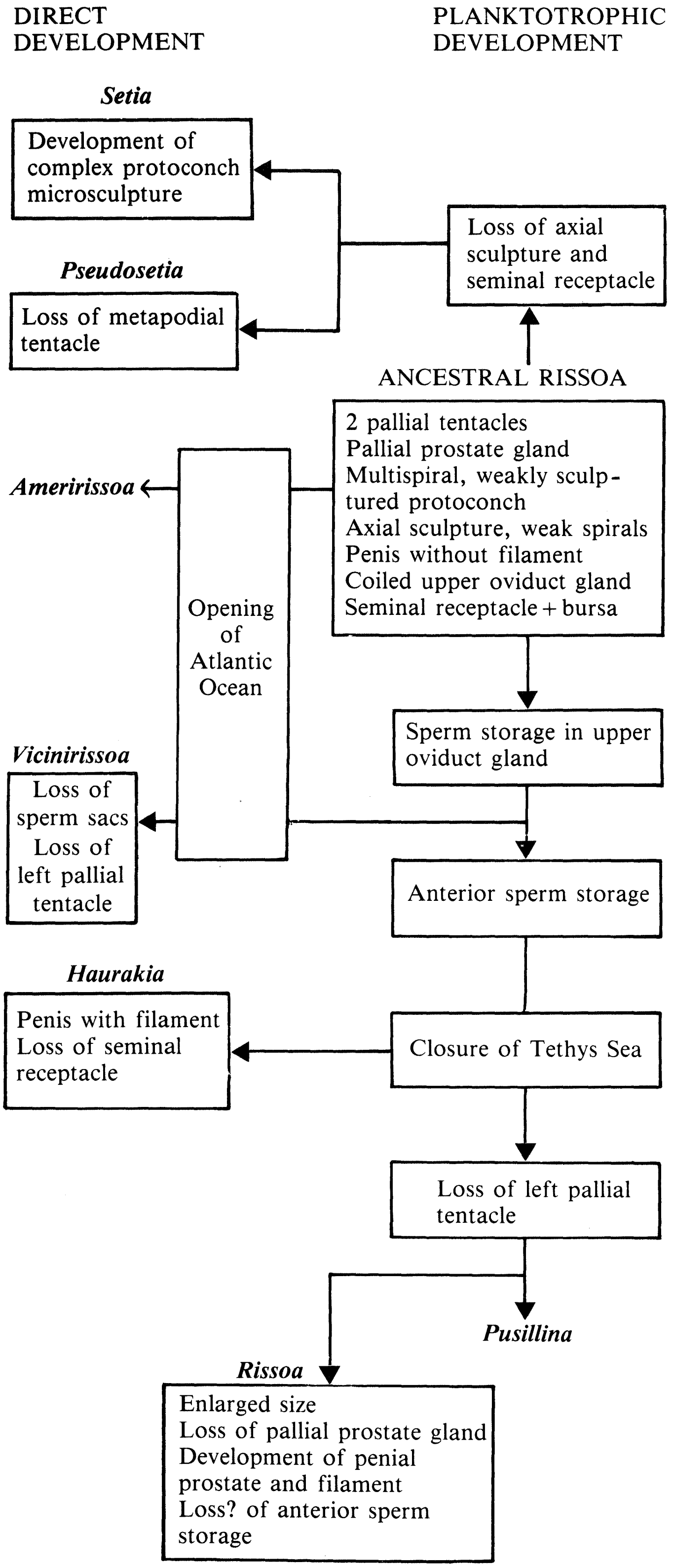

Fig. 16. Diagrammatic representation of the hypothetical relationships of *Rissoa*, *Pusillina* and *Setia*.

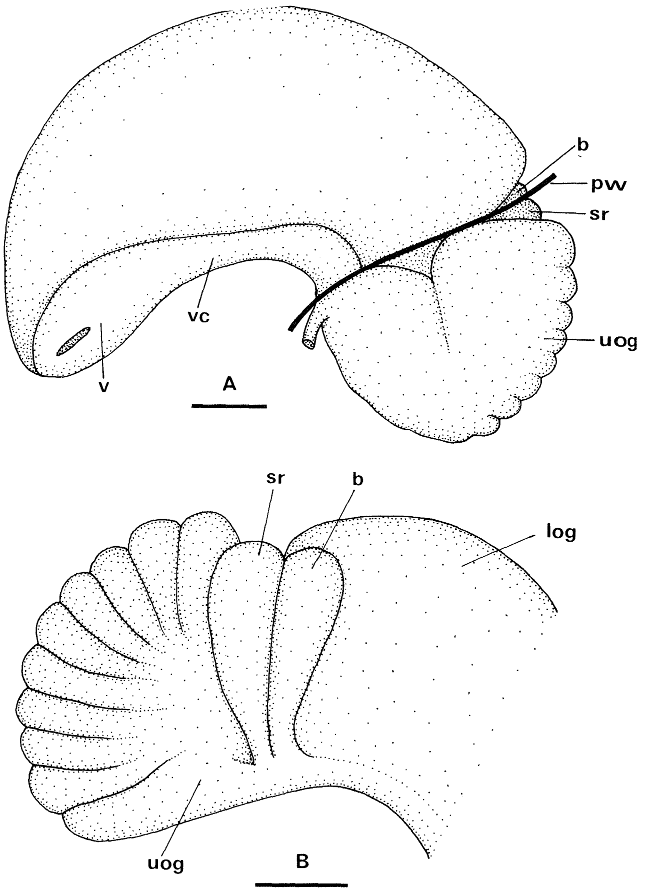

Fig. 17. Female genitalia of *Pusillina* (*Ameririssoa*) *pseudoareolata* (Warén): **A**, left side; **B**, posterior end of glandular oviduct from right side. *b*-bursa copulatrix; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sr*-seminal receptacle; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel. **Scale:** 0.1 mm.

Male with penis tapering to a point, narrowly oval in section; penial duct submarginal. Prostate gland long, bean-shaped, about half its length behind posterior pallial wall. Seminal vesicle undulates across inner side of stomach.

Female (Fig. 18) with small vestibule having no indication of sperm storage. Lower oviduct gland (*log*) terminates at posterior end of pallial cavity. Bursa copulatrix and seminal receptacle could not be located and may be absent. Upper oviduct gland (*uog*) coiled, with posterior lobe containing sperm (*sl*).

Operculum: as for genus (Fig. 83C).

Radula: central teeth $\frac{4-5+1+4-5}{1+1 \qquad 1+1}$, cusps sharp; lateral margins at 30°, thickened, with prominent denticle arising from them; ventral edge broadly convex. Lateral teeth 4+1+7−10. Inner marginal teeth with cusps on outer distal half, outer marginal teeth with no cusps visible in mount (Fig. 83D).

Egg capsules: unknown.

Development: assumed to be direct.

Distribution. Deep-water off north-eastern North America (*R. harpa*).

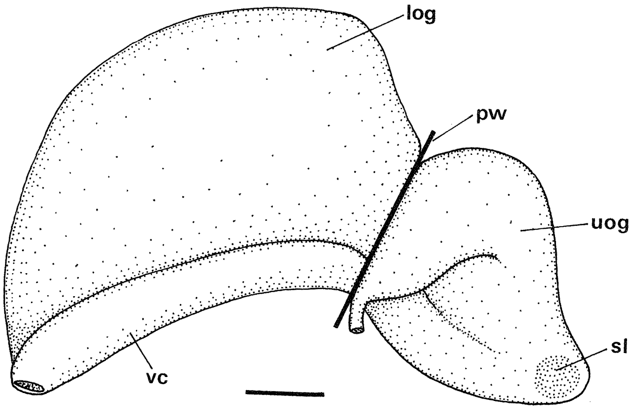

Fig. 18. Female genitalia of *Pusillina* (*Vicinirissoa*) *harpa* (Verrill), from left side. *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sl*-sperm storage in lobe of upper oviduct gland; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Material examined.
+**R. harpa*. Holotype (USNM) and a few other lots (MCZ, AMS, USNM).

Remarks. This subgenus is based on a species similar in teleoconch characters to species of *Pusillina* s.s. The head-foot is also similar in having a single (right) pallial tentacle and a narrow metapodial tentacle. It differs, however, in having a paucispiral protoconch with a large initial whorl suggesting direct development and a bean-shaped prostate gland embedded half in the kidney and half in the pallial roof. Another major difference is the apparent lack of any bursa or seminal receptacle. Although these could not be detected in dissections, this needs confirmation from sectioned material. The upper oviduct gland has a single, large posterior lobe modified for sperm storage, not several lobes as in *Pusillina* s.s.

It is probable that *Vicinirissoa*, like *Ameririssoa*, was derived from a primitive *Rissoa-Pusillina* stock in the late Cretaceous (Fig. 16) and was isolated from the evolutionary explosion of *Rissoa* and *Pusillina* s.s. in the north-eastern Atlantic by the widening of the Atlantic Ocean. The type-species of these two new subgenera are sympatric on the continental slope off eastern North America and can be regarded as relic species.

Genus *Mohrensternia* Stoliczka, 1868

Mohrensternia Stoliczka, 1868: 274. Type-species *Rissoa angulata* Eichwald, 1830; subsequent designation Nevill, 1885: 100. Miocene, Europe.

Diagnosis. *Shell*: medium to large, ovate-conic, non-umbilicate, thin, usually axially-costate, axials weak over base, spiral sculpture (if present) weak. Aperture with a shallow, broad posterior sinus, outer lip slightly sinuate, opisthocline, hardly thickened, non-varicose (Fig. 77G). Protoconch small, conical, of about 3 whorls, apparently smooth.

Animal unknown.

Distribution. Brackish and freshwater Neogene deposits of central and eastern Europe (Stoliczka, 1868).

Material examined.
Rissoa inflata Andrzejowski, 1835. Two lots (AMS, NMV).

Remarks. Pchelintsev & Korobkov (1960) have proposed a separate subfamily for this genus and some authors (e.g. Slavoshevskaya, 1975a:119) regard it as synonymous with *Pusillina* (i.e. *Turboella* auct.). There do not, however, appear to be any Recent species obviously closely allied to *M. angulata*, although it is quite possible that it is a peculiar species of *Rissoa*. It differs, however, in its simple aperture, thin outer lip, and brackish to freshwater habitat. Although the overall similarity in shell characters suggests a close relationship with *Rissoa*, the shell also has a close resemblance to some hydrobiid taxa and, when its habitat is also considered, *Mohrensternia* may prove to be a hydrobiid.

Sacco's (1895) designation of *Rissoa inflata* Andrzejowski, 1835 (Fig. 77G) as the type of *Mohrensternia* is usually the one cited, but Nevill's (1885) designation of *R. angulata* is earlier.

Genus *Setia* H. & A. Adams, 1852

Setia H. & A. Adams, 1852: 359 (not preocc. by Oken, 1815, ICZN Opin. 417). Type-species *Rissoa pulcherrima* Jeffreys, 1848; subsequent designation Kobelt, 1878: 128. Recent, Europe (Figs 81E–H; 85G).

Diagnosis. *Shell*: minute, ovate to ovate-conic, whorls convex; aperture with simple peristome, with posterior angulation but lacking distinct anterior and posterior channels; outer lip prosocline, with or without weak external varix; surface smooth or with weak to moderate spiral threads and axial growth lines. Protoconch dome-shaped, of about 1¼–1½ whorls, first ½ whorl very large; surface either smooth, except for weak spiral threads on last ¾ whorl, or with spiral rows of minute gemmae.

Head-foot: snout bilobed, metapodial and pallial tentacles present or absent.

Anatomy: ctenidium vestigial or with long to short filaments, their bases narrower than osphradium. Osphradium nearly as long as ctenidium. Stomach-style sac ratio 3–3.1, length-width ratio 1.6–2.1.

Male with penis tapering, distal end simple, pointed; duct marginal to submarginal. Prostate gland entirely within posterior pallial cavity or partly pallial and partly visceral.

Female with small vestibule, capsule gland lacking lateral fold on left. Single sperm sac present, posterior to lower oviduct gland. Upper oviduct gland with no sperm-storing lobes.

Nervous system not investigated.

Operculum: simple, thin, paucispiral, nucleus eccentric.

Radula: central teeth $\frac{2-3+1+2-3}{0-1+1 \quad 1+0-1}$, with lateral thickenings at about 30°, simple in *Setia* (*Pseudosetia*), with pair of lateral processes in *Setia* s.s. which are shorter than basal processes; U-shaped ventral extension moderate to well developed. Lateral teeth $2-4+1+4-12$. Marginal teeth with cusps at distal end of outer edge on inner marginal teeth and on distal end of inner edge on outer marginal tooth.

Development: assumed to be direct in all species.

Distribution. Eastern Atlantic and Mediterranean Sea.

Remarks. The relationships of *Setia* to *Pusillina* may be closer than implied by the classification adopted here but, on shell characters, the two groups are readily distinguished. More anatomical comparisons are required to establish their real relationship and that of *Pseudosetia*, here included, somewhat tentatively, as a subgenus of *Setia*. The assumed relationships of *Setia* to *Rissoa* and *Pusillina* are summarized in Fig. 16.

Key to Subgenera of *Setia*

— Shell smooth or spirally sculptured; radula with pair of processes from lateral margins of central teeth ...... *Setia* s.s.

— Shell smooth; radula with simple lateral margins on central teeth .... *Pseudosetia*

Subgenus *Setia* s.s.

?*Parvisetia* Monterosato, 1884a: 280. Type-species *Rissoa scillae* (Seguenza ms) Aradas & Benoit, 1876; monotypy. Recent, Mediterranean Sea.

Rudolphosetia Monterosato, 1917: 12. Type-species *Truncatella*? *fusca* Philippi, 1841. Subsequent designation Wenz, 1943: 1498. Recent, Mediterranean Sea (Figs 15A; 85A–D).

Diagnosis. *Shell*: as for genus, teleoconch with or without spiral threads (Figs 15A; 81E; 85A, E). Protoconch either smooth except for last ¾ whorl which has a few distinct spiral threads with nearly vertical wrinkles between them (Fig. 85G), or with spiral rows of minute gemmae (Fig. 85B, F).

Head-foot: cephalic tentacles rather short, thickly ciliated, with rounded tips. Foot 'divided' into two halves, with mucous pore in posterior half. Opercular lobe pigmented. Metapodial tentacle very long and pointed (*S. pulcherrima*, Clark, 1857; Jeffreys, 1867: 42). No pallial tentacles (Fretter & Graham, 1978). *Setia* sp. and *S.* (*S.*) *beniamina* (see below) have a right and left pallial tentacle, but *S. fusca* does not have any.

Anatomy: ctenidium vestigial (*S. pulcherrima*, Fretter & Graham, 1978). Additional details based on *Setia* sp. (cf. *turriculata*) Cala Rossa, near Terrasini, Sicily (1 male), *S.* (*S.*) *beniamina*, Aci Trezza, Catania, Sicily (1 male) and *S. fusca*, Monte Tauro, Sicily (3 females and 2 males). Ctenidium slightly longer than osphradium, filaments short, only slightly longer than wide, their bases ⅓ width of osphradium. Stomach-style sac ratio 3.1 (*Setia* sp.), 2.7 (*S. fusca*), length-width ratio 1.6 (*Setia* sp.), 2.04 (*S. fusca*). Intestine-rectum not examined.

Male with penis narrow, tapering, with submarginal (*Setia* sp.) to marginal, narrow duct and simple, pointed distal end. Prostate gland short, broad, in posterior pallial cavity, not projecting into kidney, except in *S. fusca* where about half lies in the pallial cavity.

Female of *S. fusca* only known. Similar to that of *Setia* (*Pseudosetia*) *turgida* (Jeffreys) (see below, and Fig. 19) but bursa copulatrix relatively smaller and lower oviduct gland relatively larger. The upper oviduct gland is not strongly indented by the intestine as in *S.* (*P.*) *turgida*.

Operculum: as for genus (Figs 81F, G; 85C).

Radula: central teeth $\frac{2+1+2}{1+1 \quad 1+1}$ with lateral thickenings at about 30° and giving rise to a pair of basal projections shorter than pair of basal denticles; median cusp small and pointed to large and wide. Lateral teeth $2-3+1+4-6$. Marginal teeth with cusps subequal in size, outer marginal with cusps on distal ¼ of each tooth, lacking on outer edge (Figs 81H; 85D).

Egg capsules: lentiform, with attachment base but neither suture nor plug (Fretter & Graham, 1978).

Development. direct (Fretter & Graham, 1978).

Distribution. Europe and Mediterranean Sea: *R. pulcherrima*, *Setia turriculata* Monterosato, 1884, *T. fusca*, *R. scillae*, ?*Cingula beniamina* Monterosato, 1884, = *Cingula concinna* Monterosato, 1869, not C.B. Adams, 1850; *Rissoa amabilis* Monterosato, 1869; *Cingula maculata* Monterosato, 1869; *Rissoa depicta* Manzoni, 1868.

Madeira: *Rissoa perminima* Manzoni, 1868 (Fig. 85E).

Van Aartsen & Verduin (1978) have revised some European species.

Material examined.

+**R. pulcherrima*. Presumed syntypes (USNM) and several other lots (BMNH, AMS).

R. scillae. A few specimens, none authenticated (BMNH, USNM).

+**T. fusca*. 1 lot ex Philippi (BMNH), 1 lot ex Monterosato (USNM), 1 lot ex S. Palazzi (AMS).

S. turriculata and *S. beniamina* (AMS).

+**R. perminima* 1 lot (AMS ex BMNH).

(*R. amabilis*, *C. maculata* and *R. depicta* are included in *Setia* on the advice of Dr. J.J. van Aartsen, *in lit.* , 1982).

Remarks. The protoconch microsculpture, small, smooth, ovate-conic teleoconch and simple aperture distinguish species of *Setia* from those of *Rissoa* and *Pusillina*. The external features of the animal indicate that the type-species of *Setia* is similar to *Rissoa* and *Pusillina* but differs chiefly in lacking a pallial tentacle. Two other species here referred to *Setia* have two pallial tentacles. Species of *Rissoa* and *Pusillina* tend to develop axial sculpture whereas species of *Setia* are smooth or spirally striate.

The type species of *Parvisetia* is known only from shells. These have the essential features of *Setia* and this name is tentatively regarded as a synonym of *Setia*. *Rudolphosetia fusca* is also similar to *Setia pulcherrima* in shell features (Figs 15A; 81E; 85A) but the central teeth of the radula have a broader median cusp (Figs 81H; 85D) and the protoconch is sculptured with rows of gemmules (Fig. 85B) rather than spiral lines (Fig. 85G). Unless additional characters can be found to separate *Rudolphosetia* from *Setia*, they can be regarded as synonyms as maintained by van Aartsen & Verduin (1978).

Wenz (1938) regarded *Setia* as a synonym of *Pseudosetia* Monterosato which he reduced to a subgenus of *Putilla* Adams. It is shown below that *Putilla* is not a rissoid.

Subgenus *Pseudosetia* Monterosato, 1884

Pseudosetia Monterosato, 1884a: 281. Type-species *Rissoa turgida* Jeffreys, 1870; subsequent designation Crosse, 1885: 140. Recent, north-western Europe (Figs 19; 80E–H).

Diagnosis. *Shell*: ovate-conic, with narrow umbilical chink, convex whorls and simple aperture. Aperture ovate, weakly angled posteriorly, not channelled or excavated anteriorly or posteriorly; outer lip thin, orthocline, inner lip very thin over parietal wall and columella; surface smooth, shining (Fig. 80E). Protoconch of about 1½ whorls, dome-shaped, with large initial whorl; sculptured with a few spiral threads sometimes broken into minute beads (Fig. 80G). Periostracum apparently absent (preserved material, as below.)

Head-foot: unpigmented; snout large, about as long as cephalic tentacles and about 2½ times as wide as one tentacle base; lips more expanded and larger than in other species of Rissoidae. Eyes relatively large. Right and left pallial tentacles present; metapodial tentacle apparently absent (preserved material, as below).

Anatomy: based on 2 males and 5 females of *S.* (*P.*) *turgida* from off Korsfjorden, W. Norway in 320 m. Ctenidial filaments finger-like, very long and narrow (up to 5 times longer than wide). Osphradium nearly as long as gill, broad in middle area, about 3 times wider than ctenidial filament bases. Style sac well developed (stomach-style sac ratio 3), length-width ratio of stomach 2.1. Rectum convoluted in front of posterior pallial wall.

Male with evenly tapering penis, with lateral, closed duct, distal end narrow. Prostate gland well developed, lying entirely within posterior pallial cavity, its height about ⅓ its length. Prostate gland with thin walls, especially ventrally.

Female (Fig. 19) with small vestibule (*v*) and well developed ventral channel (*vc*). Capsule gland lacking a lateral fold on left side. Posterior third of lower oviduct gland (*log*) with a deep saddle occupied by convolute intestine-rectum. A single, small, vertical sperm sac (*b*) present, just behind posterior pallial wall, which opens ventrally to oviduct. Upper oviduct gland (*uog*) a solid, glandular mass, with deep groove to accommodate intestine, no lobes or blisters and no indication of coiling or sperm storage.

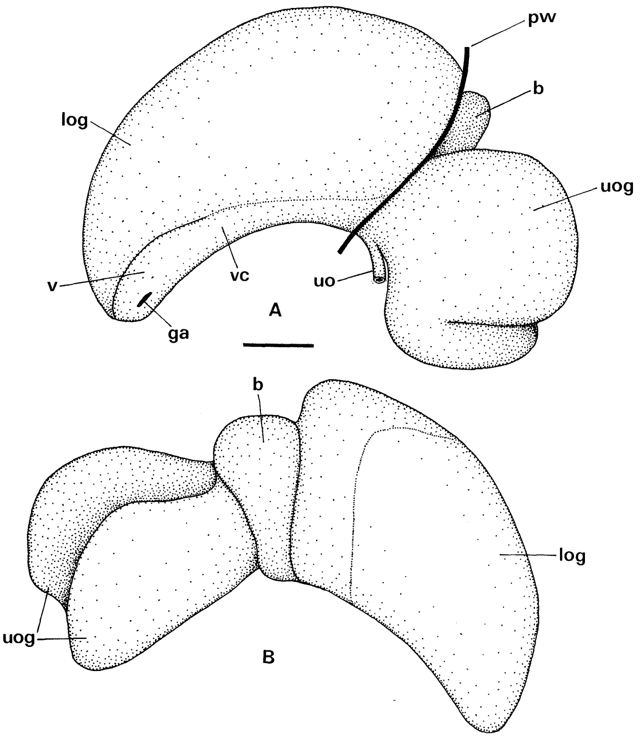

Fig. 19. Female genitalia of *Setia* (*Pseudosetia*) *turgida* (Jeffreys): **A**, left side; **B**, right side. *b*–bursa copulatrix; *ga*–pallial genital opening; *log*–lower oviduct gland; *v*–vestibule; *pw*–posterior wall of pallial cavity; *uo*–upper oviduct; *uog*–upper oviduct gland; *v*–vestibule; *vc*–ventral channel. **Scale:** 0.1 mm.

Operculum: as for genus (Fig. 80F).

Radula: central teeth $\frac{3+1+3}{1 \quad 1}$, lateral thickenings at 30°, simple. Lateral teeth 4 + 1 + 9 – 12. Inner marginal teeth with small cusps, outer marginal teeth smooth on outer edge, possibly cuspate on inner edge (folded inwards in mount so inner edge obscured) (Fig. 80H).

Egg capsules: unknown.

Development: assumed to be direct.

Distribution. Northwest Europe (*R. turgida*).

Material examined.

+**R. turgida*. Syntypes (USNM), one other lot ex Warén (AMS).

Remarks. The distinctive characters of *Setia* (*Pseudosetia*) include the apparent lack of one of the posterior sperm pouches (assumed to be the seminal receptacle), the presence of two pallial tentacles, the apparent lack of a metapodial tentacle and, in the radula, the absence of accessory denticles arising from the thickened lateral margins of the central teeth. Thus the relationships of *Pusillina* and *S.* (*Pseudosetia*) do not appear to be as close as the teleoconch characters might suggest. Smooth forms of *Pusillina inconspicua* are virtually inseparable from *S.* (*Pseudosetia*) *turgida* except on protoconch characters (compare Fig. 80A, C with 80E, G). *Pseudosetia* and *Setia* s.s. agree in their paucispiral protoconchs and similar male genitalia. The female reproductive system of the one species of *Setia* known is similar to that of *S.* (*P.*) *turgida*. *Setia* spp. have less developed ctenidial filaments (than *S.*

(*Pseudosetia*) *turgida*), relatively well developed protoconch microsculpture, fewer cusps on the lateral teeth and an accessory denticle arising from each lateral margin on the central teeth.

Some species of *Powellisetia* Ponder, 1965 resemble *S.* (*P.*) *turgida* but whereas *Powellisetia* appears to have been derived from *Onoba*, *Setia* and *Pseudosetia* are probably closer to *Pusillina*. Shells of species of *Powellisetia* can be distinguished from *S.* (*P.*) *turgida* in that almost all have an external apertural varix.

There has been considerable confusion about the relationships of *Pseudosetia*. Thiele (1929) regarded it as a subgenus of *Cingula*, Coan (1964) as a subgenus of *Barleeia* and Nordsieck (1972) as a subgenus of *Putilla*. Ponder (1967) allocated it generic rank in the Rissoinae.

Fretter & Graham (1978) reported that *S.* (*P.*) *turgida* feeds on foraminiferans. Three specimens examined by me were found to have the stomach packed with fine brown detritus and a single, small foram was present in the stomachs of two individuals.

Rissoa (*Cingula*) *canonica* Dall, 1927 from off Fernandina, Florida, U.S.A. (syntypes (USNM) examined) has shell features somewhat similar to those of *Setia* (*Pseudosetia*) *turgida* and also to some species of *Powellisetia*, but its placement cannot be confirmed on shell characters alone.

Three additional species were included in *Pseudosetia* by Nordsieck (1972): *Setia obtusispira* Seguenza, 1876; *Putilla* (*Pseudosetia*) *abyssicola* Nordsieck, 1972 and *Rissoa islandica* Friele, 1886. The first two species are probably synonyms of *Benthonella tenella* (Jeffreys) and *R. islandica* can be included in *Onoba* (decisions on these placements assisted by advice from Dr. van Aartsen *in lit.* 1982).

Genus *Alvania* Risso, 1826

Alvania (Leach ms) Risso, 1826: 140. Type-species *Alvania europea* Risso, 1826, = *Turbo cimex* Linné, 1758, subsequent designation Nevill, 1885: 105. Recent, Mediterranean Sea (Fig. 86A–E).

Acinus Monterosato, 1884a: 161. Type-species *Turbo cimex* Linné, 1758; subsequent designation Crosse, 1885: 140.

Diagnosis. *Shell*: minute to small, elongate-conic to turbiniform. Outer lip opisthocline to prosocline, with or without varix, thickened or thin, with or without denticles internally; peristome simple in most species, with or without weak posterior sinus. Axial and spiral sculpture present, sometimes spiral sculpture alone distinct; axial ribs usually continue over base but are weaker than on remainder of body whorl. Protoconch of 1⅓ to more than 2½ whorls, sculptured with raised dots to a few very strong spiral keels, often with irregular raised lines and dots in combination. Apex generally not strongly tilted in species with paucispiral protoconch.

Head-foot: cephalic tentacles long, ciliated, with parallel sides, anterior and posterior pallial tentacles present in most species; metapodial tentacles, in most species, 3–7. Anterior pedal gland present, posterior pedal gland usually inconspicuous and possibly absent in a few species.

Anatomy: ctenidium with finger-shaped filaments, narrower and slightly longer than osphradium. Stomach relatively short (length-width ratio 1.4–2.1), style sac relatively long (stomach-style sac ratio 1.7–3.0).

Penis straight or with oblique, glandular distal end, tapering, without terminal filament, reaching to posterior end of pallial cavity; duct marginal, closed. Prostate gland embedded partly in pallial roof and partly in kidney, or entirely pallial. Seminal vesicle coiled across posterior half of inner side of stomach and, in some species, just behind stomach.

Female with terminal to subterminal genital opening, with poorly developed vestibule; anterior sperm pouch not developed. Bursa copulatrix usually smaller than upper oviduct gland and lies anteriorly or dorsolaterally to it on right. Seminal receptacle absent (present in subgenus *Punctulum* where it is small relative to bursa and lies immediately posterior to it and anterior to upper oviduct gland). Ventral channel in communication with lower oviduct gland along most of gland in most species. Upper oviduct gland coiled, glandular tissue reduced in some species leaving weakly muscular duct. Upper oviduct gland opens posteriorly to thin-walled tubular extension of ventral channel (which runs along right side of gland); 1–5 sperm sacs clustered at this point (in subgenus *Punctulum* upper oviduct gland appears to open anteriorly to ventral channel).

Nervous system with cerebral ganglia separated by commissure or abutting. Supraoesophageal ganglion 1.5–2.25 times longer than ganglion. Suboesophageal connective about ⅕ length of ganglion or suboesophageal ganglion abuts against right pleural ganglion.

Operculum: simple, thin, nucleus eccentric, paucispiral.

Radula: central teeth $\frac{2-6+1+2-6}{(1)+1 \quad 1+(1)}$, basal denticles prominent; a second pair of smaller denticles sometimes formed from lateral thickenings; weak to moderate U-shaped projection at base of tooth; lateral margins at 25°–60°. Lateral teeth $3-6+1+4-12$, primary cusp relatively large. Inner marginal teeth finely cuspate on distal half of outer edge; outer marginal teeth with distal end and inner ⅕–¼ cuspate, cusps on both teeth equal in size or slightly smaller on outer marginals.

Development: direct or with planktotrophic larval stage.

Distribution. World-wide except Antarctic and Subantarctic regions. Upper Cretaceous (?) to Recent.

Remarks. Golikov & Starobogatov (1975) introduced a family and superfamily for *Alvania* mainly on the basis of Johansson's (1956) anatomical work on the genital systems of two species of *Alvania*. They state that "no gland is present in the renal gonoduct of the female, but there is a widening". Johansson has actually shown that *Alvania reticulata* (Montagu) = *A. beanii*

(Hanley) has an "upper oviduct gland" and that *A. subsoluta* (Aradas) lacks one but instead has a thickened, coiled section of the oviduct. *Alvania punctura* (Montagu) also has an upper oviduct gland (Fretter & Patil, 1961). The "renal gonoduct" referred to by Golikov & Starobogatov (1975) is shown by Johansson (1956) to be ectodermal and therefore pallial, not renal in origin. It is, as clearly stated by Johansson (1956), homologous to the upper oviduct gland. The reproductive systems of *Alvania* species thus appear to show some variation in the degree of development of the upper oviduct gland. There is also variation in the number of 'seminal receptacles', for example, *A. beanii* and *A. punctura* have two seminal receptacles and *A. subsoluta* has only one (Johansson, 1956; Fretter & Patil, 1961). My studies on the female genitalia of several species of *Alvania* have shown a gradation between species with a well developed, glandular upper oviduct gland and those with a non-glandular coiled oviduct. The number of 'seminal receptacles' varies from 1 to 5.

The opercular, sculptural and radular characters of of *Alvania* are similar to those of *Rissoa*. The external features of the animal of species of *Alvania* are somewhat similar to those of *Rissoa* but the sole is often less distinctly partitioned into anterior and posterior segments, the posterior mucous gland is sometimes indistinct and has a relatively small opening, there are always 2[1] (not 1–2) pallial tentacles (anterior and posterior) and 3–7[2] (not 1) metapodial tentacles.

Alvania species are much less common on intertidal algae than are those of *Rissoa* where they co-exist. The more poorly developed posterior mucous gland of *Alvania* species may be corelated with different habitat preferences.

The type-species designation for this genus has been the cause of some debate but the earliest valid designation appears to be that of Nevill (1885) as pointed out by Woodring (1957). Gray's (1847) designation cited by Warén (1974) is of a species not included in the original list of species cited by Risso.

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[1] Jeffreys (1867) records only one (the posterior) pallial tentacle in *A. lactea* (Michaud) but this needs to be confirmed.

[2] Jeffreys (1867) records 1 metapodial tentacle in *A. punctura, A. lactea* and *A. abyssicola* (Forbes) but Clark (1852) describes the animals of *A. 'reticulata'* (= *beanii*) and *A. punctura* and states that they are identical apart from a small difference in pigmentation. Clark also states that there are three metapodial tentacles in *A. beanii*. As the lateral metapodial tentacles are short and often difficult to observe it is probable that Jeffrey's observations are incorrect. Fretter & Graham (1978) note that in *A. abyssicola, A. subsoluta* and *A. punctura* the lateral projections of the metapodial tentacle are reduced so that it appears to be single.

Key to subgenera of *Alvania* (based on shell characters)

1.	Shell with smooth protoconch	*Punctulum*
——	Shell with variously sculptured protoconch	2
2.	Shell with axial and spiral sculpture well developed	3
——	Shell with spiral sculpture well developed, axial sculpture relatively weak	4
3.	Shell with paucispiral protoconch; protoconch microsculpture of irregularly scattered, very minute, raised dots	*Linemera*
——	Shell with multispiral or paucispiral protoconch; protoconch microsculpture variable, usually of raised spiral lines or cords, zig-zag lines or spirally arranged pustules	*Alvania*
4.	Shell with weak spiral cords	*Crisilla*
——	Shell with strong spiral keels	*Galeodina*

Subgenus *Alvania* s.s.

Turbona Leach in Gray, 1847a: 271. Type-species *Turbo reticulatus* ('Montagu') J. Adams, 1797, not Solander, 1766 (= *Cingula beanii* Hanley in Thorpe, 1844); subsequent designation, Gray, 1847b: 152. Recent, Europe (Fig. 87A–C).

Zacanthusa = Leach, 1852: 194. Type-species *Zacanthusa reticulata,* = *Turbo reticulatus* J. Adams, 1797, not Solander, 1766 (= *Cingula beanii* Hanley in Thorpe, 1844); subsequent designation Coan, 1964: 167. Recent, Europe (Fig. 87A–C).

Acinopsis Monterosato, 1884a: 162. Type-species *Turbo cancellatus* Da Costa, 1778; subsequent designation Crosse, 1885: 140. Recent, Europe (Fig. 90A–C).

Actonia Monterosato, 1884b: 61. Type-species *Rissoa testae* Aradas & Maggiore, 1843; subsequent designation Crosse, 1885: 140. Recent, Europe (Fig. 88A, B).

Massotia Bucquoy, Dautzenberg & Dollfus, 1884: 298. Type-species *Rissoa lactea* Michaud, 1830; original designation. Recent, Europe (Fig. 90D–F).

Thapsiella Fischer, 1885: 721. New name for *Thapsia* Monterosato, 1884a: 227, not Albers, 1860. Type-species *Rissoa rudis* Philippi, 1844; monotypy. Recent, Mediterranean Sea (Fig. 88D).

Arsenia Monterosato, 1891: 9. Type-species *Turbo puncturus* Montagu, 1803; subsequent designation Cossmann, 1921:24. Recent, Europe (Fig. 95A–E).

Alveniella (Monterosato ms) Sacco, 1895: 25. Type-species *Rissoa scabra* Philippi, 1844; original designation. Recent, Mediterranean Sea (Figs 89E–G; 91H).

Galeodinopsis Sacco, 1895: 28. Type-species *Rissoa tiberiana* Coppi, 1876; original designation. Pliocene, Italy.

Acinulus Seguenza, 1903: 48. Type-species *Acinulus cimicoides* (Forbes, 1844), = *Rissoa cimicoides* Forbes, 1844; original designation. Recent, Europe, Mediterranean Sea (Fig. 87D–G).

Alcidiella (Monterosato ms) Cossmann, 1921: 26. New name for *Alcidia* Monterosato, 1890: 147, not Westwood, 1879. Type-species *Alcidia spinosa* Monterosato, 1890, new name for *Rissoa angulata* Seguenza, 1873–79, not Eichwald, 1830; monotypy (see Van Aartsen, 1976). Recent Mediterranean Sea (Fig. 23C).

Pseudalvania Janssen, 1967: 129. Type-species *Pseudalvania dingdensis* Janssen, 1967; original designation. Miocene, W. Germany (Fig. 88E–G).

Conalvinia Ponder, 1967: 201. Type-species *Alvania novarensis* Frauenfeld, 1867. Recent, Australia (Figs 22A, C; 26A; 91A–D).

Andrewiella Nordsieck, 1972: 176. Type-species (*Rissoa*) *macandrewi* Manzoni, 1868; original designation. Recent, Madeira and Canary Islands (Figs 89A–D; 91I).

Massotiella Nordsieck, 1972: 182. Type-species (*Alvania* (*Massotia*)) *sublaevis* Boettger, 1906; original designation. Miocene, Rumania.

Lanciella Nordsieck, 1972: 191. Type-species (*Rissoa*) *lanciae* Calcara, 1845; original designation. Recent, Mediterranean Sea (Fig. 88C).

Alvanolira Nordsieck, 1972: 192. Type-species (*Alvania*) *lineata* Risso, 1826; original designation. Recent, Mediterranean Sea (Figs 21; 22D, E; 26B; 86F–I).

Coronalvania Nordsieck, 1972: 194. Type-species (*Alvania* (*Coronalvania*)) *corona* Nordsieck, 1972; original designation. Recent, Mediterranean Sea (Fig. 20).

Profundialvania Taviani, 1975: 207. Type-species *Alvania* (*Alvania*?) *heraelaciniae* Ruggieri, 1950; original designation. Pliocene, Italy (Fig. 91G).

Deliciosalvania Piani, 1980: 131 (*nomen nudum*).

Diagnosis. *Shell*: as for genus; ovate-conic, with cancellate sculpture, usually imperforate, whorls typically evenly convex, spiral sculpture usually weaker than axial sculpture (which it crosses), intersections weakly to strongly nodular. Microsculpture of weak, axial growth lines, irregular to spirally arranged micropustules, or spiral threads. Aperture usually with weak to very strong varix; outer lip smooth or dentate within (Figs 20; 23C; 86A, F; 87A, D; 88A, C–E; 90A, D; 91A, G–I; 92A; 93B, C; 94E; 95A, F; 102C). Protoconch of 1⅓ to over 2½ convex whorls; sculptured with few, strong spiral cords or few to many weak to strong, irregular, spirally arranged pustules or short, raised lines which sometimes form zig-zag patterns. Background sculpture of minute pustules or irregular, raised streaks which lie between spirally arranged primary elements. Apex of protoconch usually slightly inrolled (Figs 86B, C, G; 87B, G; 88B, F, G; 89A, E; 90B, F; 91B, E, F; 92B; 93A, D; 94F; 95E, H; 102D; see also Babio & Thiriot-Quiévreux, 1974; Thiriot-Quiévreux & Babio, 1975; Fretter & Graham, 1978; Bouchet, 1976 and Gofas & Warén, 1982).

Head-foot: with 1–7 (typically 3–7) metapodial tentacles, otherwise as for genus. (*A. beanii*, *A. abyssicola*, *A. cancellata*, *A. lactea* (Jeffreys, 1867), *A. punctura* (Jeffreys, 1867; Fretter & Graham, 1962), *A. lineata*, *A. pagodula* (Bucquoy, Dautzenberg & Dollfus), *A. beanii*, *A. novarensis*, *A. strangei* (Brazier) (personal observation), *A. cancellata*, *A. pagodula*, *A. montagui* (Payraudeau), *A. cimex* (A. Warén, *in lit.*) (Fig. 21).

Anatomy: based on *A. lineata*, Cala Rossa, Terrasini, Sicily (1 male, 2 females); *A. cancellata* (1 male, 3 females) and *A. pagodula* (2 males, 1 female), Calvi, Corsica; *A. subsoluta* (2 males, 2 females and sectioned material) and *A. jeffreysi* (Waller) (1 male, 1 female and sectioned material), W. of Korsfjorden, S.W. Norway, 250–300 m; *A. novarensis*, Port Stephens, N.S.W., Australia (several males and females and sectioned material). Stomach-style sac ratio 2.1–2.8, stomach length/width ratio 1.4–2.1. Stomach/rectum either straight (*A. pagodula*), convolute immediately anterior to posterior pallial wall (*A. novarensis*, *A. lineata*), or convolute mainly behind posterior pallial wall (*A. cancellata*, *A. jeffreysi* (Waller)) or both (*A. subsoluta*).

Male (Fig. 26A, B) with penis evenly tapering to a point in all species (Fig. 26B) except *A. novarensis* which has a large glandular lobe distally and a narrow, filament-like projection bearing penial duct (Fig. 26A). Penis, in all species narrowly oval in section. About ⅔ of well developed prostate gland embedded in pallial wall and ⅓ in kidney (*A. jeffreysi* has prostate spread across posterior pallial wall but does not protrude into kidney).

Female (Fig. 22) with poorly developed, inconspicuous vestibule. Bursa copulatrix (*b*) and its duct immediately behind posterior pallial wall. Bursa smaller than upper oviduct gland (*uog*) and lies on right side of oviduct glands, sometimes extending posteriorly along dorsolateral side of upper oviduct gland (as in *A. novarensis*, *A. cancellata* and *A. lineata*) with bursal duct lying beneath and opening posteriorly. Seminal receptacle absent but 1–5 small sperm pouches (*sp*) lie at posterior end of upper oviduct gland at junction of gland and narrow, thin-walled duct (*d*) to ventral channel. Upper oviduct gland (*uog*) relatively large (½–⅔ length of lower oviduct gland) and coiled. Some species (*A. subsoluta* and possibly *A. cancellata*) lack glandular tissue in coiling upper oviduct 'gland', but all others dissected had well developed glandular tissue.

Nervous system (of *A. cancellata*) with supraoesophageal ganglion separated from right pleural ganglion by a connective about 1½ times length of supraoesophageal ganglion. Suboesophageal ganglion with very short connective (about 1/5 length of ganglion) between it and left pleural ganglion. Cerebral ganglia abutting.

Operculum: as for genus (Figs 86D, I; 87E; 89B, C, F; 91C; 92C; 95B, C).

Radula: as for genus (Figs 86E, H; 87C, F; 89D, G; 90C, E; 91D; 92D; 93E; 95D).

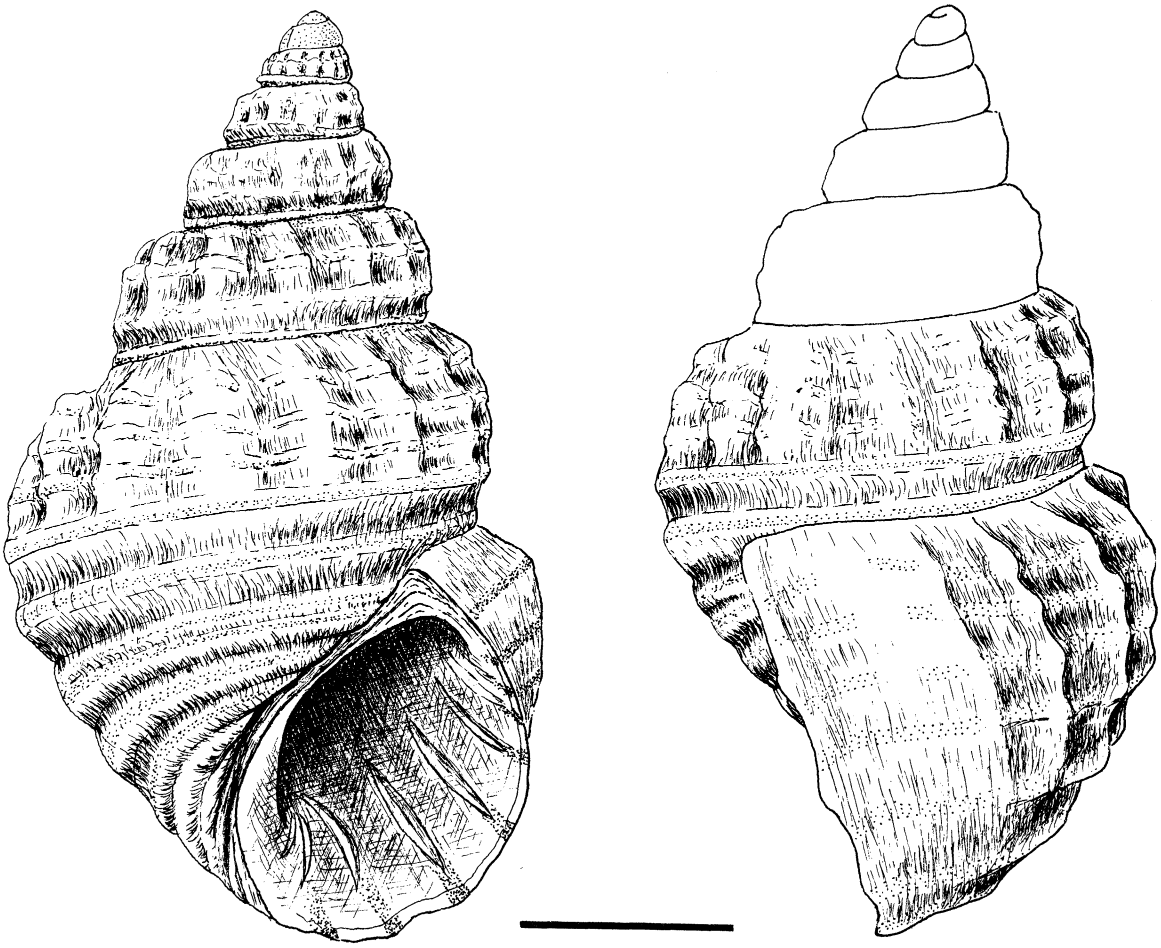

Fig. 20. Holotype of *Alvania* (*Alvania*) *corona* Nordsieck, type-species of *Coronalvania* Nordsieck; holotype, Ibiza, Balearic Islands (F. Nordsieck colln). **Scale:** 1 mm.

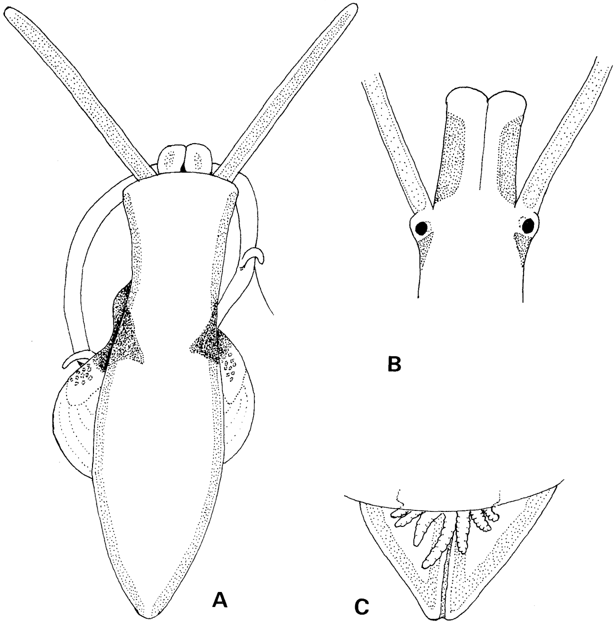

Fig. 21. Head-foot of *Alvania* (*Alvania*) *lineata* Risso, Cala Rossa, Terrasini, Sicily. **A**, ventral view of animal; **B**, dorsal view of head; **C**, dorsal view of posterior foot showing metapodial tentacles. Anterior and posterior pedal glands not shown.

Egg capsules: hemispherical to lens-shaped, attached to substrate (Lebour, 1934 (*A. punctura*); Thorson, 1946; Fretter & Graham, 1978 (*A. abyssicola*)).

Development: direct or with planktotrophic larval stage.

Distribution. North-eastern Atlantic and Mediterranean Sea: see Nordsieck (1972), van Aartsen & Nofroni (1982) and van Aartsen (1982a, b) for Recent species including *T. cimex*, *C. beanii*, *T. cancellatus*, *R. testae*, *R. lactea*, *R. rudis*, *R. scabra*, *R. cimicoides*, *A. spinosa*, *R. macandrewi*, *R. lanciae*, *A. lineata* and *A. corona*.

Western north Atlantic and Caribbean: *Rissoa auberiana* Orbigny, 1842, ? = *Rissoa minuscula* Verrill & Bush, 1900 (and also = *Rissoa lipeus* Dall, 1892 and *Rissoa lipeus floridanus* Mansfield, 1930, both from the Pliocene of Florida); *Rissoa xanthias* Watson, 1886, = *Rissoa xanthias acuticostata* Dall, 1889; *Rissoa pyrrhias* Watson, 1885, = *Rissoa listera* Dall, 1927; *Rissoa precipitata* Dall, 1889; *Cingula syngenes* Verrill, 1884.

Eastern Pacific: *Alvania tumida* Carpenter, 1856; *Rissoa inconspicua* C.B. Adams, 1852 not A. Adams, 1844, = *Alvania monserratensis* Baker, Hanna & Strong, 1930,? = *Alvania oldroydae* Bartsch, 1911, =

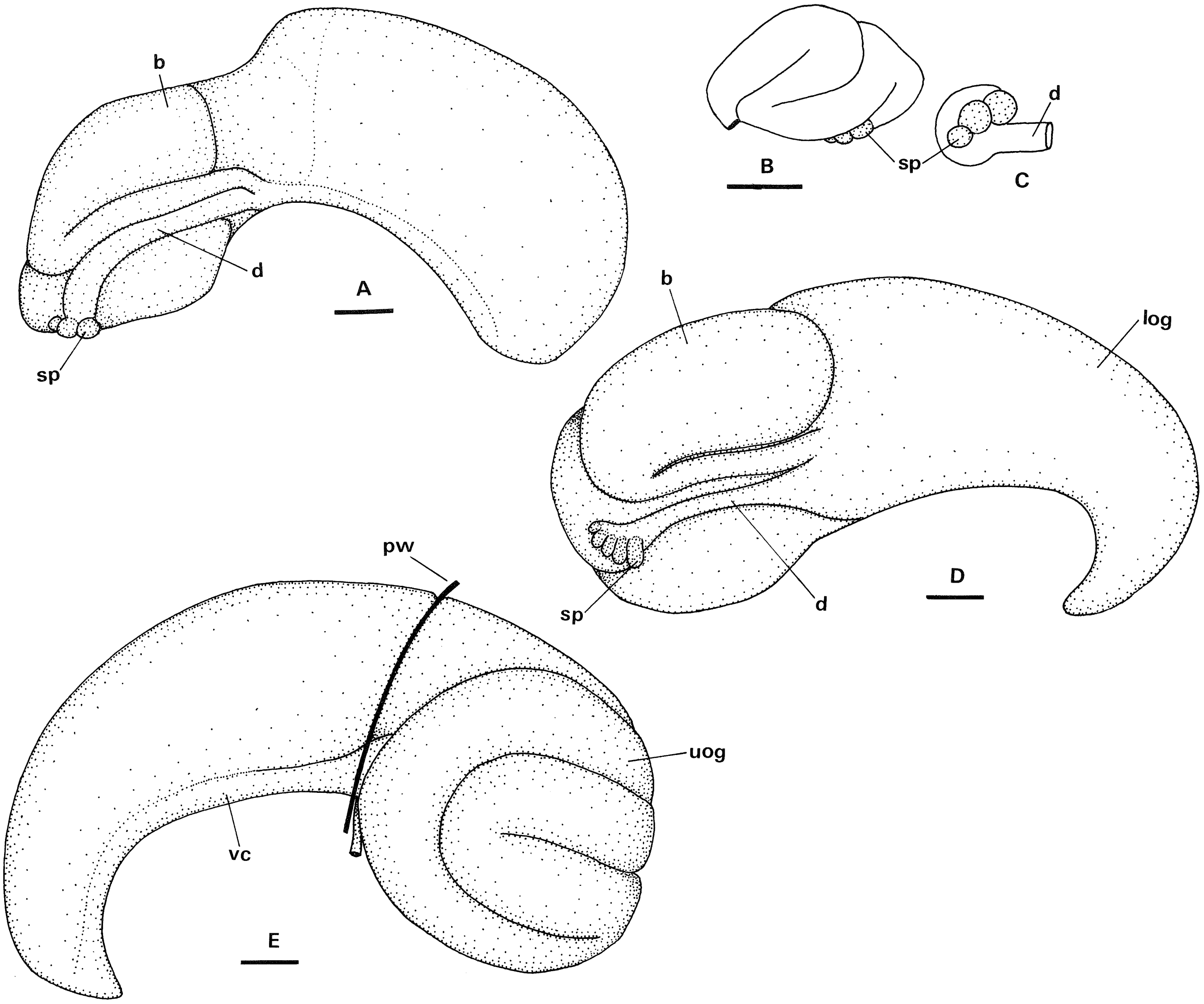

Fig. 22. Female genitalia of *Alvania* species. **A-C**, *Alvania* (*Alvania*) *novarensis* (Frauenfeld): **A**, right side; **B**, upper oviduct gland, left side; **C**, sperm sacs dissected away from upper oviduct gland. **D-E**, *Alvania* (*Alvania*) *lineata* Risso, right (**D**) and left (**E**) sides. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sp*-sperm pouch; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Alvania (*Alvaniella*) *keeleri* Palazzi, 1978, (new name for *inconspicua* C.B. Adams) (this species is very similar to the western Atlantic *A. auberiana*); *Rissoa acutelirata* Carpenter, 1864,? = *Alvania filosa* Carpenter, 1864, = *Rissoa compacta* Carpenter, 1865, = *A. iliuliukensis* Bartsch, 1911, = *A. fossilis* Bartsch, 1911, = *A. pedroana* Bartsch, 1911; *Alvania rosana* Bartsch, 1911, = *A. burrardensis* Bartsch, 1921; *Alvania profundicola* Bartsch, 1911; *Alvania trachisma* Bartsch, 1911, = *Alvania californica* Bartsch, 1911.

Indo-west Pacific: *Rissoa crystallina* Garrett, 1873; *Rissoa ogasawarana* Pilsbry, 1904; *Rissoa* (*Alvania*) *sombrerensis* Thiele, 1925; *Alvania stigmata* Frauenfeld, 1867; *Rissoa* (*Alvania*) *subcancellata* Sowerby, 1894 (? erroneous locality, may be a European species); *Rissoa townsendi* Melvill, 1910; *Rissoa versoverana* Melvill, 1893; *Rissoa* (*Alvania*) *trajectus* Watson, 1886; *Haurakia isolata* Laseron, 1956; *Haurakia firma* Laseron, 1956; *Haurakia formosita* Laseron, 1956.

Temperate Australia: *A. novarensis*; *Dunkeria fasciata* T. Woods, 1876, = *Rissoa* (*Alvania*) *hulli* Tate, 1893 (unnecessary replacement name), = *Rissoa hulliana* var. *eucraspeda* Hedley, 1911, = *Merelina eminens* Laseron, 1950; *Linemera occidua* Cotton, 1944; *Alvania hedleyi* Thiele, 1930, = *Merelina cyrta* Cotton, 1944; *Rissoa* (*Apicularia*) *strangei* Brazier, 1894, = *Rissoa lineata* Petterd, 1884, not *Alvania lineata* Risso, 1826 (also *Alvania*), = *Alvania tatei* Thiele, 1930.

South Africa: *Rissoa argentea* Sowerby, 1892, = *Alvania inflata* Turton, 1932; *Rissoa fenestrata* Krauss, 1848; *Alvania kowiensis* Tomlin, 1931, new name for *Alvania ima* Bartsch, 1915, not *Alvania ima* Bartsch, 1911.

Some Upper Cretaceous species from North America can be tentatively placed in *Alvania* (e.g. *Turboella tallahatchiensis* Sohl, 1960 (Fig. 92 E,F); *Turboella crebricostata* Sohl, 1960 (Fig. 92 G,H); *Mesostoma costatum* Wade, 1926).

Tertiary of Europe, many species named including: Paleocene, *Rissoa craticula* Briart & Cornet, 1889; Eocene, *Rissoa houdasi* Cossmann, 1907 (Fig. 91E, F); *Rissoa barreti* Morlet, 1885; *Alvania* (*Alvinia*) *bonneti* Cossmann, 1921 (Fig. 95F-H); *Alvania allixi* Cossmann, 1922. Many additional Tertiary species listed by Cossmann (1921).

Tertiary of western North America: Eocene of California, *Turbella* (sic!) *elegans* Palmer, 1923†; *Alvania vinosula* Anderson & Hanna, 1925; Oligocene of Washington, *Rissoa lettana* van Winkle, 1918.

Eocene, New Zealand (unnamed species).

Miocene, Palau, W. Pacific: *Merelina* (*Linemera*) *telkibana* Ladd, 1966.

Upper Pliocene of South Australia: *Turboella praenovarensis* Ludbrook, 1956; *Merelina* (*Linemera*) *varisculpta* Ludbrook, 1956.

Material examined. Because of the large number of European species involved, only the types of genus-group taxa are listed. Many other species were also examined including *A. montagui* (+*) and *A. pagodula* (Buquoy, Dautzenberg & Dollfus, 1884) (+*), *A. watsoni* Watson, 1873 (+), and *A. jeffreysi* (Waller, 1864) (+*).

+**T. cimex*. Syntypes (Linnaean Colln, London, which are mostly *cimex*) and many other lots (AMS and other museums).
+**C. beanii*. Several lots (BMNH, AMS and several other museums).
+**T. cancellatus*. Several lots (BMNH, AMS, and several other museums).
R. testae. Several lots (BMNH, including 1 lot ex Monterosato).
+**R. lactea*. Several lots (BMNH, AMS etc.).
R. rudis. A few lots (BMNH).
+**T. puncturus*. Many lots (BMNH, AMS, USNM etc.).
+**R. scabra*. A few lots (BMNH).
R. tiberiana. Sacco's figured specimen and 2 others (TGM).
+**R. cimicoides*. A few lots (BMNH, AMS, etc.).
A. spinosa. 1 lot, ex Monterosato (BMNH).
+ *P. dingdensis*. Holotype (GML) and topotypes (GML, AMS).
+**R. macandrewi*. 1 lot (BMNH).
+ *R. lanciae*. 1 lot (BMNH).
+**A. lineata*. Several lots (BMNH, AMS).
A. (*C.*) *corona*. Holotype (F. Nordsieck Colln).
+**R. auberiana*. Many lots (USNM, ANSP, MCZ).
R. lipeus and *R. lipeus floridanus*. Types (USNM).
R. xanthias acuticostata and *R. listera*. Types and several other lots (USNM).
+**R. xanthias* and +* *R. pyrrhias*. Types (BMNH), and a few lots (USNM, AMS).
C. syngenes. Syntypes (USNM).
+**A. tumida*. Many lots (USNM, LACM, AMS), holotype (USNM).
R. inconspicua. Holotype (MCZ).
A. monserratensis. Holotype (CAS).
A. oldroydae. Type (USNM).
+**R. compacta*. Many lots (USNM, LACM, AMS), holotype (USNM).
R. acutelirata. Holotype (PCB).
A. filosa, *A. iliuliukensis*, *A. rosana*, *A. burradensis*,*A. profundicola*, *A. trachisma*, *A. californica*. Holotypes (USNM) and other lots (USNM, LACM).
R. crystallina. Syntypes (ANSP).
R. ogasawarana. Syntypes (ANSP).
A. stigmata. Syntypes (NHMV).
R. (*A.*) *subcancellata*. Syntypes (BMNH, ANSP).
R. townsendi. Syntypes (BMNH).
R. versoverana. Holotype and paratype (BMNH).
+**R.* (*A.*) *trajectus*. Syntypes (BMNH) and many other lots (AMS).
H. isolata. Holotype and paratypes (AMS).
H. firma. Holotype, paratypes and several other lots (AMS).
H. formosita. Holotype and paratypes (AMS).
+**A. novarensis*. Syntypes (NHMV) and many other lots (AMS).
+**D. fasciata*. Syntypes (TM) and many other lots (AMS).
R. hulliana var. *eucraspeda*. Holotype and paratypes (AMS).
M. eminens. Syntypes (AMS).
+**A. hedleyi*. Syntypes (HUM) and many other lots (AMS).
M. cyrta. Holotype and paratypes (SAM).
L. occidua. Holotype and paratypes (AMS).
+**R.* (*A.*) *strangei*. Many lots (AMS).
A. tatei. Holotype (HUM).
+ *R. argentea*. Syntypes (BMNH) and a few other lots (USNM, AMS).
R. inflata. Holotype (OM).
+ *R. fenestrata*. A few lots (OM, BMNH, AMS).
A. kowiensis. Holotype (USNM).
+ *T. tallahatchiensis* (+) and *T. crebricostata* (+). A few lots (USNM).
+ *R. houdasi*. 1 lot (AMS, ex Le Renard).
R. barreti. Holotype (PCB).
T. elegans. Paratype (PCB).
A. vinosula. Holotype (CAS).
R. lettana. Paratype (PCB).
M. (L.) *telkibana*. Paratypes (USNM).

Remarks. The large number of genus-group names in the synonymy of the typical subgenus testifies to the considerable diversity in shell size and general appearance of its members. Basic characters such as protoconch ornamentation, radular structure and teleoconch sculptural pattern do not show a great diversity. Because of this, attempts to rationalise the grouping of species in many currently recognized subgenera and genera have failed. Added to these

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† Preoccupied by *Alvania elegans* Angas, 1877 but a replacement name is not required as *A. elegans* Angas is a species of *Merelina* (ICZN, Article 59(ii)).

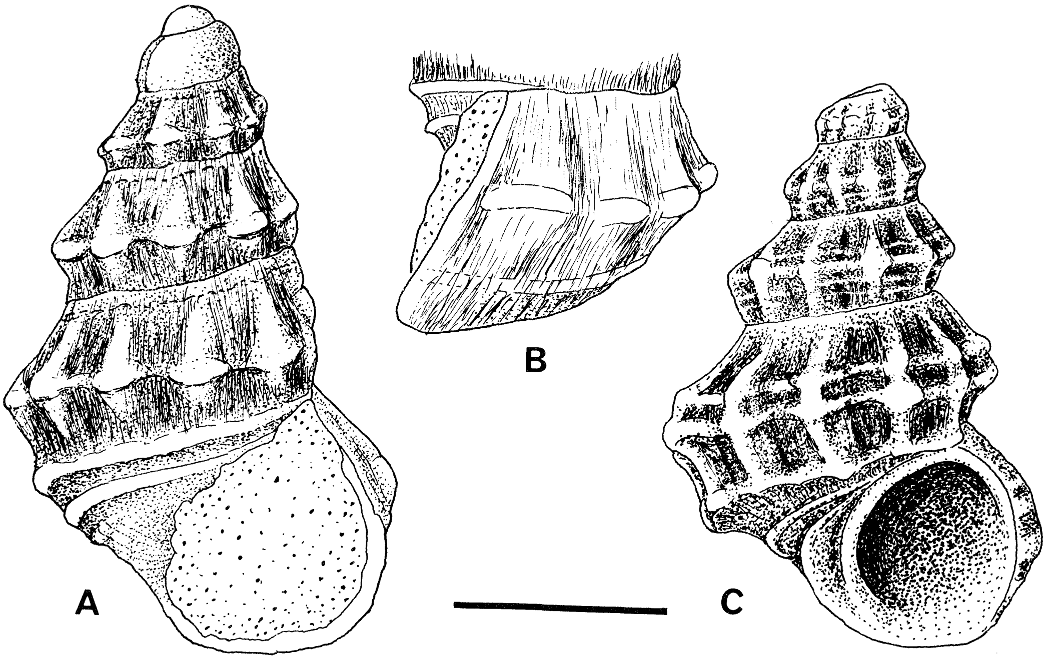

Fig. 23. **A-B**, *Alvania* (*?Linemera*) *luteophila* (Marwick), type-species of *Ihungia* Marwick; holotype, Muddy Creek, Gisborne, New Zealand, Miocene (NZGS TM1237). **C**, *Alvania* (*Alvania*) *spinosa* (Monterosato), type-species of *Alcidiella* Cossmann; Palermo, Sicily (IRSB, ex Monterosato). **Scale:** 1 mm.

problems is the apparently complete gradation between the taxa when a range of species is examined. Until such time as additional anatomical and other evidence is brought forward the available data indicates that the names listed in the synonyomy are best regarded as part of a single subgeneric grouping.

The typical subgenus has species that undergo direct development but many have a planktotrophic larval stage. The direct developing species appear to be found mostly in temperate, subtemperate and Arctic waters and can be recognized by the large initial whorl of the protoconch. As discussed above the protoconch of such species (and therefore its sculpture) is equivalent to only the initial portion of the protoconch (or protoconch 1) of planktotrophic species. A few, mostly undescribed species, from islands of the tropical Indian Ocean and east Africa have paucispiral protoconchs with strong spiral keels (Fig. 93A, D) but otherwise have shells and radulae typical of *Alvania* (Fig. 93B, C, E), although none has been examined alive. At least some species living on islands in the Atlantic also have paucispiral protoconchs and presumably undergo direct development, although their protoconch sculpture is not as strongly developed as in the Indian Ocean species *Alvania scabra* (Fig. 89E), *Alvania watsoni* (Fig. 102 D) and *Alvania macandrewi* (Fig. 89A). A zig-zag protoconch microsculpture is seen in several species and is presumably derived from the coalescing of the raised dots and dashes seen in many other species of *Alvania*. These species include *A. jeffreysi* (Fig. 94E, F), *A. vermaasi* van Aartsen, 1975, *A. imperspicua* Pallary, 1920, *A. zylensis* Gofas & Warén, 1982, and the Miocene species *A. basisulcata* Janssen, 1972. This microsculpture pattern is apparently not confined to *Alvania* as it is also found in *Rissoa perfecta* Smith (Fig. 106D-E), tentatively referred to *Cingula* below.

Of the species examined anatomically there appears to be an overall similarity in the female genital system, although differences, judged to be minor, exist. Some of the material examined was, however, poorly preserved or slightly immature so that it was not possible to determine, confidently, all details.

The male genitalia are rather uniform except for the penis of *Alvania novarensis*, the type species of *Conalvinia*. This species has a flattened, blade-like distal appendage on the penis (Fig. 26A) whereas all other species examined have simple, tapering penes. This character may eventually be a useful one in dividing *Conalvinia* and *Alvania* s.s. but more information is needed about the penes of other species of *Alvania* to determine whether or not such variation is correlated with other characters.

A small group of eastern Atlantic species including *A. xanthais*, *A. pyrrhias* and *A. precipitata* are only tentatively included in *Alvania* s.s. They have an unusual protoconch and their teleoconch sculpture is reduced to mainly axial elements. Further investigation of these species is required.

Subgenus *Galeodina* Monterosato, 1884

Galeodina Monterosato, 1884a: 163. Type-species *G. striatula* Da Costa, = *Turbo striatulus* Da Costa, 1778, not Linné, 1758, = *Turbo carinatus* 'Montagu', = Da Costa, 1778, (?) † not Born, 1778; monotypy. Recent, Europe (Fig. 94A–D).

Diagnosis. *Shell*: turbinate, with few spiral cords much stronger than axial sculpture, varix weak or absent, outer lip not dentate within (Fig. 94A). Protoconch with microsculpture of weak spiral elements (Fig. 94B; see also Thiriot-Quiévreux & Babio, 1975).

Head-foot: as in *Alvania* s.s. but only a single metapodial tentacle apparently present (Jeffreys, 1867).

Anatomy: unknown.

Operculum: typical of genus (Fig. 94C).

Radula: as for genus; central teeth $\frac{2-3+1+2-3}{1 \qquad 1}$ with simple lateral thickenings. Lateral teeth $3-4+1+6-7$ (Fig. 94D).

Egg Capsules: unknown.

Development. Thiriot-Quiévreux & Babio (1975) suggest that development is direct but the examination of a photograph of an uneroded protoconch (SEM photo supplied by Dr A. Warén) shows that it is of the type associated with planktotrophic larvae, and like that of typical species of *Alvania* such as *A. beanii.*

Distribution. Western coast of Europe and the Mediterranean Sea: *T. carinatus*, = *T. striatulus* Da Costa, 1778 not Linné, 1758, = *Turbo monilis* Turton, 1819, = *Rissoa trochlea* Michaud, 1832, ? = *Rissoa labiata* Philippi, 1836, ? = *Turbo lucullanus* Scacci, 1833, ? = *Galeodina striatula* var. *minorecarinata* Monterosato, 1884, = *Alvania russinoniacea* Locard, 1886.

Nordsieck (1972) lists the Mediterranean *Rissoa cingulata* Philippi, 1836 as a separate species of *Galeodina*. Piani (1979) and van Aartsen (1982c) also recognize that species and *Rissoa tenera* Philippi, 1844 (placed by Nordsieck (1972) in *Setia* (*Crisillosetia*)) as additional species of *Galeodina*.

Material examined.

+**T. carinatus*. Several lots (BMNH, AMS etc).

Remarks. The teleoconch characters serve to distinguish this subgenus, which is only tentatively separated from *Alvania* s.s., although some species (e.g. *A. watsoni*, Fig. 102C) included in the typical subgenus have predominantly spiral sculpture. The single metapodial tentacle recorded by Jeffreys (1867) requires confirmation.

It is probable that *A. carinata* is very closely related to species of *Alvania* s.s. but anatomical information is needed to clarify its relationship.

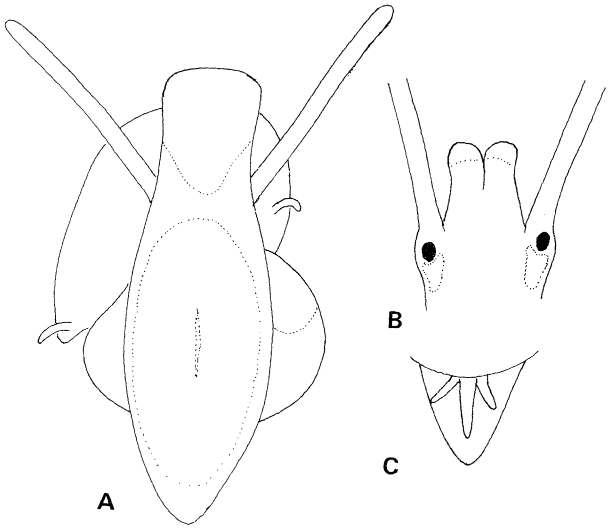

Fig. 24. Head-foot of *Alvania* (*Crisilla*) *semistriata* (Montagu), Wembury, England: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of posterior end of foot showing metapodial tentacles.

Subgenus *Crisilla* Monterosato, 1917

Crisilla Monterosato, 1917: 12. Type-species *Crisilla semistriata* (Montagu), = *Turbo semistriatus* Montagu, 1808; monotypy. Recent, Europe (Figs 24; 25B; 96A–E).

'*Cingula* Monterosato' of authors, not Fleming, 1828.

Crisella error of authors.

?*Crisillosetia* Nordsieck, 1972: 163. Type-species *(Setia* (*Crisillosetia*)) *pseudocingulata* Nordsieck, 1972; original designation. Recent, Mediterranean Sea (Fig. 102E, F).

Diagnosis. *Shell*: sculpture of spirals and axial growth lines (Fig 96B). Outer lip without varix and internal denticles (Fig. 96A). Protoconch microsculpture with spiral elements very weak, pustules small (Fig. 96C; see also Thiriot-Quiévreux & Babio, 1975).

Head foot: as in *Alvania* s.s., with 3 metapodial tentacles (Fig. 24).

Anatomy: based on *A.* (*C.*) *semistriata*, Plymouth, England (1 male, 2 females). Stomach-style sac ratio 1.7, length-width ratio 1.5–1.6. Intestine-rectum undulating and expanded in front of posterior pallial wall, otherwise straight.

Penis long, evenly tapering to a point; narrowly oval in section. Prostate gland well developed, about ¾ of its length in pallial wall.

Female (Fig. 25B) as in *Alvania* s.s., with large bursa copulatrix (*b*) about same length as, and lying laterodorsally to, upper oviduct gland (*uog*). Bursal duct short, opening to ventral channel (and to bursa) just behind posterior pallial wall. Upper oviduct gland (*uog*) coiled, glandular, with bilobed sperm pouch (*sp*) at posterior end and connected to ventral channel by narrow duct (*d*) running on outside (right side) of gland.

Nervous system not investigated.

Operculum: as for genus (Fig. 96D).

Radula: as for genus; central teeth $\frac{2-3+1+2-3}{1+1 \qquad 1+1}$,

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† I have been unable to determine which of these works has priority. If Born's work proves to be the prior one there are several alternative names available.

with lateral thickenings produced into a second, shorter pair of basal denticles. Lateral teeth 4 − 5 + 1 + 5 − 6 (Fig. 96E).

Egg capsules: hemispherical with 12–22 eggs (Lebour, 1934).

Development: planktonic larval stage present (Lebour, 1934).

Distribution. Coast of western Europe and Mediterranean Sea: *T. semistriatus*; *S.* (*C.*) *pseudocingulata*.

Van Aartsen (*in lit.*, 1982) suggests that the following species are also closely allied to *A.* (*C.*) *semistriatus*: *Rissoa callosa* Manzoni, 1868; *Rissoa* (*Cingula*) *picta* Jeffreys, 1867; *Rissoa marioni* Monterosato, 1878, ? = *R. substriata* Philippi, 1844.

Material examined.

+ **T. semistriatus*. Many lots in several museums (particularly BMNH and AMS).

+ *S.* (*C.*) *pseudocingulata*. 'Paratypes', ex F. Nordsieck (AMS).

**R.* (*C.*) *picta*. One lot (MCZ).

R. callosa. One lot (MCZ).

Remarks. The type species of *Crisilla* has often been regarded as a species of *Cingula* but the external features of the animal, its anatomy and the sculpture of the protoconch show its close relationship to *Alvania*. The main divergence from *Alvania* is in teleoconch characters, particularly in the very reduced axial sculpture and the lack of an apertural varix. Because of the shell differences *Crisilla* is regarded tentatively as being separable, as a subgenus, from *Alvania* s.s.

Crisillosetia pseudocingulata somewhat resembles *A.* (*C.*) *semistriata* in teleoconch characters but has a paucispiral protoconch with several rows of gemmules (Fig. 102 E, F). A somewhat similar protoconch sculpture is encountered in some species of *Manzonia* but those have the apex of the protoconch more strongly tilted.

Subgenus *Punctulum* Jeffreys, 1884

Punctulum Jeffreys, 1884: 122. Type-species *Rissoa wyvillethomsoni* (Jeffreys ms) Friele, 1877; here designated. Recent, bathyal, north Atlantic (Figs 25A; 97).

Diagnosis. *Shell*: ovate-conic, distinctly umbilicate in type-species, another species non-umbilicate; sculpture weakly clathrate. Aperture with thin outer lip; no varix (Fig. 97A). Protoconch conical, of 2½ whorls, smooth except for exceedingly fine spiral lines and axial striae (Fig. 97C–E; see also Gofas & Warén, 1982).

Head-foot: no pigmented eyes; snout short relative to tentacles, bilobed. Right and left pallial tentacles well developed; 5 metapodial tentacles (preserved material).

Anatomy: based on material of *A.* (*P.*) *wyvillethomsoni* collected in 1896 from 63°36′N, 7°30′W (North Atlantic), 1322 m (1 male, 2 females). Stomach-style sac ratio 3, length-width ratio 1.4 Intestine-rectum coiled in front of and behind posterior pallial wall. Penis long, strap-like, tapering to blunt point. Prostate gland mostly within pallial wall, well developed.

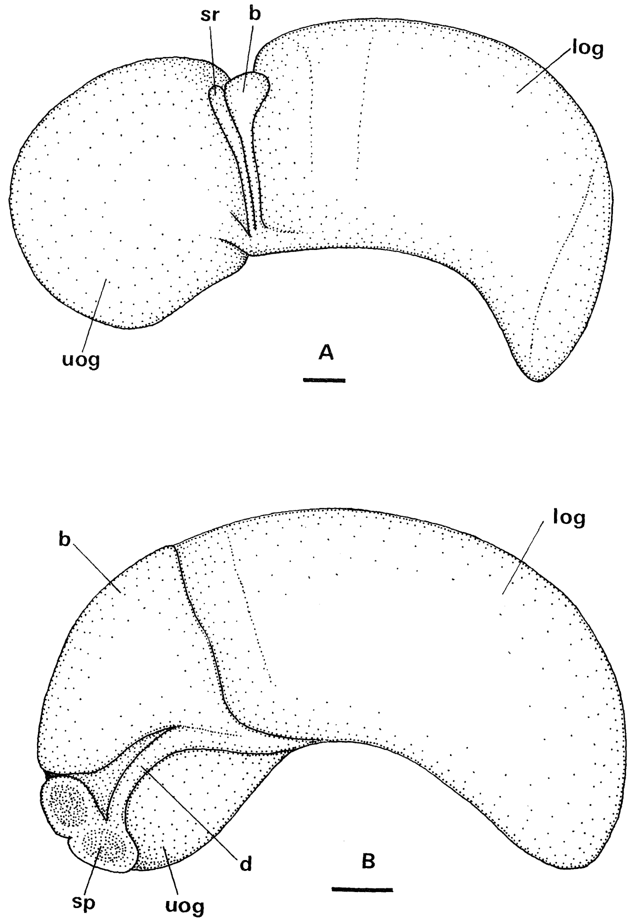

Fig. 25. Female genitalia of *Alvania* species. **A**, *Alvania* (*Punctulum*) *wyvillethomsoni* (Friele), right side; **B**, *Alvania* (*Crisilla*) *semistriata* (Montagu), right side. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *log*-lower oviduct gland; *sp*-sperm pouch; *sr*-seminal receptacle; *uog*-upper oviduct gland. **Scale:** 0.1 mm.

Female (Fig. 25A) with coiled, glandular upper oviduct gland (*uog*), immediately anterior to which is a narrow, tubular seminal receptacle (*sr*) and small bursa copulatrix (*b*), both lying dorsolaterally on right side of oviduct glands. Upper oviduct gland appears to open to ventral channel just behind seminal receptacle and is about 0.6–0.7 length of lower oviduct gland (*log*).

Cerebral ganglia separated by moderately long connective about 0.26 times length of ganglion. Supraoesophageal ganglion with connective 2.25 times longer than ganglion; suboesophageal ganglion abuts against left pleural ganglion.

Operculum: as for genus.

Radula: as for genus but central teeth more compressed than in other subgenera, about 4 times wider than high. Central teeth $\frac{2-4+1+2-4}{1+1 \quad 1+1}$. Lateral teeth 3(?) + 1 + 4 − 6 (Fig. 97B).

Egg capsules: unknown.

Development: the protoconch suggests that a planktotrophic larval stage may be present.

Distribution. Bathyal, North Atlantic: *R. wyvillethomsoni*.

North-eastern Atlantic: *Alvania porcupinae* Gofas & Warén, 1982, = *Rissoa deliciosa* var. *multicostata* Jeffreys, 1884 not *Rissoa multicostata* C.B. Adams, 1850.

Material examined.

+**R. wyvillethomsoni*: 1 lot (ZMC).

Remarks. The two species included in this subgenus can be distinguished from other species of *Alvania* by their smooth, conical protoconch and from most other species by their thin outer lip. The type-species has a distinct umbilicus, but this is not present in *A. porcupinae*.

Punctulum, a name overlooked by previous reviewers and brought to my attention by Dr A. Warén, was introduced for umbilicate species of *Rissoa*. Jeffreys (1884) included 3 species without designating one as type. One of the species listed (*Rissoa stefanisi* Jeffreys, 1869) is a pyramidellid (Warén, 1980: 23) and another (*R. subperforata* Jeffreys, 1884) is a fossil. The third species, *R. wyvillethomsoni*, is here designated as the type species of *Punctulum*.

The anatomy of *A.* (*P.*) *wyvillethomsoni* differs from that of species of *Alvania* s.s. in having a true seminal receptacle anterior to the upper oviduct gland and in apparently lacking secondary seminal receptacles. It agrees with *Alvania* in the sculptural features of the teleoconch and the multiple metapodial tentacles as well as in the anatomy of the male reproductive system.

Subgenus *Linemera* Finlay, 1924

Linemera Finlay, 1924: 483. Type-species *Linemera interrupta* Finlay, 1924, new name for *Rissoa gradata* Hutton, 1885, not Orbigny in Sagra, 1842; original designation. Uppermost Pliocene—Lower Pleistocene, New Zealand.

?*Ihungia* Marwick, 1931: 89. Type-species *Ihungia luteophila* Marwick, 1931; original designation. Miocene, New Zealand (Fig. 23A, B).

Diagnosis. *Shell*: similar to *Alvania* s.s., with rather weak to strong clathrate sculpture, the axial elements sometimes predominant. Aperture simple, varix usually weak (Figs 23A, B; 96F; 98A, E). Protoconch of 1½ bulbous whorls, sculptured with exceedingly minute granules which are sometimes coalesced to form short, horizontal striae (Figs 96G; 98B, G).

Head-foot and *anatomy*: not known.

Operculum: as for genus (Fig. 98F).

Radula: as for genus. Central teeth $\frac{4-5+1+4-5}{((1)+)1 \quad 1(+(1))}$; lateral teeth 4−5+1+4−8 (Fig. 98C, D).

Egg capsules: unknown.

Development: presumably direct in all species.

Distribution. Miocene to Recent, New Zealand, see Fleming (1966) for list of New Zealand fossil species and Powell (1979) for the Recent species.

Temperate Australia: *Alvania suprasculpta* May, 1915 (Fig. 98D–G), = *Merelina subreticulata* Laseron, 1950; *Rissoa filocincta* Hedley & Petterd, 1906; *Rissoa verconiana* Hedley, 1911.

South Africa: *Rissoa beyersi* Thiele, 1925; *Rissoa deneti* Thiele, 1925; *Rissoa nicobarica* Thiele, 1925.

Material examined.

L. interrupta. Photograph of holotype ex B.A. Marshall.

Several lots of New Zealand Recent species (AMS, NMNZ) including (+*)*A.* (*L.*) *interrupta gradatoides* (Finlay, 1930) and (+*)*A.* (*L.*) *pingue* (Webster, 1906).

I. moniliata, *I. acantha*. 1 lot of each (NMNZ).

I. aequalis. One lot (AMS).

+**A. suprasculpta*. Holotype (TM), paratypes (AMS, NMV), and several other lots (AMS).

M. subreticulata. Syntypes (AMS).

R. filocincta. Syntypes (AMS).

R. verconiana. Syntypes (AMS).

R. beyersi, *R. deneti*, *R. nicobarica*. Types (HUM).

Remarks. This subgenus appears to be restricted to the southern hemisphere where it has a known fossil history (in New Zealand) from the mid-Tertiary. Protoconchs indicate that the species are all direct developers, being paucispiral, with a large initial whorl. The shape of the protoconch and its microsculpture of small granules are the main distinguishing features.

Ihungia is based on a species which is typical of a now extinct species-group in the Neogene of New Zealand. The protoconch of one species (*I. moniliata* Marwick, Fig. 96G) was examined and found to have a few very weak spiral ridges and numerous, minute, raised dots. In two other species (*I. aequalis* Laws and *I. acantha* Marwick) it appears to be smooth although the available material is slightly worn. The teleoconch sculpture (Fig. 23A; 96F) is dissimilar to that of typical species of *Alvania* (*Linemera*) in being primarily axial with few spiral elements. While this species group can, with some certainty, be placed in *Alvania*, it is only tentatively included in the subgenus *Linemera*. *Linemera* is maintained, tentatively, as a grouping of convenience until something is known of the anatomy of at least some of the species it contains.

Alvania bonneti Cossmann, 1921 (Fig. 95F–H) from the Eocene of the Paris Basin resembles species of *Alvania* (*Linemera*) in teleoconch characters and in having a paucispiral protoconch covered with small granules (Fig. 95H). Because of the great geographic and time separation, it is more likely that *A. bonneti* and species of *Linemera* have evolved from *Alvania* by different lineages. *Linemera* probably arose in the southern hemisphere in the early Tertiary. Descent from *Alvania* s.s. is suggested by an undescribed species of *Alvania* with a multispiral protoconch known from the upper Eocene of New Zealand (specimens in NZGS).

A few deep-water species from the North Atlantic show some resemblance to species of *Linemera* (e.g. *Alvania pseudosyngenes* Warén, 1973 and *Rissoa harpa* Verrill). These species appear to have been derived independently from *Alvania*, in the case of *Alvania pseudosyngenes*, and from *Pusillina* in that of *Rissoa*

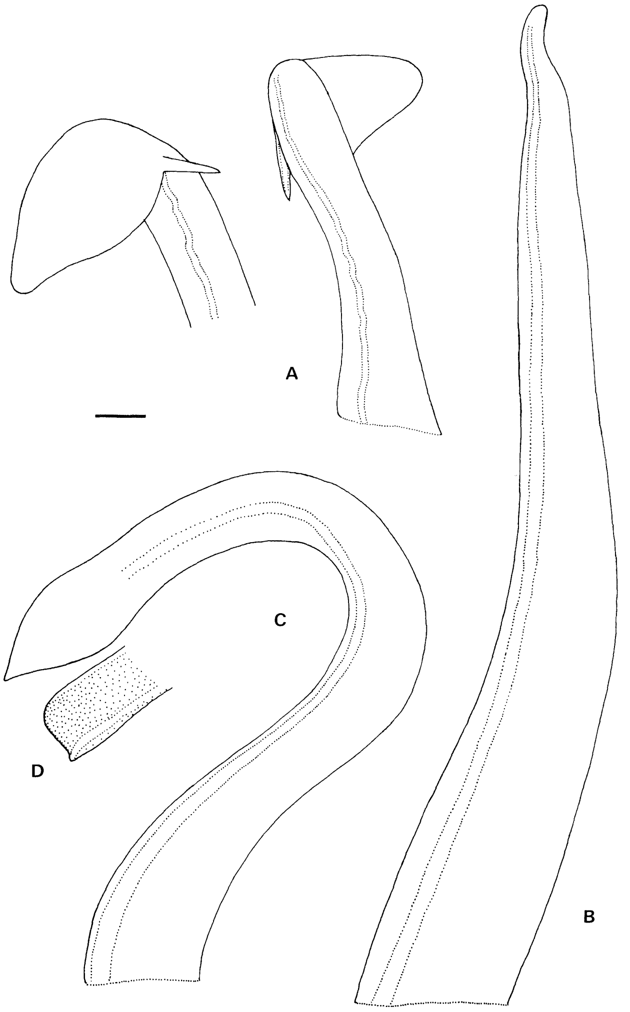

Fig. 26. Penes of species of *Alvania* and *Cingula*. **A**, two views of penis of *Alvania* (*Alvania*) *novarensis* (Frauenfeld); **B**, *Alvania* (*Alvania*) *lineata* Risso; **C-D**, *Cingula* (*Cingula*) *trifasciata* (J. Adams); **C**, preserved specimen; **D**, distal end of living specimen. **Scale:** 0.1 mm.

harpa. The similarity in shell characters of northern hemisphere species with those listed above as being typical of *Linemera* is interpreted here as convergence.

Genus *Manzonia* Brusina, 1870

Manzonia Brusina, 1870: 37. Type-species *Turbo costatus* J. Adams, 1797, not von Salis, 1793, = *Turbo crassus* Kanmacher in J. Adams, 1798; original designation. Recent, Europe and Mediterranean Sea (Figs 27; 99A-F).

Diagnosis. *Shell*: minute to small, ovate-conic, non-umbilicate, usually with strong, axial ribs (weak to absent on base), crossed by spiral cords or spiral cords predominate; axial ribs rarely absent; a few spiral cords prominent on base. Aperture oval, with or without very weak, broad excavation in rounded posterior corner, rounded anteriorly, with varix on opisthocline outer lip; peristome duplicated. Protoconch multispiral or paucispiral; if multispiral with netted microsculpture, if paucispiral with gemmate or smooth spiral keels; apex usually strongly tilted. Periostracum very thin or calcified.

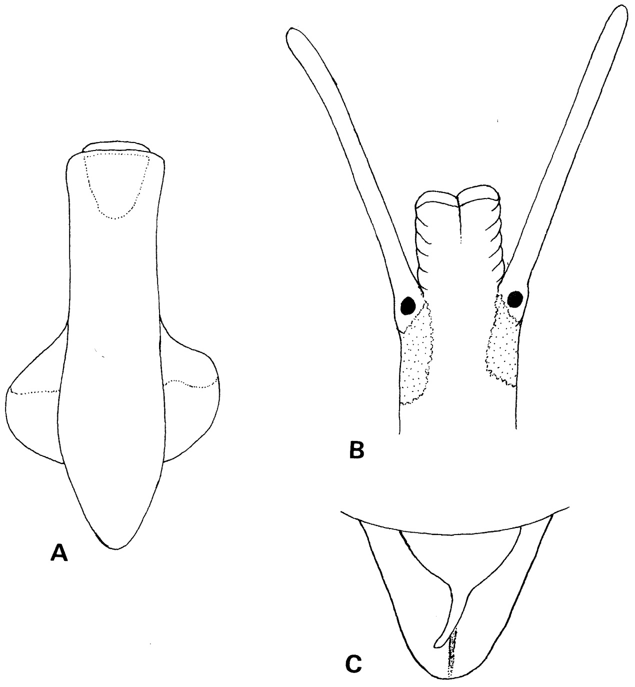

Fig. 27. Head-foot of *Manzonia* (*Manzonia*) *crassa* (Kanmacher in Adams), Wembury, England: **A**, ventral view of foot; **B**, dorsal view of head; **C**, dorsal view of posterior foot showing metapodial tentacle.

Head-foot: unpigmented, cephalic tentacles long, parallel-sided, foot not markedly constricted in middle as in *Rissoa*; posterior mucous gland apparently absent. Pallial tentacles present or absent, a metapodial tentacle present or absent.

Anatomy: ctenidial filaments finger-shaped, bases narrower than osphradium, osphradium slightly shorter than ctenidium. Stomach relatively short (length-width ratio 1.5-2), stomach-style sac ratio 2.6-3.

Penis tapering evenly to a point or with narrow terminal filament, penial duct marginal, closed. Prostate gland well developed, partly embedded in kidney, partly in pallial wall. Vas deferens coiled at posterior end of stomach.

Female with or without sac-like vestibule, genital opening subterminal. Ventral channel open to lower oviduct gland along most of its length. Bursa copulatrix between upper and lower oviduct glands on right side, just behind pallial cavity, duct short, ventral to bursa. Seminal receptacle small, immediately behind bursa, or (possibly) absent. Upper oviduct gland coiled to simple.

Nervous system not investigated.

Operculum: thin, oval, nucleus eccentric, last whorl large.

Radula: central teeth $\dfrac{2-4+1+2-4}{1 \qquad 1}$, with single pair of basal denticles; lateral margins thickened, simple, at 35°-60°; U-shaped ventral extension moderately to poorly developed. Lateral teeth $5-7+1+5-7$. Inner marginal teeth with cusps equal in size or slightly smaller than those on outer marginal teeth, confined to distal ½ of outer edge. Cusps on outer marginal on distal end and distal ½–⅓ of inner edge.

Development: direct or with planktotrophic larval stage.

Distribution. Western Europe, Mediterranean, Caribbean, eastern Pacific and Indo-Pacific.

Remarks. The species here included in *Manzonia* have a number of features in common and, as far as can be determined, appear to be a natural group that has been distinct from *Alvania* since at least the Oligocene. Species of *Manzonia* can be distinguished from most *Alvania* species by the duplicated peristome and strong, rather smooth basal spirals. The head-foot differs from that of *Alvania* in having one or no metapodial tentacles, in showing no pigmentation and in apparently lacking a posterior pedal gland. In the features of the head-foot, *Manzonia* has more in common with *Onoba*, from which it differs in its *Alvania*-like sculpture and duplicated peristome. The radula differs from that of *Rissoa*, and some species of *Alvania*, in lacking a pair of basal denticles formed from the outer margins of the central teeth. It also has more numerous (5–7) cusps on the inner edge of each lateral tooth (*Alvania* species range from 3-6 but most have 3-4).

Two of the subgenera included in *Manzonia* differ in the details of the female genitalia and in penial characters. The differences suggest that full generic status might be allowed the two groups, but because only one species in each group has been examined and the only two female specimens of *Manzonia crassa* available for examination were slightly immature, the anatomical differences are not given the weight that they may prove to deserve.

Key to Subgenera of *Manzonia*
(based on shell characters)

1. Teleoconch with strong opisthocline axial ribs; spiral sculpture conspicuously weaker than axials .... *Manzonia* s.s.

— Teleoconch with strong to very weak or absent orthocline to slightly prosocline axial ribs; spiral sculpture about equal in strength to ribs or stronger 2

2. Teleoconch with 2–3 smooth spiral cords on base, no basal axial sculpture; protoconch paucispiral, with simple spiral keels; shell shape usually elongate-ovate .... *Simulamerelina*

— Teleoconch with spiral ribs on base smooth or crossed by weak axials; protoconch paucispiral to multispiral, if paucispiral typically with spiral rows of gemmae (rarely smooth keels); shell shape ovate .... *Alvinia*

Subgenus *Manzonia* s.s.

Diagnosis. *Shell*: as for genus; with axial sculpture of strong opisthocline ribs, spiral sculpture weak to moderately strong, always weaker than axial ribs. Base with few strong spirals or keels, axial ribs absent on lower base (Figs 99A; 100A, C). Protoconch either multispiral or paucispiral. Multispiral type of about 2¼ convex whorls, initial whorl with 'netted' microsculpture, remainder with a few irregular lines or granules; mostly smooth (Fig. 99B). Paucispiral type of about 1½ whorls, with weak, spiral, finely gemmate lines (Fig. 100B) or spiral ridges. Periostracum (in type-species) well developed and apparently calcified (Fig. 99C).

Head-foot: cephalic tentacles long, slender, parallel-sided, weakly and minutely ciliated, large eyes in bulges at their outer bases. Snout distinctly bilobed, extensile. Foot rather elongate, narrow anteriorly, broader in posterior section; propodium rather narrow, with triangular anterior mucous gland. No posterior mucous gland visible. Anterior and posterior pallial tentacles present; metapodial tentacle broad proximally, narrowing to a short filament distally, sometimes extending beyond posterior end of foot. Unpigmented (Fig. 27) (*M. crassa*, Wembury, England, personal observation). *Manzonia crassa* is also described in detail by Fretter & Graham, 1978, who state that a posterior mucous gland opening to a median groove is present and that a projection from each metapodial lobe gives the appearance of a triple (metapodial) tentacle. Independent observations by A. Warén support the observation that *M. crassa* lacks a posterior pedal gland and has a simple metapodial tentacle (*in lit.*, 1981).

Anatomy: based on *M. crassa,* Calvi, Corsica (2 females, 1 male). Stomach-style sac ratio 3, length-width ratio 1.5–2. Intestine-rectum coiled anterior to posterior wall of pallial cavity.

Male with long penis tapering to a point, distal third slender, broadly oval in section, proximal portion narrowly oval in section. Prostate gland well developed, nearly half length embedded in kidney.

Female submature in the 2 specimens examined, with very small, indistinct vestibule; upper oviduct gland a coiled, apparently weakly muscular tube with slight glandular development. Bursa copulatrix small relative to upper oviduct gland, with short duct opening directly beneath to ventral channel. Seminal receptacle possibly present, immediately behind bursa, small (in one specimen this appeared to be a narrow, empty sac; not seen in second specimen).

Operculum: as for genus (Fig. 99D, E).

Radula: as for genus; U-shaped extension of ventral edge of central teeth moderately developed (Fig. 99F).

Egg capsules: unknown.

Development: planktotrophic veliger stage occurs in *M. crassa* (Fretter & Pilkington, 1970). The species which have paucispiral protoconchs presumably have direct development.

Distribution. Europe and Mediterranean Sea: *T. crassus.*

Madeira: *Rissoa crispa* Watson, 1873; *Rissoa gibbera* Watson, 1873; *Manzonia overdiepi* van Aartsen, 1983.

Oligocene of W. Germany: *Rissoa duboisii* Nyst, 1843 (Fig. 100C).

Miocene of France: *Rissoa* (*Manzonia*) *falunica* Morgan, 1915; *Rissoa* (*Manzonia*) *pontileviensis* Morgan, 1915.

Material examined.

+ **T. crassus*. Many lots in several museums (BMNH, AMS, IRSB etc).
+ *R. crispa*. 1 lot (ANSP).
R. gibbera. 1 lot (ANSP).
R. duboisii. 1 lot (NMV).

Remarks. Species included in *Manzonia* s.s. differ from those in the other subgenera included in the genus *Manzonia* in their strong, opisthocline axial ribs and weaker spiral sculpture. This group has a somewhat restricted geographic range, being found only in the Mediterranean and north eastern Atlantic.

Subgenus *Alvinia* Monterosato, 1884

Alvinia Monterosato, 1884a: 160. Type-species *Alvania weinkauffi* (Mohrenstern ms) Weinkauff, 1868; subsequent designation Crosse, 1885: 140. Mediterranean Sea (Fig. 102A, B).

Moniziella Nordsieck, 1972: 172. Type-species (*Rissoa*) *moniziana* Watson, 1873; original designation. Recent, Madeira (Fig. 102G, H).

Flemellia Nordsieck, 1972: 176. New name for *Seguenziella* Sacco, 1904: 123, not Neviani, 1901, new name for *Taramellia* Seguenza, 1903: 53, not Campana, 1903, new name for *Flemingia* Jeffreys, 1884: 116, not Johnston, 1832. Type-species *Turbo zetlandica* Montagu, 1815; subsequent designation Cossmann, 1921: 31. Recent, western Europe (Figs 99G; 100D, E).

Diagnosis. *Shell*: as for genus; with axial sculpture strong to very weak or absent, axial ribs orthocline to slightly prosocline; base with spiral ribs or keels, axial ribs weak to absent (Figs 100D, F; 101G; 102A, G). Protoconch either multispiral or paucispiral. Multispiral type as in *Manzonia* s.s. (Fig. 99G); paucispiral type with strongly tilted apex and spiral ridges which usually bear gemmules (Figs 100G; 101H; 102B, H). Periostracum thin, simple.

Head-foot and *anatomy*: unknown.

Operculum: as for genus.

Radula: as for *Manzonia* s.s. (Figs 100E; 101I).

Development: with probable planktotrophic development in *M.* (*A.*) *zetlandica*; species with paucispiral protoconchs presumably with direct development.

Distribution. Europe, eastern Atlantic, and Mediterranean Sea: *T. zetlandica*; *R. weinkauffi*; *R. moniziana*; *Rissoa* (*Alvania*) *macandrewi spreta* Watson, 1873; *Rissoa dictyophora* Philippi, 1844.

Eastern Pacific: *Alvania aequisculpta* Keep, 1887 (Fig. 101G–I), = *Rissoa* (*Alvania*) *grippiana* Dall, 1908; *Alvania cosmia* Bartsch, 1911; *Alvania almo* Bartsch, 1911; *Alvania hiala* Bartsch, 1911; ?*Alvania purpurea* Dall, 1872.

Caribbean: *Rissoa caribaea* Orbigny, 1853; *Rissoa epima* Dall & Simpson, 1901.

Material examined.

+ *R. weinkauffi*. 4 syntypes (IRSB), several other lots (BMNH, AMS, NMV, USNM).
+ **T. zetlandica*. Several lots (BMNH, USNM, AMS).
R. moniziana. Holotype and 1 other lot (BMNH).
R. (*A.*) *macandrewi spreta*. 1 lot (ANSP).
+ *R. dictyophora*. 2 lots (ANSP, S. Palazzi colln).
+ **A. aequisculpta*. Syntypes (USNM), several other lots (USNM, LACM, AMS).
R. (*A.*) *grippiana*. Holotype (USNM).
A. cosmia. Holotype (USNM).
A. almo. Type (USNM).
A. hiala. Holotype and paratypes (USNM).
R. caribaea. Many lots (USNM, MCZ, ANSP).
A. purpurea. Lectotype (USNM).
R. epima. Holotype (USNM).

Remarks. The inclusion of *Alvinia* as a subgenus of *Manzonia* can be justified by the presence of a duplicated peristome (even though weakly developed in a few species) and smooth basal spirals in some species. The large number of cusps on the inner side of the lateral radular teeth in *M.* (*A.*) *aequisculpta* and *M.* (*A.*) *zetlandica* is also a character shared with *Manzonia crassa*. In *M.* (*M.*) *crispa* the protoconch is only weakly spirally ridged, unlike species of *Manzonia* (*Alvinia*), but the apex is strongly tilted, a character also seen in species of *Manzonia* (*Alvinia*) and in the subgenus *Simulamerelina*, but usually not in *Alvania*. Another character shared by *M.* (*A.*) *zetlandica* and *M.* (*M.*) *crassa* is that both these species have a very similar netted sculpture on the protoconch (Fig. 99B, G) although this is very similar to, and could be easily derived from, typical *Alvania* protoconch microsculpture.

Alvinia species are separated from those included in the typical subgenus primarily on differences in their teleoconch sculpture and periostracum. These differences are not considered to have more than subgeneric significance, given the similarity in other characters.

While it must be admitted that the evidence is not particularly strong for placing *Alvinia* with *Manzonia* rather than with *Alvania*, it seems that there are enough shell features in common to justify this. This classification certainly needs to be tested by observations on the anatomy and head-foot of species of *Alvinia*. Certainly *Manzonia* (*Simulamerelina*) is closer to *M.* (*Alvinia*) than to *Manzonia* s.s. on the available evidence and the observations on the anatomy and head-foot of species of *M.* (*Simulamerelina*) show important differences from *Alvania*.

A few species of *Alvania*, such as *A. watsoni* (Fig. 102C, D) have teleoconch and protoconch sculpture similar to those of *Manzonia* (*Alvinia*) species but differ in their more symmetrical protoconchs and simple apertures. *Manzonia* (*Alvinia*) may have diverged from *Alvania* early in the Tertiary. Some Eocene species from the Paris Basin (e.g. *A. allixi* Cossmann, 1922) somewhat resemble some Recent species of *Manzonia* (*Alvinia*) but lack a duplicated peristome. *Manzonia* s.s. possibly arose from a species of *Manzonia* similar to *M. duboisii* (Fig. 100C) which, in teleoconch characters, is intermediate between *Manzonia* s.s. and *M.* (*Alvinia*) *zetlandica*.

Subgenus *Simulamerelina* n.subgen.

Type-species: *Merelina corruga* Laseron, 1956. Recent, north-eastern Australia (Fig. 101A, B).

Diagnosis. *Shell*: ovate-conic, solid, with clathrate sculpture gemmate at points of intersection; 2-3 spiral ribs on base usually simple; axial ribs orthocline to slightly prosocline. Aperture subcircular, with duplicated peristome, outer lip opisthocline, with moderate to strong varix (Fig. 101A, D). Protoconch of about 1½ whorls, with few, strong, smooth spiral keels, the interstices studded with minute granules (Fig. 101B, C). Periostracum very thin.

Head-foot: unpigmented, cephalic tentacles long, strap-like, snout moderately long, bilobed. No pallial or metapodial tentacles. Foot long, narrow, with large, triangular anterior pedal gland; no posterior pedal gland (*Manzonia* (*Simulamerelina*) sp., Lifu Id, Loyalty Islands). Metapodial tentacle short, blunt; right and left pallial tentacles present (*M.* (*S.*) cf. *corruga*, Lifu Id, Loyalty Islands, preserved material).

Anatomy: based on *M.* (*S.*) cf. *corruga*, Luengoni, Lifu Id, Loyalty Islands (1 male, 2 females). Stomach-style sac ratio 1.9, length-width ratio 2.6. Intestine-rectum more or less straight except for a coil just in front of posterior pallial wall.

Male with penis parallel-sided over most of its length, oval in section, distal quarter tapering, with narrow terminal filament about a quarter of length of penis. Prostate gland well developed, mostly within pallial cavity. Seminal vesicle coiled at posterior end of stomach.

Female with conspicuous pouch-like vestibule (no sperm observed in this structure). Bursa copulatrix nearly as large as upper oviduct gland and lies dorsal to it. Bursal duct opens to expanded ventral channel at posterior end of pallial cavity. Seminal receptacle a narrow pouch immediately behind bursa and in front of upper oviduct gland. Upper oviduct gland apparently not coiled: a simple, glandular lobe.

Operculum: as for genus (Fig. 101F).

Radula: as for genus $\dfrac{2-4+1+2-4}{1 \qquad 1}$, U-shaped ventral extension poorly developed. Lateral teeth $5-6+1+6-7$ (Fig. 101E).

Development: assumed to be direct in all species.

Distribution. Tropical Indo-West Pacific: *M. corruga*; *Rissoa* (*Alvania*) *mauritiana* Martens, 1880; *Merelina* (*Merelina*) *longinqua* Rehder, 1980; *Merelina* (*Mereliniopsis*) *crassula* Rehder, 1980.

Material examined.

+**M. corruga*. Holotype, paratypes and several other lots (AMS).
R. (*A.*) *mauritiana*. Syntypes (HUM).
M. (*M.*) *longinqua*. Holotype and paratypes (USNM).
M. (*M.*) *crassula*. Holotype and paratypes (USNM).
+*Two unnamed species from Lifu Id, Loyalty Islands (AMS).

Remarks. This distinctive Indo-Pacific group of *Merelina*-like species is distinguished from *Manzonia* (*Alvinia*) by its smaller shell and smooth protoconch keels. Several species of *Alvania* and *Onoba* have a similar protoconch to species of *M.* (*Simulamerelina*) but these lack a duplicated peristome. This type of protoconch appears to be a basic one amongst direct-developing species of Rissoidae as discussed above. The new subgenus differs from *Manzonia* s.s. in that species it contains have stronger spiral sculpture and orthocline to slightly prosocline axial ribs (not opisthocline).

The relationships of this group are not entirely clear. Until more information is available about the *Manzonia—Alvinia* group, it can be regarded as a subgenus of *Manzonia*. The close similarity of shell features to those of *M. aequisculpta* and the head-foot characters, support this course.

Genus *Frigidoalvania* Warén, 1974

Frigidoalvania Warén, 1974: 125. Type-species *Rissoa janmayeni* Friele, 1878; original designation. Arctic Seas (Figs 28; 103A-D).

Arctonia Golikov in Golikov & Skarlato, 1977: 322. Type-species *Rissoa jan-mayeni* Friele, 1878; original designation.

Diagnosis. *Shell*: small, broadly ovate to ovate-conic, non-umbilicate, with angled whorls and thick to thin brown or yellow periostracum. Aperture relatively large, with simple peristome, subangled anteriorly and posteriorly but not channelled (although very weak posterior excavation present). Outer lip opisthocline, with rather weak varix, not dentate within. Sculpture with few spiral elements predominant in most species, and axial ribs often present on spire whorls and upper body whorl (Fig. 103A). Protoconch with 1.1-1.5 whorls; microsculpture of a few spiral wrinkles, otherwise smooth (type-species) (Fig. 103D).

Head-foot: unpigmented, with long, parallel-sided cephalic tentacles, lacking pigmented eyes at their bases. Snout broad, distinctly bilobed. Metapodial tentacle broad, short, triangular. Right and left pallial tentacles present (*F. janmayeni*, *F. brychia* (Verrill), preserved material). Anterior pedal gland well developed, posterior pedal gland absent (sectioned material of *F. brychia*).

Anatomy: based on *F. janmayeni*, Spitzbergen, 180 m, (3 females, 1 male) and *F. brychia* (details of male genitalia only), off New York, 808 m (sectioned material). Ctenidial filaments about twice as long as high, bases about same width as osphradium which is a little shorter than ctenidium. Stomach-style sac ratio

3.6–3.7, length-width ratio 1.8–2. Intestine-rectum convolute in front of posterior pallial wall and immediately behind.

Male with large, parallel-sided, flattened penis, rapidly tapering distally to a point. Penial duct marginal, closed. Prostate gland well developed, about half its length within pallial wall. Seminal vesicle convolute over posterior half of inner stomach wall.

Female (Fig. 28) with well developed ventral channel (*vc*) not clearly differentiated into a vestibule. Genital opening subterminal. Bursa copulatrix (*b*) just behind posterior pallial wall, on right side of oviduct glands, small relative to upper oviduct gland (about ⅓ length of upper oviduct gland in width), bursal duct ventral, short, opening to swollen posterior end of ventral channel. Upper oviduct gland (*uog*) coiled, opens to ventral channel by way of narrow, nearly vertical duct (*d*). It is large in relation to lower oviduct gland (*log*), being a little over half the length of that gland. Sperm storage was observed at junction of upper oviduct gland and duct to ventral channel in one specimen and in bursa in two other specimens. Seminal receptacle apparently absent.

Nervous system with cerebral ganglia separated by connective nearly equal in width to ganglia and about half their length. Supraoesophageal ganglion attached by rather long connective (about twice length of ganglion) to right pleural ganglion. Suboesophageal ganglion abuts upon the left pleural ganglion.

Operculum: thin, chitinous, yellowish, with eccentric nucleus (Fig. 103B).

Radula: central teeth $\dfrac{3-5+1+3-5}{1 \qquad 1}$; lateral margins thickened, simple, at 35–40°; U-shaped extension of ventral edge weakly developed. Lateral teeth 7 − 8 + 1 + 5 − 7. Inner marginal teeth with small cusps on outer edge; outer marginal teeth lacking cusps on outer edge, inner sides not visible in available mounts (Fig. 103C).

Development: assumed to be direct.

Distribution. North Atlantic-Arctic: *R. janmayeni*; *Cingula brychia* Verrill, 1884, = *Rissoa americana* Friele, 1886; *Alvania cruenta* Odhner, 1915.

Material examined.

+**R. janmayeni*. 1 lot (AMS).

**C. brychia*. 1 lot (AMS), several lots and holotype (USNM).

R. americana. A few lots (USNM, MCZ).

A. cruenta. Two lots (MCZ).

Remarks. The rather thick periostracum and heavy, widely spaced sculptural elements are the only distinctive shell features of this small group, which is here regarded as generically separable from *Alvania*. The microsculpture of the protoconch is known for only the type-species and is dissimilar to that of species of *Alvania*. The animals of the type-species and of *F. brychia* are unlike those of *Alvania* in apparently lacking functional eyes and a multi-digitate metapodial tentacle. Other anatomical features are like those of *Alvania* except that the female has the opening to the upper oviduct gland at the anterior end of the gland, although dorsally placed, and the osphradium is relatively narrower, being about equal in width to the bases of the gill filaments.

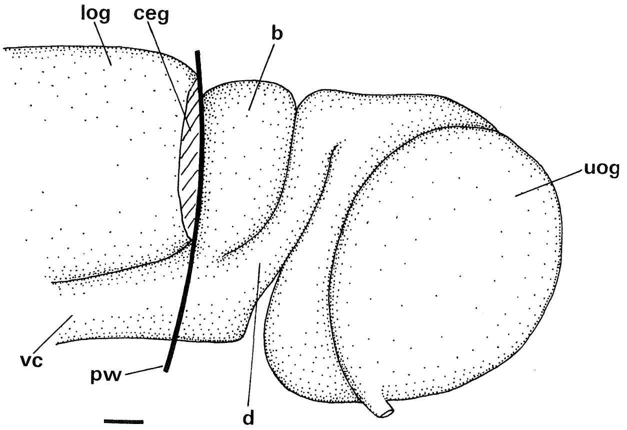

Fig. 28. A portion of the female genitalia of *Frigidoalvania janmayeni* (Friele) showing the bursa copulatrix and upper oviduct gland. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *ceg*-cut end of lower oviduct gland; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Warén (1974) included *Rissoa pelagica* Stimpson, 1851 (Fig. l03E–G) in *Frigidoalvania* but the protoconch and teleoconch characters of that species are closer to those of *Onoba*. Warén (*in lit*., 1983) has indicated that, after the examination of more material, *C. brychia* and *R. americana* appear to be the same species.

Genus *Parashiela* Laseron, 1956

Parashiela Laseron, 1956: 439. Type-species *Parashiela ambulata* Laseron, 1956; original designation. Recent, Great Barrier Reef, Australia (Figs 29; 104).

Diagnosis. *Shell*: minute, ovate-conic, non-umbilicate, with strong axial ribs which extend over base. Surface of shell with fine spiral microsculpture densely and minutely granulated (Fig. 104C). One to three strong, spiral ribs on body whorl, a single rib on spire whorls. Aperture with double peristome, almost circular, lacking anterior or posterior angulations or channels, outer lip orthocline, with varix (Fig. 104A). Protoconch smooth or spirally ridged (Fig. 104D, E).

Head-foot: cephalic tentacles rather short, parallel-sided, edged with stationary cilia, mobile cilia beneath. Eyes large, in swellings at bases of cephalic tentacles. Snout short, bilobed, longitudinally grooved dorsally. Foot elongate, narrow in anterior ¼, anterior end narrow, rounded, with very small propodial fold dorsally and long, distinct anterior mucous gland. No posterior mucous gland. A short posterior pallial tentacle present and a short, narrow metapodial tentacle arising from foot a little behind opercular lobe. Unpigmented except for a few dense-white spots (*P. ambulata*, Lizard Island, Queensland, Australia) (Fig. 29).

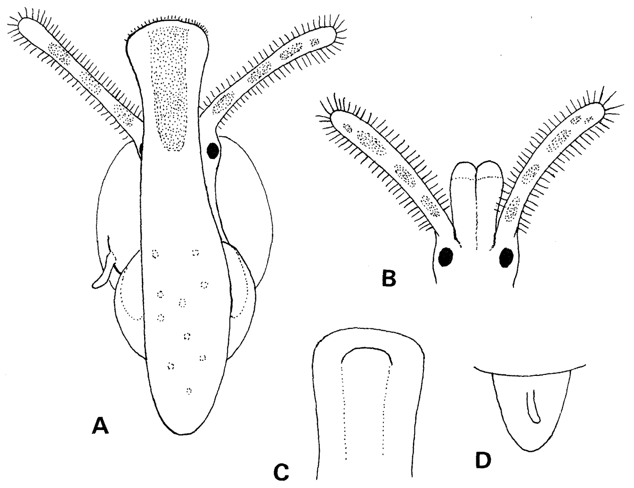

Fig. 29. Head-foot of *Parashiela ambulata* Laseron, Lizard Island, Queensland, Australia: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of anterior foot; **D**, dorsal view of posterior foot showing metapodial tentacle.

Anatomy: based on *P. ambulata*, reef near Basilisk Passage, Port Moresby, Papua-New Guinea (2 males), Moore Reef, near Cairns, Queensland (1 male). Ctenidium with finger-shaped gill filaments, shorter anteriorly than posteriorly; osphradium a little more than twice width of ctenidial filament bases and slightly shorter than ctenidium. Stomach with short style sac (stomach-style sac ratio 3.3), length-width ratio 1.8. Intestine-rectum folded in front and behind posterior pallial wall.

Male with slender, tapering penis, narrowly oval in section with long terminal filament nearly a third as long as remainder of penis. Penial duct marginal proximally, central distally. Prostate gland not clearly differentiated; a white structure observed at posterior end of pallial cavity may be a prostate gland but is more likely a modified area of hypobranchial gland. Seminal vesicle very large, a massive S-shaped coil at and behind posterior end of stomach and about equal in length to stomach.

Female and nervous system not examined.

Operculum: simple, with eccentric nucleus (Fig. 104B).

Radula: central teeth $\frac{4+1+4}{1\quad 1}$, with well developed but simple lateral thickenings at c. 50°; U-shaped ventral extension well developed. Lateral teeth 5 – 6 + 1 + 12 – 13. Marginal teeth with cusps on distal ⅓ of outer edge, outer marginal teeth lacking cusps on outer edge. All cusps relatively long and sharp (Fig. 104F, G).

Egg Capsules: unknown.

Development: the protoconch of *P. ambulata* is smooth and its morphology suggests a planktotrophic larval stage but an undescribed species from the Indian Ocean has a paucispiral protoconch with spiral sculpture and presumably undergoes direct development.

Distribution. Tropical Indo-Pacific: *P. ambulata*; *P. beetsi* Ladd, 1966; *Rissoa invisibilis* Hedley, 1899.

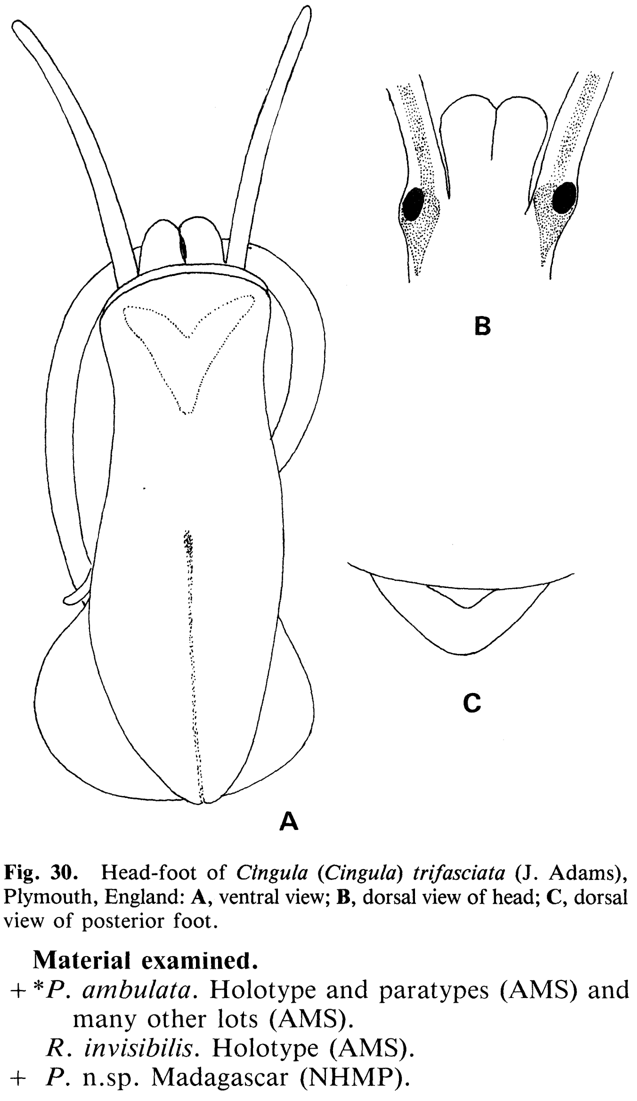

Fig. 30. Head-foot of *Cingula* (*Cingula*) *trifasciata* (J. Adams), Plymouth, England: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of posterior foot.

Material examined.

+ **P. ambulata*. Holotype and paratypes (AMS) and many other lots (AMS).
R. invisibilis. Holotype (AMS).
+ *P.* n.sp. Madagascar (NHMP).

Remarks. It is difficult to determine the relationships of this genus in the absence of information concerning the female genitalia.

The type-species has a generalised 'rissoid' radula and the shell is strongly axially sculptured but it does not appear to be closely related to *Alvania*. Species of *Parashiela* differ from those of *Alvania* notably in their duplicated peristome, in the lack of protoconch microsculpture in species with assumed planktotrophic larval stage and in their simple teleoconch macrosculpture. They are also much smaller than most species of *Alvania* and, at least the type-species, differs in having only single pallial and metapodial tentacles and no posterior pedal mucous gland.

Genus *Cingula* Fleming, 1818

Cingula Fleming, 1818: 313. Type-species '*Turbo cingellus*', = *Turbo cingillus* Montagu, 1803 (see van Aartsen & Verduin, 1978: 28), = *Turbo trifasciatus* J. Adams, 1800; subsequent designation Gray, 1847b: 152. Recent, western Europe (Figs 26C, D; 30; 31; 105).

Sabanaea Leach in Gray, 1847a: 270. Type-species *Turbo cingillus* Montagu, 1803, = *Turbo trifasciatus* J. Adams, 1800; subsequent designation Verduin, 1976: 22.

Cingilla Monterosato, 1884a: 228. Type-species *Turbo trifasciatus* J. Adams, 1800; subsequent designation Crosse, 1885: 140.

Diagnosis. *Shell*: minute to small, elongate-conic to ovate-conic, non-umbilicate, with subobsolete spiral sculpture to spiral keels; axial sculpture weak riblets or growth lines. Aperture with simple peristome, angled posteriorly, outer lip with or without varix, prosocline to orthocline. Protoconch paucispiral, with spiral striae or with spiral lirae having axial micro-lamellae between.

Head-foot: right pallial tentacle present, no left pallial tentacle; metapodial tentacle short, triangular (or absent?); unpigmented. Posterior pedal gland weakly developed (in *Cingula* s.s.).

Anatomy: ctenidial filaments finger-shaped, bases narrower than osphradium, ctenidium slightly to markedly longer than osphradium. Stomach-style sac ratio 1.3–2.4, length-width ratio 1.7–2.2. Intestine-rectum more or less straight to undulating in front of posterior pallial wall, straight behind.

Male (known only for the type-species) with tapering penis (Fig. 26C, D) slightly swollen (glandular?) distally, tapering rapidly to point; circular in section in distal area, remainder elongately oval in section. Penial duct marginal over most of penis, central distally. 'Prostate' (Fig. 31A) small, thin-walled, containing narrow, muscular papilla (*pp*).

Female (Figs 31B–D; 32) with terminal to subterminal opening, inconspicuous vestibule, relatively large, tightly coiled upper oviduct gland (Figs 31C; 32B, D) two-thirds to four-fifths length of lower oviduct gland. Bursa copulatrix (*bc*) small relative to upper oviduct gland (about half the size) to about equal in size; 1–3 sperm pouches (*sp*) at posterior end of upper oviduct gland at point of junction of gland and thin-walled duct (*d*) to ventral channel.

Nervous system not investigated.

Operculum: simple, flat, thin, oval, nucleus eccentric, last whorl large.

Radula: central teeth $\frac{2-4+1+2-4}{1+1 \quad 1+1}$, with single pair of basal denticles and a pair of smaller denticles arising from thickened lateral margins; lateral margins at 30°–47°; U-shaped ventral extension poorly to moderately developed. Lateral teeth 3 – 5 + 1 + 3 – 9. Marginal teeth with cusps subequal, inner marginal teeth with cusps on outer ⅓ of teeth, outer marginal teeth with cusps on inner distal ¼.

Egg capsules: lens-shaped.

Development: probably direct in all species.

Distribution. Western Europe, Mediterranean Sea, islands of the eastern Atlantic, north-west Africa, South Africa.

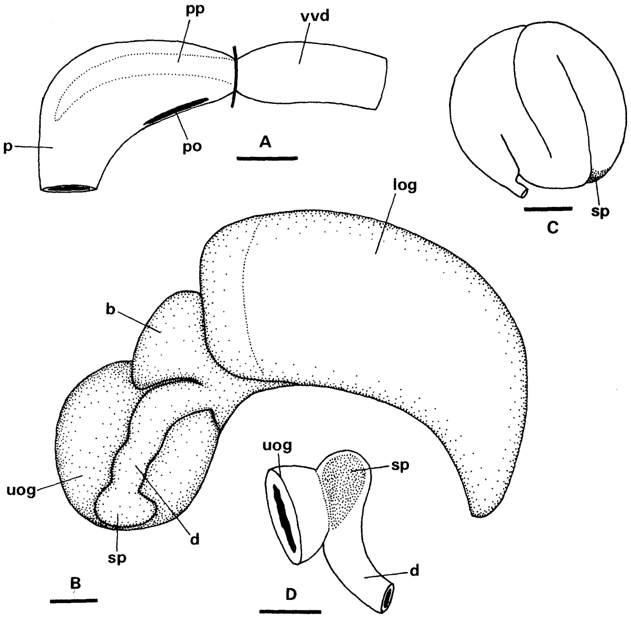

Fig. 31. Male and female genitalia of *Cingula* (*Cingula*) *trifasciata* (J. Adams): **A**, prostate, left side, papilla viewed as though walls of prostate were partly transparent; **B**, female genitalia from right side; **C**, upper oviduct gland, left side; **D**, sperm pouch dissected away from upper oviduct gland. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *log*-lower oviduct gland; *p*-prostate gland; *po*-pallial opening of prostate gland; *pp*-internal papilla; *sp*-sperm pouch; *uog*-upper oviduct gland; vvd-visceral vas deferens. **Scale:** 0.1 mm.

Remarks. The type-species of *Cingula* is unique in having a thin-walled 'prostate' with an internal muscular papilla (Fig. 31A). The female reproductive system bears a close similarity to that of *Alvania*, particularly in the coiled upper oviduct gland and the posterior sperm pouches at the junction of this gland and the duct leading to the ventral channel.

A group of species with heavy spiral cords, which is here considered to be a subgenus of *Cingula*, is known anatomically from only two species. They have a similar female reproductive system to *Cingula trifasciata* but, unfortunately, of the several specimens available for dissection, none were males. It was thus not possible to determine whether or not a papilla is present in the prostate.

Cingula differs from *Onoba* in the details of the female reproductive system, *Onoba* having a seminal receptacle and a short anterior connection of the upper oviduct gland with the ventral channel. *Onoba* species also have a glandular prostate lacking a papilla and the radula never has a second pair of denticles arising from the lateral margins of the central teeth.

Cingula trifasciata differs from species of *Alvania* in the nature of the prostate, the lack of a multidigitate metapodial tentacle and in the predominantly spiral teleoconch sculpture.

Species of *Setia* are sometimes included in *Cingula*. These species are much smaller, thinner shelled and, as far as can be judged from the available material, differ anatomically.

The genera *Hyala* and *Ceratia* are sometimes combined with *Cingula* (e.g. Fretter & Graham, 1978), but I have shown elsewhere (Ponder, 1984) that they can be included in the Iravadiidae.

Key to Subgenera of *Cingula* (based on shell characters)

— Protoconch without distinct sculpture .... *Cingula* s.s.

— Protoconch with spiral lirae with axial lamellae between .... *Lirocingula* n.subgen.

Subgenus *Cingula* s.s.

Diagnosis. *Shell*: elongate-conic to ovate-conic, non-umbilicate, sculpture of very weak spiral cords and weak, close axial growth lines. Aperture relatively small, angled and weakly channelled posteriorly, rounded anteriorly, peristome simple, outer lip weakly prosocline, without varix (Fig. 105A). Protoconch simple, dome-shaped, of about 1½ whorls, smooth except for a few very weak spiral striae (Fig. 105B, C).

Head-foot: unpigmented; cephalic tentacles long, very slightly tapering, bearing short, stationary and active cilia. Snout rather short, distinctly bilobed. Foot simple, rather short, broad, sole with inconspicuous posterior mucous pore and conspicuous anterior mucous gland. Posterior (right) pallial tentacle short, no anterior pallial tentacle; posterior edge of opercular lobe projects to form a short, triangular metapodial tentacle (personal observation, Plymouth, England) (Fig. 30).

Anatomy: based on *C. trifasciata*, Plymouth, England (3 females, 2 males). As for genus. Osphradium about 0.6 length of ctenidium. Stomach-style sac ratio 2.3-2.4, length-width ratio 1.9-2.2. Intestine-rectum almost straight to undulating.

Penis (Fig. 26C, D) as for genus; prostate (Fig. 31A; *p*) with slit-like ventral opening (*po*) in posterior section and internal papilla (*pp*). Seminal vesicle coiled over posterior end of inner side of stomach.

Female (Fig. 31B-D) as for genus; with single sperm pouch (Fig. 31D; *sp*). Upper oviduct gland (*uog*) coiled (Fig. 31C).

Operculum: as for genus (Fig. 105D, E).

Radula: as for genus; central teeth $\frac{2-3+1+2-3}{1+1 \quad 1+1}$, U-shaped ventral extension moderately developed, lateral margins at 30°. Lateral teeth 3 – 4 + 1 + 3 – 7 (Fig. 105F, G).

Egg capsules and *development*: capsules lens-shaped; development direct (Lebour, 1934; Fretter & Graham, 1962, 1978).

Distribution. Western Europe: *T. trifasciatus*.

Material examined.

+ **T. trifasciatus*. Many lots (BMNH, AMS).

Remarks. The type-species of this apparently monotypic subgenus is distinguished by the rather heavy shell with weak, spiral sculpture and weakly prosocline outer lip. Superficially it resembles some species of *Alvania* (subgenus *Crisilla*) and *Onoba*, the distinguishing characters being outlined in the 'remarks' section under the genus.

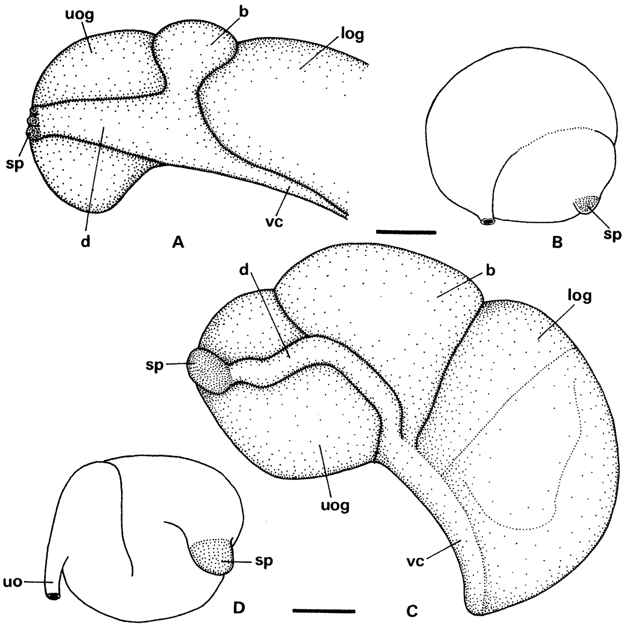

Fig. 32. Female genitalia of *Cingula* (*Lirocingula*) species. **A-B**, *C.(L.) conspecta* (Smith): **A**, right side, showing the upper oviduct gland, the bursa copulatrix and a portion of the lower oviduct gland; **B**, upper oviduct gland from the left side. **C-D**, *C.(L.) winslowae* (Bartsch): **C**, right side; **D**, upper oviduct gland from the left side. *b*-bursa copulatrix; *d*-thin-walled duct to upper oviduct gland; *log*-lower oviduct gland; *sp*-sperm pouch; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Subgenus *Lirocingula* n.subgen.

Type-species: *Alvania winslowae* Bartsch, 1928, = *Alvania almo* Bartsch, 1915, not Bartsch, 1911. Recent, South Africa (Fig. 32A, B; 107G).

Diagnosis. *Shell*: ovate-conic, non-umbilicate, with strong to sub-obsolete spiral sculpture, often with spiral keels. Aperture with simple peristome, angled but not channelled posteriorly, rounded anteriorly, with prosocline or orthocline outer lip; with or without a varix (Figs 106C, D, F; 107A, C, E, G; 108A). Protoconch sculptured with smooth spiral lirae and close, irregular, axial, lamellate threads between, or zig-zag, spiral lirae (Figs 106E, G; 107B, D, F; 108B).

Head-foot: unpigmented; snout bilobed, tentacles strap-like, longer than snout. No obvious metapodial tentacle; right pallial tentacle present (*C.* (*L.*) *conspecta* and *C.* (*L.*) *winslowae*, preserved material).

Anatomy: based on *C.* (*T.*) *winslowae* (2 females) and *C.* (*L.*) *conspecta* (3 females), Millers Point, False Bay, South Africa; as for genus. Osphradium nearly as long as ctenidium. Stomach-style sac ratio 1.3-1.5, length-width ratio 1.7-1.8. Intestine-rectum forms S-shaped curve when viewed dorsally, but not convoluted.

Male genitalia not known.

Female (Fig. 32A-D) with 1-3 (3 in *C.* (*L.*) *conspecta*) sperm pouches (*sp*) at junction of broad, thin-walled duct (*d*) from broad, posterior expansion of ventral channel to posterior end of upper oviduct. Bursa copulatrix (*b*) about half size of upper oviduct gland (*uog*) in *C.* (*L.*) *conspecta*, about equal in size in *C.* (*L.*) *winslowae*. Upper oviduct gland coiled (Fig. 32B, D).

Operculum: as for genus (Fig. 108D).

Radula: as for genus; central teeth $\dfrac{2-4+1+2-4}{1+1 \quad 1+1}$, (marginal denticles developed only intermittently in 1 specimen of *C.* (*L.*) *farquhari*), U-shaped ventral extension moderately to poorly developed; lateral margins at 35–47°. Lateral teeth $4-6+1+5-9$ (Fig. 108C).

Distribution. South Africa: *A. winslowae* (Fig. 107G); *Rissoa farquhari* Smith, 1910 (Fig. 108A–D); *Alvania outis* Tomlin, 1931, = *Alvania nemo* Bartsch, 1915, not Bartsch, 1911; *Rissoa conspecta* Smith, 1904, = *Microsetia gisna* Bartsch, 1915, = *Rissoina multilineata* Turton, 1932, = *Microsetia cingulata* Turton, 1932; *Alvania whitechurchi* Turton, 1932.

St. Helena, Eastern Atlantic: *Rissoa varicifera* (Fig. 107C, D);*Rissoa aequa* (Fig. 107A, B); *Rissoa vaga*; ?*Rissoa agapeta*; ?*Rissoa perfecta* (Fig. 106C–E); *Rissoa simulans*; *Rissoa compsa*; *Rissoa wallichi* (Fig. 107F, G) and *Barleeia wallichi* (= *Cingula* (*Lirocingula*) *helenae nom. nov.*) all Smith, 1890.

Eocene of Nantes Basin, France: an undescribed species (Fig. 107E, F).

Material examined.

+*A. winslowae*. Holotype (USNM), Turton Colln (OM), several lots (AMS).
+*R. farquhari*. Syntypes (BMNH) and several other lots (AMS).
A. outis. Holotype (USNM).
+*R. conspecta*. Syntypes (BMNH) and several other lots (AMS).
M. gisna. Holotype (USNM) and Turton Colln (OM).
R. multilineata. Holotype (OM).
M. cingulata. Holotype (OM).
A. whitechurchi. Holotype (OM).
\+ *R. varicifera*. One lot (RSM).
\+ *R. aequa*. Syntypes (BMNH, ANSP, USNM).
R. vaga. Holotype (BMNH).
R. agapeta. Syntypes and one other lot (BMNH), syntypes (ANSP, USNM).
\+ *R. perfecta*. 1 lot (RSM), syntypes (USNM).
R. simulans. Syntypes (BMNH).
R. compsa. 2 lots (IRSB), syntypes (ANSP, USNM).
\+ *R. wallichi*. Syntypes (BMNH).
B. wallichi. Syntypes (BMNH, USNM).
\+ n.sp. Nantes Basin, one lot ex Le Renard (AMS).

Remarks. The species included in this subgenus range from heavily spirally lirate, as in the type-species, to almost smooth, as in *Rissoa conspecta* and *Barleeia wallichi*. The last species requires a replacement name as it is a secondary homonym of *Rissoa wallichi* and the name *Cingula* (*Lirocingula*) *helenae nom. nov.* is provided for it.

The species in this subgenus closely resemble *Tropidorissoia taphrodes* Tomlin & Shackleford, 1915, the type-species of *Tropidorissoia* Tomlin & Shackleford, 1915, and were tentatively assigned to this genus until some preserved material was made available by S. Gofas and P. Bouchet just before the manuscript went to press. *Tropidorissoia taphrodes* (Fig. 106A, B) proves to be a barleeid and the microsculpture on its protoconch is typical of that family (Ponder, 1983a) in consisting of deep pits arranged in spiral rows (Fig. 106B). The protoconch is unusual in possessing two whorls (instead of 1½) and in being spirally lirate. The radula is like that of *Barleeia* but the operculum differs in being yellow, not red.

Most of the species in *Cingula* (*Lirocingula*) have a characteristic protoconch microsculpture of spiral cords with axial microlamellae between which distinguishes them from other rissoids, including *Cingula* s.s.

Rissoa perfecta Smith from St. Helena resembles the type-species of *Lirocingula* in shell shape and sculpture but the protoconch is strongly shouldered and sculptured with zig-zag spiral lirae (Fig. 106E). This species has an orthocline outer lip and a strong apertural varix (Fig. 106D). *Rissoa agapeta*, which shows a similar protoconch sculpture, has weaker spiral cords and a prosocline outer lip that lacks a varix. These species are only tentatively included in *Lirocingula*.The non-varicose species included in the subgenus *Lirocingula* appear similar in teleoconch characters to species of *Cingula* s.s. and will probably prove to be closely related. The female anatomy of *C.* (*L.*) *conspecta* and *C.* (*L.*) *winslowae* also suggests this. There is, too, a close resemblance to some species of *Onoba*, *Lironoba* and even *Barleeia* but these groups can all be distinguished on protoconch microsculpture.

If the relationships of the species included here in *Cingula* (*Lirocingula*) are correctly assessed, this subgenus has undergone a remarkable radiation at St. Helena and, to a lesser extent, in South Africa. This may, in part, be due to their direct mode of development.

Genus **Onoba** H. & A. Adams, 1852

Onoba H. & A. Adams, 1852: 358, new name for *Turbonilla* Leach in Gray, 1847a: 270, not Risso, 1826. Type-species *Onoba striata*, = *Turbo striatus* J. Adams, 1797, not Da Costa, 1778, = *Turbo semicostatus*[†] Montagu, 1803; subsequent designation, Gray, 1847b: 152. Recent, western Europe and the Mediterranean Sea (Figs 33; 34A–C; 109A,B).

Diagnosis. *Shell*: minute to small, ovate-conic to elongate-ovate, non-umbilicate to narrowly umbilicate, smooth or with weak to strong spiral sculpture, sometimes with a few spiral keels. Axial sculpture usually rather weak to very weak; sometimes axial ribs present but do not extend over base; sculpture rarely clathrate. Aperture with simple peristome, oval, weakly

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[†] Fretter & Graham (1978) have stated that *T. semicostatus* "was probably based on immature shells and not this species" but give no other information. Warén in Fretter & Graham (1978) has suggested that *Turbo shepeianus* (Jacobs ms) Kanmacher in G. Adams, 1798 may be an appropriate replacement name.

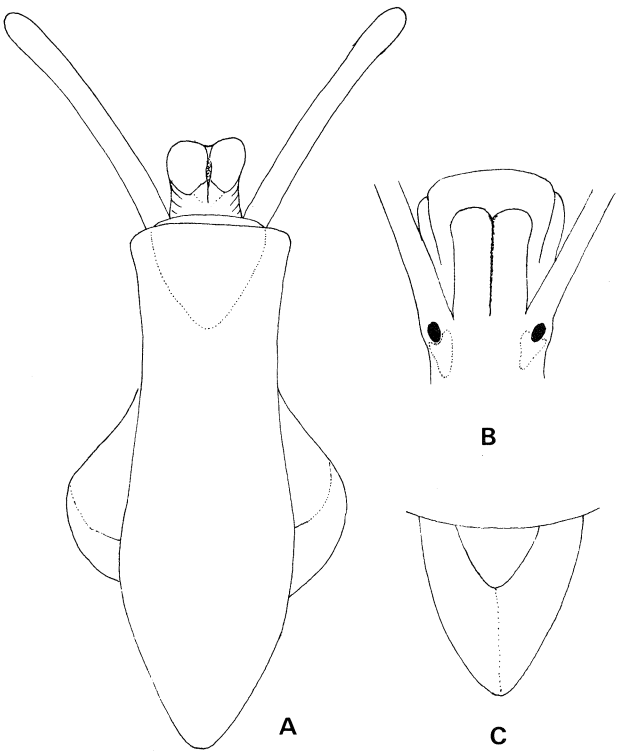

Fig. 33. Head-foot of *Onoba (Onoba) 'semicostata* (Montagu)' (? = *aculea* (Gould), Plymouth, England: **A**, ventral view; **B**, dorsal view of head and anterior foot; **C**, dorsal view of posterior foot and metapodial tentacle.

angled and channelled posteriorly, simple and rounded anteriorly; outer lip opisthocline, varix weak to heavy. Protoconch dome-shaped, sometimes with 1 or more spiral keels; smooth (*Ovirissoa*) or with microsculpture of granules, anastomosing or spirally aligned raised threads or, sometimes, wavy, spirally arranged rows of granules. Periostracum very thin to well developed.

Head-foot: cephalic tentacles strap-like, more or less parallel-sided, sometimes slightly expanded distally, eyes in small swelling at their outer bases. Snout rather long, bilobed. Foot narrow in front, broader in posterior ⅓, simple behind, with a triangular anterior mucous gland, no posterior mucous gland. A small, short, triangular metapodial tentacle sometimes present. Usually an anterior and sometimes a posterior pallial tentacle present.

Anatomy: ctenidium with finger-shaped to short, narrowly triangular filaments, osphradium wider than filament bases and nearly as long as ctenidium. Stomach-style sac ratio 2.3–4, length-width ratio 1.4–2.2. Intestine-rectum with a few folds just in front or behind posterior pallial wall.

Male with long, tapering to parallel-sided penis, narrowly oval in section, with closed, marginal penial duct and simple, pointed distal end. Prostate gland well developed, usually with a portion extending into kidney. Seminal vesicle with several loops on inner, posterior stomach wall.

Female with small, inconspicuous vestibule, a well developed ventral channel not separated from lower oviduct gland within pallial cavity. Lower oviduct gland well developed, confined to pallial cavity or extends beyond it into kidney. Upper oviduct gland well developed, about equal in length to lower oviduct gland; simple or elaborately coiled; a solid glandular mass with no accessory sperm pouches or sperm-storing lobes. Bursa copulatrix smaller than upper oviduct gland, lying vertically between upper and lower oviduct glands on right side, with a smaller seminal receptacle immediately posterior to it. Ducts of both bursa and seminal receptacle open to ventral channel immediately below.

Nervous system not known.

Operculum: simple, oval, thin, smooth, nucleus eccentric, last whorl large.

Radula: central teeth $\frac{2-7+1+2-7}{1 \quad 1}$; lateral margins thickened, at 30°–50°, simple single pair of basal denticles; U-shaped basal extension moderately to strongly developed. Lateral teeth $3-9+1+3-10$. Marginal teeth with equal-sized cusps confined to distal outer ⅓–½ on inner marginal teeth and distal inner ¼ on outer marginal teeth.

Development: probably direct in all species except one.

Distribution. Polar to subtropical in both hemispheres.

Remarks. Four subgenera are somewhat tentatively recognized within *Onoba*. *Onoba*, as here defined, is a much larger genus and encompasses a greater range of shell diversity than previous interpretations have allowed. Species of *Onoba* have a generalized rissoid radula, with only a single pair of basal denticles on the central teeth and no denticles arising from the lateral margins, a simple operculum, a non-pigmented head-foot and diverse protoconch scupture. They differ from species of *Cingula*, *Alvania* and *Rissoa* in the lack of accessory basal denticles on the central teeth and in the anatomical characters outlined below.

Species from Eocene rocks in the Paris Basin show forms that could be placed in *Onoba* s.s. and *Subonoba* (here regarded as a synonym of *Onoba*). If these have been interpreted correctly, *Onoba* appears to have diversified early in the Tertiary. Subsequently a great deal of radiation has occurred at a regional level culminating in the range of shell forms seen in the north Pacific and in the southern hemisphere.

Key to Subgenera of *Onoba* (based on shell characters)

1.	Protoconch smooth, shell surface smooth and glossy	*Ovirissoa*
—	Protoconch sculptured, shell surface dull, smooth, spirally sculptured or with spiral and axial sculpture	2
2.	Protoconch with heavy spiral lirae	3
—	Protoconch with weak spiral threads, granules or irregular raised threads	*Onoba*
3.	Teleoconch with weak to moderate spiral cords and weak or absent axial ribs; protoconch with granules between spiral keels	*Subestea*
—	Teleoconch with strong axial ribs; protoconch with smooth interspaces between spiral keels	*Manawatawhia*

Subgenus *Onoba* s.s.

Subonoba Iredale, 1915: 450. Type-species *Rissoa fumata* Suter, = *Rissoia fumata* Suter, 1898; original designation. Recent, New Zealand (Figs 34D; 111A – D).

Austronoba Powell, 1927: 541. Type-species *Rissoa candidissima* Webster, = *Rissoia candidissima* Webster, 1905; original designation. Recent, New Zealand (Figs 34E; 112E – 1).

Willettia Gordon, 1939: 31. Type-species *Alvania montereyensis* Bartsch, 1911, = *Rissoa carpenteri* Weinkauff, 1885, new name for *Alvania reticulata* Carpenter, 1864, not *Turbo (= Alvania) reticulatus* 'Montagu, 1803', = J. Adams, 1797; original destination. Recent, western North America (Figs 34F; 114A-D).

Diagnosis. *Shell*; broadly ovate-conic to elongate-ovate, rather solid, non-umbilicate, usually with many well developed spiral cords and, sometimes, weak axial ribs; microsculpture of fine spiral lirae usually present. Strong spiral cords in a few species and, in some species, surface smooth. Aperture subcircular, subangled and weakly channelled posteriorly, varix on outer lip strong to moderate (Figs 103E; 109A, C; 110A, D, F; 111A, E; 112A, G; 113A, C, E; 114A). Protoconch dome-shaped of about 1½ whorls in nearly all species, rarely up to 2¼ whorls (as in *O. 'semicostata'*); sculptured variously, for example, with exceedingly weak to moderately strong spiral lines with either parallel to oblique wrinkles or granules between, as in *O. aculea* (Gould) (Fig. 109E, F) and *O. moreleti* Dautzenberg (Fig. 113D) and in Fretter & Graham's (1978) figure of *O. 'semicostata';* with irregular, raised, wavy threads, as in *O. foveauxiana* (Suter) (Fig. 110E); with scattered granules, as in *O. fumata* (Fig. 111B, C), *O. kermadecensis* (Powell) (Fig. 112B) and several other southern species, as well as *O.* n.sp. (Fig. 111F) from the Eocene of France (Figs 109E, F; 110B, E, G; 111B, C, F; 112B, E, F; 113B, D, F; 114C; see also Thiriot-Quiévreux & Babio, 1975; Fretter & Graham, 1978).

Head-foot: cephalic tentacles rather long, parallel-sided or slightly expanded distally, with minute cilia. Snout moderately long, distinctly bilobed both ventrally and dorsally. Foot of moderate length, rather broad in middle; narrow anteriorly, tapering rapidly behind; with triangular anterior pedal mucous gland. Posterior pallial tentacle small (*O. 'semicostata'*, *O. carpenteri*, *O. candidissima*), or absent (*O. fumata*, *O. foveauxiana*); anterior pallial tentacle absent, or sometimes present in *O. 'semicostata'* (Fretter & Graham, 1978) and present in *O. carpenteri*, *O. candidissima*; metapodial tentacle short, broadly triangular (*O. 'semicostata'*, *O. carpenteri*, *O. candidissima*) or absent (*O. fumata*, *O. foveauxiana*). No external pigmentation (*O. 'semicostata'*, Plymouth England and *O. carpenteri*, Monterey, California, personal observation; *O. fumata* and *O. foveauxiana* from Ponder, 1967) (Fig. 33).

Anatomy: based on *O. 'semicostata'*, Plymouth England (several females, 2 males and sectioned material); *O. fumata*, Lyall Bay, Wellington, New Zealand (3 females and 1 male); *O. candidissima*, Leigh, New Zealand (2 females, 1 male); *O. sorenseni* (Powell) Perseverence Harbour, Campbell Island, New Zealand (3 females, 1 male); *O. carpenteri*, Monterey, California (2 females, 1 male); *O. grisea* (Martens, 1885), Signy Island, South Orkney Island (2 females, 2 males); *O. cf. kermadecensis*, Lord Howe Island (3 females, 1 male). As for genus. Ctenidium with relatively long to short, stubby ctenidial filaments, the latter condition in *O. 'semicostata'*, *O. candidissima*, *O. carpenteri*, *O. grisea* and *O. fumata* where filaments are less than twice as long as high. Stomach-style sac ratio 2. 3-3.4, length-width ratio 1.4-2.2. Intestine-rectum with 0-3 folds just in front of, or behind, posterior pallial wall.

Male with evenly tapering penis (Fig. 34C), except *O. cf. kermadecensis* which has a terminal filament about equal to ⅕ length of rest of penis. Prostate gland ½-⅓ embedded in kidney wall (*O. candidissima*, *O. carpenteri*, *O. 'semicostata'*) or about ⅕ embedded (*O. cf. kermadecensis*).

Female (Fig. 34A, B, D-F) with lower oviduct gland (*log*) extending back into kidney wall as distinct albumen gland (in *O. 'semicostata'*) or albumen gland less developed (all other species examined). Upper oviduct gland (*uog*) about equal in size to lower oviduct gland except in *O. 'semicostata')* and *O. grisea* (about ⅓ size). Seminal receptacle not observed (possibly because the specimens dissected did not contain sperm) in *O. cf. kermadecensis* and *O. sorenseni*. Seminal receptacle (*sr*) lies immediately behind bursa in all other species, although in *O. carpenteri* (Fig. 34F) it extends above,

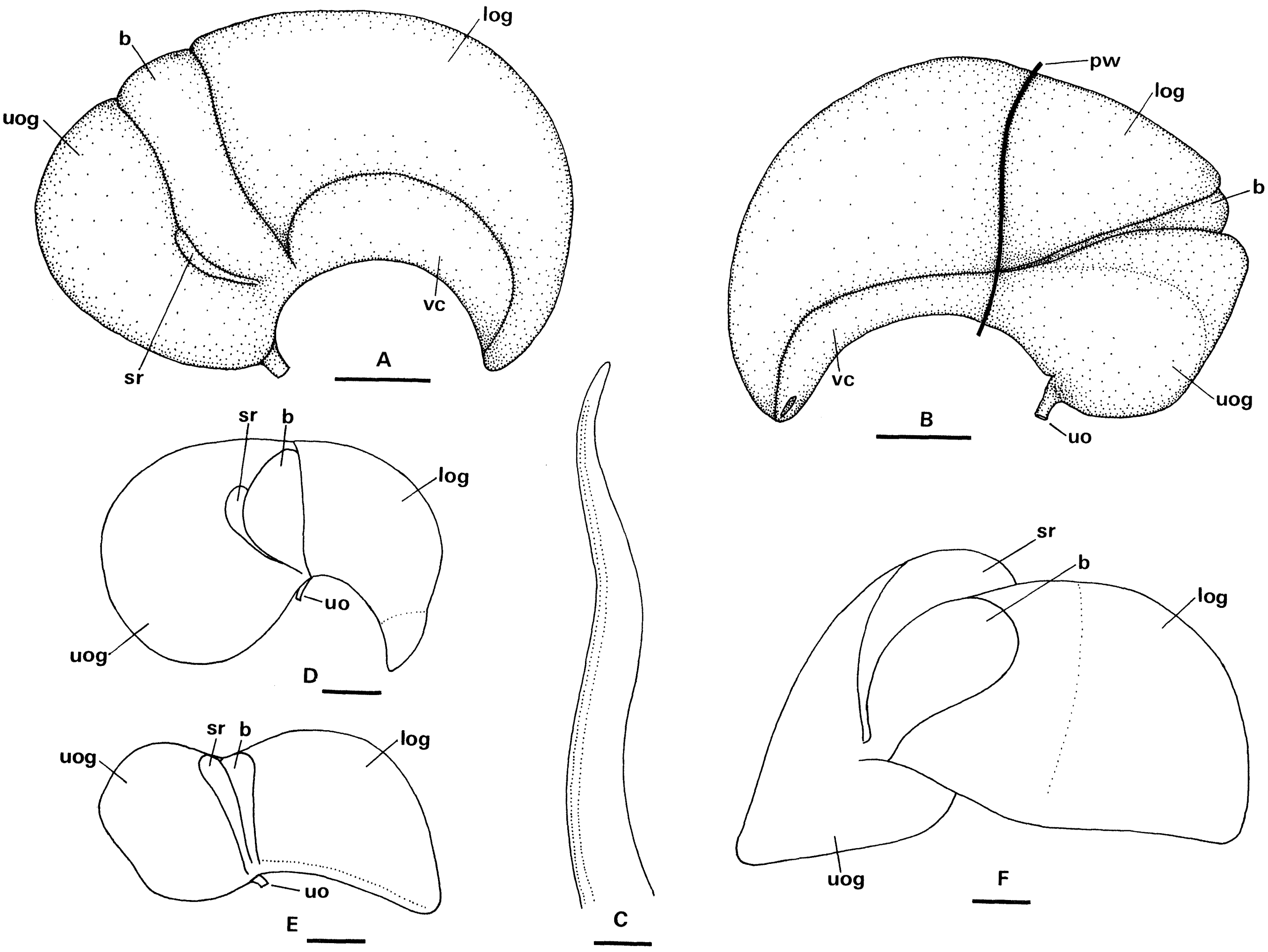

Fig. 34. Male and female genitalia of *Onoba* (*Onoba*) species. **A-C**, *O.(O.)* '*semicostata* (Montagu)' (? = *aculea* (Gould)): **A-B**, female genitalia; **A**, right side; **B**, left side; **C**, penis; **D**, *O.(O.) fumata* (Suter), female genitalia, right side; **E**, *O.(O.) candidissima* (Webster), female genitalia, right side; **F**, *O.(O.) carpenteri* (Weinkauff), female genitalia, right side. *b*-bursa copulatrix; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

and overlies, bursa. Bursa copulatrix is smaller than upper oviduct gland. It is a simple, vertically aligned sac in all species. Upper oviduct gland (*uog*) massive, simple with no sign of coiling except in *O. sorenseni* in which it is an open, S-shaped coil.

Operculum: as for genus (Figs 103G; 109G; 112C, H; 113G; 114B).

Radula: as for genus (Figs 103F, 109B, D; 110C, 111D; 112D, I; 113H, I; 114D).

Egg capsules and *development*: egg-shaped to hemispherical, without mucous plug. Development direct (*O. aculea* as *O.* '*semicostata*'); Lebour, 1934; Rasmussen, 1951, 1973; Fretter & Graham, 1978). *Onoba* '*semicostata*' may have planktotrophic larvae as judged from Fretter & Graham's (1978) figure of the protoconch of that species which clearly shows a protoconch 1 and is of about 2¼ whorls. No other species of *Onoba* is known to have a similar protoconch.

Distribution. Northern Atlantic: *T. semicostatus*; *Rissoa striata* var. *lirata* Watson, 1873; *Cingula aculeus* Gould, 1841 (Fig. 109C-G), = *Rissoa saxatilis* Möller, 1842; *Rissoa mighelsi* Stimpson, 1851; *Alvania leptalea*Verrill, 1884; *Rissoa pelagica* Stimpson, 1851 (Fig. 103E—G); *Onoba moreleti* Dautzenberg, 1889 (Fig. 113C, D).

North-eastern Pacific: *Onoba cerinella* Dall, 1886 (+*) (Fig. 113E-I), = *Onoba asser* Bartsch, 1910, ? = *Cingula forresterensis* Willett, 1934; *A. carpenteri* (+*) = *Alvania montereyensis* Bartsch, 1911, = *A. kyskaensis* Bartsch, 1917, = *A. sanjuanensis* Bartsch, 1921, = *A.* (*Willetia*) *keenae* Gordon, 1939; *Alvania dinora* Bartsch, 1917 (+*) (Fig. 113A, B),? = *Alvania dalli* Bartsch, 1927, = *Cingula eyerdami* Willett, 1934; *Cingula aleutica* Dall, 1886; *Alvania bakeri* Bartsch, 1910 (+*), ? = *Anabathron muriei* Bartsch & Rehder, 1937; *Alvania aurivillii* Dall, 1886 (+*); *Nodulus palmeri* Dall, 1919; *Nodulus kyskensis* Bartsch, 1911; *Alvania castanella* Dall, 1886; *Alvania castanea* var. *alaskana* Dall, 1886 (+*) (Fig. 110A-C).

Temperate Australia: *Rissoa multilirata* May, 1915.

Kermadec Islands: *Austronoba kermadecensis* Powell, 1927 (Fig. 112A-D).

New Zealand and New Zealand sub-Antarctic Islands: 19 species listed by Powell, 1979.

Antarctic-sub-Antarctic (excluding the New Zealand region): reviewed by Ponder (1983b), 19 species recognized.

Eocene, France: *Onoba* sp. (Fig. 110F, G); *Onoba* n.sp. (Fig. 111E, F).

Miocene, Italy: *Onoba miostriata* Sacco, 1895.

Material examined.

+*O. *'semicostata'*. Several lots (BMNH, AMS etc).
R. striata var lirata. 1 lot (ANSP).
+**C. aculeus*. A few lots (BMNH, AMS, MCZ).
+ *O. moreleti*. Possible paratypes (IRSB).

Other north-western Atlantic species: material and types (MCZ, USNM)

Alaskan (i.e. N.E Pacific) species listed above (AMS, ex LACM) and types examined for all taxa (USNM, LACM). Protoconch, radula and operculum examined for several of these species as indicated above.

New Zealand species: several have been examined in the course of this work, in particular *R. fumata* (+*), *R. candidissima* (+*), *Rissoa foveauxiana* Suter, 1898 (+) and *Rissoa insculpta* Murdoch, 1905 (+*) (NMNZ, AMS), and *Subonoba sorenseni* Powell, 1955 (AMS).

Antarctic and sub-Antarctic species: type material of the majority of species has been examined and also the radulae of several of them (see Ponder, 1983b).

+**A. kermadecensis*. Several lots (AMS).
+**R. multilirata*. Holotype (TM) and other material (AMS, NMV).
O. miostriata. Holotype (TGM).

Remarks. *Onoba* has undergone major radiations in the Antarctic-sub-Antarctic and in the sub-Arctic North Pacific. Species here included in the genus show considerable sculptural diversity but it is difficult to recognize finer generic boundaries that may be biologically valid. Although most of the species included in *Onoba* are known only from their shells, the anatomical and radular information obtained encompasses a wide range of shell-forms and is rather uniform. For these reasons a simple, broadly encompassing generic concept has been adopted.

The New Zealand-Antarctic group of species included in *Subonoba* does not appear to be separable from *Onoba* s.s. The granules on the protoconch of *Rissoia fumata* (Fig. 111B, C), the type-species of *Subonoba*, is a sculptural pattern shared by several closely related southern hemisphere species and is also found in an undescribed species of *Onoba* from the Eocene of the Paris Basin (Fig. 111F) whereas another unnamed species (Fig. 110F, G) has irregular lines bordering shallow pits. *Onoba foveauxiana* (Fig. 110D, E), a New Zealand species very like *O. fumata*, has a protoconch microsculpture (Fig. 110E) of irregular, roughly spirally oriented, short, often wavy lirae and granules like that of *O. alaskana* from Alaska (Fig. 110B). Most species of *Onoba*, unlike *O. 'semicostata'*, lack axial ribbing on the teleoconch but *O. kermadecensis* from the Kermadec Islands and *O. candidissima*, the type-species of *Austronoba*, have prominent axial ribs, and *O. kermadecensis* (Fig. 112B) has a protoconch microsculpture of granules similar to those of *O. fumata*.

I had previously assumed (Ponder, 1967) that *Subonoba* was more closely related to *Rissoina* than to *Onoba*, on the basis of the stomach morphology of *O. candidissima*, and the external appearance of the animal. Preserved specimens of *O. insculpta* and *O. fumata* were examined and found to have a short stomach containing small non-calcareous food particles. A short style sac was present but it was not established whether or not it contained a crystalline style. *Onoba 'semicostata'*, from observations on living and preserved material, has a similar stomach to that of the two New Zealand species. Re-examination of the stomach of *O. candidissima* shows that it is not significantly larger than other species of *Onoba* or other genera such as *Cingula* and *Rissoa*. The anatomical characters of the type-species of *Onoba*, *Subonoba*, *Austronoba* and *Willettia* are all very similar. For this reason, and because there do not appear to be consistent shell differences, their relationship is considered to be consubgeneric.

Shell sculpture of *Onoba lirata* from Madeira is similar to that of *O. 'semicostata'* but the spiral cords are stronger. Much stronger spiral cords are found on *Onoba aurivillii*, approaching those of species of *Lironoba*. *Onoba castanella* and *O. dinora* (Fig. 113A) have weaker spiral cords, *O. cerinella* (Fig. 113E) has fine spiral threads and *O. aleutica* is smooth. *Onoba bakeri* is sculptured with 1-2 strong spiral cords on the spire whorls. Thus the Alaskan species, which are here included in *Onoba*, show a considerable diversity in shell sculpture but are relatively uniform in radular and protoconch characters. Similar diversity in sculpture, ranging from strong spiral keels to smooth shells has also been observed in Antarctic and sub-Antarctic species (Ponder, 1983b).

There is, as remarked above, some confusion over the identity of the species described as *Turbo semicostatus*. *Onoba aculea*, and the species tentatively referred to as *O. 'semicostata'*, have a very similar teleoconch but *O. aculea* differs, according to Warén (1974), in having a larger protoconch of 1.3 whorls, *O. semicostata* having 1.7 whorls. The protoconch figured by Fretter & Graham (1978) has about 2.25 whorls and a clearly marked protoconch 1. These authors conclude that these observations may be accounted for by possible differences in reproduction between northern and southern populations. Until careful comparisons of type specimens and large series of material are made, the problem as to what species names are appropriate for the European species of *Onoba* cannot be satisfactorily resolved. It is, for example, probable that the specimens described by Lebour (1934) as having direct development were in fact *O. aculea*, as that species apparently extends into southern England (van Aartsen *in lit.*, 1982). Warén (1974), has shown that Rasmussen's (1951) description of the development of *O. 'semicostata'* applies to *O. aculea*.

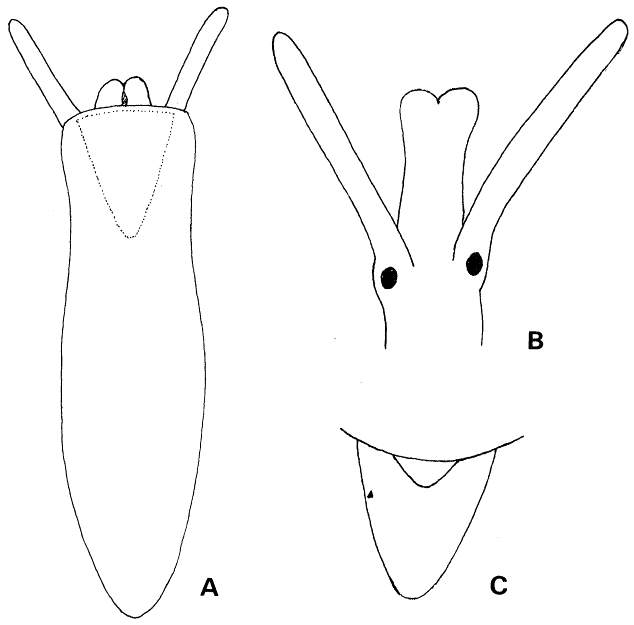

Fig. 35. Head-foot of *Onoba* (*Subestea*) *australiae* (Frauenfeld); Batemans Bay, New South Wales, Australia: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of posterior foot.

Subgenus *Subestea* Cotton, 1944

Subestea Cotton, 1944: 292. Type-species *Alvania seminodosa* May, 1915, = *Cingula australiae* Frauenfeld, 1867; original designation. Recent, S.E. Australia (Figs 35; 36; 115A–E).

Liroculma Ponder, 1967: 201. Type-species *Rissoia* (*Apicularia*) *apicilirata* Tate & May, 1900, = *Cingula australiae* Frauenfeld, 1867; original designation. Recent, S.E. Australia.

Diagnosis. *Shell*: elongate-conic to elongate-oval, rather solid, non-umbilicate, with spiral and axial sculpture varying in strength, spiral sculpture usually stronger than axial sculpture, sometimes subequal, sometimes subobsolete (Fig. 115A, F). Protoconch dome-shaped, of about 1½ whorls, sculptured with smooth spiral lirae, interspaces with granules (Fig. 115B, C, G).

Head-foot: cephalic tentacles moderately long, rather broad, with parallel sides or slightly expanded distally, somewhat triangular in section, actively ciliated ventrally, without obvious 'setae'. Snout long, slender, bilobed. Foot rather long, narrow and simple anteriorly, bluntly pointed posteriorly, with indistinct, triangular anterior mucous gland and no posterior mucous gland. Small anterior pallial tentacle and very short, broad, posterior metapodial tentacle present. (*O.* (*S.*) *australiae*, Batemans Bay, New South Wales, Australia) (Fig. 35).

Anatomy: based on *O.* (*S.*) *australiae*, Batemans Bay, New South Wales, Australia (2 females, 1 male). As for genus. Stomach-style sac ratio 3.2–3.5, length-width ratio 2. Intestine-rectum folded immediately in front of and behind posterior pallial wall.

Male with about proximal half of penis straight-sided, distal ½–⅓ tapering to point. About ⅐ of prostate gland embedded in kidney.

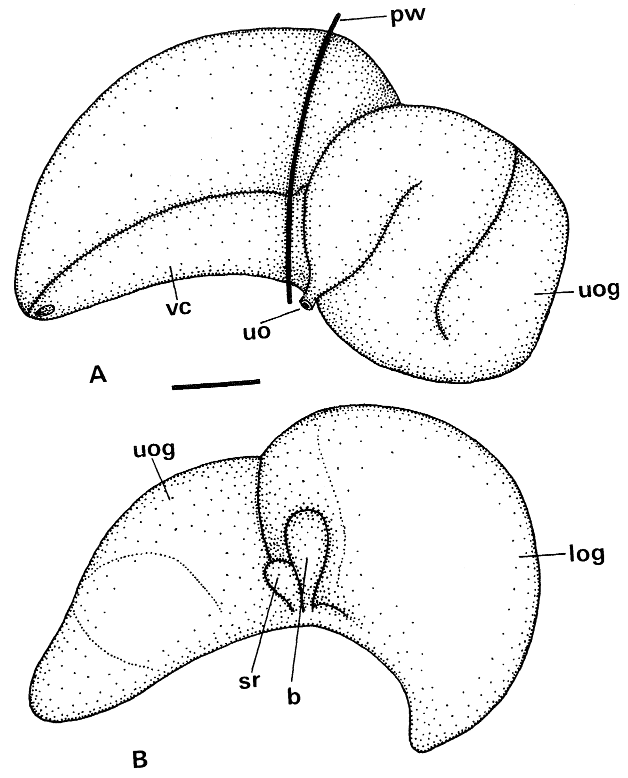

Fig. 36. Female genitalia of *Onoba* (*Subestea*) *australiae* (Frauenfeld): **A**, left side; **B**, right side. *b*-bursa copulatrix; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Female (Fig. 36) with lower oviduct gland (*log*) mostly within pallial cavity; coiled upper oviduct gland (*uog*) about equal in size to lower oviduct gland. Bursa copulatrix (*b*) and seminal receptacle (*sr*) small, opening to posterior expansion of ventral channel (*vc*) which contained sperm in one specimen. One specimen had a bilobed seminal receptacle, the other only a single pouch.

Operculum: as for genus (Fig. 115D).

Radula: as for genus; central teeth $\frac{3-6+1+3-6}{1\quad\quad 1}$, with moderate basal U-shaped projection, lateral margins at 45°. Lateral teeth 5 – 8 + 1 + 6 – 9 (Fig. 115E, H).

Egg capsules: unkown.

Development: probably direct in all species.

Distribution. Southern Australia: *C. australiae*, = *Rissoia* (*Alvinia*) *ochroleuca* Henn & Brazier, 1894, = *R.* (*A.*) *apicilirata*, = *Rissoa mixta* Tate, 1899, = *A. seminodosa*; ?*Haurakia supracostata* May, 1919.

South Africa: *Alvania alfredensis* Bartsch, 1915 (Fig. 115F–H).

?Eastern Atlantic (St. Helena): ? *Rissoa* (*Onoba*) *glypta* Smith, 1890; *Rissoa platia* Smith, 1890.

South Atlantic (Tristan da Cunha): *Rissoa* (*Alvania*) *lusciniae* Watson, 1886.

Material examined.

+ **C. australiae*. Holotype (NHMV) and many other lots (AMS).
R. ochroleuca. Syntypes (AMS).
A. seminodosa. Holotype (TM).
R. apicilirata. Holotype (TM).
+ *H. supracostata*. Holotype (TM) and paratypes (AMS).
+ **A. alfredensis*. Holotype (USNM) and several other lots (AMS).
R. (*O.*) *glypta*. 2 lots (BMNH), syntypes (USNM).
R. platia. Syntypes (BMNH, USNM).
R. (*A.*) *lusciniae*. Syntypes (BMNH).

Remarks. The species placed in *Onoba* (*Subestea*) have a strongly spirally lirate protoconch almost identical to that in species of *Attenuata*. The teleoconch of species included in that genus differ, however, in having stronger spiral sculpture and a more circular aperture with a duplicated peristome.

The protoconch of *Onoba moreleti* (Fig. 113D) is similar to that of species placed in this subgenus. It has much stronger spiral cords on the protoconch than most other species of *Onoba* and has more prominent spiral sculpture on the teleoconch. This species thus appears to provide a bridge between *Onoba* s.s. and *Subestea*.

The anatomy of the type-species of *Subestea* closely resembles species of *Onoba* s.s. except for the conspicuously coiled upper oviduct gland and the proximal half of the penis being parallel-sided, rather than tapering. These differences do not appear to be sufficient to allow full generic separation when the overall similarity of the other features is considered.

The type-species of this subgenus was also the type of *Microdryas* Laseron. Because Laseron misidentified his species the ICZN has ruled that *Epigrus iravadioides* (Gatliff & Gabriel) is now the type-species of *Microdryas* (ICZN Opin. 1181).

Subgenus *Ovirissoa* Hedley, 1916

Ovirissoa Hedley, 1916: 47. Type-species *Rissoa adarensis* Smith, 1902, = *Rissoa kergueleni* Smith, 1875; original designation. Recent, Antarctica (Fig. 114E–H).

Badenia Finlay, 1930: 403. New name for *Powellia* Finlay, 1927: 41, not Maskell, 1879. Type-species *Powellia lactea* Finlay, 1927; original designation. Miocene, New Zealand (Fig. 37).

Diagnosis. *Shell*: elongate-pupoid to elongate-conic, smooth, glossy, usually with moderate to strong varix (Figs 37; 114G). Protoconch smooth, dome-shaped, of about 1½ whorls (Fig. 114E).

Head-foot: head and tentacles appear to be typical of genus. There is a small, broadly triangular metapodial tentacle and a minute pallial tentacle on right side (*O. kergueleni*, Signy Island, South Orkney Islands; preserved material).

Anatomy: based on *O.* (*O.*) *kergueleni*, Signy Island, South Orkney Islands (1 female, 2 males). As for genus; stomach-style sac ratio 2.3–4, length-width ratio 1.6–1.9. Intestine-rectum not examined.

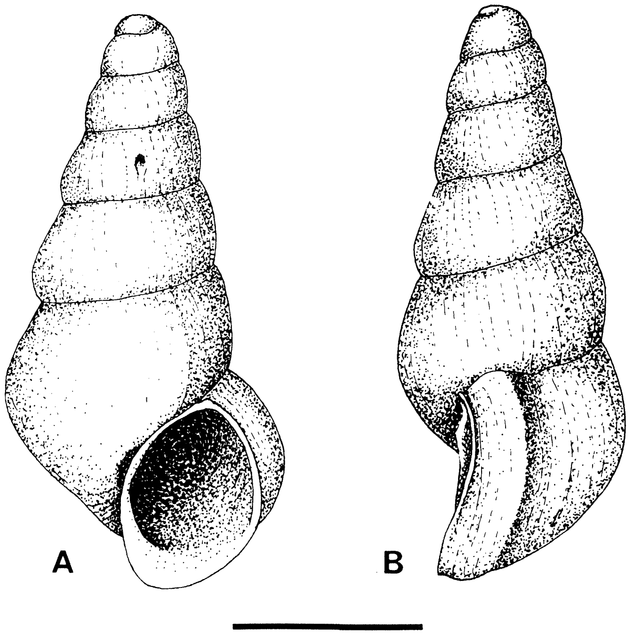

Fig. 37. *Onoba* (*Ovirissoa*) *lactea* (Finlay); type-species of *Powellia* Finlay; holotype, Pukeuri, Oamaru, New Zealand, Miocene (AIM, 637). **Scale:** 1 mm.

Male with parallel-sided penis, tapering at distal end to a point. Prostate protrudes only slightly into kidney (about ⅕ of length).

Female with lower oviduct gland protruding into kidney for about 2/7 of length. Bursa copulatrix about 4 times larger than seminal receptacle and is about half size of upper oviduct gland. Upper oviduct gland not obviously coiled.

Operculum: as for genus (Fig. 114F). Also described for *O.* (*O.*) *elegans* (Ponder, 1965).

Radula: as for genus; central teeth $\frac{6+1+6}{1\ \ 1}$, with moderate, basal U-shaped projection, lateral margins at 45°. Lateral teeth 6 – 7 + 1 + 7 – 9 (Fig. 114H).

Egg capsules: unknown.

Development: probably direct.

Distribution. Antarctic-sub-Antarctic: *Rissoa kergueleni*, = *R. adarensis*, ? = *Rissoa* (*Setia*) *columna* Pelseneer, 1903, = *Rissoa observationis* Thiele, 1912.

New Zealand: *Rissopsis* (*Peringiella*) *elegans* Ponder, 1965; *Rissoa lubrica* Suter, 1898.

Miocene of New Zealand: *P. lactea*.

South-eastern and southern Australia: *Rissoia* (*Cingula*) *rubicunda* Tate & May, 1900, = *Rissoa pulvillus* Hedley, 1906, = *Estea figula* Laseron, 1950.

Material examined.

+ **R. kergueleni*. Syntypes (BMNH) and several other lots (AMS).
R. adarensis. Holotype (BMNH).
R. observationis. Holotype (HUM).
R. lubrica. A few lots (AMS).
P. lactea. Syntypes (AIM).
+ *R. rubicunda*. Many lots (AMS).
R. pulvillus. Holotype (AMS).
E. figula. Syntypes (AMS).

Remarks. Species in this subgenus differ from *Onoba* s.s. in having smooth, glossy shells and a smooth protoconch. They are closely allied to *Onoba* s.s., judging from the anatomy of the type-species.

Ponder (1966a) described the radula and operculum of *Rissoa georgiana* Pfeffer in Martens & Pfeffer as being typical of *Ovirissoa*. This species is now regarded as belonging to *Onoba* s.s. (Ponder, 1983b).

Nordsieck (1972) incorrectly included four Mediterranean species in *Ovirissoa* which he treated as a subgenus of *Putilla*.

Ponder (1967) made *Badenia* a subgenus of *Zebina* based on an examination of the shell of the Recent species *Badenia paupereques* Finlay. This species has a peculiar shell form and may require a new genus-group taxon to accommodate it.

Subgenus *Manawatawhia* Powell, 1937

Manawatawhia Powell, 1937: 199. Type-species *Manawatawhia analoga* Powell, 1937; original designation. Recent, northern New Zealand (Fig. 108E, F).

Diagnosis. *Shell*: minute, elongate, with axial ribs, non-umbilicate. Aperture oval, weakly channelled posteriorly, with thick external varix (Fig. 108E). Protoconch relatively large, dome-shaped, of about 1½ whorls, sculptured with several smooth, spiral carinae (Fig. 108F).

Animal: not known.

Distribution. Northern New Zealand: *M. analoga*.

Material examined.

+ *M. analoga*. Holotype (BMNH), paratypes (AIM, AMS).

Remarks. This monotypic genus-group taxon is tentatively placed with *Onoba* because of the similarity of the shell features to those of *Onoba* (*Subestea*). Information about its radula and details of the soft anatomy are required to determine its relationships more accurately.

Genus *Powellisetia* Ponder, 1965

Powellisetia Ponder, 1965b: 104. Type-species *Rissoa porcellana* Suter, 1908; original designation. Recent, New Zealand (Fig. 116A–C).

Diagnosis. *Shell*: minute to small, ovate to ovate-conic, variable in shape, whorls keeled in some species, smooth or finely spirally striate, usually non-umbilicate. Aperture with simple peristome, moderate to weak posterior sinus and shallow excavation anteriorly. Outer lip orthocline to weakly opisthocline, with weak to strong varix in most species (Fig. 116A, D). Protoconch dome-shaped, paucispiral, terminated by a distinct varix; micro-sculpture of very minute, irregular, short, spirally aligned raised lirae and very indistinct wrinkles (Fig. 116B, E). Sometimes first whorl of protoconch strongly asymmetrical.

Head-foot: unpigmented, with a long, narrow, bilobed snout, long, setose cephalic tentacles slightly broader distally than proximally, eyes in swellings at their outer bases. Foot long, wide in front, tapering behind, propodium very narrow (about ⅓ width of foot). Posterior mucous gland with short opening in middle of metapodium. Unpigmented except for yellow pigment around eye. Apparently no metapodial or pallial tentacles (*P. subtenuis*, Ponder, 1965b, pl. 12, fig. 9). *P. deserta* has very short right and left pallial tentacles but no metapodial tentacle was found (preserved material).

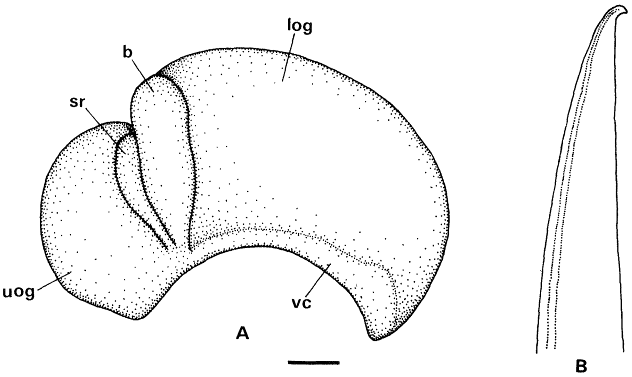

Fig. 38. Genitalia of *Powellisetia deserta* (Smith): **A**, female genitalia, right side; **B**, penis. *b*-bursa copulatrix; *log*-lower oviduct gland; *sr*-seminal receptacle; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Anatomy: based on *P. deserta*, Signy Island, South Orkney Islands (2 females, 1 male). Ctenidial filaments finger-shaped, bases slightly narrower than width of osphradium; osphradium nearly as long as ctenidium. Stomach-style sac ratio 2.8, length-width ratio 1.9. Intestine-rectum not noticeably coiled or folded.

Male with penis tapering to point (Fig. 38B), with lateral, closed duct. Nearly ½ of large prostate gland embedded in kidney.

Female (Fig. 38A) with moderately developed vestibule at anterior end of large lower oviduct gland (*log*). Upper oviduct gland (*uog*) relatively small (about two thirds length of lower gland but only half height), simple, immediately behind lower gland and with vertical bursa copulatrix (*b*) and seminal receptacle (*sr*) on right side between the two glands. Seminal receptacle appears to be single in one specimen and divided into 3 compartments lying vertically alongside one another in another specimen. Bursa copulatrix about half as wide as length of upper oviduct gland and about as long as gland. Seminal receptacle(s) about half size of bursa and lies immediately behind it. Both bursa and seminal receptacle appear to open directly to ventral channel (*vc*) below them.

Nervous system not studied.

Operculum: thin, smooth, oval, last whorl large, nucleus eccentric. The opercula of several species have been figured by Ponder (1965b; 1983b).

Radula: central teeth $\dfrac{4-6+1+4-6}{1 \qquad 1}$, cutting edge with small, sharp cusps; pair of basal denticles on face of each tooth, thickened margins simple, at 30°–47°; U-shaped ventral projection moderate to prominent. Lateral teeth $6-8+1+10-20$. Inner marginal teeth with cusps on distal outer ⅓-½; outer marginal teeth with smooth outer edges, cusps on inner edge probably present but not visible in available mounts (Fig. 116C, F. See also Ponder, 1983b).

Egg capsules: unknown.

Development: probably direct in all species.

Distribution. New Zealand: *R. porcellana*; *Notosetia subtenuis* Powell, 1937 (Fig. 116D–F). These and other species monographed by Ponder, 1965b.

Southern and south-eastern Australia: *Rissoa simillima* May, 1915.

Antarctic-sub-Antarctic: *Rissoa deserta* Smith, 1907; *Rissoa* (*Setia*) *principis* Watson, 1886; *Rissoia inornata* Strebel, 1908.

Miocene, New Zealand: *Powellia comes* Finlay, 1927; *Notosetia prisca paroeca* Finlay, 1924; *Notosetia epulata* Laws, 1941.

Material examined.

+**R. porcellana*. Several lots (NMNZ, AMS).
+**R. subtenuis*. Several lots (NMNZ, AMS). Several other New Zealand species (AMS).
R. simillima. Paratypes (AMS, NMV).
+**R. deserta*. Syntypes (BMNH) and several other lots (AMS, AIM).
R. (*S.*) *principis*. Syntypes (BMNH).
+**R. inornata*. Lectotype and paralectotypes (NHMS).
P. comes. Paratypes (AMS).
N. prisca paroeca. 1 lot (AUG).
N. epulata. Paratypes (AUG).

Remarks. The relationships of this genus are apparently with *Onoba* and it probably represents an early southern hemisphere offshoot from the ancestral *Onoba* stock. The diversity of shell-form in the species recognized as probably belonging to this genus by Ponder (1965b) may reflect a considerable antiquity of the group, or, perhaps, when anatomical information is available, it may be found to be polyphyletic.

Genera with which shells of species of *Powellisetia* can be readily confused are *Obtusella*, *Voorwindia* n.gen. and *Lucidestea* but the species in these genera have different central teeth in their radulae (they have 2–3 pairs of basal processes, not one) and *Lucidestea* has a peg on the operculum. Some small, smooth species of *Pusillina* and *Setia*, especially those in the subgenus *Haurakia*, may also have a general similarity to those in *Powellisetia*. *Pusillina* (*Haurakia*) species have a more strongly sinuate outer lip, a slightly different radula and different details of the head-foot, as well as being anatomically distinct. Species of *Setia* s.s. differ in having stronger protoconch sculpture and a pair of denticles developed from the lateral margins of the central teeth. *Setia* (*Pseudosetia*) *turgida* has a number of similarities in shell characters but differs in lacking a varix and in differences in detail of the central teeth of the radula, as well as in the anatomy of the female genitalia.

Powellisetia species can be distinguished from species of *Onoba* mainly in shell characters, their shells being more ovate, and the teleoconch sculpture is either lacking or consists of fine spiral lirae. A few New Zealand species attributed to this genus have a shoulder or even a keel developed. The lack of a metapodial tentacle, if proved to be consistent, will also be a distinguishing feature as is the orthocline (rather than opisthocline) outer lip and the lack of a substantial periostracum. The anatomy of the genital systems is very like that of *Onoba*. The radulae agree in most features but the cusps on the outer side of the lateral teeth in species of *Powellisetia* are more numerous (10–20) than in species of *Onoba* (3–10).

Genus *Peringiella* Monterosato, 1878

Peringiella Monterosato, 1878: 87. Type-species *Rissoa laevis* Monterosato, 1877 not Sowerby, 1829, = *Peringiella denticulata nom. nov.;* subsequent designation Bucquoy *et. al.*, 1884: 312. Recent, Mediterranean Sea (Fig. 117A, B).

Diagnosis. *Shell*: minute to small, elongate-conic, non-umbilicate, smooth, not glossy. Aperture with simple peristome, angled and weakly notched posteriorly, rounded anteriorly. Outer lip more or less orthocline, with weak to strong varix and weak denticles internally in type-species (Figs 117A, C; 118F). Protoconch smooth or exceedingly minutely and shallowly pitted, dome-shaped, paucispiral (Fig. 117B, D).

Head-foot and *anatomy*: not known.

Operculum: simple, oval, last whorl large, nucleus eccentric (Fig. 117E, F).

Radula: central teeth $\frac{2-4+1+2-4}{0-(1)+1\quad 1+0-(1)}$, ventral U-shaped extension moderate to prominent, thickened lateral margins at 30°–45°; with weak pair of processes in *P. denticulata*, simple in *P. balteata*; a pair of conspicuous denticles on face. Lateral teeth $3-5+1+3-6$. Marginal teeth with cusps on distal outer ⅓ of inner marginals; outer marginals presumably with cusps on inner, distal edge but obscured in mounts (Figs 117G; 118G).

Egg capsules: not known

Development: assumed to be direct.

Distribution. Mediterranean Sea: 5 Recent species are recognized by Nordsieck, 1972, including *Rissoa nitida* Bucquoy *et. al.*, 1884, not Defrance, 1827 (Fig. 117C–G) and *Cingula epidaurica* Brusina, 1866.

Madeira: *Rissoa* (*Cingula*) *balteata* Manzoni, 1868 (Fig. 118F, G).

Material examined.

+ *P. denticulata*. One lot (NMW).
+**R. nitida*. Several lots (BMNH, including one lot from Brusina, AMS, HUM, including one lot from Brusina).
+**R. balteata*. 1 lot, identified as *C. epidaurica*, ex Brusina (BMNH).

Remarks. Only the shell of the type-species has been examined. It is unique in its weakly dentate inner lip, so that it is not possible to establish convincingly its relationship with other species placed in *Peringiella*. Species included in *Onoba* (*Ovirissoa*), are very similar

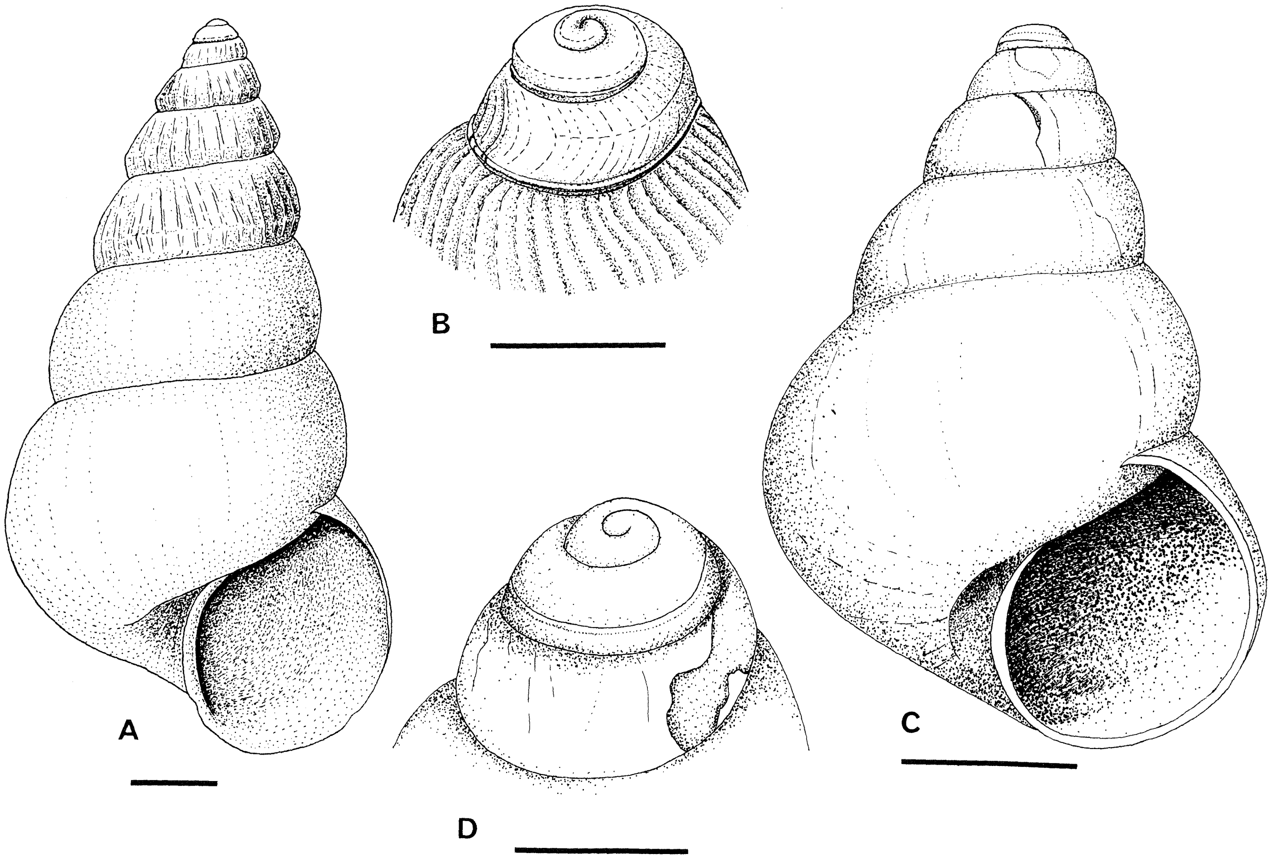

Fig. 39. *Benthonella* species. **A-B**, *Benthonella gaza* Dall, type-species of *Benthonella* Dall; holotype, 1256 m, S. of St Kitts, West Indies: **A**, shell; **B**, protoconch. (USNM, 95397). **C-D**, *Benthonella tenella* (Jeffreys), syntype of *Assiminopsis abyssorum* Locard, type-species of *Assiminopsis* Locard: **C**, shell; **D**, protoconch. 1205 m, S. of Portugal (NHMP). **Scale:** A, C - 1 mm; B, D - 0.5 mm.

to those of *Peringiella*, the only observable differences being that the shells of *Onoba* (*Ovirissoa*) species tend to have more convex whorls, a narrower spire and that the anterior part of the aperture projects forward. New Zealand species included in *Peringiella* by Ponder (1965b) can be placed in *Onoba* (*Ovirissoa*) using these characters.

This generic name was introduced for five species and four varieties. The type-species designation is erroneously given as monotypy by Coan (1964) and Ponder (1965b, 1967). Cossmann (1921) and Wenz (1939) give *R. nitida* (Brusina) as the type-species. The first valid type designation appears to be that of Bucquoy *et. al.* (1884).

The introduction of the name *Rissoa nitida* by Monterosato is in a list with no figure or description or references to these and so it must be regarded as a *nomen nudum*. The name was validly introduced by Bucquoy, *et al* (1884, p. 314) as *Rissoa* (*Peringiella*) *nitida* (Brusina ms). This name is preoccupied by *R. nitida* Defrance, 1827 and Grateloup, 1828. A replacement name is not provided since it is almost certain that an alternative name exists from amongst the nominal species referred to *Peringiella*. Van Aartsen (*in lit.*, 1982) has suggested that *Cingula elegans* Locard 1892, may be the same species.

Genus *Benthonella* Dall, 1889

Hela Jeffreys, 1870: 78, not Münster, 1830. Type-species *Lacuna tenella* Jeffreys, 1869; monotypy. Recent, Mediterranean Sea and eastern Atlantic Ocean (Figs 39C, D; 40; 119A-E).

Benthonella Dall, 1889: 25. Type-species *Benthonella gaza* Dall, 1889, ? = *Benthonella fischeri* Dall, 1889; original designation. Recent, western Atlantic (Fig. 39A, B).

Assiminopsis Locard, 1897: 466. Type-species *Assiminopsis abyssorum* Locard, 1897, = *Lacuna tenella* Jeffreys, 1869; monotypy. Recent, eastern Atlantic Ocean (Fig. 39C, D).

Diagnosis. *Shell*: small to medium size, thin, ovate-conic to elongate-conic, narrowly umbilicate, smooth with fine spiral sculpture and/or axially ribbed; axial ribs usually not extending over base. Aperture subangled posteriorly but not channelled, rounded to subangled anteriorly; peristome simple. Inner lip very thin, fused to parietal wall; outer lip orthocline to slightly prosocline, with thin edge, no varix (Figs 39A, C; 119A, F). Protoconch dome-shaped, of about 2½ whorls, with a few (2-3) spiral carinae; 'protoconch I' sculptured with spiral lirae and small granules. Growth lines strongly sinuate (Figs 39B, D; 119B, C; see also Bouchet, 1976).

Head-foot: cephalic tentacles short and broad, with bulges at outer bases but no pigmented eyes. No pallial or metapodial tentacles discernable (preserved material, as below). Anterior pedal mucous gland but no posterior pedal gland present (sectioned material).

Anatomy: based on *B. tenella*, 1950 m, Bay of Biscay, N.E. Atlantic (2 males, 2 females and sectioned material). Ctenidium with very long, finger-shaped filaments about 3 times longer than width of bases. Osphradium more than twice as wide as filament bases, nearly as long as ctenidium. Stomach-style sac ratio 2.8, length-width ratio 1.7. Intestine-rectum with a few undulations just behind and in front of posterior pallial wall.

Male with long penis (Fig. 40B), narrowly oval in section, with parallel sides, marginal, closed duct and very small terminal filament (*f*). Prostate thickly glandular, about ⅓ embedded in kidney. Seminal vesicle coiled at posterior end of inner side of stomach.

Female (Fig. 40A) with short, high, lower oviduct gland (*log*), vestibule and ventral channel inconspicuous, opening terminal. Bursa copulatrix (*b*) about half size of upper oviduct gland (uog), lies vertically on right side between upper and lower oviduct glands and opens ventrally to ventral channel. Seminal receptacle (*sr*); about half size of bursa, not visible in dissected specimens but located in sectioned material immediately behind bursa. Upper oviduct gland simple, containing sperm in upper dorsal part of lumen (confirmed in sections as well as dissections), about ⅓ size of lower oviduct gland. A posterior continuation of ventral channel (*rgo*), just behind its connection with upper oviduct gland, opens to kidney. Sperm in kidney of 2 of 3 females sectioned. Renal oviduct (*uo*) opens separately to upper oviduct gland.

Nervous system not examined.

Operculum: subcircular, simple, thin, nucleus subcentral (Fig. 119D).

Radula: central teeth $\dfrac{5-9+1+5-9}{0-1+1 \quad 0+1-0}$, with short denticle from thickened lateral margins in some specimens, basal denticles prominent; cutting edge narrowly V-shaped; U-shaped ventral extension weak to moderate; lateral margins at 35°-50°. Lateral teeth $3-6+1+3-8$, cutting edge V-shaped. Marginal teeth with equal-sized cusps; inner marginal teeth with cusps in middle of outer edge (i.e. distal and proximal ⅓ of each smooth). Outer marginal teeth with cusps on middle ½ of inner edge (Fig. 119E).

Egg capsules: unknown.

Development. planktonic larval stage present in *B. tenella* (Bouchet, 1976) and probably in the other species.

Distribution. Atlantic Ocean: *L. tenella*, = *Rissoa amblia* Watson, 1886, = *A. abyssorum*; *Benthonella fischeri* Dall, 1889, ? = *B. gaza*.

Pacific and Indian Oceans: *Cithna margaritifera* Watson, 1886; *Cithna decorata* Thiele, 1925; *Cithna sculpta* Thiele, 1925.

Material examined.

+ **B. tenella*. Syntypes (USNM), several other lots (NHMP, AMS).

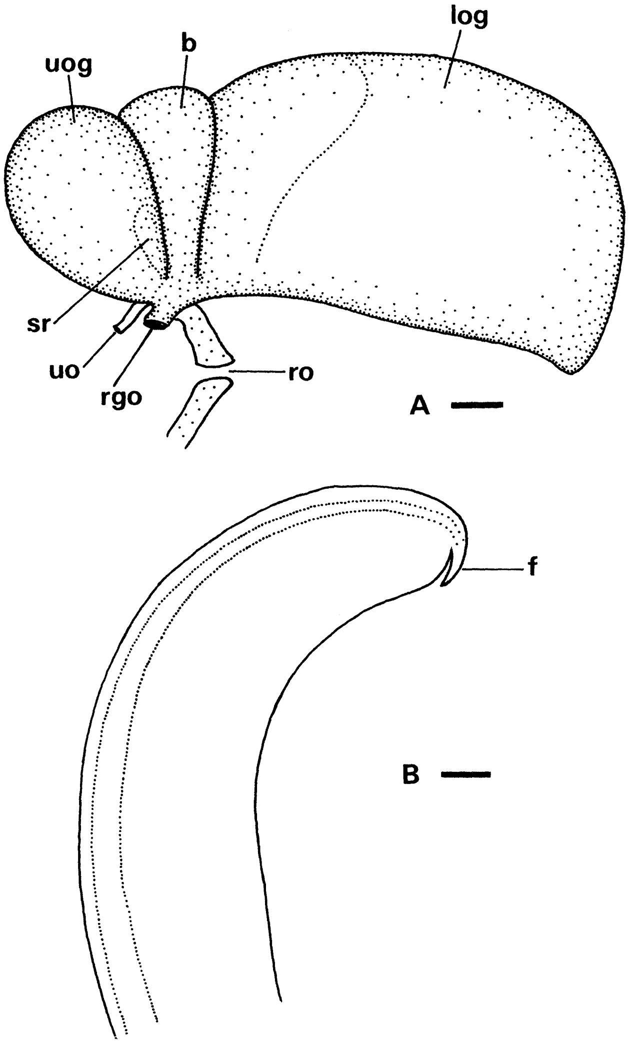

Fig. 40. Genitalia of *Benthonella tenella* (Jeffreys): **A**, female genitalia, right side; **B**, penis, distal half. *b*-bursa copulatrix; *f*-filament; *log*-lower oviduct gland; *rgo*-reno-genital opening; *ro*-renal opening to pallial cavity; *sr*-seminal receptacle (shown by dotted line); *uo*-upper oviduct; *uog*-upper oviduct gland. **Scale:** 0.1 mm.

R. amblia. 5 lots (IRSB).

B. gaza. Holotype (USNM). A few other lots (NHMP, AMS).

A. abyssorum. Syntypes (NHMP) and several other lots so identified by Locard (NHMP, IRSB).

C. margaritifera. Holotype (BMNH).

Radulae and opercula also examined from 2 unidentified species.

Remarks. Species of *Benthonella* occur from the outermost part of the continental shelf down to the abyssal plains of the Atlantic and Indo-Pacific. Rex *et. al.* (1979) have recently described the reproductive biology of *B. tenella* in some detail and Bouchet (1976) has discussed its larval ecology.

Benthonella can be distinguished from other rissoid genera by the thin, simple shell with a large, multispiral, spirally sculptured protoconch. Anatomically it is similar to *Onoba* although the gono-renal duct observed in *B. tenella* has no known counterpart in *Onoba*. The

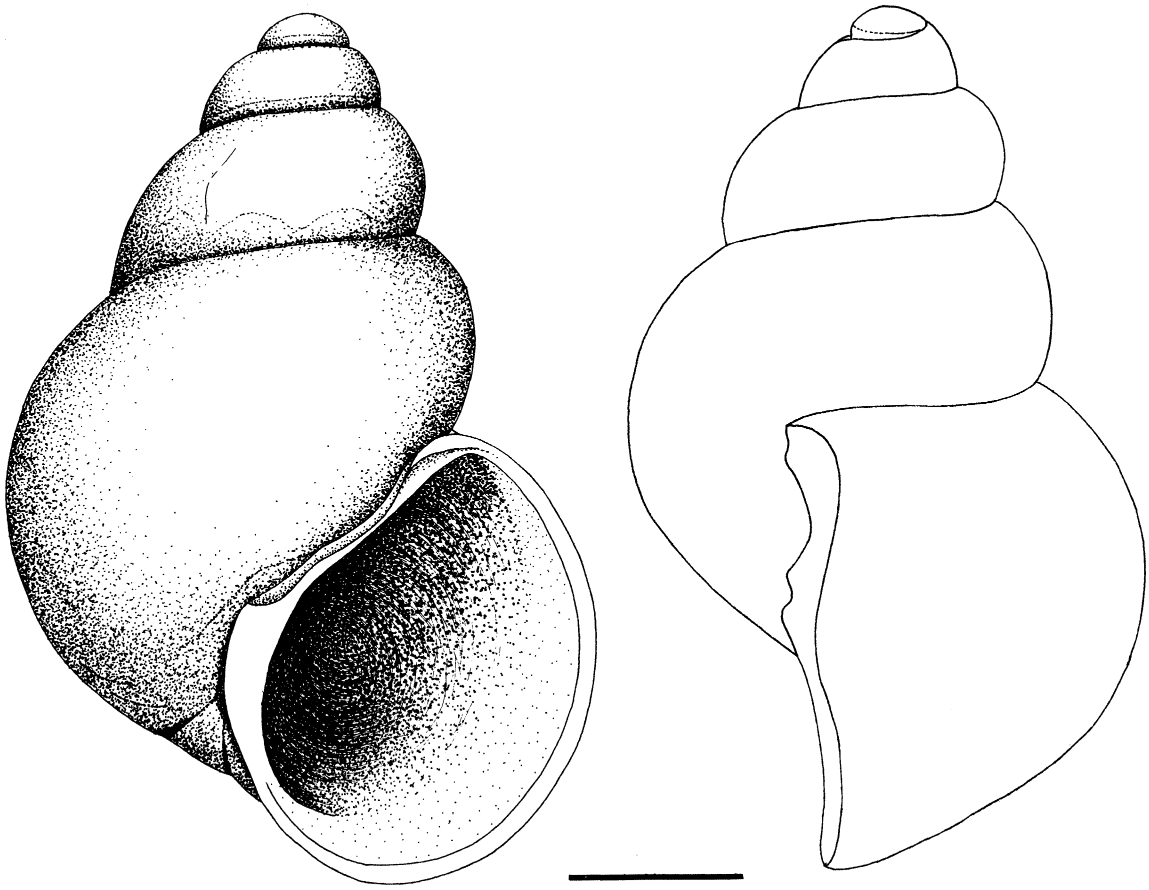

Fig. 41. *Boreocingula martyni* (Dall), type-species of *Boreocingula* Golikov & Kussakin; holotype, Kuska Harbour, Aleutian Islands, Alaska (USNM, 206036). **Scale:** 1 mm.

radula, too, is distinctive, especially in the smooth, pointed distal ends of the marginal teeth and the narrow, V-shaped cutting edge on the central and lateral teeth.

Genus *Boreocingula* Golikov & Kussakin, 1974

Boreocingula Golikov & Kussakin, 1974: 291. Type-species *Cingula martyni* Dall, 1886, = *Cingula robusta* var. *martyni* Dall, 1886; original designation. Recent, Aleutian Islands, north Pacific (Figs 41; 42; 120A–E).

Diagnosis. *Shell*: small, ovate, rather thin, non-umbilicate, with weakly convex to convex whorls, smooth or with weak spiral lines or cords. Aperture ovate, weakly channelled posteriorly, broadly rounded anteriorly, peristome simple, outer lip weakly prosocline, without external varix (Figs 41; 120F). Protoconch paucispiral; microsculpture of minute pits in spiral rows (Fig. 120A, B, G). Periostracum thin to well developed.

Head-foot: unpigmented, snout short relative to narrow cephalic tentacles. Eyes in bulges at outer bases of tentacles. Foot moderately elongate, anterior edge slightly convex, anterior corners rounded; posterior end tapering, rounded. Anterior pedal gland well developed, posterior pedal gland with epithelial and subepithelial gland-cells but apparently not invaginated (from sectioned material). No metapodial or pallial tentacles (based on drawing and description of living animal of *B. martyni* by R. Baxter, *in lit.* and on examination of preserved specimens, as below).

Anatomy: based on *B. martyni*, Kasitsna Bay, Kachemak Bay, Cook Inlet, Alaska (several specimens, dissection and sections). Ctenidium with very long filaments (about 4.5 times longer than width of bases); **bases narrower than osphradium. Osphradium ⅔ to ⅞** length of ctenidium. Stomach-style sac ratio 2.3, length-width ratio 1.6. Intestine-rectum more or less straight behind pallial cavity, folded immediately in front of posterior pallial wall.

Male with penis tapering to point, oval in section, with closed, marginal penial duct. Prostate gland massive, about one third protrudes into kidney, this portion being broader than pallial part which tapers anteriorly.

Female (Fig. 42) with well developed lower oviduct gland scarcely extending behind pallial cavity with small vestibule (*v*) and with ventral channel (*vc*) along most of its length. Upper oviduct gland (*uog*) about half size of lower oviduct gland (*log*), not obviously coiled and contains sperm in lumen. Bursa copulatrix (*b*) and seminal receptacle (*sr*) aligned vertically between upper and lower oviduct glands. Bursa anterior to seminal receptacle and about 2–3 times larger. Bursa much smaller than upper oviduct gland. Short ducts to the kidney (*grd*) and to the pericardium (*gpd*) arise from the renal oviduct (*uo*).

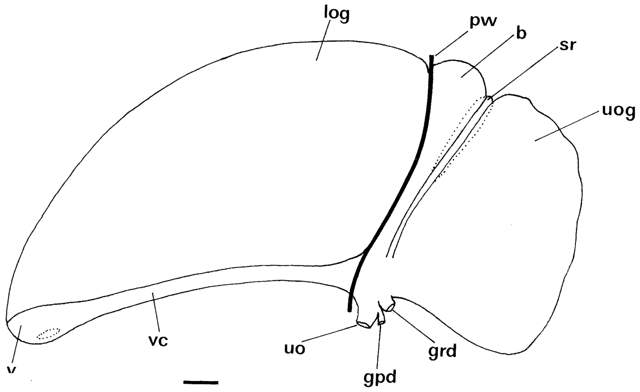

Fig. 42. *Boreocingula martyni* (Dall), female genitalia viewed from left side. *b*-bursa copulatrix; *gpd*-gono-pericardial opening; *grd*-gono-renal opening; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel. **Scale:** 0.1 mm.

Kidney with several massive, longitudinal folds on outside wall; a development not seen in other genera.

Nervous system not studied.

Operculum: thin, simple, horny, nucleus eccentric, last whorl large.

Radula: central teeth $\frac{4-7+1+4-7}{1 \qquad 1}$, lateral margins at 23°–53°, simple; U-shaped ventral extension prominent; second pair of basal denticles present in one specimen (Fig. 120D). Lateral teeth 3 – 10 + 1 + 6 – 12. Inner marginal teeth with cusps on distal ¼–⅓ mostly on outer edge; outer marginal teeth with simple outer edges; inner edges not visible in mounts (Fig. 120C–E, H).

Egg capsules: not known.

Development: assumed to be direct.

Distribution. North Pacific: *C. martyni*, = *Cingula katherinae* Bartsch, 1912.

North Atlantic-Arctic: *Rissoa globulus* Möller, 1842; *Rissoa castanea* Möller, 1842 (Fig. 120F-H).

Material examined.

+**C. martyni*. Holotype (USNM) and several other lots (USNM, LACM, AMS).
+**R. globulus*. 1 lot, ex A. Warén (AMS).
+**R. castanea*. 1 lot, ex A. Warén (AMS).

Remarks. *Boreocingula* was included in the Hydrobiidae by its authors on the basis of its shell shape. The shell characters also suggest a relationship with *Falsicingula*, species of which are sympatric with species of *Boreocingula*. The radulae of the type-species of *Falsicingula* and *Boreocingula* are similar to those of most Rissoidae but differ from each other in detail, particularly in the presence of two pairs of basal cusps on the central teeth of species of *Falsicingula* and fewer cusps on the cutting edge of the central teeth. There are also differences in protoconch microsculpture (compare Figs 120A, B, G with 147A, B, G-I). The anatomy of the female reproductive system of *Falsicingula* species has been examined (Lasareva, 1971; Slavoshevskaya, 1975b, 1982, and unpublished observations of my own) and found to be different from that of the Rissoidae. *Boreocingula* on the other hand has an anatomy typical of the Rissoidae and generally similar to that of species of *Onoba*. The genus differs from *Onoba* in having a more ovate shell, a punctate protoconch microsculpture and in apparently lacking metapodial and pallial tentacles.

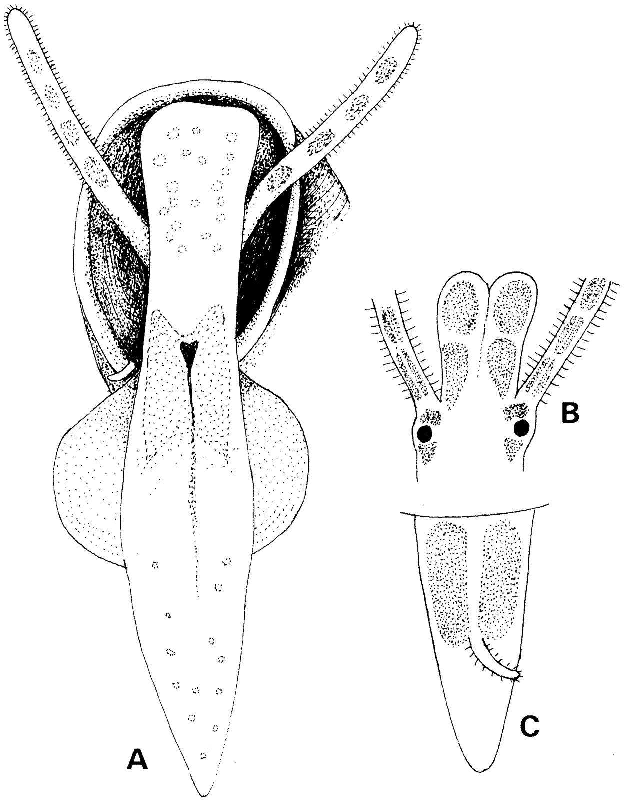

Fig. 43. Head-foot of *Lucidestea* species. **A**, *L.* cf. *nitens*, N. Stradbroke Island, Queensland, Australia, ventral view. **B-C**, *Lucidestea* sp., Lee Point, Darwin, Australia: **B**, dorsal view of head; **C**, dorsal view of posterior foot.

The protoconch and radula of *Rissoa castanea* (Fig. 120G, H) and *R. globulus* are like those of *B. martyni* and, because the general teleoconch features are also similar, they are considered to be congeneric.

Genus *Lucidestea* Laseron, 1956

Lucidestea Laseron, 1956: 448. Type-species *Lucidestea vitrea* Laseron, 1956; original designation. Recent, Queensland, Australia (Fig. 121A-E).

Falsisetia Golikov & Kussakin, 1967: 35. Type-species *Falsisetia ornata* Golikov & Kussakin, 1967; original designation. Recent, North Pacific (Fig. 121F-I).

Diagnosis. *Shell*: minute, conic to ovate-conic, rather solid, non-umbilicate to narrowly umbilicate, smooth or with fine spiral sculpture, aperture with simple peristome, oval, with weak posterior angulation but no channel. Outer lip orthocline with weak to moderate external varix (Fig. 121A, F). Protoconch dome-shaped, of about 1½ whorls, smooth except for a weak spiral cord on last ½ whorl; growth lines strongly curved in sinusigera form (Fig. 121B, H).

Head-foot: tentacles long, ciliated, strap-like, eyes in bulges at their outer bases; snout rather long, bilobed.

Foot elongate, rather narrow, with constriction in middle portion; anterior and posterior mucous glands present, posterior mucous gland opening by way of a short slit which does not extend to posterior end of foot. Metapodial tentacle short, ciliated, arises from dorsal side of metapodium about ½ way between operculum and posterior end of foot. A short posterior pallial tentacle usually present. Semitransparent white with dense white spots on tentacles and foot, or orange spots near eyes in some species. (Based on several Australian species, including the type-species) (Fig. 43).

Anatomy: based on *L. atkinsoni*, Pelican Lagoon, American River, Kangaroo Island, S. Australia (several specimens, dissection and sections). Osphradium long, ctenidium reduced to a few short stubs at posterior end of pallial cavity. Stomach-style sac ratio 2.8, length-width ratio 1.6. Intestine-rectum not studied.

Male with very broad, long, parallel-sided penis (Fig. 44C), narrowly oval in section, with central duct and relatively short, very narrow terminal filament (*f*). Prostate gland well developed; appears to be entirely within pallial wall but posterior end pressed against posterior pallial wall.

Female (Fig. 44A, B) with relatively massive U-shaped anterior sperm pouch (*ss*) lying dorsally and anteriorly to genital opening (*go*). Lower oviduct gland posterior to anterior limb of sperm pouch, posterior limb on left side of anterior end of gland, the two limbs joined by a narrow connection dorsally. Posterior limb of sperm pouch opens to lower oviduct gland just anterior to slit-like genital opening. Lower oviduct gland (*log*) about as long as it is high and about equal in length to upper oviduct gland (*uog*) which abuts on to it at posterior pallial wall. Upper oviduct gland a thick, U-shaped tube with narrow lumen not containing sperm. Bursa copulatrix (*b*), between upper and lower oviduct glands on right side, opens to ventral channel (*vc*) between the glands. A long tube runs ventrally from this part of ventral channel to small ovoid seminal receptacle (*sr*) which lies immediatey behind and below upper oviduct gland. Both bursa and seminal receptacle approximately equal in size and much smaller than upper oviduct gland.

Nervous system not studied.

Operculum: oval, thin, simple except for a short peg which emerges from eccentric nucleus, and does not reach columellar edge (Fig. 121C, G).

Radula: central teeth $\frac{3-5+1+3-5}{1+2 \quad 2+1}$, outermost pair of basal denticles shortest and are derived from lateral margins; inner pair of basal denticles about ½ as long as outer pair; U-shaped basal projection weak to absent, lateral margins at 40°-60°. Lateral teeth $6-11+1+10-16$. Marginal teeth with cusps subequal; outer distal half of inner marginal teeth and inner distal half of outer marginal teeth cuspate (Fig. 121D, E, I).

Egg capsules: unknown.

Development: planktonic larval stage probably present in most species.

Distribution. Tropical Indo-west Pacific: *L. vitrea*; *Rissoella mundula* A. Adams, 1860; *Rissoella minima* A. Adams, 1860; *Rissoella fulgida* (A. Adams ms), Dunker, 1882; *Rissoa poolei* Hedley, 1899; *Rissoa* (*Setia*) *microscopica* Thiele, 1925; *Cithna milium* Thiele, 1925; *Rissoa ina* Thiele, 1925; *Setia* (*Obtusella*) *pallaryi* Hornung & Mermod, 1928; *Cingula* (*Ovirissoa*) *intermedia* Thiele, 1930, = *Cingula* (*Ovirissoa*) *nitidula* Thiele, 1930; *Lucidestea laterea* Laseron, 1956; *Lucidestea obesa* Laseron, 1956.

Miocene, Palau, Pacific Ocean: *Putilla* (*Parvisetia*) *goikulensis* Ladd, 1966; *Barleeia* (*Barleeia*) *meiauhana* Ladd, 1966.

Miocene, Fiji: *Putilla* (*Parvisetia*) *suvaensis* Ladd, 1966.

Temperate Australia: *Setia nitens* Frauenfeld, 1867; *Rissoa* (*Cingula*) *atkinsoni* T. Woods, 1876; *Notosetia muratensis* Cotton, 1944.

North Pacific: *F. ornata*.

Material examined.

+**L. vitrea*. Holotype and paratypes (AMS) and many other lots (AMS).
R. mundula. Probable syntypes (SMF, BMNH).
R. minima. Syntypes (BMNH, SMF).
R. fulgida. Possible syntypes (SMF).
R. poolei. Syntypes (AMS).
R. (*S.*) *microscopica*. Holotype and paratypes (HUM).
C. milium. Holotype and paratypes (HUM).
R. ina. Syntypes (HUM).
S. (*O.*) *pallaryi*. Types (NHMG).
C. (*O.*) *intermedia*. Holotype (HUM).
C. (*O.*) *nitidula*. Syntypes (HUM).
+**L. laterea*. Holotype and paratypes (AMS) and many other lots (AMS).
L. obesa. Holotype and paratypes (AMS).
P. (*P.*) *goikulensis*. Type material (USNM).
B. (*B.*) *meiauhana*. Type material (USNM).
P. (*P.*) *suvaensis*. Type material (USNM).
+**S. nitens*. Syntypes (NHMV) and many other lots (AMS).
+**R.* (*C.*) *atkinsoni*. Syntypes (TM) and many other lots (AMS).
N. muratensis. Holotype and paratypes (SAM).
+**F. ornata*. One lot ex Golikov (AMS).

Remarks. The species of this genus are among the most abundant of the Australian and tropical Indo-west Pacific rissoids. They are characterized by their simple, rather conical shells, minute size and, in several species, by a dark brown line or band on the base. The radula with the three pairs of heavy denticles on the face of the central teeth differs from all other Rissoidae, although it is somewhat similar to that of *Voorwindia* and *Obtusella*. In *Voorwindia* the inner-most pair of basal cusps on the central teeth is the longest and in *Obtusella* there are only two pairs of basal denticles. The operculum also separates these genera; species of *Lucidestea* have a peg on the operculum; the other two do not.

The operculum and radula of the type-species of *Falsisetia* are nearly identical to those of *Lucidestea vitrea* and, because the shells show no important differences, these two species are considered to be congeneric.

The female reproductive system is unusual for the Rissoidae in having a massive, U-shaped, anterior sperm sac which lies in front of the genital opening. This sac opens immediately in front of the genital opening into a wide, very short groove probably homologous with the sperm groove of some other rissoids (e.g. *Merelina*, *Stosicia*). This suggests that the sperm groove has closed over anteriorly to develop a sperm-storing structure similar to the anterior bursa copulatrix found in some Vitrinellidae (Fretter, 1956), Caecidae (Marcus & Marcus, 1963) and Iravadiidae (Ponder, 1984). The other characters of this genus, however, closely resemble those of other Rissoidae. In some other rissoids closure of the sperm groove has apparently occurred behind the genital opening (e.g. *Rissoina*, *Schwartziella*) but in most the sperm groove has either been lost within the ventral channel or excluded from it during closure of the lower oviduct gland and lost. The ventral seminal receptacle is also unusual although this configuration could easily be obtained by displacement from the normal right lateral position.

The virtual loss of the ctenidium in *L. atkinsoni* is unusual in the Rissoidae, although *Voorwindia umbilicata* n.gen. n.sp. also has no ctenidium and *Obtusella intersecta* (Wood) (herein) and '*Setia inflata*' (= *Obtusella*? sp.) (Fretter & Patil, 1961) have a rudimentary ctenidium.

The sinusigera growth lines on the protoconch (Fig. 121B, H) of the species in this genus strongly suggest that they have a planktonic larval stage despite the small number of whorls of the protoconch. This supposition is supported by the extensive distributions of some of the tropical Indo-Pacific species in this group.

The nominal species listed under 'Distribution' have not been critically revised and there are probably fewer species than the available names would indicate.

Genus *Obtusella* Cossmann, 1921

Obtusella (Monterosato ms) Cossmann, 1921: 43. New name for *Cingulina* Monterosato, 1884a: 228, not A. Adams, 1860. Type-species *Rissoa obtusa* Cantraine, 1842 (not Brown, 1841), = *Putilla* (*Obtusella*) *cantrainei* Nordsieck, 1972, new name for *R. obtusa* Cantraine, not Brown, ? = *Rissoa intersecta* Wood, 1856 (van Aartsen, 1982); monotypy. Recent, Mediterranean (Figs 44D–F; 118A–E).

Diagnosis. *Shell*: minute, ovate to ovate-conic, narrowly umbilicate to non-umbilicate, with convex whorls, smooth or finely spirally striate. Aperture of moderate size, peristome simple, angled but not channelled posteriorly, rounded anteriorly. Outer lip orthocline to opisthocline, with or without weak varix (Fig. 118A). Protoconch dome-shaped, of about 2 whorls, protoconch 1 with few, very weak spiral lirae with minute granules between; remainder smooth (Fig. 118B; see also Fretter & Graham, 1978; Babio & Thiriot-Quiévreux, 1974).

Head-foot: "Like that of *C. cingillus* (= *Cingula trifasciata*) in general organization. The tentacles are delicate and setose; the eyes rarely seen beyond the edge of the shell; there is only one pallial tentacle, on the right". The head-foot is unpigmented (from Fretter & Graham, 1978). Clark (1852) gives additional details noting the bilobed snout and the lack of a metapodial tentacle but in the AMS there is an annotated copy of his work in which he notes a long tentacle reaching nearly to the end of the foot and the presence of a posterior pallial tentacle. Jeffreys (1867) says there is a very long metapodial tentacle and a conspicuous pallial tentacle in '*R. soluta*' (= *intersecta*). Fretter & Patil (1961) describe the head-foot of their '*Setia inflata*' as having a bilobed snout, short, cylindrical, sparsely setose cephalic tentacles, slightly dilated at tips; large eyes in protuberances at bases. Foot short, rounded in front, bluntly pointed behind. Anterior pedal gland present, no posterior pedal gland. Metapodial tentacle short, not projecting beyond borders of foot; no pallial tentacles (Fretter & Patil, 1961) (Fig. 3A).

Anatomy: based on *O. intersecta*, from Vattenholmen, Koster area, Sweden in 10–20 m (5 females, 2 males) and from Calvi, Corsica (3 females). Osphradium short and broad, large relative to pallial cavity. Ctenidial filaments absent. Stomach-style sac ratio 2.2–2.9, length-width ratio 1.4–1.9. Intestine-rectum more or less straight.

Male with very broad, long, parallel-sided penis, narrowly oval in section, with long, narrow, terminal filament (Fig. 44F; *f*). Prostate gland pallial + visceral in one male (with reduced penis), hardly developed in second specimen.

Female (Fig. 44D, E) with large U-shaped sperm sac (*ss*) only slightly shorter than oviduct gland. Lower oviduct gland (*log*), about as long as high, terminated at posterior pallial wall (*pw*) and lying largely behind anterior sperm sac. Pallial opening of gland (*go*) appears to be a slit along most of ventral side. Anterior sperm sac with separate opening (*sso*) anterior to oviducal opening. Oviduct and sperm sac share common closed area just behind sperm sac opening. Upper oviduct gland (*uog*) small relative to lower oviduct gland (constricted ventrally by style sac) and with no obvious coils. Bursa copulatrix (*b*) on right side between upper and lower glands. Seminal receptacle (*sr*) elongate and placed posteroventrally.

Nervous system not studied.

Operculum: simple, oval, flat, thin, smooth, nucleus eccentric, last whorl large (Fig. 118C).

Radula: central teeth $\frac{4-6+1+4-6}{1+1 \qquad 1+1}$, thickened lateral margins at about 47° with outer pair of basal denticles longer than inner pair; U-shaped basal projection moderately developed. Lateral teeth 6 – 9 + 1 + 14 – 19. Marginal teeth with subequal cusps on distal ½ of outer edge of inner marginal and distal ⅓ of inner edge of outer marginal teeth (Fig. 118D, E).

Egg capsules: unknown.

Development: probably with planktotrophic larval stage (Babio & Thiriot-Quiévreux, 1974).

Distribution. Western Europe and the Mediterranean Sea: several species including *R. intersecta*; ?*Setia macilenta* Monterosato, 1880, = *Rissoa concinnata* Jeffreys, 1883 (van Aartsen, 1982).

?Miocene of Rumania: *Cingula* (*Cingulina*) *communis* Boettger, 1906.

Material examined.

+**R. intersecta*. A few lots (BMNH, USNM, as *R. obtusa* and *R. alderi*; AMS).

Remarks. The relationships of this genus appear to be with *Lucidestea*. The shell is similar, as is the radula in having two pairs of basal denticles on the central teeth. However, it lacks the marginal denticles present in species of *Lucidestea*, and the operculum lacks a peg. Anatomically the two genera are also similar. Both have a ventral, posterior seminal receptacle, a slit-like ventral opening in the lower oviduct gland (although this has not been confirmed in sectioned material of *O. intersecta*), and a penial filament. *Lucidestea atkinsoni* has only a single genital opening but *Obtusella intersecta* appears to have two. This latter character may have arisen from a *Lucidestea*-like genital system by the anterior migration of the vestibule and the retention of the posterior slit-like lower oviduct gland opening. The very reduced gill filaments seen in *Lucidestea* appear to have entirely disappeared in *Obtusella* but a large osphradium remains and its ciliation probably supplies a water current.

Minor differences in the female genitalia occur between the Swedish and Corsican specimens identified as *O. intersecta* suggesting that different taxa may be represented (compare Fig. 44D and E).

Nordsieck (1972) recognizes five European species in this genus and at least some of the species he includes in *Ovirissoa* could also be placed here. The type-species is usually considered to be close to *Rissoa alderi* Jeffreys, 1858 (see Warén, 1980) but that species appears to be very distinct and may not be congeneric. The species identified as *Setia inflata* Monterosato, 1884 by Fretter & Patil (1961), is tentatively assumed to belong here. Their description of the shell and their illustration of the radula agree rather well with *O. intersecta* although the head-foot characters differ. Van Aartsen & Verduin (1978) have shown that *Setia inflata* Monterosato is a form of *Setia fusca* (Philippi, 1841), a species restricted to the Mediterranean Sea. Fretter & Graham (1978, p. 162) suggest that the *Setia inflata* of Fretter & Patil is a variety of *Setia pulcherrima*. Their (1961) illustration of the radula, however, suggests that this is not the case.

Monterosato (1884a) included a single species (*obtusa*) under *Cingulina* so that the type designation is by monotypy as indicated by Coan (1964). Monterosato (1884b), in what is assumed to be a slightly later publication, includes a second species in the genus. Nordsieck (1972) incorrectly cites (*Cingula* (*Cingulina*)) *communis* Boettger, 1906 as the type of this genus. This Miocene species may belong to *Obtusella* but I have not seen any specimens.

Obtusella intersecta is unique among the north Atlantic-Mediterranean Rissoidae that I have studied in having two pairs of basal denticles on the central teeth of the radula. The compact, ovate shell with its fine spiral sculpture is also distinctive and cannot be confused with any other groups except, perhaps, some species of *Setia*. The protoconch differs from *Setia* species in having about two whorls and a distinct protoconch 1.

Genus *Voorwindia* n.gen.

Type-species: *Voorwindia umbilicata* n. sp. Recent, south-eastern Australia (Figs 45; 46; 122A-E).

Diagnosis. *Shell*: small (up to about 2.6 mm in length), broadly ovate-conic, narrowly umbilicate to imperforate, with convex whorls and periphery. Sculpture of teleoconch of weak axial growth lines, and spiral microstriae or minute granules. Aperture ovate, angled but not channelled posteriorly, rounded and simple anteriorly. Outer lip thin, orthocline, with or without weak varix behind outer lip (Fig. 122A). Protoconch of about 1¾–2¼ whorls, initial whorl small, with weak, axial growth striae V-shaped at a weak spiral cord on last whorl. Periostracum very thin, transparent.

Head-foot: snout bilobed, moderately extensile; cephalic tentacles strap-like with active cilia and stationary setae laterally and distally; eyes in bulges at outer bases. Foot elongate, with straight to slightly convex anterior edge, slightly expanded and rounded laterally, posteriorly elongate, pointed. Anterior pedal mucous gland triangular, conspicuous; posterior sole with epithelial glands only. Metapodial tentacle short, narrow, emerges from foot about midway between posterior end and posterior edge of operculum. Pallial tentacle on right side short, none on left. Black smudge on mantle roof and visceral mass; remainder of animal translucent-white with conspicuous dense-white spots on cephalic tentacles, dorsoposterior-foot, and sole (*V. umbilicata*, Port Hacking and North Harbour, Sydney, New South Wales) (Fig. 45).

Anatomy: based on *V. umbilicata*, North Harbour, Sydney (several specimens examined by dissection and sections). Ctenidium absent, a ciliated ridge on left side of head presumably provides water current. Osphradium long, relatively wide (about ½ as wide as long), lateral ridges relatively wide. Stomach-style sac ratio 3.1, length-width ratio 2.1. Intestine-rectum not investigated.

Male with penis (Fig. 46C) broadly oval in section, slightly wider in distal half than in proximal half and with very short terminal papilla (*p*) or a short filament. Penial duct submarginal, closed. Prostate gland (Fig. 46D, *pr*); entirely behind (but abutting against) posterior pallial wall. Seminal vesicle U-shaped, at posterior end of stomach.

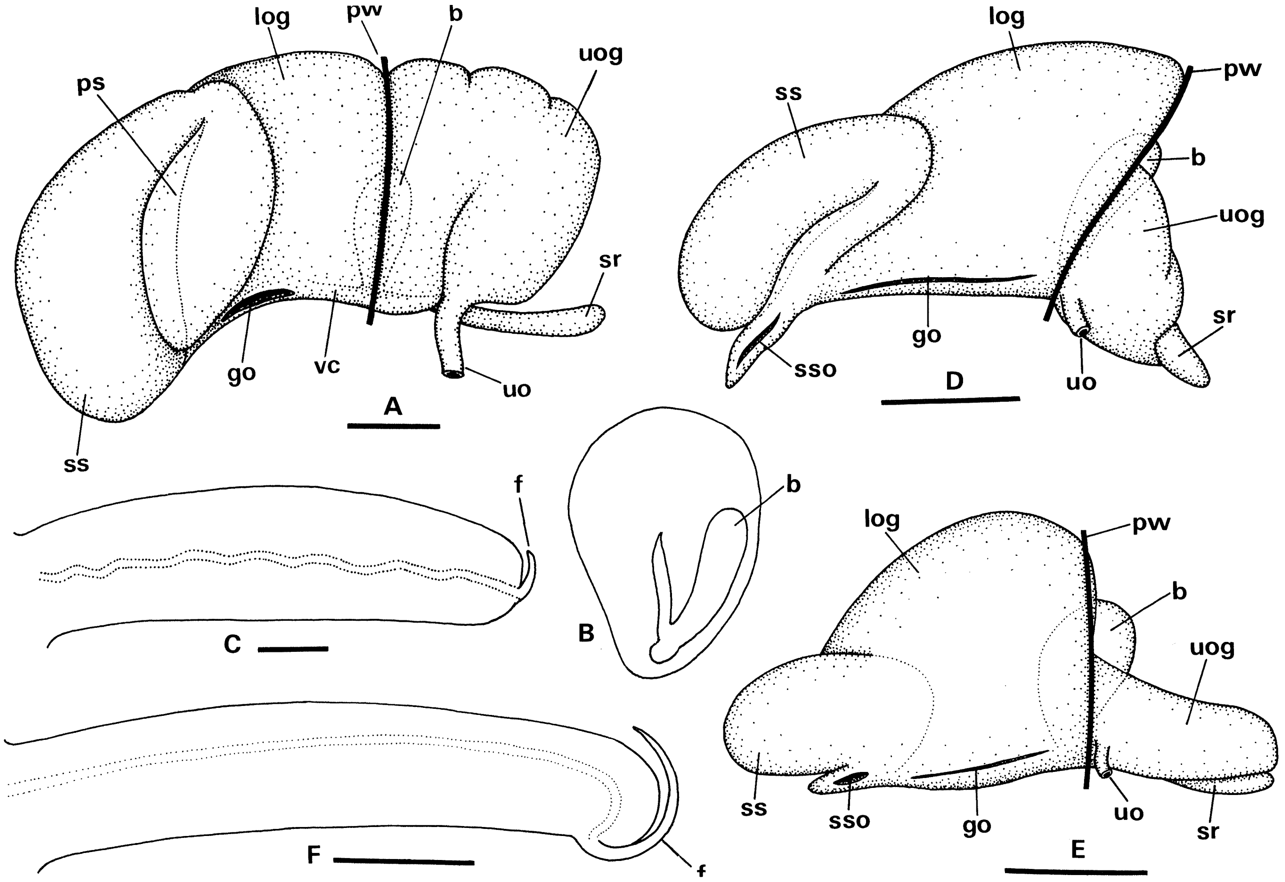

Fig. 44. Genitalia of *Lucidestea* and *Obtusella*. **A-C**, *Lucidestea atkinsoni* (T. Woods): **A**, female genitalia, left side; **B**, transverse section at the posterior-most part of the lower oviduct gland; **C**, penis. **D-F**, *Obtusella intersecta* (Wood): **D-E**, female genitalia, left side; **F**, penis (D, F, East of Vattenholmen, near Koster, Sweden; E, Calvi, Corsica). *b*-bursa copulatrix (indicated by dotted line in A); *f*-penial filament; *go*-pallial genital opening; *log*-lower oviduct gland; *ps*-proximal arm of anterior sperm sac; *pw*-posterior wall of pallial cavity; *ss*-anterior sperm sac; *sso*-sperm sac opening; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Female (Fig. 46A, B) with two anterior sperm sacs, a small, narrow, dorsal sac (Fig. 46A, *asp*) and a large lateral pouch (Fig. 46A, B, *msp*). Anteriodorsal sac small, circular in section, left laterodorsal to capsule gland, ends blindly near point of commencement of lateral sperm sac and contains unorientated sperm. It opens into separate sperm groove in narrow vestibule anterior to capsule gland. Lateral (or median) sperm pouch (*msp*) about half length of lower oviduct gland, on left side, opens directly to lower oviduct gland and contains spermatozoa with heads embedded in epithelium lining sac. Upper oviduct gland (*uog*) apparently simple, small relative to lower oviduct gland (*log*) (which is about 2½ times longer), with lumen and two dorsoposterior, thin-walled lobes containing sperm (*sl*). No bursa copulatrix present. Seminal receptacle (*sr*) narrow, vertical, on right side between upper and lower oviduct glands.

Operculum: simple, thin, with eccentric nucleus (Fig. 122E).

Radula: central teeth $\frac{3+1+3}{2-0+1 \quad 1+0-2}$, cutting edge straight with small, parallel-sided lateral cusps, median cusp longer and fused to face of tooth below cutting edge; basal denticles massive, two smaller pairs derived from lateral margins in type-species, lateral margins simple in *V. sublacuna*; slope of lateral margins 40°-45°; ventral margin slightly convex. Lateral teeth $2-6+1+13-16$, cusps narrow. Marginal teeth with subequal cusps, relatively larger than in most Rissoidae, on distal half of outer edge of inner marginal teeth and on inner distal third of outer marginal teeth (Fig. 122B-D, F).

Egg capsules: unknown

Development: assumed to have a planktotrophic larval stage.

Distribution. South-eastern Australia: *V. umbilicata* n.sp.

North-eastern Australia: *Lucidestea sublacuna* Laseron, 1956 (Fig. 122F).

?Japan: *Rissoella omphalotropis* A. Adams, 1860.

?Red Sea: *Cingula tiberiana* Issel, 1869.

Somali Republic: one unnamed species.

Material examined.

+**V. umbilicata*. Type material and many other lots (AMS).

+ **L. sublacuna*. Holotype, paratypes and several other lots (AMS).

R. omphalotropis. Material ex Adams (USNM).

C. tiberiana. Syntypes (NHMG), 1 lot (SMF).

**V*. sp. (Somali Republic). One lot (AMS)

Remarks. This genus differs from all other known Rissoidae in the characters of the male and female genitalia and in the characters of the central teeth of the radula. *Obtusella intersecta* and *Lucidestea* species have two pairs of true basal denticles, (the inner-most pair being the shorter. In *Voorwindia umbilicata* the inner pair of basal denticles (the only true basal denticles) are massive, being much longer than the outer two pairs.

The shell characters of the type-species of the new genus most closely resemble some species of *Powellisetia* and, to a lesser extent, a few species of *Lucidestea*. *Powellisetia* species have, however, a paucispiral protoconch with a large initial whorl and only a single pair of basal denticles on the central teeth of the radula. *Lucidestea* species differ in the radular features noted above and in the operculum bearing a peg.

The distinctive features of the reproductive system include the prostate gland which lies entirely behind the posterior pallial wall and, in the female, the small, anterior, dorsal sperm sac and the large lateral sperm pouch which opens directly to the capsule gland. The upper oviduct gland stores sperm in posterodorsal lobes as in *Rissoa* and *Pusillina* and there is no bursa copulatrix. The sperm-storing lobes of the upper oviduct gland and the morphology of the head-foot suggest relationship with *Rissoa-Pusillina* but these genera differ significantly in a number of characters (e.g. the lack of a posterior pedal gland, in *Voorwindia*, the visceral position of the prostate gland and the radular characters).

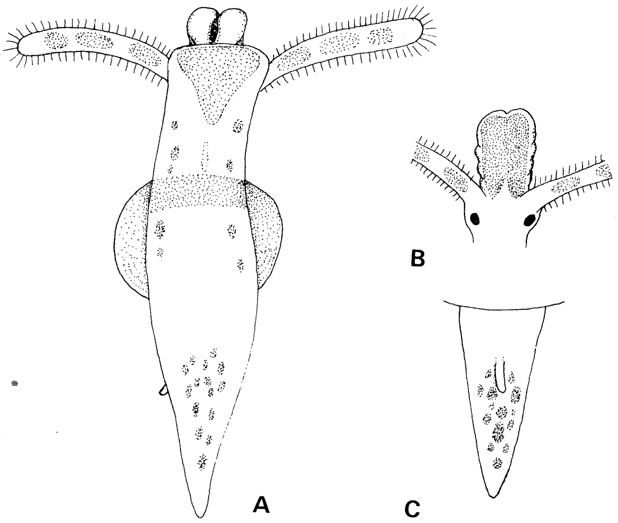

Fig. 45. Head-foot of *Voorwindia umbilicata* n.sp., Port Hacking, New South Wales, Australia: **A**, ventral view; **B**, dorsal view of head; **C**, dorsal view of posterior foot.

Two of the species included in the genus other than the type-species, are known only from their shells so that their inclusion in *Voorwindia* is tentative. Radular and opercular characters are known for a third species, *V. sublacuna* (Fig. 122F). These agree closely with the type-species except that the central teeth of the radula lack any processes derived from the lateral margins. In all other respects, including the fusion of the median cusp of the central tooth to the face of the tooth, the radulae of the two species agree very closely. The teleoconch of *V. sublacuna* is unusual in being sculptured with minute granules. An unnamed species from Somaliland has a radula similar to that of the type-species.

The new genus is named for the late Mr Jacques Voorwinde, as a small mark of recognition of his considerable help and encouragement over many years.

Voorwindia umbilicata n.sp.

(Figs 45; 46; 122A-E)

Notosetia simillima May. — Laseron, 1950: 280, not May, 1915.

Diagnosis. *Shell*: as for genus; teleoconch of 3-3⅔ whorls, narrowly-umbilicate, surface dull to slightly shining with exceedingly fine spiral microstriae. Colour parchment white.

Dimensions:

	Length	Width	Length of aperture	Width of aperture
Holotype	1.90	1.24	0.80	0.64
Paratypes	2.13	1.38	0.98	0.65
	2.27	1.53	0.92	0.73
	1.90	1.25	0.76	0.61
	1.96	1.35	0.83	0.63
	1.99	1.29	0.77	0.64

Head-foot, anatomy and *operculum:* as for genus.

Radula: central teeth with 2 pairs of basal processes derived from lateral margin. Lateral teeth 6 + 1 + 13, otherwise as for genus (Fig. 122B, C, D).

Material examined.

Holotype: 4–7 m, off Chinamans Beach, Middle Harbour, Sydney, New South Wales, coll. J. Voorwinde, AMS, C.134536 (Fig. 122A).

Paratypes: Same data as for holotype (AMS, C.134537), and 8 (AMS, C.83587, C.134529–134535) additional lots, Chinamans Beach, 0–11 m.

Additional material: 34 lots from Port Hacking, New South Wales to Hervey Bay, southern Queensland (all AMS).

Remarks.

The new species differs from *Notosetia simillima* May, which is here considered to be a species of *Powellisetia*, in its broader, umbilicate shell as well as in the characters separating *Voorwindia* and *Powellisetia*.

Voorwindia umbilicata feeds, in part, on Foraminifera. It is found in sheltered bays and estuaries on the northern half of the New South Wales coast where it is associated with seagrasses.

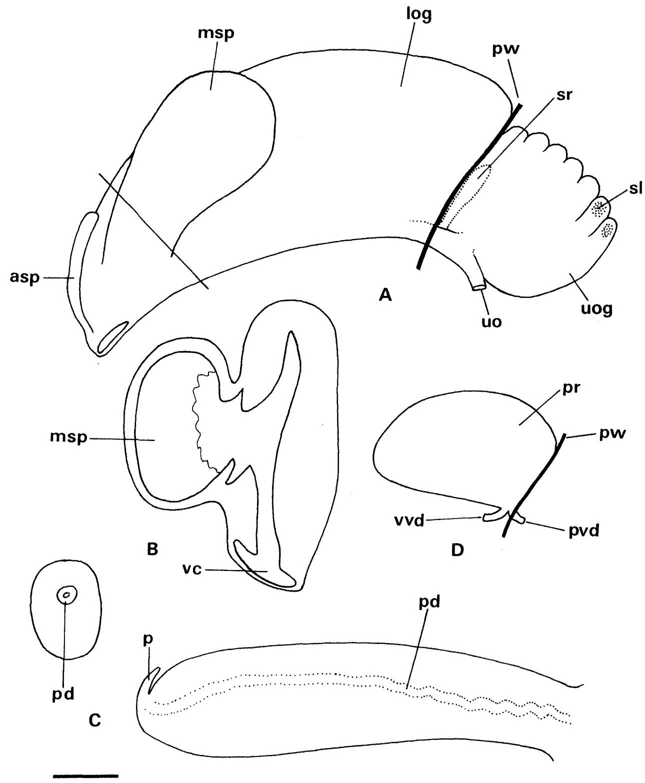

Fig. 46. Genitalia of *Voorwindia umbilicata* n.sp. **A-B**, female: **A**, left side; **B**, Section through anterior part of lower oviduct gland and lateral sperm pouch (*msp*), position of section indicated in A. **C**, penis and transverse section; **D**, prostate gland. *asp*-anterior sperm pouch; *log*-lower oviduct gland; *msp*-lateral (or median) sperm pouch; *p*-papilla; *pr*-prostate; *pd*-penial duct; *pvd*-pallial vas deferens; *pw*-posterior wall of pallial cavity; *sl*-sperm in lobe of upper oviduct gland; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel; *vvd*-visceral vas deferens. **Scale:** 0.1 mm.

Genus *Striatestea* Powell, 1927

Striatestea Powell, 1927a: 544. Type-species *S. bountyensis* Powell, 1927; original designation. Recent, Bounty Island, south of New Zealand.

Diagnosis. *Shell*: minute, thin, shining, elongate-conic, non-umbilicate. Aperture somewhat D-shaped, peristome simple; outer lip orthocline, sometimes flanged, with weak, narrow varix, slightly thickened internally; inner lip narrow, slightly concave. Weak but distinct spiral cords on base, remainder of shell smooth (Fig. 93F). Protoconch conical, apex pointed with about 1½ whorls, microsculpture of minute, shallow pits (Fig. 93G).

Head-foot: not known.

Operculum: oval, thin, simple, transparent (*S. bountyensis*, Ponder, 1967).

Radula: central teeth $\frac{2+1+2}{1\quad 1}$. Lateral and marginal teeth typical of family, marginal teeth possibly lacking cusps (*S. bountyensis*, Ponder, 1967).

Distribution. New Zealand sub-Antarctic: *S. bountyensis*.

New Zealand: *Striatestea poutama* Ponder, 1967; *S.* n. sp.(Fig. 93F, G).

Material examined.

S. bountyensis. Holotype (AIM).
S. poutama. A few specimens (NMNZ).
\+ *S.* n.sp. Several specimens (NMNZ).

Remarks. This genus can be distinguished from all others in the Rissoidae by its minute, elongately conical shell, pointed protoconch and the (spiral) sculpture restricted to the periphery-base. The characters of the radula and operculum separate it from *Microdryas* (Barleeidae, Anabathrinae), which it resembles superficially. Species of *Microdryas* also have a more solid shell with a straighter inner lip and a dome-shaped protoconch. *Striatestea* is included in the Rissoidae somewhat tentatively, the microsculpture (of the one species examined using the SEM) and form of the protoconch being atypical.

Genus *Amphirissoa* Dautzenberg & Fischer, 1897

Amphirissoa Dautzenberg & Fischer, 1897: 40. Type-species *A. cyclostomoides* Dautzenberg & Fischer, 1897; monotypy. Recent, Azores, abyssal (Fig. 47).

Diagnosis. *Shell*: minute, helicoid, very finely spirally striate, with convex whorls and narrowly umbilicate. Aperture subcircular, with duplicated peristome and sharply reflected outer lip (Fig. 47). Protoconch large, of 1¼ whorls, apparently with very fine spiral striae.

Animal unknown.

Development: probably direct.

Distribution. Azores, Atlantic Ocean: *A. cyclostomoides*.

Material examined.

A. cyclostomoides. Holotype (MOM), and paratypes (BMNH, IRSNB, NHNP).

Remarks. Known only from the type specimens. The holotype was regrettably destroyed during an attempt to clean it because it was nearly completely covered with crystals.

This species may belong in the Skeneidae but has an aperture unlike any known skeneid. It is unlikely that *A. cyclostomoides* is a rissoid but may continue to be placed tentatively in this family until its radula, at least, is examined. The shell has some general similarity to that of species of *Parashiela*.

Genus *Merelina* Iredale, 1915

Merelina Iredale, 1915: 449. Type-species *Rissoa cheilostoma* T. Woods, 1877; original designation. Recent, Tasmania (Fig. 123A, B).

Promerelina Powell, 1926: 593. Type-species *Promerelina crosseaformis* Powell, 1926; original designation. Recent, New Zealand (Fig. 124E, F).

Mereliniopsis Ponder, 1967: 214. Type-species *Merelina*

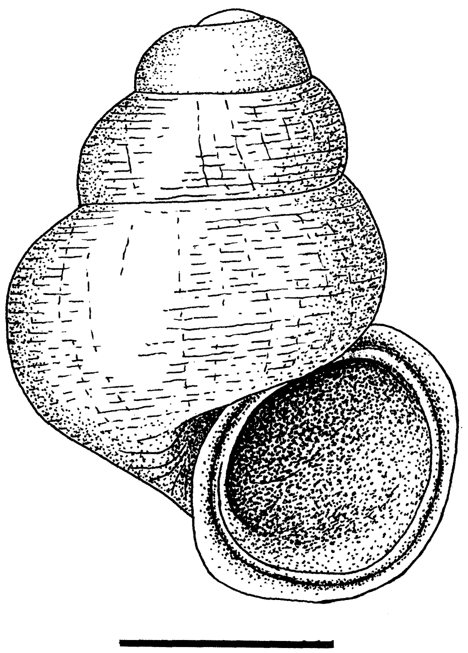

Fig. 47. *Amphirissoa cyclostomoides* (Dautzenberg & Fisher), type-species of *Amphirissoa* Dantzenberg & Fischer; paratype, 1600 m, Azores (NHMP). **Scale:** 0.5 mm.

queenslandica Laseron, 1956; original designation. Recent, Queensland, Australia (Fig. 123C, D).

Diagnosis. *Shell*: small, elongate, solid, non-umbilicate, with a few spiral cords usually predominant; axial ribs usually render sculpture cancellate, weak to absent on base. Aperture relatively small, subcircular, with double peristome, no distinct anterior or posterior channel or angulation. Outer lip opisthocline, with varix (Figs 123A, C, E; 124A, E). Protoconch paucispiral (about 1½ whorls), with several spiral cords on which lie closely spaced, prominant, rounded nodules; interspaces almost smooth (Figs 123B, D, F; 124B, F).

Head-foot: cephalic tentacles rather short for family, compressed, not tapered, with stationary cilia on edges, mobile cilia ventrally, distal ends bluntly rounded; eyes in swellings at outer bases. Snout short, bilobed. Foot long, narrow anteriorly, anterior mucous gland large, propodium well developed; no posterior mucous gland. No pallial or metapodial tentacles (Ponder, 1967 pl. 6, fig. 3; *M. elegans*, Batemans Bay, N.S.W., Australia, *M. gracilis*, Sydney, N.S.W.).

Anatomy: based on *M. gracilis*, Jervis Bay and Port Stephens, New South Wales, Australia (several specimens from dissection and sections). Ctenidium with finger-shaped filaments up to four times longer than wide. Osphradium nearly three times wider than filament bases and nearly as long as ctenidium. Stomach-style sac ratio 4.3, length-width ratio 2.5. Intestine-rectum with single loop immediately behind or in front of posterior pallial wall.

Male with long penis with deep penial groove along entire length making penis (Fig. 48D) V-shaped in section; tapers to point in distal third, remainder parallel-sided. Prostate gland small, open, at posterior end of pallial cavity. Seminal vesicle S-shaped and massive, at and behind posterior end of stomach.

Female (Fig. 48A-C) with long, narrow, lower oviduct gland (*log*) open ventrally within pallial cavity except for about posterior fifth. Pallial opening (*ga*) with narrow sperm groove (*sg*) on left lip. Upper oviduct gland (*uog*) small, about half length and height of lower oviduct gland, coiled. Bursa copulatrix (*b*) a little larger than upper oviduct gland, lies between the two oviduct glands and opens via a very short duct to an expanded, muscular sac (*bd*) lying just behind posterior pallial wall. This sac, like the bursa, contains sperm and may be homologous with the bursal duct of other rissoids. Seminal receptacle (*sr*) very small, on right side of bursa copulatrix and opens to narrow duct from upper oviduct gland. This duct opens at posterior end of lower oviduct gland, just behind pallial opening, and separately from muscular sac into which bursa opens. Bursa with unorientated sperm; swollen bursal duct containing orientated sperm with heads embedded in epithelium. Seminal receptacle with orientated sperm lying loose in lumen.

Nervous system with cerebral ganglia abutting, supraoesophageal ganglion with connective to right pleural ganglion about two-thirds as long as ganglion. Suboesophageal ganglion with connective to left pleural ganglion about half as long as ganglion. Pleural ganglia fused to cerebrals.

Operculum: subcircular, thin, simple, nucleus subcentral (Fig. 123G).

Radula: central teeth $\frac{2-4+1+2-4}{2\quad 2}$, cutting edge a little less than half width of tooth, triangular, lateral margins simple (an occasional denticle in one specimen of *M. gracilis* (Fig. 124D)), at 30°-65°; ventral margin slightly convex to flat. Two pairs of basal denticles, outermost pair longer. Lateral teeth $4-6+1+7-9$. Marginal teeth with subequal cusps; inner marginal teeth with cusps on distal half of outer edge; outer marginal teeth with cusps on distal third of inner edge (Figs 123H; 124C, D).

Egg capsules: unknown.

Development: assumed to be direct in all species.

Distribution. Tropical Indo-Pacific: *M. queenslandica*; *Alvania pisinna* Melvill & Standen, 1896; ? *Rissoa* (*Manzonia*) *petronella* Melvill & Standen, 1901, ? = *Anabathron pagodiformis* Sowerby, 1914; ? *Rissoina granulosa* Pease, 1862; *Rissoa tokyoensis* Pilsbry, 1904; *Merelina* n.sp, east Africa.

Temperate Australia: *M. cheilostoma*; *Alvania elegans* Angas, 1877 (Fig. 123E-H); *Alvania gracilis* Angas, 1877 (Fig. 124A-D), = *Rissoa devecta* Tate, 1899, unnecessary replacement name.

New Zealand: *P. crosseaformis* and 19 other species; listed by Powell, 1979.

Miocene to Pliocene, New Zealand: *Merelina kaawaensis* Laws, 1936; *Merelina saginata* Laws, 1939; *Merelina waiotemarama* Laws, 1948.

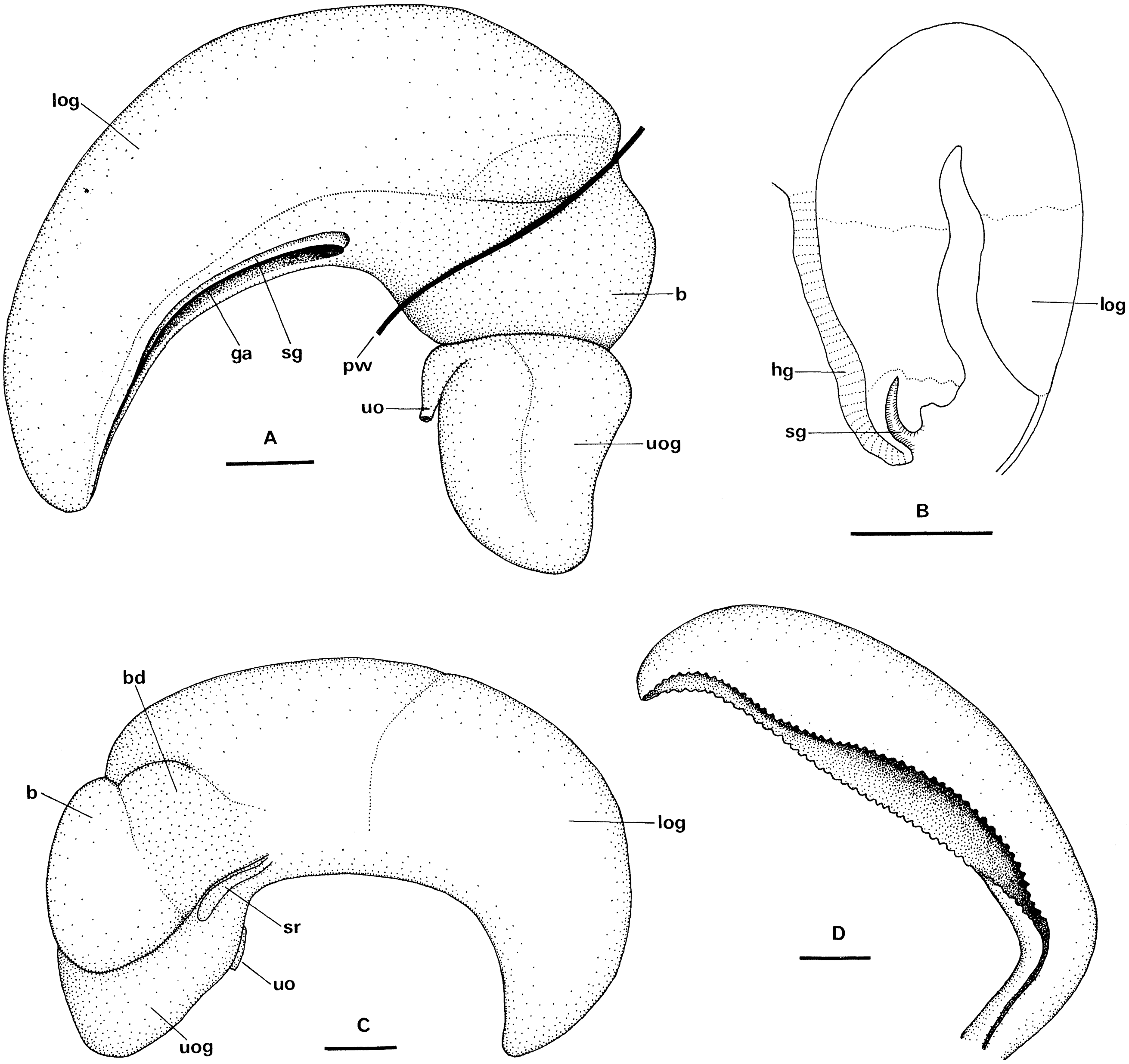

Fig. 48. Genitalia of *Merelina gracilis* (Angas): **A**, left side; **B**, transverse section through middle part of capsule gland; **C**, view from right side; **D**, penis. *b*-bursa copulatrix; *bd*-bursal duct; *hg*-hypobranchial gland; *ga*-pallial genital opening; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sg*-sperm groove; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland. **Scale:** 0.1 mm.

Material examined.

+ **M. queenslandica*. Holotype and paratypes and several other lots (AMS).
+ **A. pisinna*. Holotype (MUM), and several other lots (AMS).
R. (*M.*) *petronella*. Holotype (BMNH).
A. pagodiformis. Holotype (BMNH).
R. granulosa. A few lots (ANSP, AMS).
R. tokyoensis. Syntypes (ANSP).
+ **M.* n.sp. 1 lot, N. of Dar es Salaam, Tanzania (AMS).
+ *M. cheilostoma*. Holotype (TM) and a few other lots (AMS).
+ **A. elegans*. Many lots (BMNH, AMS).
+ **A. gracilis*. Syntypes (BMNH) and many other lots (AMS).
+ *P. crosseaformis*. A few lots (AIM, AMS, NMNZ).
M. kaawaensis, *M. saginata* and *M. waiotemarama*. Paratypes (AUG).

Remarks. Members of this genus are superficially similar to some species of *Alvania* but differ in anatomical, radular, and several shell characters. Most species of *Merelina* have a taller spire, more distinctly convex whorls and an aperture with a double peristome that is usually relatively smaller than found in species of *Alvania*. In addition, the protoconch is distinctly spirally keeled, the keels bearing regular, closely spaced nodules. Similar protoconch sculpture is unknown in *Alvania* species, although the protoconch of some species of *Manzonia* approach it. A new subgenus of *Manzonia*, *Simulamerelina*, that is described above, contains species convergent with *Merelina* in teleoconch characters (apertural and sculptural features) but these differ in their anatomical and radular characters and in their protoconch microsculpture.

Powell separated *Promerelina* from *Merelina* by the granular spiral ridges of the protoconch, the predominantly spiral sculpture of the teleoconch and the single basal keel. The first character is shared with *Merelina*, the second is not justified because the axial sculpture in the type-species of *Promerelina* is just as strong as in several other *Merelina* species. The single basal keel does not seem sufficient justification for separating two genera or even subgenera, as proposed by Wenz (1939) and Ponder (1967).

Nordsieck (1972:177) placed the Mediterranean species *Rissoa pagodula* Bucquoy, Dautzenberg & Dollfus, 1884 in *Merelina* (*Promerelina*) but examination of the shell (Fig. 92A), head-foot, radula (Fig. 92D) and anatomy of that species has shown it to be an *Alvania*.

Mereliniopsis was introduced as a subgenus to cover species differing from *Merelina* only in the possession of a smooth protoconch. Examination of the types of the type-species shows it to have a protoconch typical of *Merelina* (Fig. 123D) (despite Laseron's (1956) contention that it was smooth) therefore this name must become a synonym of *Merelina*. Several species referred to *Merelina* by Laseron (1956) are now placed in *Iravadia* (Ponder, 1984).

The Merelinidae Golikov & Starobogatov, 1975 was erected for *Merelina* on the basis of the 'anatomical' information given by Ponder (1967). *Merelina* may prove to require a separate subfamily along with *Lironoba*. If so, the family-group name Lironobinae Ponder, 1967 would have priority.

Merelina differs from the other rissoid genera, except *Lironoba*, in having both an open penial groove and two pairs of basal denticles on the central teeth of the radula. It is unique in the Rissoacea in having a completely open pallial genital duct, but the remainder of its anatomy is essentially similar to that of other rissoids, as is the basic structure of the female genital tract. *Obtusella intersecta* also appears to have a ventrally open lower oviduct gland but that species has a large, U-shaped anterior sperm sac.

The peculiarities in the female and male genitalia as well as the head-foot characters, are interpreted as primitive character-states, suggesting that *Merelina* has been independent of the mainstream of rissoid evolution for a long time. There are, however, character-states that can be interpreted as derived. These include the thin operculum with its subcentral nucleus (a modification in response to the subcircular aperture) and the second pair of denticles on the face of the central teeth of the radula.

Genus *Lironoba* Iredale, 1915

Lironoba Iredale, 1915: 451. Type-species *Rissoa suteri* Hedley, 1904; original designation. Recent, southern New Zealand (Fig. 126E–G).

Diagnosis. *Shell*: minute to small, elongate-conic to ovate-conic, non-umbilicate, with few, strong spiral keels (1–3 on penultimate whorl). Aperture subcircular, slightly angled and very weakly channelled posteriorly; peristome duplicated, with thin, opisthocline inner lip, outer lip with strong varix (Figs 125A; 126A, E). Teleoconch microsculpture between spiral cords of raised, close spiral striae crossed by finer axial striae (Figs 125F; 126G). Protoconch of about 1½ dome-shaped whorls, first half whorl large, rounded, with weak keel and/or spiral lirae on last whorl; microsculpture of extremely minute pits and, in some species, minute pustules (Figs 125D, E; 126C, F).

Head-foot: cephalic tentacles rather short, minutely and actively ciliated, slightly flattened and slightly swollen distally, with eyes in small bulges at their outer bases. Snout moderately long, bilobed. Foot (Fig. 49A) rather narrow in front, tapering posteriorly, without a posterior mucous gland; anterior mucous gland conspicuous. No pallial tentacles; a short, triangular metapodial tentacle present (Fig. 49B). Exposed animal unpigmented (*L. australis*, Eaglehawk Neck, Tasmania).

Anatomy: based on *L. australis*, Flinders, Victoria and Eaglehawk Neck, Tasmania, Australia (a few specimens, rather poorly preserved; one subadult male sectioned). Ctenidium with finger-like filaments, bases considerably narrower than osphradium. Stomach-style sac ratio 3.1–5.5, length-width ratio 2–2.7. Intestine-rectum with coil at posterior pallial wall.

Male with penis similar in shape to *Merelina* but with much shallower, open groove. Prostate gland apparently closed, mostly within pallial wall, a small portion protruding into kidney. Seminal vesicle of several coils over inner side of posterior end of stomach.

Female with long, lower oviduct gland open over anterior half in one specimen, about anterior ¼ in another. Bursa copulatrix globular, on left side of oviduct glands, small relative to oviduct glands, duct narrow, muscular, opens to ventral channel anteroventrally. Upper oviduct gland small relative to lower oviduct gland (details not known due to poor preservation of material). Seminal receptacle not found (but possibility of presence not excluded).

Nervous system not studied.

Operculum: oval, flat, thin, simple, except (in *L. australis*) for ridge-like structure on inner face emerging from nucleus towards columellar edge, nucleus subcentral (Fig. 125B, C); *L. unilirata* has a simple operculum with eccentric nucleus (Fig. 126B).

Radula: central teeth $\frac{4-6+1+4-6}{2 \quad 2}$, with large outer pair of denticles on face and smaller inner pair; outer margins simple, thickened, at 45°–50°; U-shaped process on ventral edge weak to moderate. Cutting edges of central and lateral teeth triangular. Lateral teeth

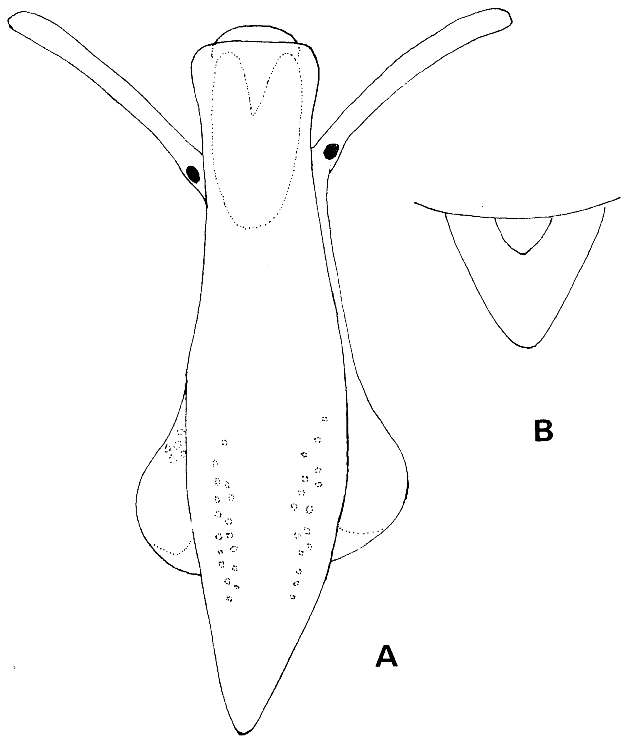

Fig. 49. Head-foot of *Lironoba australis* (T. Woods), Eaglehawk Neck, Tasmania: **A**, ventral view; **B**, dorsal side of posterior end of foot.

3 – 7 + 1 + 8 – 9, cusps small. Inner marginal teeth with cusps on distal ⅓–½ of outer edge; outer marginal teeth with cusps on distal ¼ of inner edge; cusps subequal on inner and outer marginals (Figs 125G; 126D).

Egg capsules: unknown.

Development: assumed to be direct in all species.

Distribution. Southern New Zealand: *R. suteri*.

Southern Australia and Tasmania: *Cingulina australis* T. Woods, 1877 (Figs 49, 125), = *Rissoia* (*Onoba*) *tenisoni* Tate, 1899, unnecessary replacement name; *Rissoina unilirata* T. Woods, 1878 (Fig. 126A–D).

South Africa: ? *Rissoa rara* Thiele, 1925.

Material examined.

\+ *R. suteri*. Holotype and paratypes (AMS) and several other lots (AMS, NMNZ).
+**C. australis*. Many lots (AMS).
+**R. unilirata*. Many lots (AMS).
R. rara. Holotype (HUM).

Remarks. Unfortunately the type-species of *Lironoba* is only known from its shell and conclusions about its relationships must be drawn from *L. australis* which, although assumed to be congeneric, is probably not very closely related to *L. suteri*. *Rissoina unilirata* (Fig. 126A–D) is probably also congeneric. Some other Tasmanian species (such as *Rissoa freycineti* May, 1915 and *Rissoa agnewi* T. Woods, 1877) are similar to *Lironoba suteri* but lack a duplicated peristome. They are probably species of *Onoba*.

This genus is clearly related to *Merelina* although it differs in both teleoconch and protoconch sculpture. The duplicated peristome of the shell and two pairs of denticles on the face of the central teeth of the radula are characters shared with *Merelina* as are the somewhat subcentral position of the nucleus of the operculum (in *L. australis*) and the characters of the head-foot. In addition, the penis of *L. australis* has an open seminal groove as in *Merelina*, although the female genitalia differ, principally in that species of *Merelina* have an open pallial oviduct whereas this duct is only partially open in *L. australis*. Another difference is the simple bursal duct in *L. australis*, compared with the swollen, muscular sperm chamber representing the bursal duct in *M. elegans*.

In possessing strong spiral cords on the teleoconch, *Lironoba* closely parallels three other genera, *Attenuata*, *Onoba* and *Cingula* (subgenus *Lirocingula*), but these can be distinguished by their protoconch sculpture. In addition these genera have only a single pair of denticles on the face of the central teeth of the radula.

The peculiar, ridge-like structure on the inside of the operculum of *L. australis* (Fig. 125B, C) is probably a remnant of an opercular peg such as that seen in *Rissoina* and some other genera. It is not present in the only other species examined but its presence has been confirmed in several specimens of *L. australis*.

Ponder (1967) erected the Lironobinae for *Lironoba* and *Nobolira*. The status of this group is further discussed under *Attenuata* and *Merelina*. Any further use of this family-group name should be suspended until at least the radula of the type-species of *Lironoba* has been examined.

Genus *Attenuata* Hedley, 1918

Attenuata Hedley, 1918: M.52. Type-species *Rissoa integella* Hedley, 1904; original designation. Recent, south-eastern Australia (Fig. 127A–C).

Nobolira Finlay, 1926: 227. Type-species *Lironoba polyvincta* Finlay, 1924; original designation. Miocene, New Zealand (Figs 50; 127D–F).

Adolphinoba Powell, 1930: 537. Type-species *Adolphinoba finlayi* Powell, 1930; original designation. Recent, New Zealand (Fig. 128D–H).

Diagnosis. *Shell*: minute to small, tall-spired to conic, non-umbilicate, with prominent, well spaced spiral ridges and, rarely, axial folds. Aperture usually with duplicated peristome, oval, without distinct channels. Outer lip opisthocline, with varix (Figs 50; 127A, D; 128A, D). Teleoconch microsculpture of close, axial rugae (Fig. 127C, F) and, in some species, fine spiral threads, the latter crossing the axial rugae and rendering them minutely gemmate. Protoconch dome-shaped, of about 1½ whorls, with several (6–11) simple spiral cords with irregular, minute, granules between them (Figs 127B, E, G; 128B, F).

Head-foot: tentacles rather short to moderately long, rather flat, not tapering; snout short, bilobed. Eyes present or (possibly) absent. No accessory tentacles apparently present (from dried material of *N.* '*bollonsi*' (= *A. manawatawhia* Powell) Ponder, 1967; and *A. finlayi*, off Mayor Island, New Zealand, 59–74 m).

Anatomy: unknown.

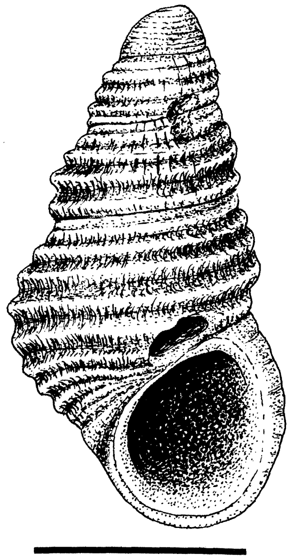

Fig. 50. *Attenuata polyvincta* (Finlay), type-species of *Nobolira* Finlay; holotype; Pukeuri, Oamaru, New Zealand, Miocene (AIM). **Scale:** 1 mm.

Operculum: simple, thin, nucleus eccentric to subcentral; last whorl large (*A.* '*bollonsi*' (= *manawatawhia*), Ponder 1967, *A. archensis* (May) and *A. finlayi*) (Fig. 128E).

Radula: central teeth $\dfrac{6-21+1+6-21}{(0-1)\qquad(1-0)}$, very broad and narrow dorsoventrally (about 3-4 times wider than high), with small lateral cusps and small, blunt median cusp; basal denticles lacking in *A. finlayi*, blunt, short in *A. archensis*, although apparently absent from some teeth; lateral margins at about 25°-30°, simple, thickened; ventral margin almost straight. Lateral teeth rather short $4-5+1+14-19$ in *A. archensis*, c.$3+1+$c.12 in *A. finlayi*, or apparently smooth except for prominent primary cusp (in *A. manawatawhia*). Marginal teeth with few to several rather long cusps on distal ⅓ of inner edge of inner marginal teeth and distal ¼-½ of inner edge of outer marginal teeth in *A. archensis* and *A. finlayi*; apparently smooth to weakly dentate in *A. manawatawhia* (data on *A. manawatawhia* from Ponder, 1967) (Fig. 128C, G, H).

Egg capsules: unknown.

Development: assumed to direct in all species.

Distribution. New Zealand: several species including *Nobolira manawatawhia* Powell, 1937 and *A. finlayi*; see Powell (1979) for a list of species.

Temperate Australia: *R. integella; Rissoa lockyeri* Hedley, 1911; *Rissoa archensis* May, 1913 (Fig. 128 A-C); *Alvania praetornatilis* Hedley, 1912; *Rissoa schoutanica* May, 1913; *Rissoa wilsonensis* Gatliff & Gabriel, 1913.

Miocene and Upper Eocene of southern Australia: undescribed species.

Miocene of New Zealand: *L. polyvincta*; *Lironoba charassa* Finlay, 1927; *Nobolira inflata* Laws, 1939.

Eocene of New Zealand: an undescribed species.

Material examined.

+ **R. integella.* Holotype, paratype and a few other lots (AMS).

+ **A. finlayi.* 2 lots (NMNZ).

+ **N. manawatawhia.* A few lots (AMS, NMNZ, AIM).

R. lockyeri. Holotype, paratypes and a few other lots (AMS).

+ **R. archensis.* Broken holotype (TM), paratypes and several other lots (AMS).

A. praetornatilis. Holotype and several other lots (AMS).

R. schoutanica. Holotype (TM), paratype and several other lots (AMS).

R. wilsonensis. Holotype and partypes (NMV) and a few other lots (AMS).

+ **L. polyvincta.* Holotype (AIM) and one other lot (NZGS).

L. charassa. One lot (AUG).

N. inflata. Paratypes (AUG).

Three additional New Zealand species examined for protoconch microsculpture: *N. bollonsi* Powell, *N. cochlearella* Powell (both NMNZ) and *Attenuata* sp. (Eocene) (NZGS).

Remarks. The peculiar radular characters (Fig. 128 C, G, H) set this genus apart from all other Rissoidae. Unusual features include the relatively broad central teeth, the rather short, multicuspate lateral teeth and the inner marginal teeth having cusps on the inner, not the outer edge. Ponder (1967) erected a subfamily (Lironobinae) on the basis of the radula in *Lironoba* (*Nobolira*) '*bollonsi*' (= *manawatawhia*). Species assumed to be congeneric with the type-species of *Lironoba* herein have a typical rissoid radula so the Lironobinae should not be recognised, at least on that basis. There may, eventually, be anatomical grounds for placing *Attenuata* in a separate subfamily or family but until further details are known, such as the nature of the radula of the type-species, there are insufficient grounds for doing so.

Species of *Attenuata* differ from other rissoid genera with spirally lirate teleoconchs in their usually duplicated peristome and spirally sculptured protoconchs, as well as in the peculiar, broad central radular teeth. The radulae of more species of *Attenuata* need examination to confirm the constancy of the characters of the central teeth.

This genus appears to be confined to the Continental Shelf and upper Continental Slope of New Zealand and Australia. Several undescribed species are known from Australia and the genus is known to extend into tropical waters in eastern Australia. It has a fossil history reaching back to the Eocene in southern Australia and New Zealand, suggesting that it has been isolated in Australasia since early Tertiary times.

Genus *Rissoina* Orbigny, 1840

Rissoina Orbigny, 1840: 395. Type-species *Rissoina inca* Orbigny, 1840; original designation. Recent, Peru and Chile (Fig. 129A-D).

Diagnosis. *Shell*: small to large; elongate-conic, non-umbilicate, solid, with axial ribs and/or spiral sculpture, or smooth; basal sculpture sometimes distinctive. Aperture D-shaped, distinctly angled and channelled anteriorly and posteriorly, anterior channel narrow, immediately adjacent to columella; peristome simple. Columella and inner lip form an almost straight line at about 45° to vertical axis of shell. Outer lip opisthocline, usually with strong varix. Protoconch paucispiral or multispiral, dome-shaped, smooth or weakly sculptured. Periostracum often calcified.

Head-foot: cephalic tentacles long, slightly tapering, very inconspicuously ciliated; eyes in bulges at their outer bases. Snout rather long, narrow, bilobed. Foot rather narrow in front, propodium moderately well developed. Anterior mucous gland distinct, triangular, opening at anterior edge of foot; posterior mucous gland absent. Two pallial tentacles, anterior or posterior sometimes bilobed. Metapodial tentacle short, broad, triangular, absent in *Rissoina* (*Apataxia*). External parts of animal unpigmented.

Anatomy: ctenidial filaments broadly to narrowly triangular, length slightly less than width to about ⅓ longer. Osphradium narrower to slightly wider than filament bases. Stomach very long due to elongation of posterior chamber; stomach-style sac ratio 4.5-5.6, length-width ratio 3-4, crystalline style present or absent. Intestine-rectum almost straight, faecal pellets packed sideways in some species.

Male with open or closed penial duct, penis with or without large glandular distal swelling, which is complexly fluted in some species. Prostate gland long and narrow, open or closed, not massively glandular. Prostatic tissue in penial duct in some species. Seminal vesicle coiled on posterior part of inner side of stomach.

Female (Fig. 52) with large (small in one subgenus) distal vestibule (*v*) modified as sperm storage area and with short, slit-like, subterminal opening (*ga*). Ventral channel (*vc*) and sperm groove (*sd*) separated; sperm groove usually closed to form a separate duct along most of capsule gland which opens to bursa copulatrix. Bursa copulatrix (*b*) larger than upper oviduct gland (*uog*) to subequal in size; entirely, to mainly, within pallial cavity, mainly in space between upper and lower oviduct glands but overlapping both glands on their right side. Seminal receptacle (*sr*) very small, vertical to subvertical, at anterior edge of upper oviduct gland (and thus either within pallial cavity or just behind it in smaller species); opening to oviduct immediately anterior to upper oviduct gland. Upper oviduct gland (*uog*) about ¼ to ½ length of lower oviduct gland (*log*), U-shaped, thickly glandular, without obvious sperm-storing capacity, partly within pallial cavity in large species, immediately behind posterior pallial wall in smaller species.

Nervous system with cerebral ganglia abutting or joined by a short commissure; supraoesophageal commissure equal to, or about twice length of suboesophageal commissure or up to about three times as long as supraoesophageal ganglion. Left pleural ganglion and suboesophageal ganglion abut in one species.

Operculum: thick, yellow, with strong, curved, hollow or grooved peg arising from nucleus on inner side, distal end of peg sometimes bilobed. Nucleus eccentric, submarginal, last whorl very large. A weak ridge runs parallel to columellar edge.

Radula: central teeth $\frac{2\text{-}5+1+2\text{-}5}{(0\text{-}3)+1\;1+(0\text{-}3)}$; lateral margins thickened, at 40°-55°, with 0-3 small denticles arising from them; U-shaped ventral extension weak to strong. Lateral teeth 4-7 + 1 + 2-9. Marginal teeth with subequal cusps; inner marginal teeth with cusps on distal ¼-⅓ of outer edge (and inner edge in *R. ferruginea* (Hedley)); outer marginal teeth with cusps on distal ¼-⅓ of inner and outer edges.

Egg capsules: pear-shaped, point of attachment very small, with one embryo (*R. anguina* Finlay, Ponder, 1968).

Development: direct or with planktotrophic larval stage (deduced from protoconch morphology).

Distribution. World wide in temperate and tropical seas. Upper Jurassic to Recent. Many species.

Remarks. There have been a large number of genus-group taxa proposed for species of *Rissoina*. These have been variously interpreted as synonyms and subgenera (Wenz, 1939, Kosuge, 1965a, b, Voorwinde, 1966 and Ponder, 1967) and some have been given subfamily status in a separate family, the Rissoinidae (Coan, 1964). Kosuge (1965b) described the anatomy, operculum and radula of several Japanese species and Ponder (1967, 1968) described the anatomy, radula and operculum of a New Zealand species. The sculptural variation exhibited by species of *Rissoina* (s.l.) is considerable, ranging from smooth to axially costate, cancellate and spirally striate. Broad groupings can be achieved on the basis of sculpture but these do not appear to exhibit any other features peculiar to these groupings. It is possible that the sculptural groupings are polyphyletic so that the arrangement given below may be artificial. Any finer subdivision based on the available names does not appear to be justifiable, given the overall similarity in shell, radula, operculum and anatomy. If all the presently available names were upheld several additional subgenera would be necessary to accommodate the sculptural patterns not already catered for and the subgeneric units here recognised would have to be elevated to generic rank. As these generic units would be based on sculpture alone this would, I believe, be a retrograde step. A few species exhibit shell sculpture intermediate between the subgenera here recognised. This is another reason why these groups should not be given more than subgeneric status. A key based primarily on sculptural differences between the subgenera here recognised is provided.

Rissoina exhibits a number of primitive character-states that may be a reflection of its long history. It has apparently remained little changed since the Upper Jurassic. Some of the primitive states include the head-foot characters (triangular metapodial tentacle, lack of a posterior pedal gland and presence of right and left pallial tentacles), the presence of glandular structures associated with the penis, and open pallial prostate gland, seminal groove and penial duct in some species. The retention of a separate sperm groove and duct in the capsule gland is also regarded as primitive. The radula has a single pair of denticles on the face of the central teeth and a variable number of cusps arising from the lateral margins. The outer marginal teeth have cusps on their outer as well as their inner edges, a character that may also be primitive.

Key to subgenera of *Rissoina* (based on shell characters)

1. Shell with axial and spiral sculpture forming a cancellate pattern over whole surface.. *Phosinella*

—— Shell with axial or spiral sculpture predominating, or with 1–2 strong spiral ribs and axial ribs, or smooth...2

2. Shell with strong axial sculpture, very weak or no spiral sculpture and a spiral ridge on lower base... *Rissolina*

—— Shell with or without strong axial sculpture, with or without spiral sculpture and usually lacking a well defined spiral ridge on lower base.......................3

3. Shell with axials abruptly terminated at periphery by a strong spiral cord. .... *Pachyrissoina*

—— Shell with axials (when present) not abruptly terminated by a strong spiral cord at periphery...4

4. Shell with spiral cords crossing stronger axials; protoconch sometimes strongly sculptured; aperture about equal in length to greatest height of penultimate whorl; lirae inside outer lip; body whorl subangled.......................... *Apataxia*

—— Shell with spirals and/or axials; protoconch smooth or weakly sculptured; aperture longer than greatest height of penultimate whorl; outer lip smooth within; body whorl convex to subangled...5

5. Shell with 1-2 strong spiral cords and weak to moderate axial ribs; whorls angled by spiral cords.. *Buvignieria*

—— Shell with spirals or axials predominating; spire whorls evenly rounded. .... *Rissoina* s.s.

Subgenus *Rissoina* s.s.

Zebinella Mörch, 1876: 47. Type-species (*Helix*) *decussata* Montagu, 1803; subsequent designation Martens, 1878: 30. Recent, West Indies (Fig. 133A-C).

Moerchiella Nevill, 1885: 73,88. Type-species *Rissoa gigantea* Deshayes, 1850; original designation. Recent, Indo-Pacific (Fig. 131A).

Parazebinella Boettger, 1893: 108. Type-species *Rissoina* (*Parazebinella*) *crenilabris* Boettger, 1893; monotypy. Recent, Philippines (Fig. 133F).

Stiva Hedley, 1904: 192. Type-species *Stiva ferruginea* Hedley, 1904; original designation. Recent, south-eastern Australia (Fig. 130A-C).

Chiliostigma Melvill, 1918: 147. Type-species *Rissoina* (*Chiliostigma*) *refugium* Melvill, 1918; subsequent designation Coan, 1964: 169. Recent, Gulf of Oman.

Caporista Iredale, 1955: 81. Type-species *Rissoina iredalei* Laseron, 1950; original designation. Recent, New South Wales, Australia (Fig. 132C-E).

Austrosina Laseron, 1956: 393. Type-species *Rissoina pulchella* Laseron, 1956, not Brazier, 1877 (Fig. 129 E-G), = *Pyramidella ambigua* Gould, 1849 (misidentified type-species); original designation. Recent, north-eastern Australia.

Peripetella Laseron, 1956: 400. Type-species *Peripetella queenslandica* Laseron, 1956, = *Pyramidella ambigua* Gould, 1849; original designation. Recent, north-eastern Australia (Figs 53B; 129E-G).

Pleneconea Laseron, 1956: 402. Type-species *Pleneconea angulata* Laseron, 1956; original designation. Recent, north-eastern Australia (Fig. 132A, B).

Zymalata Laseron, 1956: 416. Type-species *Zymalata concinna* Laseron, 1956; original designation. Recent, north-eastern Australia (Fig. 133D, E).

Condylicia Laseron, 1956: 418. Type-species *Condylicia collaxis* Laseron, 1956; original designation. Recent, north-eastern Australia (Fig. 51).

Laseronia Cotton, 1959: 355. Type-species *Rissoina cretacea* T. Woods, 1878; original designation. Recent, south-eastern Australia (Fig. 130D-G).

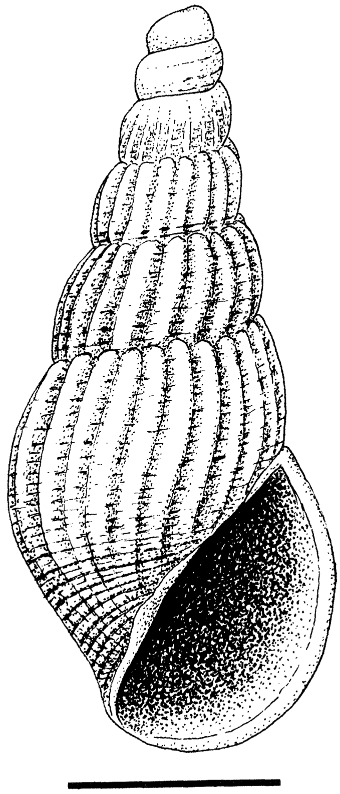

Fig. 51. *Rissoina* (*Rissoina*) *collaxis* (Laseron), type-species of *Condylicia* Laseron; holotype, Howick Islands Group, Queensland, Australia (AMS, C.41445). **Scale:** 1 mm.

Sulcorissoina Kosuge, 1965a: 108. Type-species *Rissoina imbricata* Gould, 1861, = *Rissoina striatula* Pease, 1867, = *Rissoina enteles* Melvill & Standen, 1896, = *Rissoina striatula hawaiensis* Pilsbry, 1920; original designation. Recent, Indo-Pacific.

Ailinzebina Ladd, 1966: 65. Type-species *Zebina* (*Ailinzebina*) *abrardi* Ladd, 1966; original designation. Miocene to Recent, Pacific Ocean.

Fercurtia Gougerot & Le Renard, 1977: 33, 40. Type-species *Rissoina semistriata* (Lamarck), = *Melania semistriata* Lamarck, 1804; original designation. Eocene, Paris Basin, France.

Diagnosis. *Shell*: as for genus; sculpture of weak to moderate axial ribs and (usually) with weaker spiral sculpture; sometimes spiral sculpture predominates, sometimes smooth. Base lacks a strong spiral fold (Figs 51; 53B; 129A, E; 130A, D; 131A; 132A, C; 133A, D, F). Protoconch paucispiral to multispiral, sometimes minutely pitted, usually smooth, rarely with granules in spiral series (Figs 129C; 130F; 132B; 133C, E).

Head-foot: as for genus (Several species examined; Ponder, 1967, pl. 4, figs 2, 3; 1968, fig. 27).

Anatomy: based on *Rissoina ambigua*, Lizard Island, Queensland, Australia (sectioned material); *R. variegata* Angas, Port Stephens, New South Wales, Australia (several specimens), and *R. striata* (Quoy & Gaimard), Norsup, Malakula, Vanuatu (1 female). Data also on *Rissoina* (*Zebinella*) *striata* (not of Quoy & Gaimard) (Kosuge, 1965b) and *R. chathamensis* (Hutton) (Ponder, 1968). As for genus; male with distal penial enlargement (male of *R. striata* not examined) which is sometimes complexly fluted. Penial duct open (at least over proximal portion of penis) distally enclosed and containing prostatic tissue in some species (confirmed in *R. ambigua*, absent from *R. chathamensis*). Prostate gland open, long and narrow, with thin, glandular walls.

Female genitalia (Fig. 52) as for genus; vestibule (*v*) large.

Nervous system (of *R. striata* only) with abutting cerebral ganglia and left pleural and suboesophageal ganglia also abutting. Supraoesophageal commissure about three times length of supraoesophageal ganglion.

Operculum: as for genus; with hollow peg (Figs 129D, F; 130E; 131B, D; 132D; 133B).

Radula: as for genus (Figs 129B, G; 130B, C, G; 131C, E, F; 132E).

Egg capsules: as for genus.

Development: direct or with planktonic larval stage.

Distribution. World-wide in temperate to tropical seas. Many species.

Upper Jurassic of Europe: *Rissoa obliquata* Sowerby, 1829; *Rissoa acuta* Sowerby, 1829 not Fréminville, 1814, = *Rissoina ancliffensis* Cox & Arkell, 1950.

Cretaceous: *Melania incerta* Deshayes, 1842.

Examples of Eocene species (all Paris Basin, France): *M. semistriata*; *Melania clavula* Deshayes, 1824; *Melania cochlearella* Lamarck, 1804; *Melania polita* Deshayes, 1825; *Rissoina discreta* Deshayes, 1861; *Rissoina puncticulata* Deshayes, 1861; *Rissoina raincourti* Cossmann, 1885. See also Gougerot & Le Renard, 1977.

Material examined.

+*_R. inca._ 15 syntypes (BMNH) and one other lot (AMS ex LACM).
+*_R. decussata._ A few lots (USNM).
R. gigantea. Several lots (AMS etc.)
*_S. ferruginea._ Types and several other lots (AMS).
_R._ (_P._) _crenilabris._ Lectotype and paralectotype (SMF), a few other lots (AMS).
_R._ (_C._) _refugium._ Holotype (BMNH).
+*_R. iredalei._ Syntypes and several other lots (AMS).
R. pulchella. Syntypes (AMS).
+*_P. queenslandica._ Holotype and paratypes and many other lots of _R. ambigua_ (AMS).
P. angulata. Holotype and paratypes and several other lots (AMS).
Z. concinna. Holotype and paratypes and several other lots (AMS).
+*_L. cretacea._ Holotype and several other lots (AMS).
C. collaxis. Holotype (AMS).
R. imbricata. Holotype (USNM), a few lots (NSMT, AMS, ANSP, USNM).
R. striatula. Holotype (MCZ).
R. striatula hawaiensis. Syntypes (ANSP).
_Z._ (_A._) _abrardi._ Holotype and 2 paratypes (USNM).
R. obliquata. One lot (BMNH).
R. ancliffensis. One lot (BMNH).
M. incerta. One lot (BMNH).
Eocene _Rissoina._ All PCB.

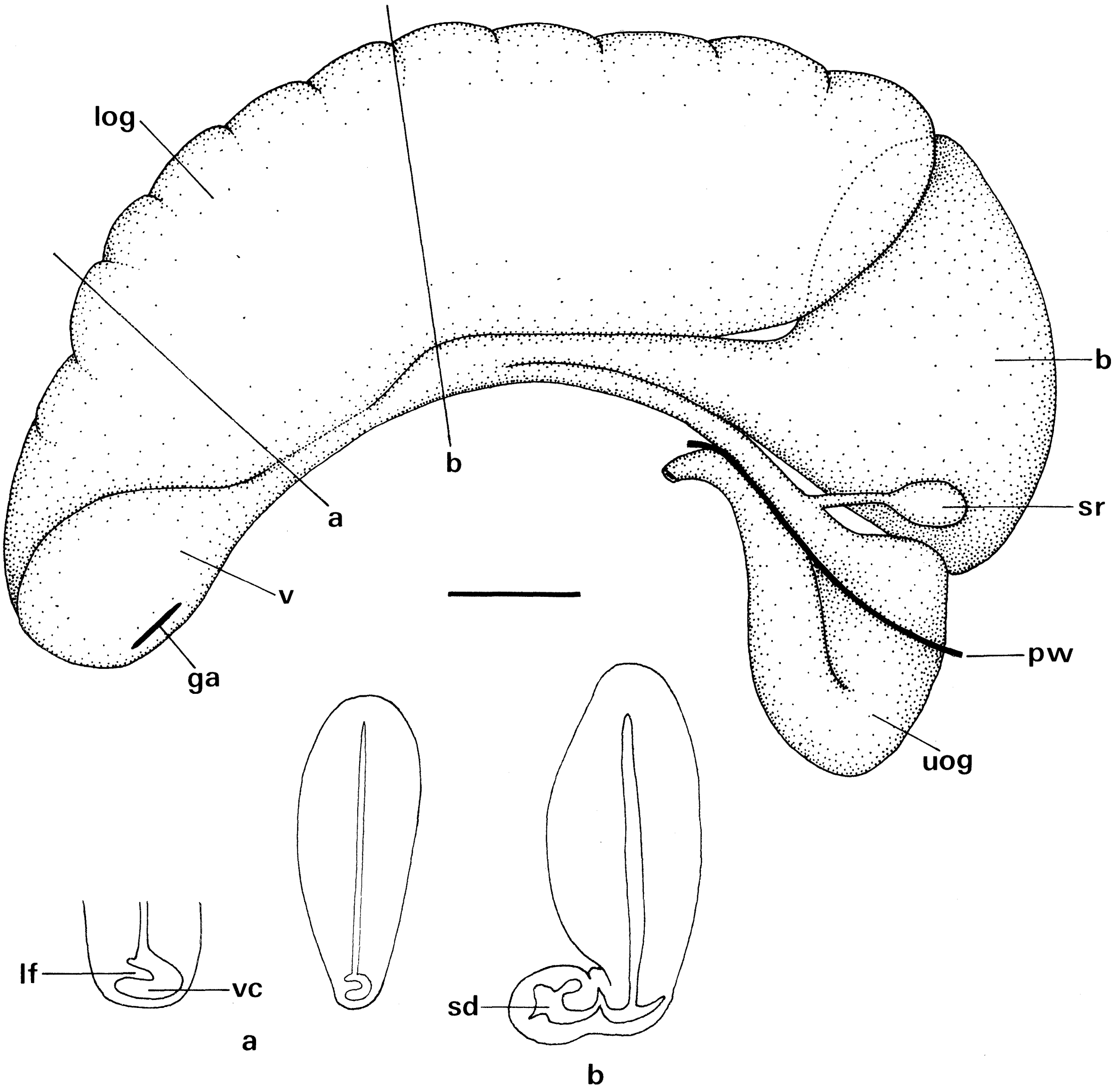

Fig. 52. Female genitalia of *Rissoina* (*Rissoina*) *striata* (Quoy & Gaimard), left side. Transverse sections a and b taken at positions indicated through lower oviduct gland. *b*-bursa copuatrix; *ga*-pallial genital opening; *lf*-longitudinal fold in ventral channel; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sd*-sperm duct; *sr*-seminal receptacle; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel. **Scale:** 0.5 mm.

Radulae and opercula also examined of *Rissoa spirata* Sowerby, 1820-24, *Rissoa striata* Quoy & Gaimard, 1832, and *Rissoina variegata* Angas, 1867. Shells of many additional species examined.

Remarks. Species in this subgenus range from smooth to strongly axially or spirally sculptured. They lack a strong spiral ridge on the lower base, a feature distinguishing them from species in the subgenus *Rissolina*. Some species of *Rissoina* s.s. have a weak basal fold so that this structure alone cannot be used to separate the two subgenera. Species of *Rissoina* s.s. also differ from those of *Rissoina* (*Rissolina*) in usually being less coarsely axially sculptured and in often having spiral sculpture. These two subgenera are, however, sometimes not readily distinguished and are retained as groupings of convenience only.

The sculptural forms exhibited by the type-species of the genus-group taxa listed in the synonymy all appear to integrade with one another. Members of one group, typified by *Zebinella* (includes *Chiliostigma, Pleneconea, Zymalata* and *Ailinzebina*) (Figs 132A; 133A, D) are all sculptured with rather weak, sharp axial ribs and have distinct spiral sculpture. These merge, through numerous gradations, to species similar to the type-species of *Rissoina* (Fig. 129A). *Rissoina* (*Parazebinella*) *crenilabris* (Fig. 133F) is unusual in having strongly angled whorls and a large aperture with a distinctly crenulated edge. A somewhat similarly shaped shell, but with much finer axial ribbing and convex whorls, is *Zymalata concinna* (Fig. 133D), which approaches species typical of *Zebinella* through species such as *Rissoina triangularis* Watson, 1886.

Rissoina lepida Woodring, the fossil type-species of *Mirarissoina*, has sculpture similar to that of species of the *Zebinella* group, but has a small, deep notch in the posterior corner of the aperture. The operculum of a closely related Recent species is simple. These species are placed in *Folinia*.

Members of the group of species formerly included in *Moerchiella* (Fig. 131A) are all tropical and probably closely related. They are typical of *Rissoina* in anatomy (based on that of *R. striata*) and have no distinctive shell features except their change from a predominance of axial to spiral sculpture with shell growth. Some of the species are larger than the majority of those in *Rissoina* s.s., but otherwise there do not appear to be any reasons why this species-group should be separated. Consequently, it is reduced to a synonym of *Rissoina* s.s.

Stiva has been used to include three species, all restricted to south-eastern Australia, and, apart from the large size of the type-species (Fig. 130A), they are distinguished by lacking spiral sculpture and in having an angled to subangled body whorl. These differences alone do not seem sufficient to warrant the recognition of *Stiva* as a distinct subgenus. The external features of the animal and the radula and operculum are typical of *Rissoina* s.s. except that there is only a simple, very short pallial tentacle in the anterior and posterior corners of the aperture in *R. ferruginea*.

Sulcorissoina was separated because of the uniform spiral sculpture of the type-species but this is considered to be insufficient reason for its recognition as a distinct group. Some temperate Australasian species are smooth or weakly to moderately spirally striate and these appear to be similar anatomically to more typical species of *Rissoina*.

Subgenus *Rissolina* Gould, 1861

Rissolina Gould, 1861: 401. Type-species *Rissoina plicatula* Gould, 1861; subsequent designation, Nevill, 1885: 73, 77. Recent, Indo-Pacific (Fig. 134A-D).

Eurissolina Woodring, 1928: 368 (= *Eurissoina* error of authors). Type-species *Rissoina* (*Eurissolina*) *ditomus* Woodring, 1928; original designation. Miocene (= Pleistocene), Bowden, Jamaica.

Costalynia Laseron, 1956: 394. Type-species *Rissoina cardinalis* Brazier, 1877; original designation. Recent, north-eastern Australia (Fig. 134E).

Fractoralla Laseron, 1956: 398. Type-species *Fractoralla praecida* Laseron, 1956; original designation. Recent, northern Australia (Fig. 53A).

Diagnosis. *Shell*: as for genus but axial sculpture always strong, spiral sculpture weak or absent except for a few spiral cords on periphery and upper base in some species. Lower base with a strong spiral fold (Figs 53A; 134A, E, F). Protoconch as for *Rissoina* s.s. (Fig. 134C).

Head-foot: as for genus. Kosuge (1965) states that *R.* (*Rissolina*) *costulata* has the left pallial tentacle 'three-forked' and *R.* (*Rissolina*) *plicata* has a single right and left pallial tentacle.

Anatomy: based on *R.* (*Rissolina*) cf. *crassa* Angas, Thevenard, near Ceduna, South Australia (1 male, 1 female). *Rissoina* (*Rissolina*) *plicata* (A. Adams) and *R.* (*R.*) *costulata* (Dunker) (Kosuge, 1965b) have also been described and appear to be similar. As for genus; male with penis having complex, expanded distal portion nearly as long as narrow, stalk-like proximal portion. Penial groove visible externally as a line but possibly sealed (Fig. 54C). Prostate open, with about ⅙ of length embedded in kidney. Kosuge (1965b) does not describe the male genitalia.

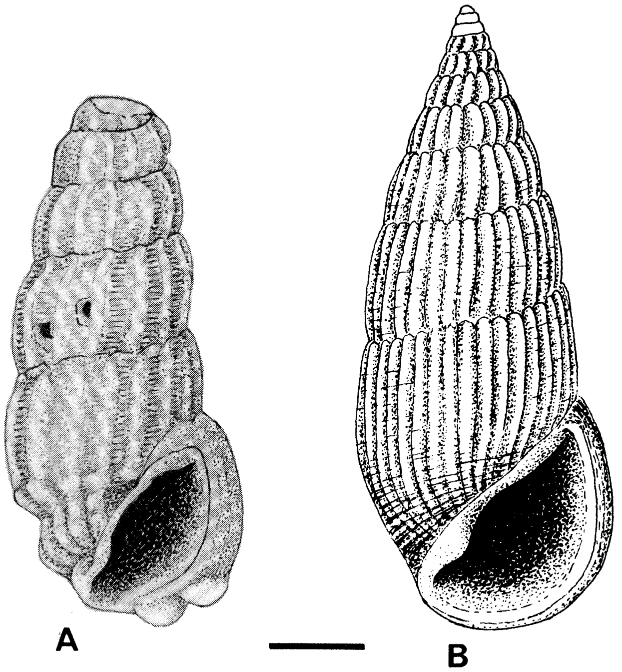

Fig. 53. **A**, *Rissoina* (*Rissolina*) *praecida* (Laseron), type-species of *Fractoralla* Laseron; holotype, Darwin, Northern Territory, Australia (AMS, C.102435). **B**, *Rissoina* (*Rissoina*) *ambigua* (Gould); holotype of *Peripetella queenslandica* Laseron, type-species of *Peripetella* Laseron; Bowen, Queensland, Australia (AMS, C.102387). **Scale:** 1 mm.

Female with posterior portion of bursa copulatrix and seminal receptacle (but not its duct) behind posterior pallial wall. Anterior sperm pouch massive, about half as long as entire glandular oviduct.

Nervous system (described by Kosuge, 1965b), with cerebral ganglia abutting and supraoesophageal connective about twice as long as suboesophageal connective, in *R.* (*R.*) *costulata*, or, as in *R.* (*R.*) *plicata*, cerebral ganglia separated by short commissure and suboesophageal and supraoesophageal commissures about equal in length.

Operculum: as for *Rissoina* s.s. (Fig. 134B, H).

Radula: central teeth $\frac{2\text{-}5+1+2\text{-}5}{(0\text{-}1)+1 \quad 1+(0\text{-}1)}$ lateral margins at 45°-50°, U-shaped basal extension moderate to well developed. Lateral teeth 6-7 + 1 + 4-6. Inner marginal teeth with cusps on distal ⅓ of outer edge; outer marginal teeth with cusps on inner and outer edges of distal ¼ (Fig. 134D, G).

Egg capsules: unknown.

Development: direct or with planktotrophic larval stage.

Distribution. Indo-Pacific, temperate to tropical: several species including *Rissoina crassa* Angas, 1871

(Fig. 134F-H); *R. plicatula*, = *Rissoina laevicostulata* Pilsbry, 1904.

Miocene, Borneo: *Rissoina* (*Rissolina*) *semari* Beets, 1941.

Miocene, Pacific: several species, see Ladd, 1966.

Miocene of France: *Rissoina* (*Rissolina*) *aturensis* Cossmann & Peyrot, 1918.

Material examined.

+ * *R. plicatula*. Holotype (USNM), and several other lots (as *R. laevicostulata*) (USNM, AMS).
R. laevicostulata. Holotype (ANSP).
R. (*E.*) *ditomus*. Holotype (USNM).
F. praecida. Holotype and paratype (AMS).
R. cardinalis. Syntypes (AMS).

The operculum, radula and protoconch of *R.* cf. *crassa* were also examined, in addition to the shells of several other species.

Remarks. This subgenus forms a compact group of species exhibiting strong axial ribs, weak or absent spiral sculpture and a spiral fold on the lower base. *Rissolina* is very close to *Rissoina* s.s. but is maintained largely as a subgenus of convenience for a distinctive species-group centred in the Indo-Pacific. The species illustrated give an indication of the small range of shell variation in this group.

Subgenus *Phosinella* Mörch, 1876

Phosinella Mörch, 1876: 51. Type-species *Rissoa pulchra* C.B. Adams, 1850 (not Forbes, 1844), = *Rissoina cancellata* Philippi, 1847; subsequent designation Nevill, 1885; 73, 83. Recent, West Indies (Fig. 135A-D).

Phintorene Iredale, 1955: 81. Type-species *Rissoina allanae* Laseron, 1950; original designation. Recent, eastern Australia (Figs 54A; 135E-H).

Planapexia Laseron, 1956: 408. Type-species *Planapexia fractura* Laseron, 1956; original designation. Recent, northern Australia (Fig. 135I).

Diagnosis. *Shell*: as for *Rissoina* s.s. but teleoconch with clathrate sculpture. Inside outer lip smooth (Fig. 135B, G, I). Protoconch multispiral or paucispiral, weakly sculptured or smooth (Fig. 135A, E).

Head-foot: as for genus. Kosuge (1965) states that *R.* (*P.*) *media* Mohrenstern has single right and left pallial tentacles but *R.* (*P.*) *allanae* has a bifid left tentacle and a single right tentacle.

Anatomy: based on *R.* (*Phosinella*) *allanae*, Arrawara, near Coffs Harbour, New South Wales, Australia (1 male, 1 female). *Rissoina* (*Phosinella*) *media*, described by Kosuge (1965b), is similar. As for genus; male without prostate gland in *R.* (*P.*) *media*, pallial vas deferens an open groove. *R.* (*P.*) *allanae* has a very narrow, but probably thinly glandular tube in posterior pallial cavity, which appears to be closed except for narrow posterior opening. Penis with penial duct closed (*R.* (*P.*) *allanae*) or open proximally (*R.* (*P.*) *media*). Penial duct with associated (prostatic ?) glandular tissue in *R.* (*P.*) *media*. Distal end of penis with simple swelling bearing cuticular warts (*R.* (*P.*) *media*) or with separate, simple, glandular lobe (*R.* (*P.*) *allanae*) (Fig. 54A).

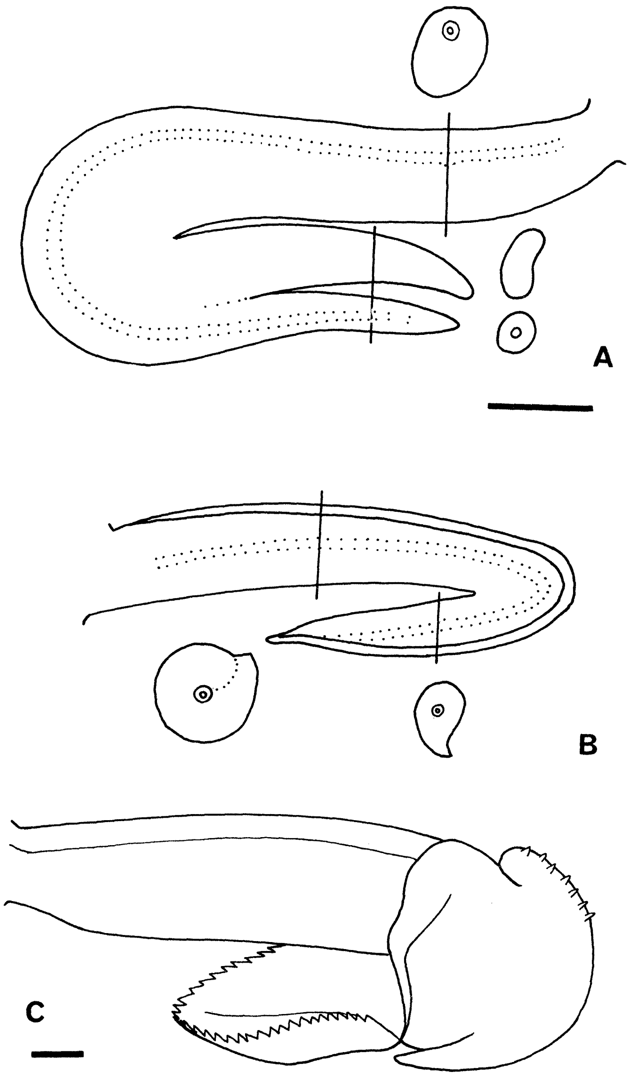

Fig. 54. Penes of *Rissoina* species. **A**, *Rissoina* (*Phosinella*) *allanae* Laseron. **B**, *Rissoina* (*Apataxia*) *miltozona* Tomlin. **C**, *Rissoina* (*Rissolina*) cf. *crassa* Angas. **Scale:** A, B - 0.1 mm; C - 0.2 mm.

Female with upper oviduct gland and a portion of bursa copulatrix behind posterior pallial wall (in *R.* (*P.*) *allanae*) and large vestibule.

Nervous system (of *R.* (*P.*) *media*) with cerebral ganglia separated by short commissure; supraoesophageal connective about twice as long as suboesophageal connective.

Operculum: as for *Rissoina* s.s. (Fig. 135C, F).

Radula: as for genus; central teeth $\frac{2\text{-}3+1+2\text{-}3}{1 \qquad 1}$, ventral margin with moderate to strong U-shaped extension. Lateral teeth 4-6 + 1 + 3(+). Marginal teeth as in *Rissoina* (*Rissolina*) (Fig. 135D, H).

Egg capsules: unknown.

Development: direct or with planktotrophic larval stage.

Distribution. Indo-Pacific; warm-temperate and tropical: several species.

Caribbean: a few species, e.g. *R. cancellata*.

Miocene, Pacific: see Ladd, 1966.

Material examined.

+ **R. cancellata*. 1 lot (USNM).
+ **R. allanae*. Syntypes and many other lots (AMS).
P. fractura. Holotype and paratypes (AMS).

The shells of several additional species have also been examined.

Remarks. The cancellate sculpture readily distinguishes species of *Phosinella* from those of the other subgenera of *Rissoina*. Species attributable to *Phosinella*, like those included in *Rissolina*, appear to belong predominantly to the Indo-Pacific fauna and to be of relatively recent origin.

Subgenus *Apataxia* Laseron, 1956

Apataxia Laseron, 1956: 401. Type-species *Apataxia erecta* Laseron, 1956, = *Rissoina miltozona* Tomlin, 1915; original designation. Recent, north-eastern Australia (Figs 54B; 55; 132F-H).

Apataxis error of authors.

Diagnosis. *Shell*: of small size, narrower than most *Rissoina* species. Sculpture of axial ribs crossed by weaker spiral cords. Aperture small, with a few weak ridges inside outer lip (Fig. 55). Protoconch typically conical, sculptured with raised chevron-shaped markings and granules in spiral series; apical whorl smooth; last whorl weakly keeled (Fig. 132G). Some species with apparently smooth, dome-shaped protoconch.

Head-foot: typical of genus except cephalic tentacles very weakly ciliated; no metapodial tentacle; left pallial tentacle bifid (*R. miltozona*, Lizard Island, Queensland).

Anatomy: based on *R.* (*A.*) *miltozona*, Komave, Fiji (several males), also described by Kosuge (1965b) as *R.* (*Apataxis* (sic!)) *cerithiformis* (sic!). As for genus; male with slender, simple penis with deep slit leading to central duct (Kosuge, 1965b). Specimens from Fiji appear to have slit fused with central duct and a lip externally marking edge of fused groove. Penis with short papilla-like structure distally (Fig. 54B) Prostate gland poorly developed, open, very narrow.

Female system not examined but Kosuge (1965b) states that 'vagina' (= vestibule) small and not inflated.

Nervous system not studied.

Operculum: typical of genus; but peg more massive than in *Rissoina* s.s. and grooved rather than hollow (Fig. 132F).

Radula: central teeth $\frac{2\text{-}3+1+2\text{-}3}{1+1\quad 1+1}$, lateral margins at 50°, with small denticle arising from them; ventral margin with moderate U-shaped exterior. Lateral teeth c.5 + 1 + 5. Marginal teeth as in *Rissoina* (*Rissolina*) (Fig. 132H).

Egg capsules: unknown.

Development: direct with planktotrophic larval stage.

Distribution. Indo-West Pacific: *Rissoa cerithiiformis* Dunker, 1887 (*nom. nud.*), ? = *Rissoina balteata* Pease, 1869, = *Rissoina costulata* Pease, 1868 (not Dunker, 1860), = *Rissoina miltozona* Tomlin, 1915, = *Apataxia erecta* Laseron, 1956, = *Apataxia eripona* Laseron, 1956.

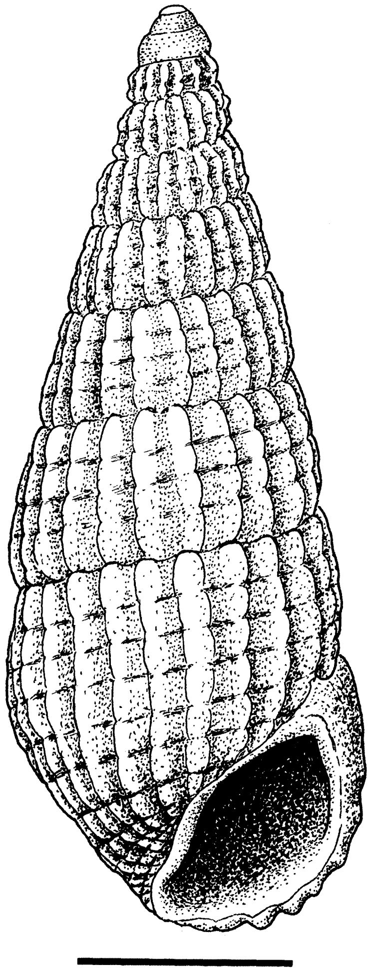

Fig. 55. *Rissoina* (*Apataxia*) *miltozona* Tomlin; holotype of *Apataxia erecta* Laseron, type-species of *Apataxia* Laseron; Heron Island, Queensland, Australia (AMS, C.102429). **Scale:** 1 mm.

Miocene, Pacific Islands: *Rissoina* (*Rissoina*) *waluensis* Ladd, 1966; *Rissoina* (*Phosinella*) *bikiniensis* Ladd, 1966; *Rissoina* (*Rissoina*) *goikulensis* Ladd, 1966.

Material examined.

R. cerithiiformis. 3 specimens *ex* Dunker (HUM).
R. costulata. Syntypes (ANSP, MCZ).
+ * *R. miltozona*. Holotype and paratype (BMNH), and many other lots (AMS).
A. erecta. Holotype (AMS).
A. eripona. Holotype and 3 paratypes (AMS).

Remarks. *Apataxia* is recognised because of the shell differences noted in the description, the different opercular peg, the simple penis and the small vestibule in the female genital system. The subgenus appears to contain only one Recent species and a few fossil species. It is restricted to the Indo-Pacific.

Subgenus *Pachyrissoina* Boettger, 1893

Pachyrissoina Boettger, 1893: 104. Type-species *Rissoina walkeri* Smith, 1893; subsequent designation Wenz, 1939: 628. Recent, Indo-Pacific (Fig. 56).

Diagnosis. *Shell*: rather broad, large, whorls lightly convex, narrowly shouldered just below sutures, with strong, rounded axial ribs and weak spiral striae. Axials terminated at periphery by a strong spiral cord (Fig. 56). Protoconch not known.

Animal unknown.

Distribution. Central Indo-Pacific: *R. walkeri*.

Material examined.

R. walkeri. Holotype and 3 paratypes (BMNH) and a few other lots (AMS).

Remarks. *Rissoina walkeri* does not appear to be closely related to any other species of *Rissoina*. The aperture is typical of *Rissoina* and suggests placement in that genus but its affinities need to be confirmed.

Boettger (1893) included *Rissoina basteroti* Mohrenstern, 1860 in his section *Pachyrissoina* but that species differs from *R. walkeri* in having axial ribs extending on to the base and it lacks a spiral keel on the periphery. *Rissoina basteroti* is thus best included in *Rissoina* s.s.

Subgenus *Buvignieria* Cossmann, 1921

Buvignieria Cossmann, 1921: 64. Type-species *Rissoina unicarina* Buvignier, 1843; original designation. Upper Jurassic, Europe.

Diagnosis. *Shell*: small, with spiral and axial sculpture, 1–2 spiral cords causing angulation of whorls. Aperture more weakly channelled anteriorly than in *Rissoina* s.s. (Fig. 133G). Protoconch multispiral (about 3 whorls) with regularly increasing convex whorls, the first minute; apparently smooth.

Animal unknown.

Development: presumably a planktonic larval stage present.

Distribution. Upper Jurassic of Europe: *Rissoa duplicata* Sowerby, 1829 (Fig. 133G); *Rissoa bisulca* Buvignier, 1843; *R. unicarina*.

Material examined.

R. duplicata. Several lots (including material *ex* Sowerby) (BMNH, WAM).

Remarks. *Buvignieria* contains species very similar to *Rissoina* s.s. in apertural and other features and probably represents an early group of *Rissoina* s.l.

The three species names listed above are probably all variants of the same species as far as can be judged from illustrations and the amount of variation seen in material of *R.* (*B.*) *duplicata* (Fig. 133G). Cossmann (1921) listed several additional species of *Buvignieria*, some of which are here regarded as being better located in *Rissoina* s.s., since they lack prominant spiral ribs.

Buvignieria carixensis Cox and *B. biornata* (Tate) are cerithiiaceans, as shown from examination of material in the BMNH.

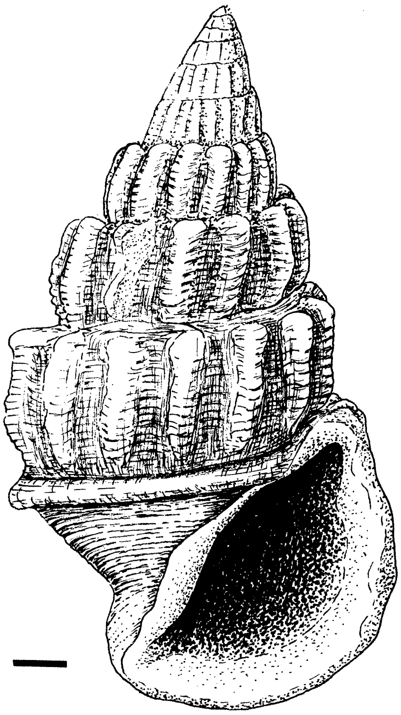

Fig. 56. *Rissoina* (*Pachyrissoina*) *walkeri* Smith; type-species of *Pachyrissoina* Boettger; Onslow, Western Australia (AMS, C.134887). **Scale:** 1 mm.

Genus *Zebina* H. & A. Adams, 1854

Zebina H. & A. Adams, 1854: 328. Type-species *Rissoina semiglabrata* A. Adams, 1854, ? = *Rissoa tridentata* Michaud, 1830 (Fig. 136 A-D); subsequent designation Rehder, 1980: 27. Recent, Indo-Pacific.

Diagnosis. *Shell*: small to large in size; non-umbilicate, ovate-conic to elongate-conic, smooth, often shining, often with axial ribbing on upper teleoconch whorls; sometimes with spiral sculpture and, in one species, with thin axial lamellae over whole surface. Aperture pyriform, channelled posteriorly, rounded or weakly channelled anteriorly, peristome simple; outer lip usually with heavy varix, sometimes dentate within, opisthocline. Protoconch smooth, sometimes decollate, multispiral to paucispiral.

Head-foot: as in *Rissoina* but pallial tentacles simple, slender.

Anatomy: similar to *Rissoina* but with relatively short stomach (see under *Zebina* s.s. for details).

Operculum: smooth, flat, thin, nucleus eccentric, last whorl large.

Radula: central teeth $\frac{2\text{-}6+1+2\text{-}6}{(0\text{-}1)+1\ 1+(0\text{-}1)}$, lateral margins thickened, at 40°–55°, simple or with small denticle arising from them; ventral margins with moderate to well developed U-shaped process. Lateral teeth 4-9 + 1 + 5-11. Marginal teeth with subequal cusps; inner marginal teeth with cusps on distal ⅓ of outer edge; outer marginal teeth with cusps on distal ⅓ of inner and outer edge (in *Z. tridentata*) or outer edge smooth.

Egg capsules: unknown.

Development: direct or with planktonic larval stage.

Distribution. Tropical and subtropical seas; worldwide. Several species. ?Upper Jurassic to Recent.

Remarks. *Zebina* and *Rissoina* are readily distinguished on stomach morphology, the lack of an opercular peg and the form of the anterior apertural channel in *Zebina*. *Zebina* and *Schwartziella* are, however, very closely related and differ mainly in shell-features. *Schwartziella* is not known in the fossil record until the Miocene and it is thus possible that it evolved from *Zebina*, which was well represented in the early Tertiary. The shell surface of *Zebina* is, however, smooth and glossy whereas some species of *Schwartziella* have a calcified periostracum like that seen in some species of *Rissoina*. More detailed anatomical studies are required to show if the two groups can be maintained as separate genera.

Key to Subgenera of *Zebina* (based on shell characters)

1. Shell usually lacking an anterior channel in aperture; with or without axial and spiral sculpture.......2

—— Shell with weak anterior channel in aperture; with spiral sculpture, lacking axial sculpture.......*Takirissoina*

2. Shell elongate-conic, body whorl smooth or with fine spiral sculpture (one species has widely spaced spiral ridges).......3

—— Shell ovate-conic, with closely-spaced spiral ridges and, in one species, with fine axial lamellae.......*Tomlinella*

3. Shell with curved spire, protoconch usually decollate, axial ribs well developed on spire whorls.......*Tiphyocerma*

—— Shell with straight spire, protoconch rarely decollate, axial ribs weak to absent on spire whorls.......*Zebina* s.s.

Subgenus *Zebina* s.s.

Iopsis Gabb, 1873: 272. Type-species *I. fusiformis* Gabb, 1873; monotypy. 'Miocene' of Santo Domingo.

Cibdezebina Woodring, 1928: 369. Type-species *Rissoina browniana* Orbigny, 1842; original designation. Recent, West Indies (Fig. 58A, B).

Diagnosis. *Shell*: As for genus; elongate conic; whorls more or less flat to lightly convex, sutures not much impressed; smooth or with very weak spiral threads (one species with spiral cords) and, in some species, axial ribs on upper teleoconch whorls (Figs 136A, G; 137G).

Head-foot: As for genus (several Indo-Pacific species examined and *Z. browniana*, Missouri Key, Florida) (Fig. 58A, B).

Anatomy: Based on *Zebina* '*nitens* Laseron, 1956' Lizard Island, Queensland, Australia (2 females, and sectioned females and male). Ctenidial filaments about twice as long as their bases; osphradium about equal in width to ctenidial filament bases and nearly as long as ctenidium. Stomach-style sac ratio 2.4, length-width ratio 1.7. Crystalline style present. Intestine-rectum not examined.

Male with open penial groove, penis with expanded, non-glandular distal portion (details not ascertained as only observed in sectioned material). Prostate gland narrow, open; pallial vas deferens an open ciliated groove.

Female genital tract (Fig. 57) similar to that of *Rissoina*, but with bursa copulatrix (*b*) on right side of oviduct glands, about half size of upper oviduct gland, its mid-point being opposite posterior pallial wall. Vestibule (*v*) of moderate size about ⅓ length of lower oviduct gland. Both vestibule and swollen, muscular pallial sperm duct (*bd*) leading back to bursa, contain sperm. Seminal receptacle (*sr*) about size of bursa and lies vertically immediately behind bursa and on right side of upper oviduct gland. Upper oviduct gland (*uog*) about half size of lower oviduct gland (*log*). Ventral channel and sperm duct separate, seminal receptacle duct opens to ventral channel.

Nervous system not examined.

Operculum: as for genus (Fig. 136B, C, F).

Radula: as for genus (Fig. 136D, E).

Distribution. Tropical and subtropical; Caribbean Sea, Western Atlantic, Indo-Pacific (several species). ?Upper Jurassic of Europe: *Rissoa laevis* Sowerby, 1829 (Fig. 137G), to Recent.

Examples of Eocene species (France) are *Rissoina laevigatissima* Deshayes, 1861; *Rissoina schwartzi* Deshayes, 1861 and *Rissoina* (*Zebina*) *pygmaea* Cossmann, 1888.

Material examined.

* *R. semiglabrata*. Type (BMNH).
* *R. tridentata*. Several lots (AMS, BPBM).
+* *R. browniana*. A few lots (USNM, AMS).
R. laevis. 3 lots (BMNH, WAM).
Several other species from the Indo-Pacific region. Eocene species. All PCB.

Remarks. These smooth, colourless rissoids are frequently mistaken for eulimids but their apertural characters are quite distinctive; in particular the heavy

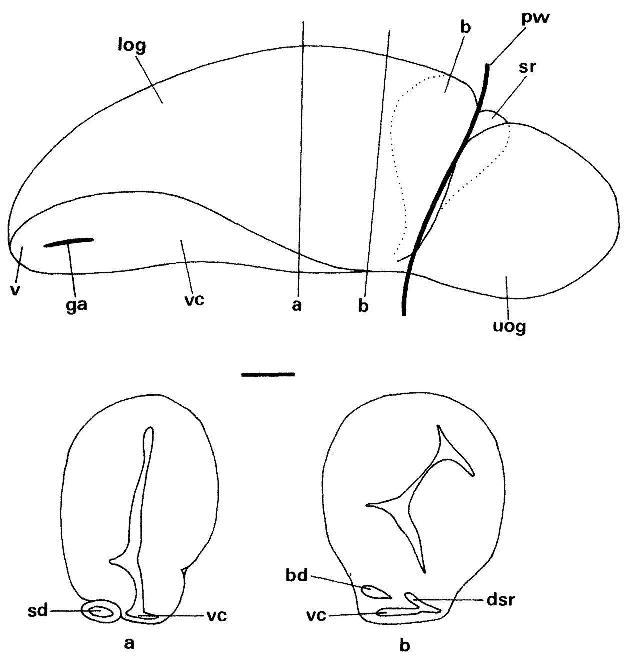

Fig. 57. Female genitalia of *Zebina* (*Zebina*) '*nitens* Laseron', left side. Transverse sections **a** and **b** taken at positions indicated through lower oviduct gland. *b*-bursa copulatrix; *bd*-bursal duct; *dsr*-duct of seminal receptacle; *ga*-pallial genital opening; *log*-lower oviduct gland; *pw*-posterior wall of pallial cavity; *sd*-tubular part of oviduct; *sr*-seminal receptacle; *uog*-upper oviduct gland; *v*-vestibule; *vc*-ventral channel. **Scale:** 0.1 mm.

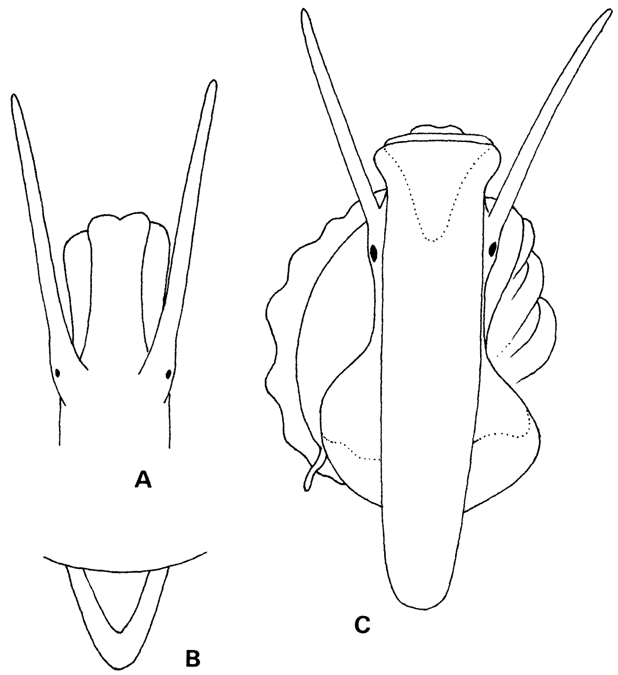

Fig. 58. A-B, *Zebina* (*Zebina*) *browniana* (Orbigny), Missouri Key, Florida: **A**, dorsal view of head; **B**, dorsal view of posterior end of foot; **C**, *Stosicia* (*Stosicia*) *annulata* (Dunker); Mersing, Malaya; ventral view of head-foot.

apertural varix and distinct posterior canal at the suture. The shell texture also differs, being more opaque and thicker than that of most eulimids.

There appear to be a large number of species of *Zebina* s.s. in the Indo-Pacific but their taxonomy is in a chaotic state.

Ladd (1966) placed *Moerchiella* (here regarded as a synonym of *Rissoina*) as a subgenus of *Zebina* and included in it some typical species of *Zebina*, as well as species of *Rissoina*.

Iopsis Gabb is placed in synonymy with *Zebina* on the authority of Pilsbry (1922: 382) who states that *I. fusiformis* is the neanic stage of *Zebina laevigata* (C. B. Adams).

Leaella Cossmann is usually regarded as a synonym or subgenus of *Zebina*. Cossmann (1921) designated *Pasithea notata* Lea, 1833, from the Eocene of Alabama as the type of *Leaella* but, as pointed out by Aldrich (1910) and Palmer (1937), Cossmann (1921) misidentified the specimens he illustrated and described as *P. notata*. Examination of the holotype in ANSP shows it to be an eulimid. Aldrich (1910) supplied a replacement name for Cossmann's species (*Eulima cossmanni*), based on an earlier (1893) illustration of Cossmann's. Palmer (1937) has taken *cossmanni* to be the type-species of *Leaella* but, because the shells illustrated by Cossmann (1893, 1921) differ in the number of whorls, there remains some doubt as to whether *cossmanni* is the species illustrated by Cossmann (1921) when he introduced *Leaella*. Dr A. Warén *(pers. comm.)* has indicated that *Pasithea lugubris* Lea, 1833 is probably based on a specimen of the species Cossmann had before him when naming his new genus. A submission to the ICZN will have to be made to resolve this matter.

One species, *Rissoa laevis* Sowerby, 1829 (Fig. 137G) from the Upper Jurassic of England, is possibly a *Zebina*. Cossmann (1921) recognises the genus in the Paleocene.

Rissoina vittata Gardner, 1947 is an unusual member of the genus in that it possesses strong spiral cords giving it a superficial resemblance to some species of *Stosicia*. Examination of the holotype in the USNM shows that it is probably a *Zebina*. Some other species of *Zebina* (e.g. *Rissoina exeliana* Hertlein & Strong, 1951) have weak spiral sculpture. Their shells can be distinguished from superficially similar species of *Rissoina* by the lack of an anterior channel in the aperture.

Subgenus *Tomlinella* Viader, 1938

Tomlinella Viader, 1938: 6. Type-species *Tomlinella miranda* Viader, 1938; here designated. Recent, Indian Ocean (Figs 59B; 143E).

Dentrissoina Laseron, 1956: 415, = *Dentirissoina* error of authors. Type-species *Dentrissoina thornleyana* Laseron, 1956, = *Rissoa insignis* Adams & Reeve, 1850; original designation. Recent, Indo-Pacific (Figs 59A; 143F, G).

Ishimoria Kuroda, 1960: 72. Type-species *Ishimoria lamellata* Kuroda, 1960; original designation. Recent, Okinawa Is., Ryukyu Group.

Diagnosis. *Shell*: medium to large, ovate-conic, with narrowly shouldered to convex whorls. Upper whorls of teleoconch with or without distinct axial ribs, penultimate and body whorls with spiral lirae or spiral

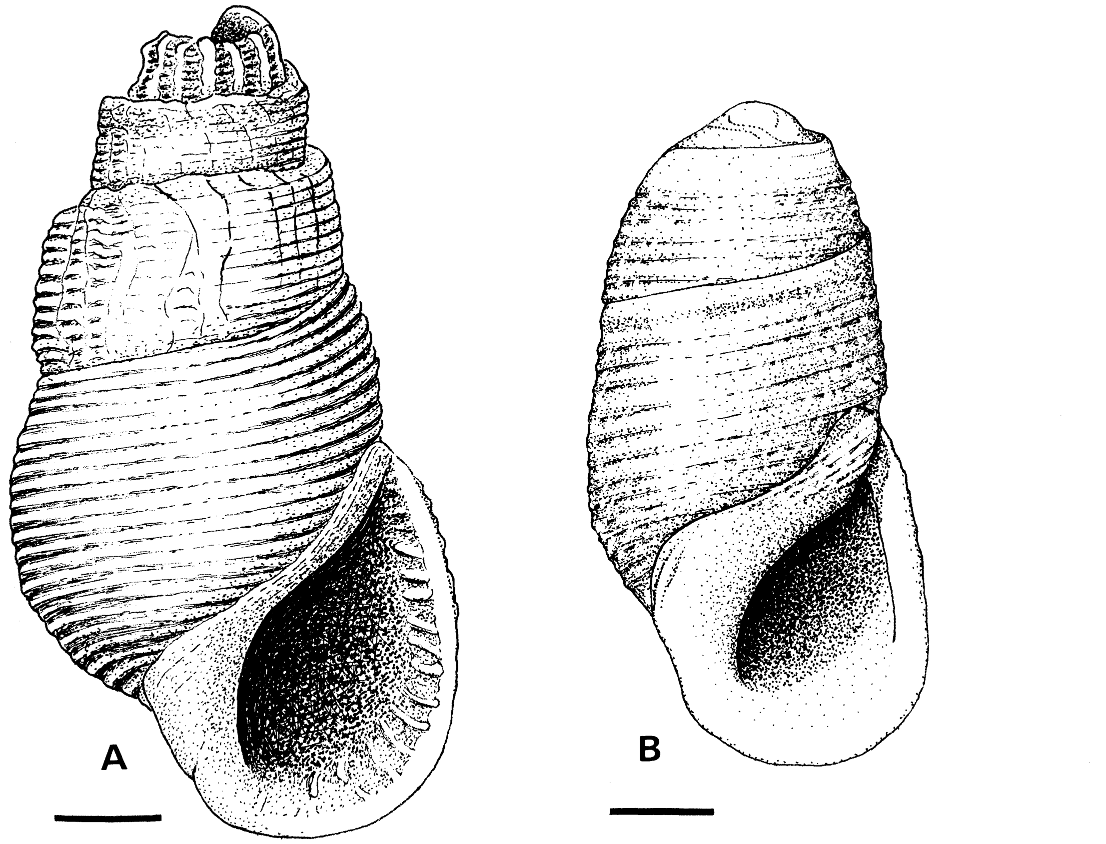

Fig. 59. **A**, *Zebina* (*Tomlinella*) *insignis* (Adams & Reeve), holotype of *Dentrissoina thornleyana* Laseron, type-species of *Dentrissoina* Laseron; Murray Island, Torres Strait, Queensland, Australia (AMS, C.102433). **B**, *Zebina* (*Tomlinella*) *miranda* (Viader), type-species of *Tomlinella* Viader; West Island, Cocos Keeling Islands, Indian Ocean (AMS, C.134886). **Scale:** 1 mm.

striae and thin axial lamellae (Figs 59A, B; 143E). Protoconch (of *Z.* (*T.*) *miranda*) small, of about 1½ whorls, surface eroded in only available non-decollate specimen.

Head-foot and *anatomy*: not known

Operculum: as for genus (Fig. 143F).

Radula: as for genus. Central teeth $\frac{4\text{-}6+1+4\text{-}6}{1 \quad\quad 1}$; lateral margins at 40°, lacking denticles. Lateral teeth c.8 + 1 + 6-7 (Fig. 143G).

Distribution. Tropical Indo-west Pacific: *R. insignis*, = *Rissoina turrita* Garrett, 1873, = *D. thornleyana*; *T. miranda.*

Material examined.

+ *T. miranda.* A few specimens (Cocos Keeling Is) (AMS).

* *R. insignis.* Holotype (NMW) and several other lots (AMS, BMNH, IRSB, USNM).

R. turrita. Holotype (ANSP).

D. thornleyana. Holotype and paratype (AMS).

Remarks. *Tomlinella* was introduced for two species from Mauritius and the Chagos Archipelago, Indian Ocean. The type specimens have not been examined and only a few specimens referable to the type-species of this genus have been seen. The shell has obvious affinities with *Zebina* but, because of its large aperture, spiral sculpture and decollate spire, it is referred to the same group as *Dentrissoina.*

Rissoina insignis and *Ishimoria lamellata* are similar to some of the larger species of *Zebina* s.s. but have well developed sculpture over the whole teleoconch, a more ovate shell and each whorl has a narrow shoulder and incised suture.

No specimens of *I. lamellata* have been examined but Kuroda's (1960) illustrations are excellent and, as he suggests, his species and *insignis* are closely related. There does not appear to be any good reason why these two species should be retained in separate subgenera or genera on the available evidence.

?Subgenus *Takirissoina* Oyama, 1962

Takirissoina Oyama, 1962: 56. Type-species *Rissoina japonica* Weinkauff, 1881; original designation. Recent, Japan (Fig. 136H).

Diagnosis. *Shell*: small, similar to *Rissoina* but with a very weak anterior channel, and sharp, strong spiral lirae (Fig. 136H). Protoconch dome-shaped, paucispiral, ?smooth.

Animal unknown.

Distribution. Japan: *R. japonica.*

Material examined.

R. japonica. 1 lot (NSMT).

Remarks. Although generally similar to some spirally lirate species of *Rissoina*, *R. japonica* differs in having a much weaker anterior apertural channel suggesting that its relationships are with *Zebina* or *Schwartziella* rather than with *Rissoina*. Examination of the operculum will help to clarify its taxonomic position but, in the absence of any material containing an operculum, *Takirissoina* is tentatively regarded as a subgenus of *Zebina*.

Subgenus *Tiphyocerma* Berry, 1958

Tiphyocerma Berry, 1958a: 83. Type-species *Tiphyocerma preposterum* Berry, 1958; original designation. Recent, western North America (Fig. 137A-D).

Diagnosis. *Shell*: small, rather solid, ovate-conic, non-umbilicate, spire usually slightly twisted with weak axial ribs on upper whorls; remainder of shell with weak, irregularly zig-zag ridges (Fig. 137B). Aperture ovate, strongly channelled posteriorly, rounded to weakly channelled anteriorly, with external varix (Fig. 137A, C). Protoconch pupoid, of about 3 whorls, apparently smooth; decollated in adults (Fig. 137D).

Animal unknown.

Distribution. Tropical west America: *T. preposterum*.

Material examined.

\+ *T. preposterum*. 2 specimens (LACM)

Remarks. *Tiphyocerma* is probably very close to (and perhaps synonymous with) *Zebina*. It is tentatively regarded as a subgenus because of its somewhat distorted appearance, weak axial sculpture and pupoid protoconch. Keen (1971) has illustrated the type specimen of *T. preposterum*.

Genus *Schwartziella* Nevill, 1881

Schwartziella Nevill, 1881: 162. Type-species *Rissoina orientalis* Nevill, 1881 ? = *Rissoina triticea* Pease, 1861, (Fig. 138D-G); original designation. Recent, Indo-Pacific.

Diagnosis. *Shell*: minute to small, elongate-conic, non-umbilicate, solid, with axial ribs. Aperture oval, channelled posteriorly, rounded anteriorly; inner lip concave, thickened; peristome simple. Outer lip opisthocline, with strong varix. Base with or without spiral fold. Protoconch multispiral or paucispiral, weakly sculptured with a spiral row of raised gemmules and very minute, scattered granules or minute, irregular pits.

Head-foot: very similar to *Rissoina* but with a simple, single, short anterior and posterior pallial tentacle. Metapodial tentacle broadly triangular when present.

Anatomy: ctenidial filaments triangular, a little longer than wide; osphradium slightly wider than bases of ctenidial filaments, and nearly as long as ctenidium. Stomach-style sac ratio 2.3; length-width ratio 2. Intestine with a loop just in front of posterior pallial wall, and curving below upper oviduct gland.

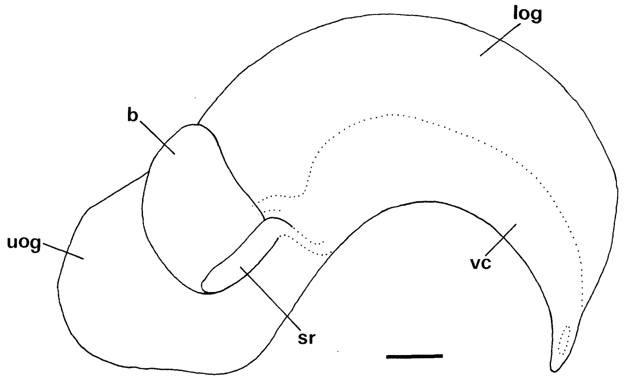

Fig. 60. Female genitalia of *Schwartziella inconspicua* (Brazier), right side. *b*-bursa copulatrix; *log*-lower oviduct gland; *sr*-seminal receptacle; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

Male with tapering penis with open sperm groove and few small rugae at commencement of distal ⅓ which is otherwise simple and narrowly tapering. Prostate gland very poorly developed, apparently closed, a narrow tube protruding behind posterior pallial wall into kidney for a small proportion of its length. Seminal vesicle coiled over posterior inner end of stomach.

Female (Fig. 60) similar to *Rissoina*, with muscular pallial sperm tube separate from ventral channel, approximately equal in width throughout; narrows immediately before opening to bursa copulatrix. Bursa copulatrix (*b*) immediately behind posterior pallial wall and on right side of oviduct glands; about half size of upper oviduct gland. Upper oviduct gland (*uog*) smaller than lower oviduct gland (*log*), behind bursa copulatrix. Seminal receptacle (*sr*) much smaller than bursa, lying horizontally below it and opening to ventral channel *(vc)*.

Schwartziella catesbyana (Orbigny), as described by Marcus & Marcus (1964) under the name *Rissoina chesneli*, agrees with the above description except that the ctenidial filaments are described as 'finger like'. The penis is more swollen and there is a broad ciliated tract instead of a prostate or pallial vas deferens. The female genital tract has a larger vestibule but is otherwise similar. The nervous system of *S. catesbyana* has a rather long supraoesophageal connective and a short suboesophageal connective. The cerebral commissure is short and thick. Marcus & Marcus also give additional details about the nervous system.

Operculum: thin simple, oval; nucleus eccentric.

Radula: central teeth $\frac{3\text{-}5+1+3\text{-}5}{1 \qquad 1}$; a single pair of basal denticles, and no denticles on lateral margins; U-shaped ventral extension moderate to well developed; lateral margins thickened, at 30°-45°. Lateral teeth 5-9 + 1 + 4-7. Marginal teeth with subequal cusps; inner marginal teeth with cusps on distal ⅓ of outer edge; outer marginal teeth with cusps on distal ¼-⅓ of inner edge.

Egg capsules: unknown.

Development: direct or with planktotrophic larval stage, deduced from protoconch morphology.

Distribution. Caribbean Sea (Western Atlantic), eastern Pacific and Indo-Pacific. Miocene to Recent.

Remarks. Species of *Schwartziella* can be distinguished from *Rissoina* species by the lack of an anterior canal in the aperture and their simple operculum. They differ from *Zebina*, to which *Schwartziella* is closely allied, in having prominent, axial sculpture over the entire teleoconch (including the base). Two subgenera are recognised.

Key to subgenera of *Schwartziella*

——Shell without spiral basal fold, surface dull to shining.................... *Schwartziella* s.s.

——Shell with spiral basal fold, surface shining .... *Pandalosia*

Subgenus *Schwartziella* s.s.

Schwartziella Nevill, 1885: 73, 82, not Nevill, 1881. Type-species *Rissoina bryerea* Montagu, 1803; original designation. Recent, West Indies (Fig. 138A-C).

Rissoinella Oyama, in Taki & Oyama, 1954: 52. Type-species *Rissoina zeltenerioides* Yokoyama, 1920, ? = *Rissoina adamsiana* Weinkauff, 1881; original designation. Yokosuka, Japan, Upper Tertiary or Plesitocene (see Oyama, 1973: 7) (Fig. 137E, F).

Atlantorissoina Kosuge, 1965a: 108. Type-species *Rissoa chesnelii* (= *chesnelli*) Michaud, 1830, based on misidentified specimens of *Rissoina catesbyana* Orbigny 1842; original designation. Recent, Caribbean.

Diagnosis. *Shell*: as for genus but lacking basal fasciole. Whorls weakly convex; surface dull to shining (Figs 137E; 138A, D, H). Protoconch relatively small, multispiral or paucispiral (Fig. 138E, 1).

Head-foot: as for genus. Metapodial tentacle broadly triangular (several Indo-Pacific species examined and *S. catesbyana*, Fort Pierce, Florida; *S.* '*chesneli*' (= *catesbyana*) Marcus & Marcus, 1964, fig. 1).

Anatomy: based on *Schwartziella inconspicua*, Point Hunter, Norfolk Island (1 male, 2 females); *S. catesbyana* (Marcus & Marcus, 1964). As for genus (Fig. 60).

Operculum: as for genus (Fig. 138B, F).

Radula: as for genus; lateral margins of central teeth at 45° (Fig. 138C, G).

Development: direct or with planktotrophic larval stage.

Distribution. Caribbean Sea and Western Atlantic: *R. bryerea*; *R. chesnelli*, = *Rissoa scalaroides* C.B. Adams, 1850; *Rissoina catesbyana* Orbigny, 1842, = *Rissoa scalarella* C.B. Adams, 1845, = *Rissoina bermudensis* Peile, 1926.

Western America: *Rissoina dalli* Bartsch, 1915; *Rissoina hannai* Smith & Gordon, 1948; *Rissoina willetti* Strong, 1938; *Rissoina coronadoensis* Bartsch, 1915; *Rissoina nereina* Bartsch, 1915; *Rissoina cleo* Bartsch, 1915; *Rissoina bakeri* Bartsch, 1902.

Tropical Indo-Pacific: *R. triticea*; *Rissoina inconspicua* Brazier, 1877 (Fig. 138H, I); *Schwartziella lata* Laseron, 1956; *Rissoina* (*Rissoina*) *bilabiata* Boettger, 1893.

Pliocene (?) to Recent of Japan: *R. zeltenerioides.*

Temperate Australia: *Rissoina fiscina* Cotton, 1952; *Rissoina grata* Cotton, 1952.

South Africa: *Rissoina rietensis* Turton, 1932.

Miocene of Bikini Atoll, Pacific: *Rissoina* (*Schwartziella*) *rilebana* Ladd, 1966.

Material examined.

+* *R. bryerea*. A few lots (USNM, AMS).

R. chesnelli. A few lots (USNM).

+* *R. catesbyana*. Several lots (USNM, AMS).

\+ *R. triticea*. Holotype (BMNH), paratype (MCZ) and several other lots (AMS).

\+ *R. inconspicua*. Syntypes and several other lots (AMS).

S. lata. Holotype, paratypes and a few other lots (AMS).

R. (*R.*) *bilabiata*. Syntypes (SMF).

R. zeltenerioides. 1 lot (ANSP).

R. fiscina. Syntypes (SAM) and several other lots (AMS).

+* *R. grata*. Syntypes (SAM) and several other lots (AMS).

+* *R. rietensis*. Holotype and paratypes (OM) and a few other lots (AMS).

Western American species all examined at LACM.

Remarks. Nevill (1885) changed the type designation of his subgenus *Schwartziella* from *Rissoina orientalis* Nevill to *Rissoina bryerea* (Montagu) without explanation. Subsequently Kosuge (1965a) erected *Atlantorissoina* for the species investigated anatomically by Marcus & Marcus (1964) and incorrectly identified as *Rissoina chesneli* (Michaud). Moore (1969) has shown that the species investigated was actually '*Rissoina*' *catesbyana*, which is very closely related to *Schwartziella bryerea*.

The Indo-Pacific species of *Schwartziella* have not been properly delineated, and considerable revision is required. Nevill (1885) placed his *R. orientalis* in the synonymy of *R. triticea* Pease, 1860. The mamillate apex mentioned in the description of *R. orientalis* does not agree well with the holotype of *R. triticea*, although the illustration given by Kay (1965) shows the protoconch to be narrower than it really is. Both *R. orientalis* and the type of *R. triticea* have 11 ribs on the body whorl but the latter is slightly larger. I have not been able to examine the type material of *R. orientalis* but it appears likely that the taxon it represents is very closely related to *R. triticea*.

A well developed mamillate protoconch is seen in *S. inconspicua* (Brazier) (Fig. 138H, I). The existence of both paucispiral and multispiral types of protoconchs indicates that some species of *Schwartziella*, as also seen in species of *Rissoina*, have adopted direct development while others have maintained a planktonic larval stage. These differences in larval strategy do not appear to be associated with any other characters and are not interpreted as being of taxonomic importance at the supraspecific level.

Rissoinella is based on a species with weak, oblique ribs but, in other shell characters, it is similar to typical species of *Schwartziella*. Several other species also show reduction in strength of the axial ribs, and a tendency for them to become oblique. One such species, *R. rietensis*, has an operculum and radula like that of other *Schwartziella* species.

Kosuge (1965a) placed his new species *S. otohimeae* in *Schwartziella* but his description of the shell and operculum show that it belongs in *Rissoina* s.s.

Subgenus *Pandalosia* Laseron, 1956

Pandalosia Laseron, 1956: 391. Type-species *Pandalosia excelsis* Laseron, 1956; original designation. Recent, north-eastern Australia (Fig. 139A, B).

Diagnosis. *Shell*: as for genus; with strong, spiral basal fold. Whorls convex, surface shining (Fig. 139A, C). Protoconch relatively large, multispiral, with weak growth lines, and inconspicuous granules and raised dashes arranged spirally (Fig. 139B, D, E).

Head-foot: as for genus. Metapodial tentacle represented by a short, thin flap from opercular lobe (*Schwartziella* (*Pandalosia*) *ephamilla*, 30 m, Carter Reef, Great Barrier Reef, Queensland, Australia).

Anatomy: not known.

Operculum: as for genus (Fig. 139F).

Radula: as for genus; lateral margins of central teeth at 30° (Fig. 139G, H).

Development: with planktotrophic larval stage.

Distribution. Tropical Indo-Pacific: *P. excelsis*; *Rissoina minuta* Nevill, 1874; *Rissoina scalariformis* Watson, 1886, not Adams, 1852, = *Rissoina ephamilla* Watson, 1886 (Fig. 139C-H), = *Pandalosia oceanica* Laseron, 1956; *Rissoina subfirmata* Boettger, 1887; *Pandalosia darwinensis* Laseron, 1956; *Pandalosia obtusa* Laseron, 1956; *Pandalosia subulata* Laseron, 1956.

Tropical west America: *Rissoina porteri* Baker, in Hanna & Strong, 1930.

Material examined.

\+ *P. excelsis*. Holotype and paratypes (AMS).
R. minuta. Syntypes (BMNH).
\+ * *R. ephamilla*. Holotype (BMNH), and several lots (AMS).
P. oceanica. Holotype and paratypes (AMS).
R. subfirmata. Holotype (SMF).
P. darwinensis. Holotype and paratypes (AMS).
P. obtusa. Holotype and paratypes (AMS).
P. subulata. Holotype (AMS).

Remarks. The group of species referred to *Pandalosia* by Laseron (1956) is separable from species of *Schwartziella* s.s. by their small size, slender form, relatively large, elongate protoconchs, shining surface and prominent basal fold. The one species that has been examined alive appears to be virtually identical to typical *Schwartziella* species in head-foot, radular and opercular characters.

Genus *Folinia* Crosse, 1868

Folinia Crosse, 1868: 218. Type-species *Rissoa insignis* Folin, 1867, not A. Adams & Reeve, 1850, = *Rissoina* (*Folinia*) *signae* Bartsch, 1915; monotypy. Recent, west coast of Panama (Fig. 140A-D).

Mirarissoina Woodring, 1928: 365. Type-species *Rissoina* (*Mirarissoina*) *lepida* Woodring, 1928. 'Miocene' (= Pleistocene), Bowden, Jamaica (Fig. 61).

Diagnosis. *Shell*: small, elongate-conic, non-umbilicate, with strong axial ribs and spiral threads, or smooth and glossy with punctate microsculpture. Aperture D-shaped, with anterior and posterior angulations and channels; anterior channel narrow, weak to deep; posterior channel a narrow, deep notch. Outer lip opisthocline, with varix and duplicated edge. Base with prominent spiral fold (Figs 61; 140A, E; 142F). Protoconch elongately conic, about 3½ convex or shouldered whorls with weak spiral lirae or prominant spiral ridge (Fig. 140B, F).

Head-foot and *anatomy*: not known.

Operculum: oval, simple, thin, yellowish; nucleus eccentric (Fig. 140C, G).

Radula: central teeth $\frac{3\text{-}5 + 1 + 3\text{-}5}{1 \qquad 1}$; lateral margins at 45° thickened, simple; U-shaped ventral extension moderately developed. Lateral teeth 4-6 + 1 + 4-5. Inner marginal teeth with small cusps on distal ⅓ of outer edge; outer marginal teeth with outer edge smooth; inner edge obscured in available mounts (Fig. 140D, H).

Egg capsules: unknown.

Development: probably with planktotrophic larval stage.

Distribution. Central W. America: *F. insignis*; *Rissoina* (*Folinia*) *ericana* Hertlein & Strong, 1951 (Fig. 140E-H); *Rissoina histia* Bartsch, 1915 (Fig. 142F).

Caribbean: *Rissoina bermudezi* Aguago & Rehder, 1936.

Pleistocene of Jamaica: *R. lepida*; *Rissoina* (*Mirarissoina*) *xesta* Woodring, 1928.

Material examined

\+ **F. insignis*. 2 syntypes (BMNH); several lots (LACM).
R. (*M.*) lepida. Holotype (USNM).
\+ **R.* (*F.*) *ericana*. Holotype (CAS) and several lots (LACM).
R. histia. Holotype (USNM), 1 lot (LACM).
R. bermudezi. Holotype and a few other lots (USNM).

Remarks. The shell of the type species of this genus is superficially similar to that of *Manzonia crassa* whereas the other species included here are more like *Rissoina* in shell features (Fig. 140E). The characteristic feature of *Folinia* is the strongly notched posterior corner of the aperture. The two species included in *Mirarissoina* by Woodring (1928) have similar apertural notches to *F. insignis*. There are also no significant differences in the radula and operculum of *R. ericana*, a species closely similar to *R. lepida* Woodring (the type-species of *Mirarissoina*) and *F. insignis*. If the species included in *Folinia* are indeed a single genus, the

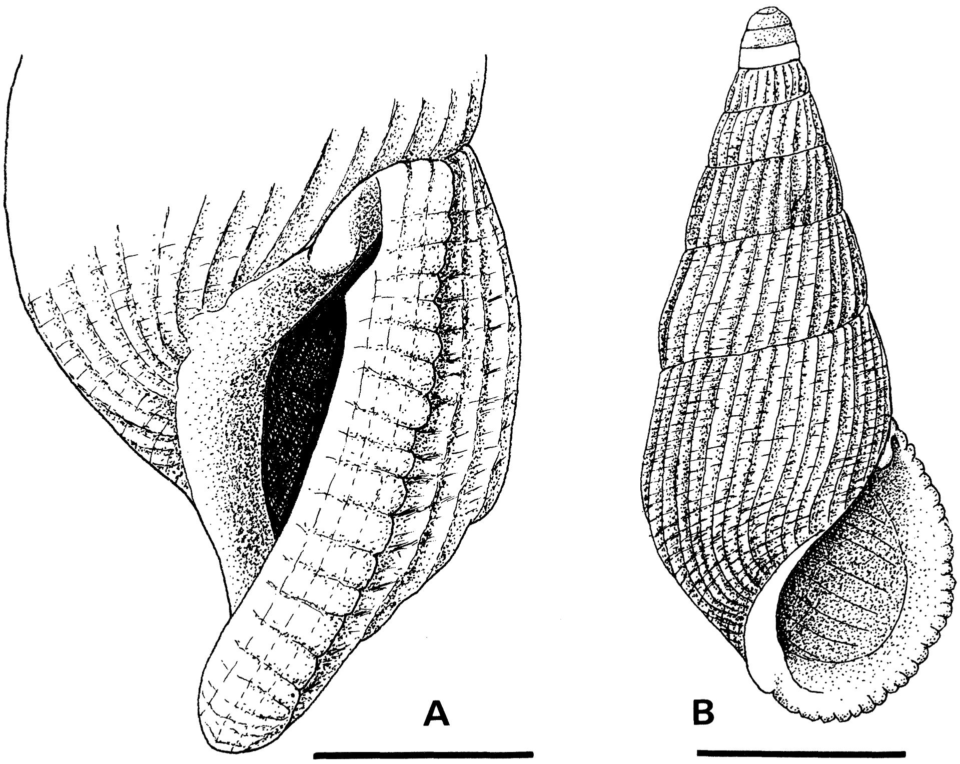

Fig. 61. *Folinia lepida* Woodring; type-species of *Mirarissoina* Woodring; holotype, Bowden, Jamaica, 'Miocene' (USNM, 369509). **Scale:** A - 0.5 mm, B - 1 mm.

sculptural diversity is considerable, and parallels that seen within *Rissoina* and *Zebina*.

Folin in Folin & Périer (1867) described two unfigured species from Egypt, and he attributed them to this genus.

Genus *Cossmannia* Newton, 1891*

Cossmannia Newton, 1891: 233. New name for *Diastictus* Cossmann, 1888: 237, not Mulsant, 1842, not Amyot, 1846. Type-species *Rissoina expansa* Deshayes, 1861; original designation. Eocene, Paris Basin, France (Fig. 62; 133H).

Diagnosis. *Shell*: of medium size, shining, elongate-conic, with angled periphery, non-umbilicate. Sculpture of spiral and axial threads of equal strength, with pits in the interspaces (Fig. 133H) on upper spire whorls, remainder of teleoconch smooth, shining. Aperture with simple peristome, pyriform, with weak subangulation; no channel anteriorly; narrow posterior channel (not notched); columella deeply excavated; varix thick, outer lip prosocline (Fig. 62). Protoconch apparently smooth, of nearly 3 whorls (Fig. 133H).

Development: planktotrophic larval stage was probably present.

Distribution. Eocene of France, Paris Basin: *C. expansa*.

Material examined.

+ *C. expansa.* 2 lots, Cossmann Colln (UMC).

Remarks. This genus is probably most closely related to *Zebina* as it agrees with its shining surface, weak sculpture and pyriform aperture. The outer lip is prosocline, not opisthocline as in *Zebina*, and the sculptural details and angled periphery are also distinctive.

The sculpture is very similar to that of *Rissoina refugium* Nevill, the type-species of *Chiliostigma* Nevill (= *Rissoina* s.s.), but *R. refugium* has an aperture typical of the genus *Rissoina* and lacks a peripheral angulation.

Genus *Stosicia* Brusina, 1870

Stosicia Brusina, 1870: 214. Type-species *Rissoa buccinalis* Grateloup, 1828, not Lamarck, 1804, = *R. planaxoides* Grateloup, 1838; monotypy. Miocene, France (Figs 63; 141F, G).

Stossicia, and *Stossichia* invalid emendations.

Diagnosis. *Shell*: small, ovate-conic, solid, non-umbilicate, with spiral cords or clathrate sculpture. Microsculpture of fine, close axial lamellae in interstices (Fig. 141D, G). Aperture ovate, with shallow posterior channel and an anterior channel which is usually broad and deep; peristome simple. Outer lip with prominent varix, more or less orthocline to slightly opisthocline. Columella simple or with prominent angulation (sometimes swollen to form a denticle) at inner end of anterior canal. Protoconch multispiral or paucispiral, dome-shaped to conical, smooth (Fig. 141B, F).

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* *Liocium* Gabb, 1869, type-species *L. punctatum* Gabb, 1869 from the Cretaceous of Colorado, may be an earlier name for this genus.

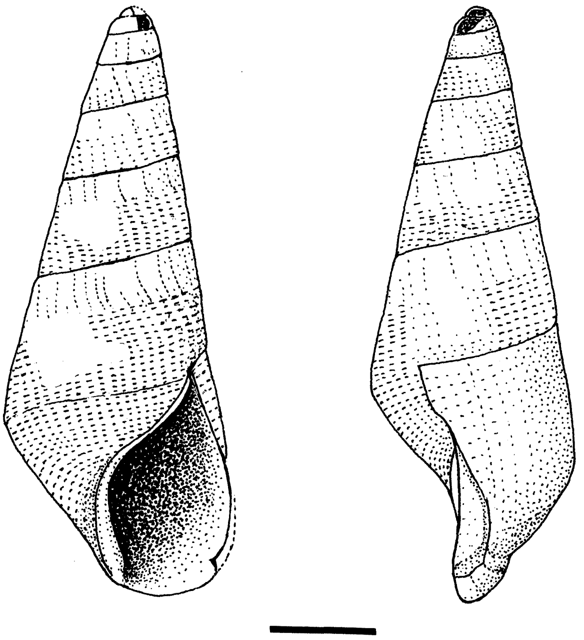

Fig. 62. *Cossmannia expansa* (Deshayes); type-species of *Cossmannia* Newton; Thionville, Paris Basin, France, Eocene (UMC). **Scale:** 1 mm.

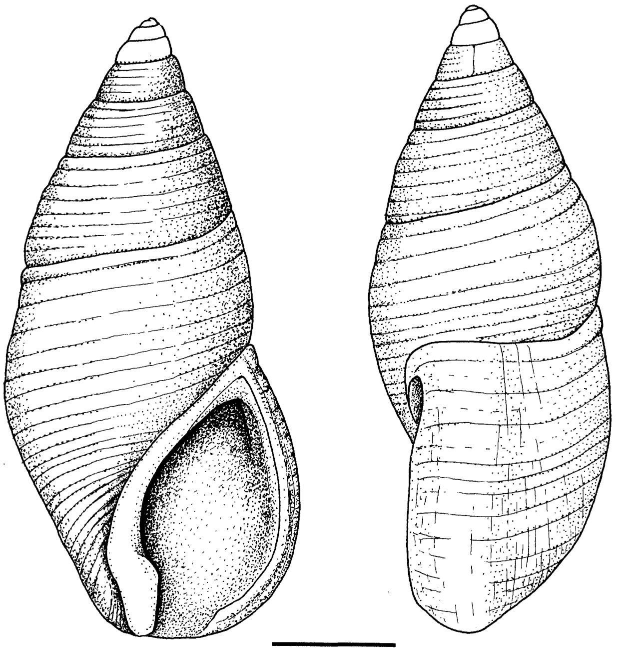

Fig. 63. *Stosicia* (*Stosicia*) *planaxoides* (Grateloup); type-species of *Stosicia* Brusina; Steinabrunn, Austria, Miocene (BMNH, 61881). **Scale:** 1 mm.

Head-foot: similar to *Rissoina* (see under *Stosicia* s.s. below).

Anatomy: based on *S. annulata* (Dunker). Ctenidial filaments about twice as long as wide, bases about half as wide as osphradium. Osphradium slightly shorter than gill. Stomach relatively very short compared with length of style sac (stomach-style sac ratio 1.7), length-width ratio 1.5. Intestine-rectum not examined.

Male: penis (Fig. 64D) with narrow proximal half and open penial groove, distal half swollen, with small, sharp 'warts' on distal end, and on terminal papilla-like structure. Prostate gland within posterior end of pallial cavity, rather large, narrow in section, about 4 times longer than high. Ventral edges apparently fused with very thin tissue except for a short, open portion at posterior end. Seminal vesicle coiled over inner face of stomach.

Female (Fig. 64A-C) with terminal genital pore (*ga*) opening to expanded end of sperm duct. Lower oviduct gland opens to anterior expanded vestibular region (*as*) which is lined with mucous cells and opens to anterior end of expanded sperm duct. Seminal receptacle (*sr*), bursa copulatrix (*b*) and anterior portion of upper oviduct gland lie within pallial wall. Bursa and upper oviduct gland about equal in size; upper oviduct gland about ⅓ size of lower oviduct gland. Seminal receptacle small, globular, about half height of bursa copulatrix and ¼ of length. Both bursa and seminal receptacle lie between upper and lower oviduct glands with seminal receptacle at about middle of base of bursa on its right side. Some of bursa visible on left but partly overlapped by oviduct glands. Sperm duct (Fig. 64C, *sd*) and lower oviduct gland separate; anterior part of lower oviduct gland narrow and with low glandular cells. Ventral channel (*vc*)thin-walled with a weak flap on inner (left) side. Upper oviduct gland (*uog*) apparently simple.

Nervous system not examined.

Operculum: smooth, simple, rather elongate, pointed, at end opposite nucleus; nucleus small, markedly eccentric.

Radula: central teeth $\frac{2\text{-}6+1+6\text{-}2}{1 \qquad 1}$; low, with a pair of prominent denticles on face; ventral margin with moderately developed U-shaped extension; lateral margins simple, at 23°-35°. Lateral teeth 3-4 + 1 + 5-10(+). Numerous sharp cusps on distal half of outer edge of inner marginal teeth; outer sides of outer marginal teeth smooth, inner sides obscured in mounts.

Egg capsules: unknown.

Development: unknown. Probably both direct and with planktotrophic larval stage, judged by the protoconch morphology.

Distribution. Tropical Indo-west Pacific, southern Australia, Caribbean and the Miocene of Europe.

Remarks. *Stosicia* resembles *Rissoina*, *Schwartziella* and *Zebina* in having an open penial groove, a partly open (and only partially fused) prostate gland, a sperm duct separate from the ventral channel and triangular, rather than finger-shaped ctenidial filaments. *Stosicia* differs from these genera in having what is presumably a more primitive female reproductive system, in which the sperm channel is open to the capsule gland. This is also seen in *Rissoina* but over a much shorter portion of the capsule gland. In shell characters species of *Stosicia* differ from related genera in having a broad, deep, anterior apertural channel.

Stosicia and *Isseliella* appear to be closely related groups as realized by Boettger (1887), who combined

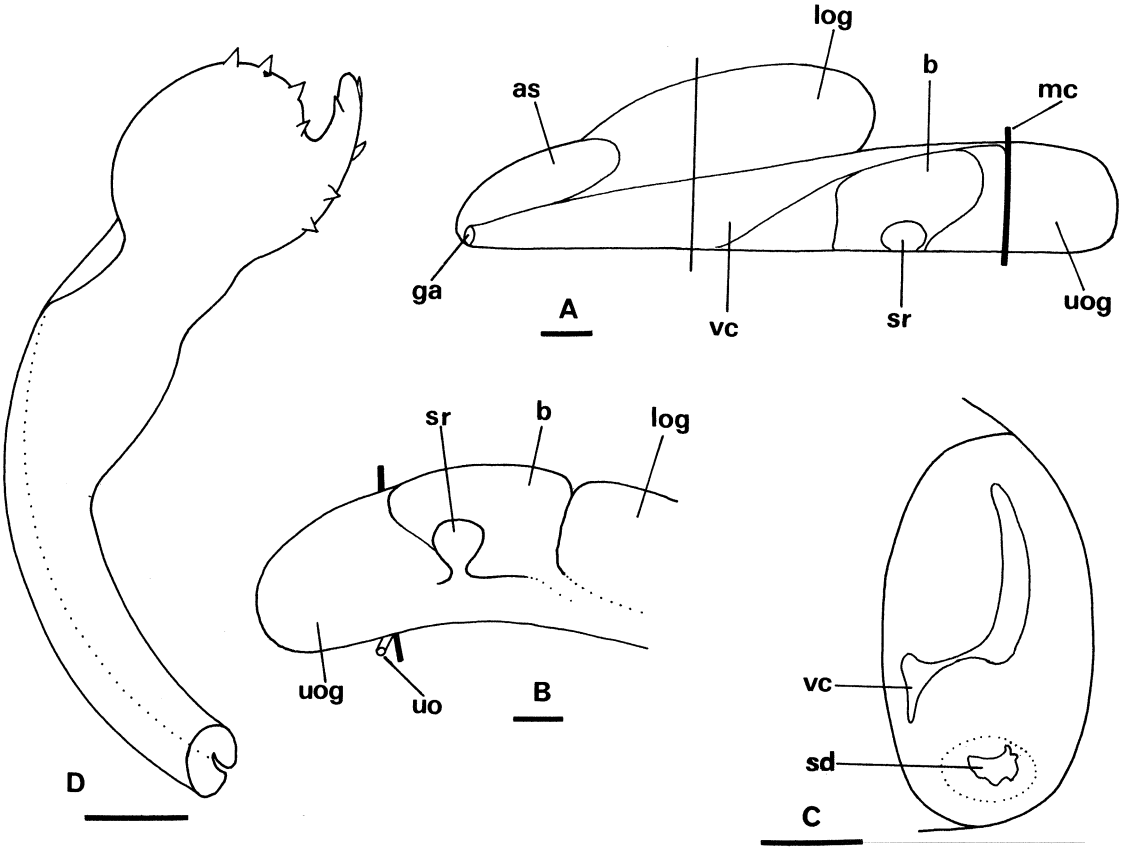

Fig. 64. Genitalia of *Stosicia (Stosicia) annulata* (Dunker). **A-C**, female genitalia: **A**, left side; **B**, right side of posterior portion of oviduct glands; **C**, transverse section at position indicated in middle of lower oviduct gland. **D**, penis. *as*-anterior sperm sac; *b*-bursa copulatrix; *ga*-pallial genital opening; *log*-lower oviduct gland; *mc*-posterior wall of pallial cavity; *sd*-sperm duct; *sr*-seminal receptacle; *uo*-upper oviduct; *uog*-upper oviduct gland; *vc*-ventral channel. **Scale:** 0.1 mm.

them into a single genus. They are here regarded as subgenera. Their apertural features and general shell form are very similar, the difference being mainly in shell sculpture. That of *Isseliella* species is usually clathrate whereas *Stosicia planaxoides* has only spiral cords.

Key to subgenera of *Stosicia*

— Shell with spiral sculpture only, protoconch multispiral. . . . . *Stosicia* s.s.

— Shell usually with clathrate sculpture, protoconch paucispiral. . . . . *Isseliella*

Subgenus *Stosicia* s.s.

Diagnosis. *Shell*: as for genus. Sculpture of teleoconch of strong spiral cords. Columella simple or with prominent denticle-like swelling at inner end of anterior canal. Outer lip with or without a few weak denticles within (Figs 63; 142A). Protoconch multispiral, conical (Figs 141F; 142C).

Head-foot: very similar to that of *Rissoina* species. Cephalic tentacles long, slightly tapering, without obvious ciliation; eyes in small bulges at their outer bases. Snout highly extensile, bilobed. Foot without posterior mucous gland but anterior gland well developed. A long, slender posterior (right) pallial tentacle present, but no metapodial tentacle. (*S. annulata* (Dunker); Mersing, Malaya; Fig. 58C).

Anatomy: based on *S. annulata*, Mbodya Island, N. of Dar es Salaam, Tanzania (1 male and 1 female) and Tolo Harbour, Hong Kong (2 males, 2 females sectioned). As for genus.

Operculum: as for genus (Fig. 142B).

Radula: central teeth $\frac{2\text{-}3+1+2\text{-}3}{1\quad 1}$; cutting edge narrowly triangular. Lateral teeth 3 + 1 + 5-6. Marginal teeth as for genus (Fig. 142D).

Development: planktotrophic larval stage assumed to be present in all species.

Distribution. Japan, south-east Asia, India and east Africa: *Rissoina annulata* Dunker, 1860 (Fig. 142A-D), = *Rissoina trochlearis* Gould, 1861, = *Alvania ligata* Gould, 1861.

?Peru: *Rissoina sulcifera* Troschel, 1852 (possibly based on mislocalised *S. annulata*).

Miocene of Eniwetok and Bikini Is, Pacific: *Iravadia gardnerae* Ladd, 1966.

Miocene of France and Italy: *R. planaxoides*, ? = *Stossichia planaxoides paucisulcata* Sacco, 1895, = *Stossichia ovatulina* Sacco, 1895; *Stossichia multicingulata* Boettger, 1887.

Material examined.

\+ *R. planaxoides*. A few lots (BMNH; Cossmann Colln UMC).
S. planaxoides paucisulcata. Holotype (TGM).
S. ovatulina. Holotype (TGM).
\+ * *R. annulata*. Many lots in several museums (USNM, AMS, BMNH etc.).
R. trochlearis. Holotype (USNM).
R. ligata. Holotype (USNM).
I. gardnerae. 2 paratypes (AMS).

Remarks. *Stosicia planaxoides* is somewhat similar to *S. annulata* (Dunker) but differs in its much flatter and more numerous spiral cords and the more prominent anterior notch in the aperture. Despite these differences the two species are considered to be consubgeneric because they have most other features in common. *Rissoina annulata*, and two other species here placed in *Stosicia*, have been included previously in *Iravadia* but they differ from that genus in protoconch characters and, in the case of *S. annulata*, in radular and opercular characters, as well as in anatomy and the morphology of the head-foot.

Subgenus *Isseliella* Weinkauff, 1881

Isselia Semper in Schmeltz, 1874: 104, 110, not Bourguignat, 1877. Type-species *Rissoina mirabilis* Dunker in Schmeltz, 1874; original designation. *nom. nud.*

Isseliella (Nevill ms) Weinkauff, 1881: 61, 67. Substitute name for *Isselia* Semper in Schmeltz, 1874, which was based on a *nomen nudum*. Type-species *Rissoina mirabilis* (Dunker ms) Weinkauff, 1881; original designation. Recent, western Pacific (Figs 141A-E; 142E).

Isselliella error of authors.

Diagnosis. *Shell*: as for genus but usually with clathrate sculpture (one species has predominantly spiral sculpture). Columella with prominent angulation at inner end of siphonal canal (Figs 141A, 142E). Protoconch dome-shaped, with about 1½ convex, smooth whorls (Fig. 141B).

Head-foot and *anatomy*: not known.

Operculum: as for genus (Fig. 141C).

Radula: central teeth $\frac{3\text{-}6+1+3\text{-}6}{1 \qquad 1}$; cutting edge broadly triangular. Lateral teeth 4+1+10(+). Marginal teeth as for genus (Fig. 141E).

Development: assumed to be direct in all species.

Distribution. Tropical Indo-west Pacific: *R. mirabilis*, ? = *Rissoina* (*Isseliella*) *pseudoconcinna* Nevill, 1885 (new name for *Rissoa concinna* Sowerby, 1879 not Adams, 1851), = *Rissoina polytropa* Hedley, 1899, = *Rissoina* (*Phosinella*) *paschalis* Melvill & Standen, 1901, = *Isselia polytropa augerea* Laseron, 1956; *Rissoina* (?) *abnormis* Nevill, 1875; *Rissoina* (*Stossichia*) *bougei* Bavay, 1917; *Isselia chiltoni* Oliver, 1915; *Isselia incisa* Laseron, 1956; *Alvania bourguignati* Issel, 1869, = *Nassa semitexta* Hedley, 1899, = *Tritonidea seurati* Couturier, 1907; *Bittium hiloense* Pilsbry & Vanatta, 1908, = *Isselia undulata* Laseron, 1956, = *Isselia lateralis* Laseron, 1956.

South and south-western Australia: *Rissoina hedleyi* Tate, 1899.

Tropical western America: *Stossichia serrei* Bavay, 1922.

Caribbean: *Rissoa aberrans* C.B. Adams, 1850.

Miocene of Europe: *Stossichia semicostulata* Boettger, 1887; *Stossichia costata* Boettger, 1887.

Material examined.

\+ * *R. mirabilis*. 5 lots, 1 ex Dunker (HUM), several other lots (AMS).
R. (*S.*) *bougei*. Holotype (Dautzenberg Colln, IRSB).
N. semitexta. Syntypes (AMS).
R. polytropa. Holotype and paratypes (AMS).
R. (*P.*) *paschalis*. Holotype (BMNH).
Isselia species of Laseron 1956. Types (AMS).
I. chiltoni. 2 lots, 1 ex Oliver (AMS).
R. hedleyi. Several lots (AMS).
S. serrei. Paratypes (Dautzenberg Colln, IRSB).
R. aberrans. Several lots (USNM, MCZ, ANSP), holotype (MCZ).

Remarks. All of the described species have clathrate sculpture except *Rissoina bougei*, which has only spiral sculpture. The small size of *R. bougei*, rather thin shell and paucispiral protoconch are features that place it in the subgenus *Isseliella* rather than in *Stosicia* s.s. Cossmann (1921) was apparently unaware of the name *Isseliella* and included two Recent species of *Isseliella* in '*Stossichia*' (= *Stosicia*).

Genus *Lapsigyrus* Berry, 1958

Lapsigyrus Berry, 1958b: 92. Type-species *Alvania contrerasi* Jordan, 1936, = *Alaba mutans* Carpenter, 1857; original designation. Pleistocene, W. Mexico (Figs 65, 143A-D).

Diagnosis. *Shell*: small, ovate-conic, moderately solid, imperforate, with lightly convex whorls, sharp spiral ribs and weak axial threads. Aperture rather large, pyriform to D-shaped, rounded anteriorly, sharply angled and very narrowly channelled posteriorly, with simple peristome. Outer lip slightly opisthocline, with a narrow, rather weak varix; inner lip closely applied to parietal wall. Base simple, lacking a basal fold (Figs 65; 143A). Protoconch small, somewhat conical, of 2-3 convex whorls, apparently smooth except for sinuous growth lines (Fig. 143C).

Head-foot and *anatomy*: not known.

Operculum: simple, thin, horny, elongate; end nearest eccentric nucleus convex, other end sharply pointed (Fig. 143B).

Radula: central teeth $\frac{(4\text{-}5)+1+(4\text{-}5)}{(1) \qquad (1)}$; broad, low (about 4 times wider than high), lacking distinct lateral cusps (about 4-5 rudimentary cusps visible on each side in some teeth); median cusp moderately long, sharp;

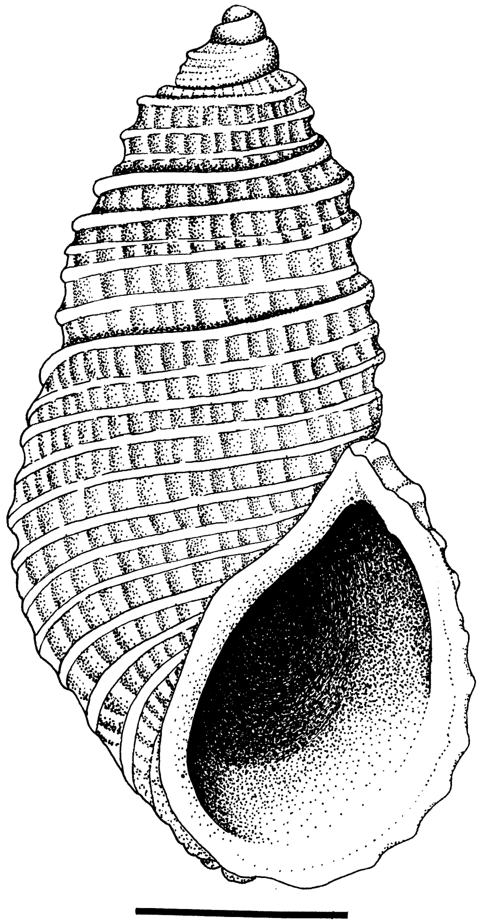

Fig. 65. *Lapsigyrus mutans* (Carpenter), type-species of *Lapsigyrus* Berry; holotype of *Alvania contrerasi* Jordan; Magdalena, Lower California, Pleistocene (CAS, 5565). **Scale:** 1 mm.

lateral edges of each tooth at about 45° to cutting edge, moderately thickened, each with a very small, almost obsolete, denticle (assumed to be basal denticle) on inner edge; U-shaped process on ventral margin moderately developed. Lateral teeth 0 + 1 + 0, with large, pointed median cusp; no other cusps present. Inner marginal teeth with numerous small, sharp cusps, on distal ¼ of outer edge, forming straight cutting edge. Outer marginal teeth smaller with fewer, smaller cusps on distal ¼ of inner side (Fig. 143D).

Egg capsules: unknown.

Development: probably with planktotrophic larval stage.

Distribution. West coast of north and central America: *A. mutans*, = *A. contrerasi*, = *Alvania milleriana* Hertlein & Strong, 1951; *Lapsigyrus myriosirissa* Shasky, 1970.

Material Examined.

+ **A. mutans*. A few lots (LACM).
L. contrerasi. Holotype (CAS).
A. milleriana. Holotype (CAS).
L. myriosirissa. Holotype (LACM).

Remarks. Species of *Lapsigyrus* are distinctive in having a large, pyriform aperture, and sharp spiral sculpture with weak axial riblets between the spiral ribs, giving the surface a somewhat netted appearance. The relationships of *Lapsigyrus* are not altogether clear. The sculpture resembles that of some species of *Iravadia* (*Fairbankia*) (Iravadiidae), and some features of the radula are similar to members of that family, but all known iravadiids have a depressed protoconch (Ponder, 1984). The genus is probably related to species of *Stosicia* (*Isseliella*) which have generally similar shells, opercula and radulae.

Genus *Pseudotaphrus* Cossmann, 1888

Pseudotaphrus Cossmann, 1888: 238. Type-species *Bulimus buccinalis* Lamarck, 1804; original designation. Eocene, Paris Basin (Fig. 66).

?*Microtaphrus* Cossmann, 1888: 240. Type-species *Pseudotaphrus (Microtaphrus) proavius* Cossmann, 1888; original designation. Paleocene, Paris Basin, France.

Pezantia Cossmann, 1896: 22 Type-species *Rissoa dactyliosa* Deshayes, 1861; original designation. Eocene, Paris Basin.

Diagnosis. *Shell*: of medium size, rather thin, elongate-conic, non-umbilicate, with close, low spiral cords. Whole surface very minutely pitted. Aperture with distinct anterior and posterior angulations, weakly channelled at angles; simple perisome and strong varix on orthocline outer lip. Occasional varices formed, particularly on body whorl (Fig. 66). Protoconch dome shaped, with about 3 convex whorls; smooth.

Animal unknown.

Development: judging from the protoconch morphology a planktotrophic larval stage was probably present.

Distribution. Paleocene of France, Paris Basin: *P(M.) proavius*.

Eocene of France: *B. buccinalis*, = *Rissoa fayellensis* de Rainc, 1876 (*fide* Cossmann, 1888); *R. dactyliosa*; *Rissoa cincta* Deshayes, 1861.

Miocene of France and Italy: *Rissoa desmoulinsii* Orbigny, 1852; *Pseudotaphrus desmoulinsii tauroinflata* Sacco, 1895.

Cossmann (1921) also includes *P. moloti* Cossmann, 1907 (Paleocene, France) and 4 species additional to *B. buccinalis* from the Eocene of Europe.

Material Examined.

+ *B. buccinalis*. A few lots (BMNH; Cossmann Colln UMC; PCB).
R. cincta. 1 lot (PCB).
P. desmoulinsii tauroinflata. Type (TGM).

Remarks. The immediate relationships of *Pseudotaphrus* are not clear. It is possibly related to *Stosicia*, but the rather thin shell, the formation of occasional varices and the different microsculpture suggest otherwise. This genus may not be closely related to the *Rissoina* group of genera at all, its relationships possibly being with *Microstelma*. Judging only from illustrations, *Rissoa dactyliosa* does not appear to differ enough from *Pseudotaphrus buccinalis* for even subgeneric distinction to be maintained.

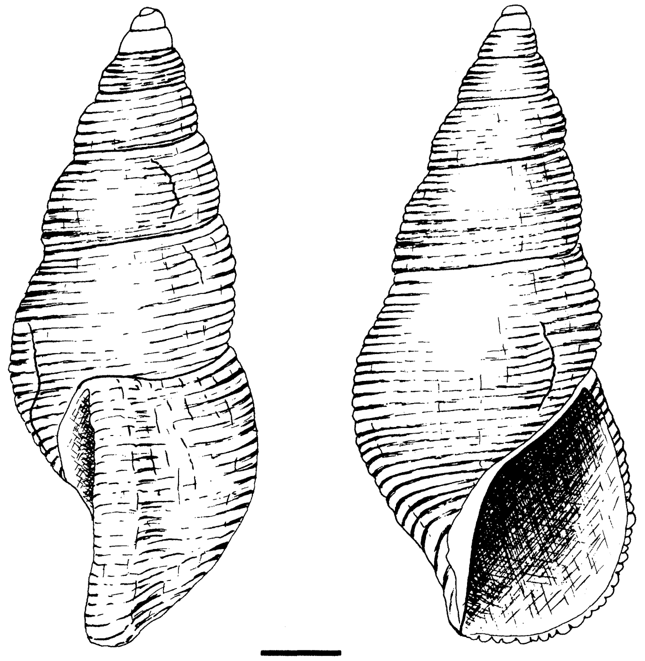

Fig. 66. *Pseudotaphrus buccinalis* (Lamarck); type-species of *Pseudotaphrus* Cossmann; le Fayel, Oise, France, Eocene (UMC). **Scale:** 1 mm.

Genus *Microstelma* A. Adams, 1863

Microstelma A. Adams, 1863: 347. Type-species *Microstelma daedala* A. Adams, 1863; monotypy. Recent, Japan (Fig. 68A).

Amaurella A. Adams, 1867: 311. Type-species *Macrocheilus japonicus* A. Adams, 1867; subsequent designation Cossmann, 1909: 81. Recent, Straits of Korea (Figs 67; 68F; 142G).

Crepitacella Guppy, 1867: 500. Type-species *Melanopsis cepula* Guppy, 1866; monotypy. Miocene, 'Cumana, Venezuela', ? = Bowden, Jamaica, *fide* Woodring, 1928: 361. (Fig. 68C, D).

Dolophanes Gabb, 1873: 272. Type-species *Dolophanes melanoides* Gabb, 1873; monotypy. Miocene, Dominican Republic (Fig. 68B).

Diagnosis. *Shell*: of medium to large size, ovate-conic, with narrow to absent umbilical chink; weak to moderate axial ribs and weak spiral striae; axial ribs (if present) do not extend over base. Base with prominent fasciole. Aperture with simple peristome, prominently channelled and angled anteriorly and posteriorly. Outer lip opisthocline, with weak varix externally; inner lip rather narrow (Figs 67; 68). Protoconch conical, multispiral or paucispiral (about 3½ whorls in *M. melanoides*, about 2 in *M. cepula* and *M. japonica*, and 1½ in *M. daedala*), microsculpture absent (known only in *M. japonica*, Fig. 142G).

Animal unknown.

Egg capsules: unknown.

Development: planktotrophic and direct development, deduced from protoconch morphology.

Distribution. Indo-Pacific: *M. daedala*; *M. japonicus*.

Caribbean region: *Dolophanes gabbi* Dall, 1889 (Fig. 68E); *Crepitacella vestalis* Rehder, 1943.

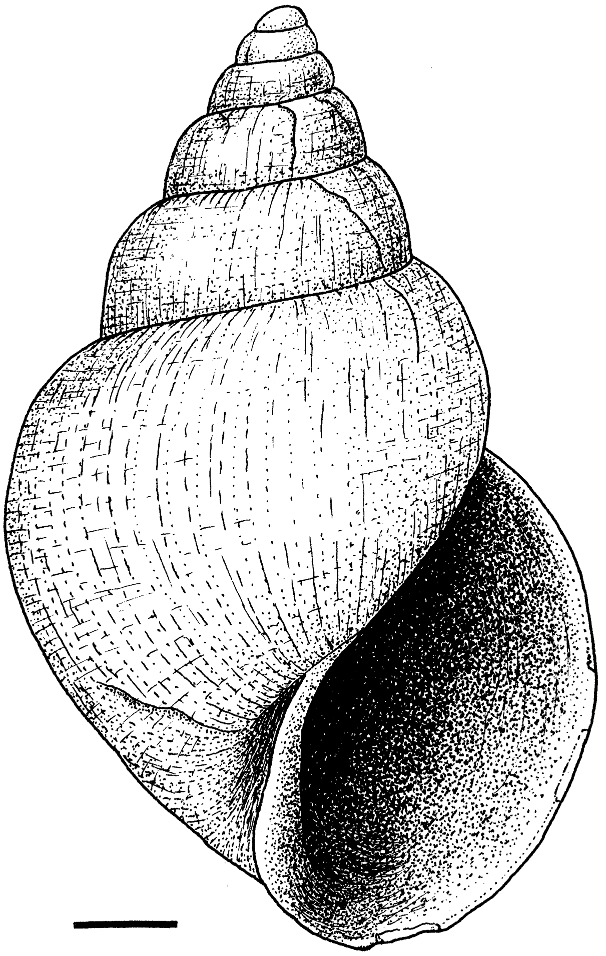

Fig. 67. *Microstelma japonica* (A. Adams); type-species of *Amaurella* A. Adams; probable syntype, 'Japan' (= Straits of Korea) (BMNH, 1878.1.28.425). **Scale:** 1 mm.

Miocene of the Caribbean region: *D. melanoides*; *C. cepula*; *Crepitacella aresca* Woodring, 1928.

Material Examined.

M. daedala. 3 lots, 2 ex H. Adams (BMNH).

\+ *M. japonicus*. 2 syntypes (BMNH); a few other lots (AMS).

M. cepula. Lectotype and 4 paralectotypes (USNM).

D. melanoides. 1 specimen (holotype?) (USNM).

D. gabbi. Holotype (USNM).

Remarks. Woodring (1928) discussed the type-species of *Crepitacella* at length. While *Dolophanes* has long been considered to be a synonym of *Crepitacella*, the relationship with *Microstelma* and *Amaurella* has not been noted previously. Examination of material of the type-species of the four genera listed in the synonymy here suggests that they can be regarded as being congeneric. The known distribution of the genus is extended by several records of *Microstelma japonica* in deep water off eastern Australia.

The relationships of *Microstelma* are not clear. It is possibly allied to *Pseudotaphrus* but otherwise does not appear to be closely related to any other genus. It may not be a rissoid.

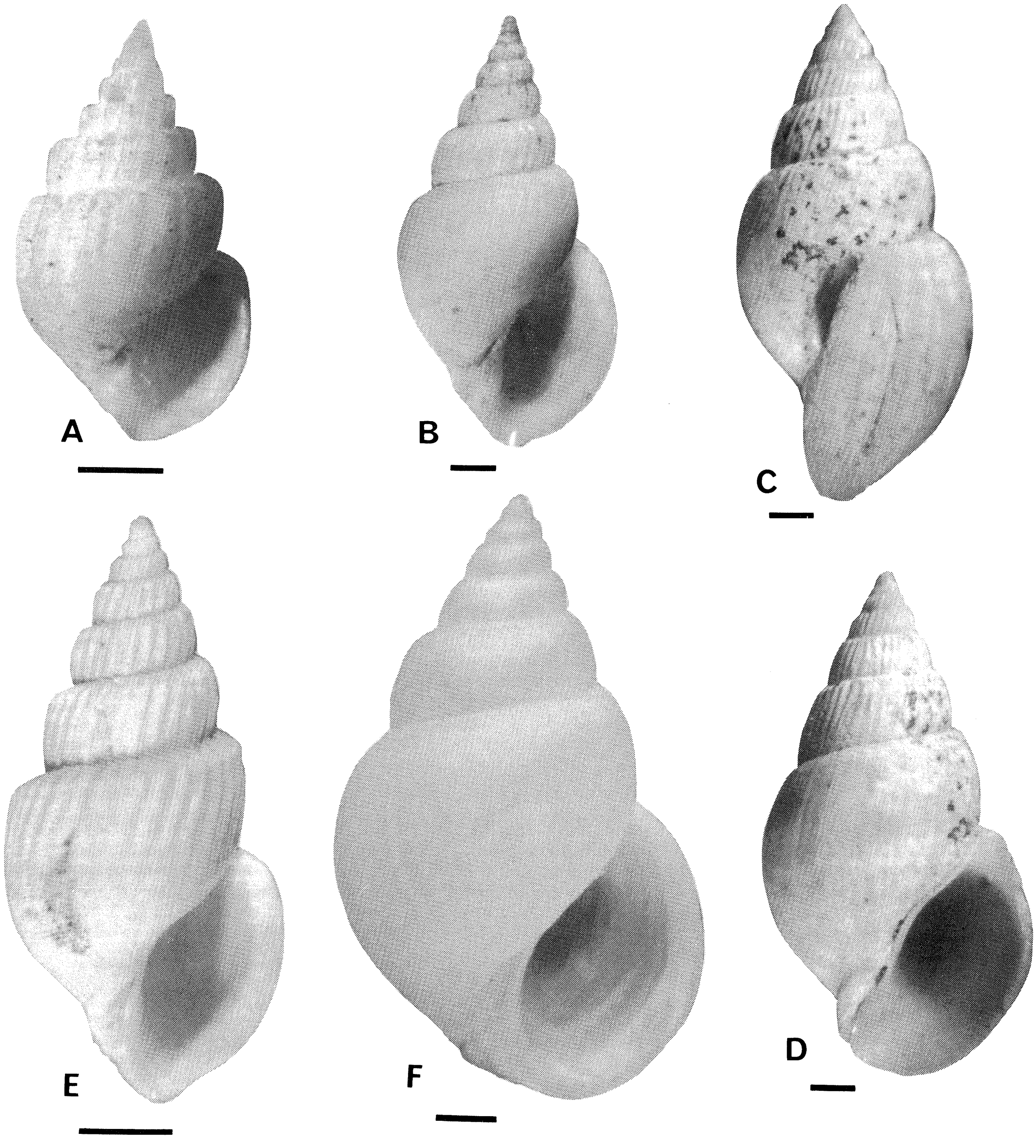

Fig. 68. Shells of *Microstelma* species. **A**, *Microstelma daedala* A. Adams, type-species of *Microstelma* A. Adams; syntype, 'Japan' (BMNH, 78.1.28.115). **B**, *Microstelma melanoides* (Gabb), type-species of *Dolophanes* Gabb; Miocene, Dominican Republic (USNM, 113392). **C-D**, *Microstelma cepula* (Guppy), type-species of *Crepitacella* Guppy; lectotype, Miocene, 'Cumana, Venezuela' (? = Bowden, Jamaica) (USNM, 115513). **E**, *Microstelma gabbi* (Dall); holotype, 785 fathoms (1436m), off St. Vincent, Windward Islands (USNM, 508719). **F**, *Microstelma japonica* (A. Adams); type-species of *Amaurella* A. Adams; 210-219 m, off S. end of Fraser Island, Queensland, Australia (AMS, C.134889). **Scale:** 1 mm.

Genera of Uncertain Relationship

Mesozoic genera of uncertain relationships are listed below. They have been included in the Rissoidae and may, possibly, belong there. No material of the type-species has been available to the writer for examination.

Genus *Trochoturbella* Cossmann, 1921

Trochoturbella Cossmann, 1921: 6. Type-species *Rissoa moreyensis* Cossmann, 1885; original designation. Middle Jurassic, Europe.

Remarks. Species in this group are axially, or spirally and axially, sculptured with a prosocline outer lip. They resemble species of *Alvania* and *Rissoa* in a general way and may represent an early rissoid group.

Genus *Calvadosiella* Wenz, 1939

Calvadosiella Wenz, 1939: 620 new name for *Calvadosia* Cossmann, 1921: 7, not Clark, 1863. Type-species *Trochoturbella (Calvadosia) brasili* Cossmann, 1921; original designation. Upper Jurassic, Europe.

Remarks. This genus is possibly related to *Rissoina* (*Buvignieria*).

Genus *Hirsonella* Fischer, 1969

Hirsonella Fischer, 1969: 156. Type-species *Hirsonella costifera* (Piette, 1855, *nom. nud.*), Fischer, 1969; original designation. Upper Jurassic (Bathonian), France.

Remarks. This genus is based on a species with a tall spire, a small aperture and a slightly twisted anterior canal. The teleoconch is sculptured with strong axial ribs. The relationships of this genus are obscure but are probably with the Cerithiacea.

Genus *Thierachella* Fischer, 1969

Thierachella Fischer, 1969: 156. Type-species *Euchrysalis rissoaeformis* (Piette, 1855, *nom. nud.*) Cossmann, 1885; original designation. Upper Jurassic (Bathonian), France.

Remarks. Species in this group have tall-spired, smooth shells with a prosocline outer lip. Fischer also includes *T. microstoma* (Piette, 1855 *nom. nud.*) Fischer, 1969. There is little in the shell characters of *Thierachella* indicative of its relationships although they may be with the Rissoidae or, possibly, Barleeidae.

Genera Wrongly Incuded in the Rissoidae

The generic names below are, with few exceptions, confined to those listed by Wenz (1939), Coan (1965) and Ponder (1967). They are grouped in what is considered to be correct taxonomic order. The type-species of many of these genera are figured to assist in substantiating the taxonomic position.

Subclass PROSOBRANCHIA
Order Archaeogastropoda

Family TROCHIDAE

Genus *Anxietas* Iredale, 1917

Anxietas Iredale, 1917: 334. Type-species *Anxietas perplexa* Iredale, 1917; original designation. Recent, Christmas Island, Indian Ocean (Fig. 145A, B).

Remarks. Iredale tentatively included his new genus in the Trochidae but Wenz (1939) reduced it to a synonym of *Amphithalamus* Carpenter, and Coan (1964) included it as a subgenus of *Scrobs* Watson, both genera now being included in the Barleeidae (Anabathrinae) (Ponder, 1983a). Ponder (1967) allowed *Anxietas* generic rank within the Anabathrinae. Iredale's illustration and description do not indicate any trochid features but examination of the syntypes (AMS) shows them to have a distinctive iridescent surface and an internal nacreous layer not mentioned by Iredale but probably influencing his decision to place his genus in the Trochidae. The aperture is channelled anteriorly and is similar in shape to that of *Putilla*.

Anxietas can be included in the Trochidae, although its relationships within the family are unclear.

Genus *Nevillia* H. Adams, 1868

Nevillia H. Adams, 1868: 289. Type-species *Nevillia picta* H. Adams, 1868; subsequent designation Nevill, 1885: 129. Recent, Mauritius.

Remarks. Tomlin (1938) suggested that this genus should be placed near *Euchelus* Philippi in the Trochidae. Examination of Adam's material of *N. picta* in the BMNH confirms that it is a trochid.

Genus *Botelloides* Strand, 1928

Botelloides Strand, 1928: 66. New name for *Botellus* Iredale, 1924: 183, 244, not Moniez, 1887. Type-species *Onoba bassiana* Hedley, 1911; original designation. Recent, Australia (Fig. 144D-F).

Remarks. It is shown elsewhere (Ponder, in press) that the radula and operculum of species of *Botelloides* indicate that the genus is related to *Halistylus* Dall, 1890, which is included in the subfamily Halistylinae in the Trochidae. The radula of both of these genera is unusual in that the central and lateral teeth are poorly developed; almost non-existent in *Botelloides* (Fig. 144E, F). Their placement in the Trochacea is undoubted but species of both genera are atypical of the Trochidae in lacking an inner nacreous layer in their shells. The shell of species of *Botelloides* (Fig. 144A, B) is strongly convergent with *Onoba* but can be distinguished by the circular aperture. The operculum (Fig. 144D) is multispiral and circular.

Family TURBINIDAE

Genus *Kaurnella* Ludbrook, 1941

Kaurnella Ludbrook, 1941: 88. Type-species *Kaurnella denotata* Ludbrook, 1941; original designation. Pliocene, South Australia (Figs 144C;145C).

Remarks. Examination of author's material (SAM) shows that the species on which this monotypic genus was based belongs in the Trochacea and resembles some turbinids, but lacks a nacreous layer. No entirely satisfactory familial designation can be determined and it is tentatively assigned to the Turbinidae on the basis of the shell sculpture and the similarity of its protoconch microsculpture (Fig. 144C) to some species of the Homalopomatinae.

Family SKENEIDAE

Genus *Putilla* A. Adams,1867

Putilla A. Adams, 1867: 312. Type-species *P. lucida* A. Adams, 1867; monotypy. Recent, Japan (Fig. 69A).

?*Notosetia* Iredale, 1915: 452. Type-species *Barleeia neozelanica* Suter, 1898; original designation. Recent, New Zealand (Fig. 69B).

?*Wanganella* Laseron, 1954: 13. Type-species *Wanganella fissura* Laseron, 1954, = *Cyclostrema porcellana* Tate & May, 1900; original designation. Recent, S.E. Australia (Fig. 69D).

?*Conicella* Laseron, 1954: 12. Type-species *Cyclostrema porcellana* Tate & May, 1900; original designation. Recent, S.E. Australia (Fig. 69C, D).

Remarks. The type-species of *Putilla* is known only by the holotype (BMNH). Its shell shows a strong resemblance to *Notosetia neozelanica* (Suter), the type-species of *Notosetia*, and the two genera can be regarded tentatively as congeneric on the evidence only of shell characters. This genus name has recently been used by Nordsieck (1972) for several small European rissoids.

The type-species of *Notosetia* was placed by Ponder (1965b) in the Liotiidae but a better family placement would be the Skeneidae. Two other genera from south-east Australia, originally described as liotiids, appear to be synonyms of *Putilla* and are listed above.

The type-species of *Conicella* is the same species as the type of *Wanganella*, from comparison of material in the AMS and the types (TM, AMS). *Rissoa pertranslucida* May, 1912 (Fig. 69C) is another synonym. The specimen Laseron (1954) identified as *Conicella porcellana* is an apparently undescribed species which is only superficially similar to *P. porcellana* (Tate & May) and not congeneric with it. Thus *Conicella* is based on a misidentified type-species.

Family PELYCIDIIDAE

This family was created recently for *Pelycidion* by Ponder & Hall (1983) for a small group of species previously included in the Rissoidae. It contains only one valid genus, *Pelycidion* Fischer in Fischer & Périer, 1873. *Allixia* Cossmann, 1912 and *Nannoteretispira* Habe, 1961, are synonyms. The family has been provisionally included in the Archaeogastropoda.

Order Mesogastropoda

Family EATONIELLIDAE

The genus-group taxa *Eatoniella* Dall, 1876, *Cerostraca* Oliver, 1915, *Dardanula* Iredale, 1915, *Pellax* Finlay, 1927 and *Skenella* Pfeffer (in Martens & Pfeffer), 1886 were separated into a new littorinacean family, the Eatoniellidae, by Ponder (1965a). *Skenella* is now known to be a cingulopsid (Ponder, 1983b).

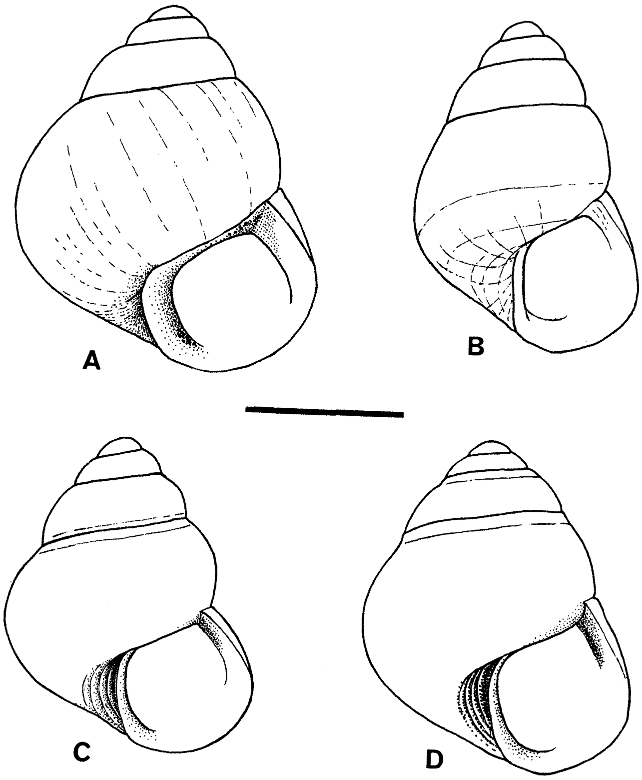

Fig. 69. **A**, *Putilla lucida* A. Adams; type-species of *Putilla* A. Adams; probable holotype, 54 fathoms (99m), Gotto Islands, Japan (BMNH, 78.1.28.310). **B**, *Putilla neozelanica* (Suter); type-species of *Notosetia* Iredale; Halfmoon Bay Stewart Island, New Zealand (AMS, C.16669). **C-D**, *Putilla porcellana* (Tate & May), nominal type-species of *Conicella* Laseron: **C**, paratype of *Rissoa pertranslucida* May, 183 m, off Cape Pillar, Tasmania (AMS, C.34117); **D**, syntype of *Wanganella fissura* Laseron, type-species of *Wanganella* Laseron; Port Stephens, New South Wales, Australia (AMS, C.101112). **Scale:** 0.5 mm.

Family CINGULOPSIDAE

Ponder (1965b) and Ponder & Yoo (1980) have shown that the following genus-group taxa are members of the Cingulopsidae Fretter & Patil, 1958: *Coriandria* Tomlin, 1917, new name for *Microsetia* Monterosato, 1884, = *Cingulopsis* Fretter & Patil, 1958 and *Globisetia* Nordsieck, 1972; *Mistostigma* Berry, 1947; *Eatonina* Thiele, 1912; *Boogina* Thiele, 1913, new name for *Watsonella* Thiele, 1912; *Eatoniopsis* Thiele, 1912. Ponder (1983b) has shown that *Skenella* Pfeffer (in Martens & Pfeffer), 1886 is a cingulopsid genus and is an earlier name for *Eatoniopsis*.

Family BARLEEIDAE

Many genus-group taxa previously referred to the Rissoidae have been included recently in the Barleeidae by Ponder (1983a). Two subfamilies are recognised within the family: the Barleeinae and Anabathrinae. The Barleeinae includes *Barleeia* Clark, 1853 (synonyms are *Pseudodiala* Ponder, 1967 and *Ansola* Slavoshevskaya, 1975); *Caelatura* Conrad, 1865; *Fictonoba* Ponder, 1967 and two new genera. The Anabathrinae includes *Anabathron* Frauenfeld, 1867 and its subgenus *Scrobs*

Watson, 1886 (synonyms of *Scrobs* are *Nannoscrobs* Finlay, 1927 and *Ultiscrobs* Iredale, 1955); *Amphithalamus* Carpenter, 1865 (synonyms are *Microfossa* Laseron, 1950 and *Obescrobs* Iredale, 1955), with a subgenus *Notoscrobs* Powell, 1927; *Microdryas* Laseron, 1950; *Badepigrus* Iredale, 1955 (synonyms are *Laseronula* Whitley, 1959, new name for *Saltatricula* Laseron, 1956, new name for *Saltatrix* Laseron, 1950); *Pseudestea* Ponder, 1967; *Pisinna* Monterosato, 1878 (synonyms are *Hagenmulleria* Bourguignat, 1881, *Estea* Iredale, 1915, *Nodulestea* Iredale, 1955, *Feldestea* Iredale, 1955 and *Microestea* Ponder, 1965) and *Nodulus* Monterosato, 1878. A related genus, *Emblanda* Iredale, 1955, is currently being investigated and may require a new family-level group to accommodate it.

Since the above was written preserved material of *Tropidorissoia taphrodes* Tomlin & Shackleford, 1915 (Fig.106A, B), the type-species of *Tropidorissoia* Tomlin & Shackleford, 1915, has been made available and this species proves to be a barleeid. See discussion under *Cingula* (*Lirocingula*) for further details.

Family EPIGRIDAE new family

Diagnosis. *Shell*: small, elongately-oval, imperforate, smooth, shining, with lightly-convex whorls. Protoconch dome-shaped, smooth, paucispiral. Aperture D-shaped, peristome simple, continuous. No inner chitinous layer. Periostracum absent.

Operculum: simple, thin, nucleus eccentric, last whorl large.

Radula: ribbon very broad and short, very small in relation to animal. Central teeth minute, simple, very narrow, with 1 cusp. Lateral teeth rectangular, with several small, blunt cusps, innermost slightly larger than others. Inner marginal teeth slightly larger than lateral teeth, with very broad, straight cutting edges parallel to base which is about ½ width of cutting edge; third or fourth cusp on inner side large, blunt, others small, blunt. Outer marginal teeth about same size as lateral teeth, subrectangular, ventral edge parallel to, but narrower than, straight cutting edge; cusps small, blunt, outermost longest.

Head-foot: snout very broad, bilobed, short; cephalic tentacles simple, rather narrow, shorter than snout, eyes at their outer bases.

Anatomy: ctenidium and osphradium present. Penis arises some distance behind right cephalic tentacle, slightly curved, with enclosed penial duct and very small distal swelling which appears to be glandular. Stomach rather large (radular, opercular and anatomical details based on 2 specimens of *Epigrus cylindraceus* from 113 km S. of Lakes Entrance, Victoria, 95 m and 1 specimen from off Sydney, 79 m).

Remarks. The new family is created because of the very distinctive radular features of *Epigrus*. The minute central tooth and the peculiar subrectangular lateral and marginal teeth are completely different from those of any other described taenioglossan radula known to the writer. The family can be provisionally included in the Rissoacea because of the presence of a penis, a snout and the simple, small shell.

A single alcohol-preserved specimen of *E. cylindraceus* from off Sydney in 79 m contained a large foraminiferan that occupied the entire anterior end of the stomach. A second specimen had only 2 small calcareous fragments in its stomach. The unusual radula is presumably not simply an adaptation to feeding on Foraminifera because *Rissoina* has a normal rissoid radula and some species feed, at least in part, in the same way (Kosuge, 1965b; Ponder, 1968).

Genus *Epigrus* Hedley, 1903

Epigrus Hedley, 1903: 355. Type-species *Rissoina cylindracea* T. Woods, 1878; original designation as *Rissoia ischna* Tate, 1899, new name for *Rissoina cylindracea* T. Woods, not preocc. by *Rissoa cylindracea* Krynicki, 1837 (Fig. 70; 146).

Diagnosis. Shell and protoconch (Figs 70; 146A, B), head-foot, operculum (Fig. 146C) and radula (Fig. 146D-F) as for family.

Development: probably direct.

Distribution. Australia: *R. cylindracea*, = *R. ischna* (unnecessary replacement name), = *Rissoa* (*Amphithalamus*) *simsoni* Tate & May, 1900, = *Epigrus borda* Cotton, 1944; *Eulima dissimilis* Watson, 1886; *Epigrus obesa* Laseron, 1956; ?*Aclis columnaria* May, 1910.

Material Examined.

+ **R. cylindracea*. Holotype and many other lots (AMS).
R. (*A.*) *simsoni*. Holotype (TM).
E. borda. Holotype (SAM).
E. dissimilis. Many lots (AMS).
E. obesa. Holotype and paratypes (AMS).

Remarks. This genus contains only three (or possibly four) known species, and appears to be confined to Australia even though it is found around the entire Australian coast. The thick shells of species of *Epigrus* preserve well in sediments and are consequently commonly encountered. Living material has proved, however, to be extremely difficult to obtain. The species appear to be living amongst coarse sediments on the continental shelf and in the sublittoral zone.

Wenz (1939) and Thiele (1929) listed *Epigrus* as a synonym of *Pelycidion* but that genus probably belongs in the Archaeogastropoda (Ponder & Hall, 1983).

UNNAMED FAMILY

A new family name will be proposed (Ponder, in press) for the genus *Elachisina* Dall, 1918 (synonym *Microdochus* Rehder, 1943).

Family HYDROBIIDAE

The following genus-group taxa have previously been shown to be hydrobiids: *Hemistomia* Crosse, 1872 (Starmühlner, 1970; Climo, 1974; Ponder 1982a); *Heterocyclus* Crosse, 1872 (Starmühlner, 1970); *Tatea* T. Woods, 1879 (Ponder, 1967; Climo, 1974); *Lanzaia*

Brusina, 1906. Wenz (1943: 1499) pointed out the similarity of *Lanzaia* to *Costellina* Kušćer, 1933 (type-species *C. turrita* Kušćer), a genus placed in the Hydrobiinae. The type-species of *Lanzaia* has been illustrated by Schütt (1968, fig. 1) and the genus is included in the Orientaliidae (= Hydrobiidae *s.l.)* by Radoman (1973).

Goniatogyra Cossmann, 1921 (type-species *Rissoa tenuis* Briart & Cornet, 1889 (Fig. 71); monotypy) from the Paleocene of Belgium can be tentatively included in this family.

It is noted above that the type-species of *Mohrensternia* Stoliczka may be a hydrobiid.

Family ?POMATIOPSIDAE/ASSIMINEIDAE

Genus *Floridiscrobs* Pilsbry & McGinty, 1949

Floridiscrobs Pilsbry & McGinty, 1949:15. Type-species *Amphithalamus* (*Floridiscrobs*) *dysbatus* Pilsbry & McGinty, 1949; original designation. Recent, Florida, U.S.A. (Figs 72; 148A-C).

Remarks. The shell of the holotype (ANSP) of the type-species has been examined and appears to be hydrobioid (*sensu* Davis, 1979). Ponder (1967) suggested affinity with *Stenothyra*, but the examination of a dried animal (Key West, edge of mangrove lagoon, LACM) revealed a typical hydrobioid animal with an operculum which has no calcareous material. The radula is unusual for North American hydrobiids in having three pairs of basal denticles on the central teeth (Fig. 148B, C). The radula is very like that of some Assimineidae and it is possible that *Floridiscrobs* is an atypical member of that family. The animal, however, is not typical of the Assimineidae and the rather heavy, elongately-oval operculum is also atypical (Fig. 148A). The cephalic tentacles are rather long with the eyes in very weak swellings at their outer bases. The snout is bilobed and large (nearly as long as the tentacles in the resuscitated animal), the dorsal foot is dark grey and the head (including the snout and tentacles) black.

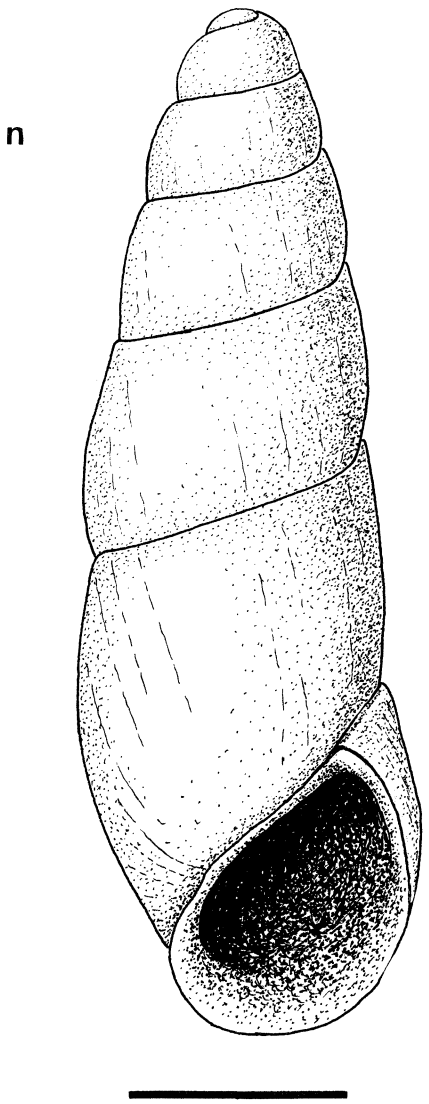

Fig. 70. *Epigrus cylindraceus* T. Woods, type-species of *Epigrus* Hedley; holotype; 82 m, off Sydney, New South Wales, Australia (AMS, C.246a). **Scale:** 1 mm.

Family FALSICINGULIDAE Slavoshevskaya, 1975b

Diagnosis. Shell ovate-conic to ovate, smooth or spirally sculptured, non-umbilicate, without internal chitinous shell layer; aperture simple, without varix. Periostracum well developed. Protoconch paucispiral, sculptured with spiral threads. Radula very similar to that of Rissoidae, with large pair of basal denticles on central teeth and small pair of denticles derived from lateral margins; cusps few, primary cusps of central and lateral teeth large. Operculum thin, horny, simple; nucleus eccentric. Foot wide, with a longitudinal furrow, no posterior mucous gland, anterior gland large. No metapodial or pallial tentacle. Penis well developed, prostate gland large. Female with upper oviduct communicating with kidney or pericardium. Pericardium and/or kidney modified to store sperm. Two posterior sperm sacs present. Albumen and capsule glands not separated; with central duct (i.e. no ventral channel).

Distribution. North Pacific.

Remarks. This family is convergent with the Rissoidae in most characters but differs fundamentally in lacking a ventral channel in the pallial oviduct. In this respect it resembles *Barleeia* but differs from that genus and other members of the Barleeidae in radular characters, in having a simple operculum, and in lacking a spermathecal duct. The Pomatiopsidae and Assimineidae also have a similar oviduct gland. Some species in the Pomatiopsidae also copulate via the kidney (Davis 1979), and in other respects (radula, shell) there are few differences between the two groups. Slavoshevskaya (1982) notes that the structure of the anterior pedal gland and the style sac agree closely with that of some Pomatiopsidae but differ from most other Rissoacea.

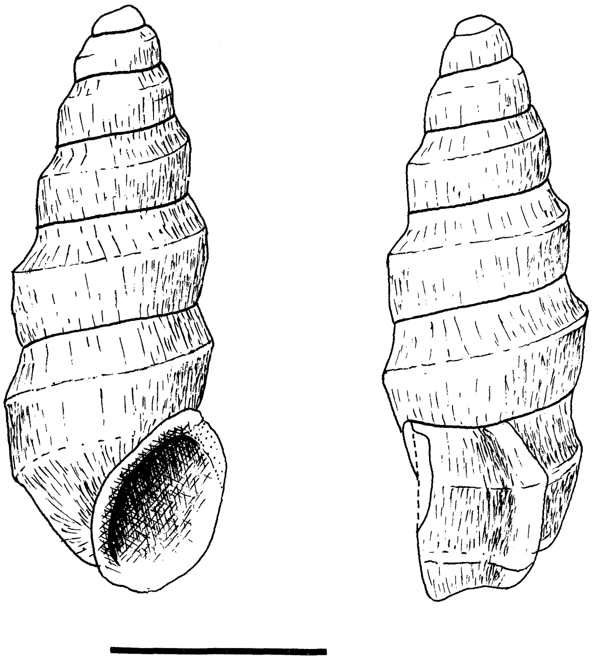

Fig. 71. *Goniatogyra tenuis* (Briart & Cornet); type-species of *Goniatogyra* Cossmann; no locality given on label, = Mons, Belgium (UMC). **Scale:** 1 mm.

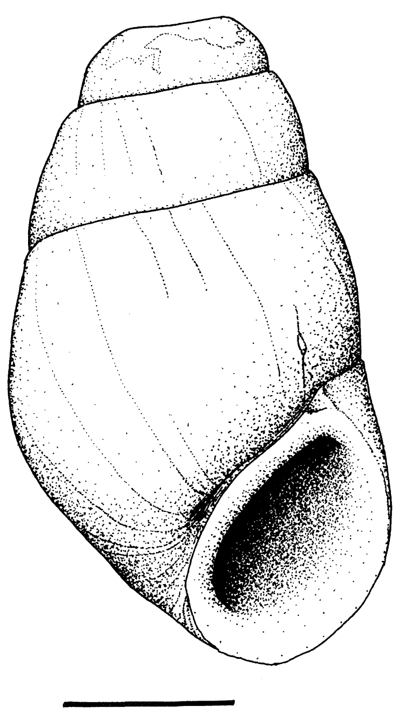

Fig. 72. *Floridiscrobs dysbatus* (Pilsbry & McGinty); type-species of *Floridiscrobs* Pilsbry & McGinty; edge of mangrove lagoon, E. end of Key West, Florida, U.S.A. (LACM, 70-32). **Scale:** 1 mm.

Genus *Falsicingula* Habe, 1958

Falsicingula Habe, 1958: 6. Type-species *Cingula kurilensis* Pilsbry, 1905; original designation. Recent, Kuril Islands, north-west Pacific (Fig. 147A-E).

Diagnosis. *Shell*: ovate-conic, rather thin, non-umbilicate, with weakly convex whorls, smooth except for fine spiral scratches and axial growth lines, usually with a thin to moderately well developed periostracum. Aperture ovate, weakly channelled posteriorly, broadly rounded anteriorly, outer lip weakly prosocline, without external varix. Protoconch about 1½ whorls, sculptured with very weak, irregular spiral ridges and pustules (Fig. 147A, B, G-I).

Head-foot: black; cephalic tentacles longer than bilobed snout, parallel-sided, with prominent eyes in swellings at their outer bases. No metapodial or pallial tentacles. Foot slightly expanded anteriorly, anterior edge convex, posterior end rounded. Sole with median longitudinal groove but no posterior mucous gland (based on *F. aleutica*, from notes by R. Baxter *in lit.* and on *F. athera*, Slavoshevskaya, 1982).

Operculum: thin, simple, horny, nucleus eccentric, last whorl large (Fig. 147E, F).

Radula: central teeth $\frac{1\text{-}3 + 1 + 1\text{-}3}{1 + 1 \quad 1 + 1}$; with 2 pairs of denticles on face of each central tooth, outermost pair minute, derived from lateral margins; cutting edge triangular, with relatively large median cusp; ventral margin with moderately developed U-shaped extension. Lateral teeth 1-2 + 1 + 2-6, primary cusp relatively large. Marginal teeth similar to those of Rissoidae, with numerous small cusps on outer distal ⅓ of inner marginal teeth and inner distal ¼ of outer marginal teeth (Fig. 147C, D, J).

Egg capsules: minute, lens-shaped, with only one embryo (*F. kurilensis*, Golikov & Kussakin, 1975, fig. 60b; *F. athera*, Slavoshevskaya, 1982).

Development: direct.

Distribution. North Pacific: *C. kurilensis*; *Falsicingula athera* (Bartsch ms) Golikov & Kussakin, 1967; *Onoba aleutica* Dall, 1886 (Fig. 147F-J). The north-western Pacific species have been reviewed by Golikov & Kussakin, 1978.

Material Examined.

+ * *C. kurilensis*. Types (ANSP) and several other lots (ANSP, USNM, AMS).

+ * *O. aleutica*. A few lots (AMS).

Remarks. The anatomy of *F. athera* has been investigated by Slavoshevskaya (1975b, 1982) and of *F. kurilensis* by Lazareva (1971). Slavoshevskaya (1975b, 1982) has shown that female *F. athera* store sperm in the pericardium, which is modified (in females) as a gametolytic organ. The female also has a peculiar modified kidney that is probably part of a sperm receiving structure, although Slavoshevskaya (1982) was unsure of its function. My unpublished investigations on *F. aleutica* have shown that in this species, the modified area of the kidney appears to receive and store sperm. The pericardium in that species does not appear to have a sperm storage function.

Family IRAVADIIDAE

I have reviewed this family recently (Ponder, 1984). Several of its genera have been previously included in the Rissoidae. These include: *Iravadia* Blanford, 1867; *Pellamora* Iredale, 1943, a synonym of *Iravadia* (*Fairbankia*) (Blanford ms) Stoliczka, 1868; *Mesodestea* Laseron, 1956, = *Iravadia* (*Fluviocingula*) Kuroda & Habe, 1954; *Pseudonoba* Boettger, 1902 as a subgenus of *Iravadia* with *Paronoba* Laseron, 1950, *Dipsotoma* Laseron, 1956, *Lucidinella* Laseron, 1956 and *Iraqirissoa* Dance & Eames, 1966 as synonyms; *Chevallieria* Cossmann, 1888, with *Nanadoma* Laseron, 1956 as a synonym; *Hyala* H. & A. Adams, 1852; *Ceratia* H. & A Adams, 1852; *Nozeba* Iredale, 1915, with *Antinodulus* Cossmann in Cossmann & Peyrot, 1919 as a synonym; *Rissopsis* Garrett, 1873.

Family STENOTHYRIDAE

Stenothyra Benson, 1856 (*Obesitena* Iredale, 1943 is a synonym) and *Gangetia* Ancey, 1890 were included in the Rissoidae, subfamily Stenothyrinae by Coan (1964). The Stenothyridae has, however, generally been given familial rank and this view is supported by the anatomical information given by Kosuge (1969).

Family VITRINELLIDAE

Genus *Discrevinia* Laseron, 1956

Discrevinia Laseron, 1956: 437. Type-species *Discrevinia balba* Laseron, 1956; original designation. Recent, Christmas Island, Indian Ocean (Fig. 73A, B).

Remarks. Examination of Laseron's type specimen (AMS) shows that it is an elongated species related to *Sansonia* Jousseaume, 1892. Some species referred to *Alvania* (*A.* (*Taramellia*) *kenneyi* Ladd, 1966 and *A.* (*Taramellia*) *corayi* Ladd, 1966) belong in *Sansonia.*

The familial position of this group is questionable. It is usually placed in the Archaeogastropoda but the examination of the radula of the similar and probably related *Lophocochlias minutissimus* (Pilsbry) shows it to be typical of the Vitrinellidae. The animal of any species of *Sansonia* has yet to be investigated. Bavay (1922) has reviewed this genus and Iredale (1936) has introduced a family name, Pickworthiidae, which could be used for the group if, after anatomical investigation, it was found to be distinct from the Vitrinellidae.

Microliotia Boettger, 1901 (type-species *Microliotia brandenburgi* Boettger, 1901 (Fig. 73C, D), Miocene of Europe) was placed in the Rissoidae by Wenz (1939). The shell features of the type-species closely resemble those of *Sansonia* and it can be included in that genus.

Genus *Scrupus* Finlay, 1927

Scrupus Finlay, 1927: 376. Type-species *Fossarus hyalinus* Odhner, 1924; original designation. Recent, New Zealand.

Remarks. The shell, operculum and radula of the Australian species *Scrupus minutus* (Petterd) agree well with those of *S. hyalinus*. The Australian species has a head-foot and anatomy similar to some Vitrinellidae and consequently *Scrupus* is tentatively placed in the family. The relationships of *Scrupus* and a description of its anatomy will be dealt with elsewhere.

Superfamily CERITHIACEA

Several genera included in the Rissoidae by Coan (1964) and Laseron (1950, 1956) are members of the Cerithiacea (Ponder, 1967). Many of them have been examined alive in the course of this work. Kosuge (1964) has described the anatomy of '*Diala*' (= *Styliferina*) *goniochila* Adams. *Styliferina* A. Adams, 1860 (? = *Dialessa* Iredale, 1955) is closely related to *Alaba* H. & A. Adams, 1853. These genera, and *Australaba* Laseron, 1956, should be tentatively included in the Litiopidae (*s.l.*) on the basis of head-foot characters.

Coan (1964) apparently included *Diala* A. Adams and its relatives in the Rissoidae on the basis of the *Barleeia*-like operculum of '*Diala*' *marmorea* Carpenter, 1864. The group of species to which *D. marmorea* belongs were placed with *Barleeia* by Ponder (1967; 1983a).

The following genus-group taxa appear to be closely related to, and may belong in, the Cerithiidae (*s.l.*). The family name Dialidae Ludbrook 1941, is available for them if they should prove to be a distinct family or subfamily. These taxa differ from those included in the Litiopidae in lacking epipodial tentacles: *Diala* A. Adams, 1861; *Dialopsis* Cossmann, 1889 (Fig. 145D); *Laevitestea* Laseron, 1950; *Mellitestea* Laseron, 1956; *Rissoalaba* Oyama, 1954; and *Paradiala* Laseron, 1956.

Laseron (1950, 1956) included *Obtortio* Hedley, 1899 (? = *Finella* A. Adams, 1860, error for *Fenella* A. Adams, 1864, not *Fenella* Westwood, 1840) in the Rissoidae but this genus belongs in the Cerithiacea. The familial position of *Obtortio* will be dealt with elsewhere.

Family DIASTOMATIDAE?

Genus *Keilostoma* Deshayes, 1848

Keilostoma Deshayes, 1848: 46. Type-species *Keilostoma turricula* Bruguière, = *Bulimus turriculus* Bruguière, 1792; monotypy. Eocene, Paris Basin.

Paryphostoma Bayan, 1873: 93, new name for *Keilostoma* Deshayes, 1848, not *Chilostoma* Fitzinger, 1833 (unnecessary replacement name).

Remarks. This extinct genus seems to have achieved a wide distribution in the early to middle Tertiary and has a fossil history from the Cretaceous. The species contained in it do not appear to be rissoids but are possibly related to *Diastoma* Deshayes, as far as can be judged from shell characters.

Family FOSSARIIDAE

Ponder (1967) suggested that *Nilsia* Finlay, 1927 might belong in this family. Another genus probably

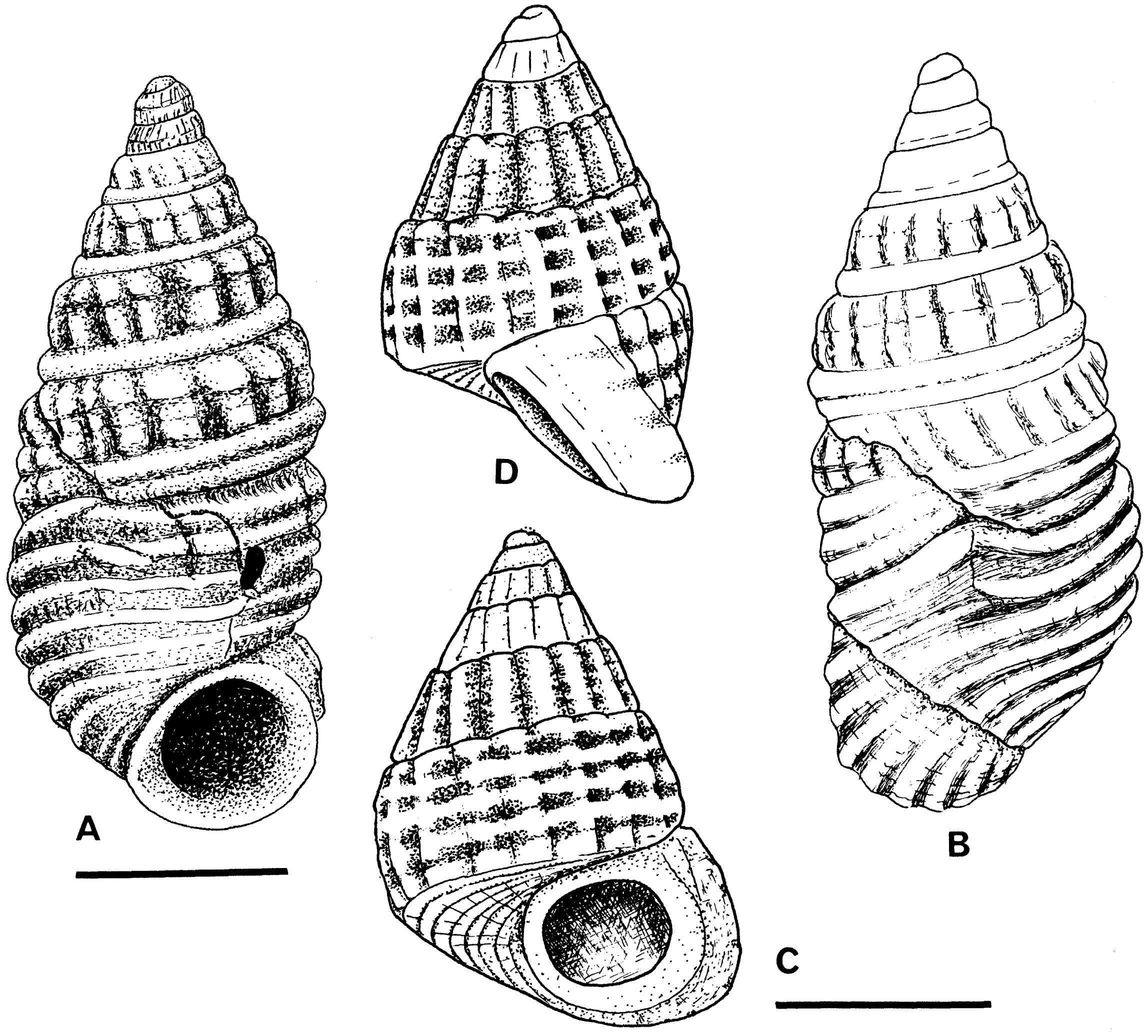

Fig. 73. **A-B**, *Discrevinia balba* Laseron; type-species of *Discrevinia* Laseron; holotype; Christmas Island, Indian Ocean (AMS, C.102475). **C-D**, *Microliotia brandenburgi* Boettger; type-species of *Microliotia* Boettger; Kostej, Rumania, Miocene (UMC). **Scale:** 1 mm.

related to *Nilsia* is *Constantia* A. Adams, 1860, at present included in the Epitoniidae. *Rissoa* ? *macrostoma* Thiele, 1925, *Rissoa coriacea* Manzoni, 1868 and *Rissoa tenuisculpta* Watson, 1873 may be related to *Nilsia* which in turn appears to be close to *Couthouyia* A. Adams, 1860. It is also possible that this group may belong in the Vanikoridae.

Family TURRITELLIDAE?

Genus *Actaeonema* Conrad, 1865

Actaeonema Conrad, 1865b: 147, new name for *Caelatura* Conrad, 1865b: 35, not Conrad, 1865a: 28. Type-species *Pasithea striata* Lea, 1833; monotypy. Eocene, Alabama, U.S.A.

Remarks. Palmer (1937) has suggested that *Pasithea striata* is based on a turritellid protoconch. Wenz (1939) tentatively included *Actaeonema* in the Iravadiidae, following Cossmann (1921).

Caeltura Conrad, 1865a, is now included in the Barleeidae (Ponder, 1983a).

Order Heterogastropoda

Family ACLIDIDAE

Genus *Awanuia* Powell, 1927

Awanuia Powell, 1927a: 538. Type-species *Merelina* (*Awanuia*) *dilatata* Powell, 1927; original designation. Recent, New Zealand.

Remarks. Although this genus has been regarded as a member of the Rissoidae by all previous writers a re-examination of the shell (Fig. 149A-C) of a species very similar to the type-species has shown that it is probably an aclidid. There are two species named in the genus, both from northern New Zealand. *Awanuia* is very similar to *Coenaculum* Iredale, 1924 (Fig. 149F-H) (= *Parascala* Cotton & Godfrey, 1931), a genus sometimes included in the Rissoidae but tentatively placed in the Aclididae by Wenz (1940). The examination of a preserved specimen of *Coenaculum minutulum* (Tate & May, 1900) and a reconstituted dried animal of *A. porcellana* Ponder failed to obtain a radula from either species. The animals lacked a true snout, there being only a slight protuberance between the tentacles, and there was a short retracted proboscis. The large eyes were situated in the centre of the bases of the tentacles.

Genus *Scalaronoba* Powell, 1927

Scalaronoba Powell, 1927b: 116. Type-species *Scalaronoba costata* Powell, 1927: original designation. Recent, New Zealand.

Remarks. Ponder (1967) placed *Scalaronoba* in the Pyramidellidae but re-examination of the shell suggests that is closely related to *Coenaculum* and *Scalaronoba*, and should thus be included in the Aclididae.

Another genus, at present included in the Epitoniidae, that is closely related to *Coenaculum* and *Scalaronoba* is *Dissopalia* Iredale, 1936 (type-species *Scala turrisphari* Hedley, 1905). This appears to be congeneric with *Bouryiscala* Cossmann, 1902, as pointed out by A. Warén (*in lit.*, 1982).

Genus *Cyclonidea* Laseron, 1956

Cyclonidea Laseron, 1956: 453. Type-species *Cyclonidea carina* Laseron, 1956; original designation. Recent, Christmas Island, Indian Ocean (Fig. 74C, D).

Remarks. Ponder (1967) reduced *Cyclonidea* to a synonym of *Teretianax* Iredale, 1938 on the basis of Laseron's description and figure. Examination of the holotype (AMS), however, shows that it is an aclidid.

Genus *Ruapukea* Dell, 1952

Ruapukea Dell, 1952: 417. Type-species *Ruapukea carolus* Dell, 1952; original designation. Recent, New Zealand (Fig. 74A, B).

Remarks. Examination of the holotype (NZGS) of the type-species shows that this genus should be included in the Aclididae.

Genus *Larochella* Powell, 1927

Larochella Powell, 1927a: 539. Type-species *Larochella toreuma* Powell, 1927; original designation. Recent, New Zealand (Fig. 149D, E).

Remarks. Examination of the shell confirms that this genus should be placed in a new group including *Graphis* Jeffreys, 1867, near the Aclididae. This group is currently being investigated by Dr. A. Warén and Prof. A. Graham. There are two species of *Larochella* described from New Zealand.

Genus *Austrorissopsis* Ponder, 1965

Austrorissopsis Ponder, 1965b: 115. Type-species *Rissopsis brevis* May, 1919, = *Rissopsis consobrina* Tate & May, 1900); original designation. Recent, Tasmania.

Remarks. Ponder (1974) has suggested that the type-species of this genus is probably a pyramidellid and tentatively regarded *Austrorissopsis* as a subgenus of *Eusetia*. Ponder (1974) also figured the holotype of the type-species of *Austrorissopsis*.Warén (*in lit.*) has suggested that this genus, and *Rissopsetia* Dell, 1956, may be related to *Cima* Jeffreys.

Genus *Eusetia* Cotton, 1944

Eusetia Cotton, 1944: 306. Type-species *Rissopsis expansa* Powell, 1930; original designation. Recent, New Zealand.

Remarks. Ponder (1967) has suggested that this genus is a member of the Pyramidellidae but Warén (*in lit.*) suspects it is probably an aclidid. The holotype of *E. expansa* has been refigured by Ponder (1974).

Family EULIMIDAE

Remarks. This family appears to contain several genus-group taxa previously included in the Rissoidae. Some of these are being revised currently by Dr A. Warén. In most cases little is known about these animals apart from their shells and the external appearance of the living animal of a few species.

The genera listed below differ from typical eulimids in their solid, rather opaque shells, often strong external sculpture, lack of a highly glossy surface and, in some, in having duplicated peristomes. They closely parallel some rissoid genera in shell characters but can be distinguished by their subulate protoconchs, porcellanous shell texture, and (usually) by the presence of distinct varices.

Genus *Pyramidelloides* Nevill, 1885

Pyramidelloides Nevill, 1885: 95. Type-species *Rissoina miranda* A. Adams, 1861; original designation. Recent, Japan (Fig. 150F-I).

Isselia auct., *nom. nud.*, not Bourguignat, 1877.

Remarks. This genus appears to contain 3-4 species in the Indo-West Pacific, although there are more names available. The shells differ from other related genera in having nodulose spiral ribs. Scale-like rugae cover the outer surface of the operculum (Fig. 150F). The anatomy of the type-species and *P. angusta* (Hedley) has been described in detail by Warén (1984). He has found it to be very similar to that of *Eulima*.

Species names that belong in this genus include *R. miranda*, = *Rissoina insolita* Deshayes, 1863, = *Rissoina bellardi* Issel, 1869, = *Rissoina* (*Pyramidelloides*) *insolita* vars *deformis*, *major* and *depauperata* Nevill, 1885, = *Rissoina hystrix* Souverbie, 1877, = *Rissoina eucosmia* Bartsch, 1915, = *Rissoina gemmulata* Turton, 1932, = *Pyramidelloides cylindrica* Laseron, 1956, = *P. pacifica* Laseron, 1956, = *P. turris* Laseron, 1956; and *Rissoina angusta* Hedley, 1898, = *Rissoa gracilis* Pease, 1861 (not *R. gracilis* Macgillivray, 1843, not Philippi, 1844), = *Rissoina viaderi* Tomlin, 1939.

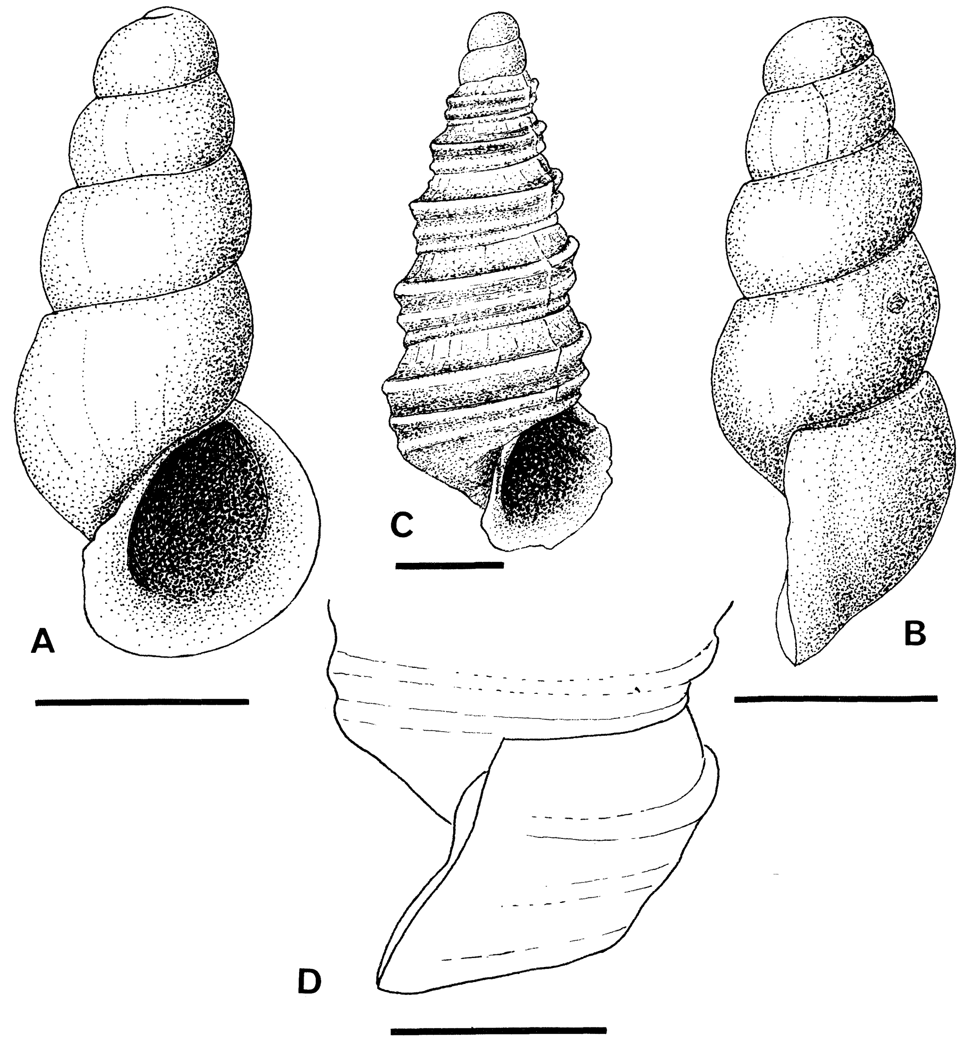

Fig. 74. **A-B**, *Ruapukea carolus* Dell; type-species of *Ruapukea* Dell; holotype; 24 m off Ruapuke Island (NZGS, TM786). **C-D**, *Cyclonidea carina* Laseron; type-species of *Cyclonidea* Laseron; holotype; Christmas Island, Indian Ocean (AMS, C.102477). **Scale**; 0.5 mm.

?Subgenus *Chrystella* Laseron, 1956

Chrystella Laseron, 1956: 427. Type-species *Chrystella islandica* Laseron, 1956; original designation. Recent, Christmas Island, Indian Ocean (Fig. 75I).

Remarks. The type-species is similar to species of *Pyramidelloides* but lacks the axial ribs that render the spirals nodulous. The spire is also shorter in two of the known species than in species of *Pyramidelloides*. *Rissoa finckhi* Hedley, 1899 is also a member of this subgenus.

?Subgenus *Teretianax* Iredale, 1919

Teretianax Iredale, 1919: 39. Type-species *Scalenostoma suteri* Oliver, 1915; original designation. Recent, Kermadec Islands (Fig. 150D, E).

Remarks. Ponder (1967) removed *Teretianax* from the Eulimidae on the basis of the external similarity of the animal to that of *Rissoina*. The shell characters and the probable lack of a radula (I failed to find a radula in *Teretianax pagoda* Powell, 1926), suggests, however, that *Teretianax* is related to *Pyramidelloides*. I (1967) reported a snout in *P.* (*T.*) *pagoda* but reference to my original notes suggests that this was a mistaken observation. I (1967) also regarded *Cyclonidea* Laseron as a synonym of *Teretianax* but examination of the holotype of the type-species has shown that it is an aclidid.

Additional species of *Teretianax* are *Rissoina baculumpastoris* Melvill & Standen, 1896 from Lifu Island, Loyalty Islands (Fig. 150C) and *Turritella minuta* Turton, 1932 from South Africa.

Both *Chrystella* and *Teretianax* are, as far as can be judged from shell characters, very closely related to *Pyramidelloides* but differ in lacking axial sculpture. They are only tentatively maintained as subgenera.

Genus *Palisadia* Laseron, 1956

Palisadia Laseron, 1956: 431. Type-species *Palisadia subulata* Laseron, 1956; original designation. Recent, Christmas Island, Indian Ocean (Fig. 150A, B).

Remarks. This genus appears to be related to *Chileutomia* Tate & Cossmann, 1898 and *Menon* Hedley, 1900 but differs in its very heavy varices, distinctly duplicated peristome, deeply incised sutures and the presence of sharp axial ribs over the surface between the varices. The protoconch is tall, multispiral and appears to be smooth. A few shells of this rare species have been obtained in north-eastern Australia (AMS).

Genus *Plagyostila* Fischer, 1872

Plagyostila Fischer (in De Folin & Périer), 1872: 50, for *Plagiostyla* Fischer (in De Folin & Périer), 1871, *nom. nud.* Type-species *Plagyostila asturiana* Fischer (in De Folin & Périer), 1872; monotypy. Recent, southern Atlantic coast of Europe and Mediterranean Sea (Fig. 148D, E).

Remarks. This genus is placed tentatively in the Eulimidae because of the shell 'texture'. It also resembles some Pyramidellidae but the columella lacks a distinct plait, although a weak bulge is present in some specimens, and the protoconch is not noticeably heterostrophic.

Genus *Anteglosia* Vokes, 1948

Anteglosia Vokes, 1948: 146. Type-species *Anteglosia essoensis* Vokes, 1948; original designation. Lower Cretaceous, Maryland, U.S.A.

Remarks. The three specimens in the type series (USNM) are all imperfect but the paratypes show strong varices similar to those in *Chileutomia*, although these are weaker in the holotype. The aperture appears to be rather simple and oval but is not well preserved in any of the specimens. This genus can be placed in the Eulimidae near *Chileutomia* on the available shell characters. Vokes also included two Maastrichtian species in *Anteglosia*: *Rissoina tennesseensis* Wade, 1926, which is a *Rissoina*, and *Rissoina subornata* Wade, 1926, which is probably a tall-spired fossariid related to *Nilsia* and *Couthouyia*.

Family MATHILDIDAE

Genus *Veterator* Laws, 1944

Veterator Laws, 1944: 306. Type-species *Brookesena quadricincta* Marwick, 1931; original designation. Miocene, New Zealand (Fig. 75H).

Remarks. This genus was included in the Rissoidae by Coan (1964), where it was originally placed by Laws. It was separated from *Brookesena* Finlay, 1927, another genus sometimes included in the Rissoidae, on the basis of the smooth protoconch of *V. quadricinctus* compared with the spirally ridged protoconch of *Mathilda neozelanica* (Suter) (Fig. 145F), the type-species of *Brookesena*. The two 'genera' are probably very closely related and both appear to belong to the Mathildidae, despite the absence of a heterostrophic protoconch. Ponder (1967) tentatively included *Brookesena* in the Aclididae but examination of the shell (Fig. 145E), operculum (Fig. 145G) and radula (Fig. 145H) of *B. neozelanica* shows that its placement in the Mathildidae by Wenz (1940) was correct. Neither of these two genera has a heterostrophic protoconch but, because the protoconch is paucispiral with a bulbous initial whorl (suggesting direct development), all trace of heterostrophy may have been lost.

Subclass OPISTHOBRANCHIA

Family PYRAMIDELLIDAE

Genus *Contraxiala* Laseron, 1956

Contraxiala Laseron, 1956: 421. Type-species *Contraxiala obliqua* Laseron, 1956; original designation. Recent, Queensland, Australia (Fig. 75A, B).

Remarks. Examination of the holotype (AMS) shows that it is a pyramidellid with the initial whorl of the protoconch strongly inverted and shell 'texture' typical of that family.

Genus *Costabieta* Laseron, 1956

Costabieta Laseron, 1956: 421. Type-species *Costabieta paucina* Laseron, 1956, = *Rissoina horrida* Garrett, 1873; original designation. Recent, Queensland, Australia (Fig. 75C, D).

Remarks. Examination of the holotypes of *C. paucina* (AMS) and *R. horrida* (ANSP) have shown them to be the same species. *Costabieta horrida* is a pyramidellid with the first whorl of the protoconch inverted and a very weak columellar plication. Examination of living material from Queensland shows the animal to be typical of the Pyramidellidae.

Genus *Herewardia* Iredale, 1955

Herewardia Iredale, 1955: 81. Type-species *Rissoina kesteveni* Hedley, 1907; original designation. Recent, Queensland, Australia (Fig. 75E, F).

Remarks. The type-species of this genus appears to be a pyramidellid from examination of the shell.

Subclass PULMONATA

Genus *Corena* A. Adams, 1870

Corena A. Adams, 1870: 122. Type-species *Corena tuberculifera* A. Adams, 1870; monotypy. Recent, Gulf of Suez (Fig. 75G).

Remarks. The presumed holotype (UC, ex MacAndrew Collection) is a badly damaged shell (Fig. 75G) of what is probably a stylommatophoran

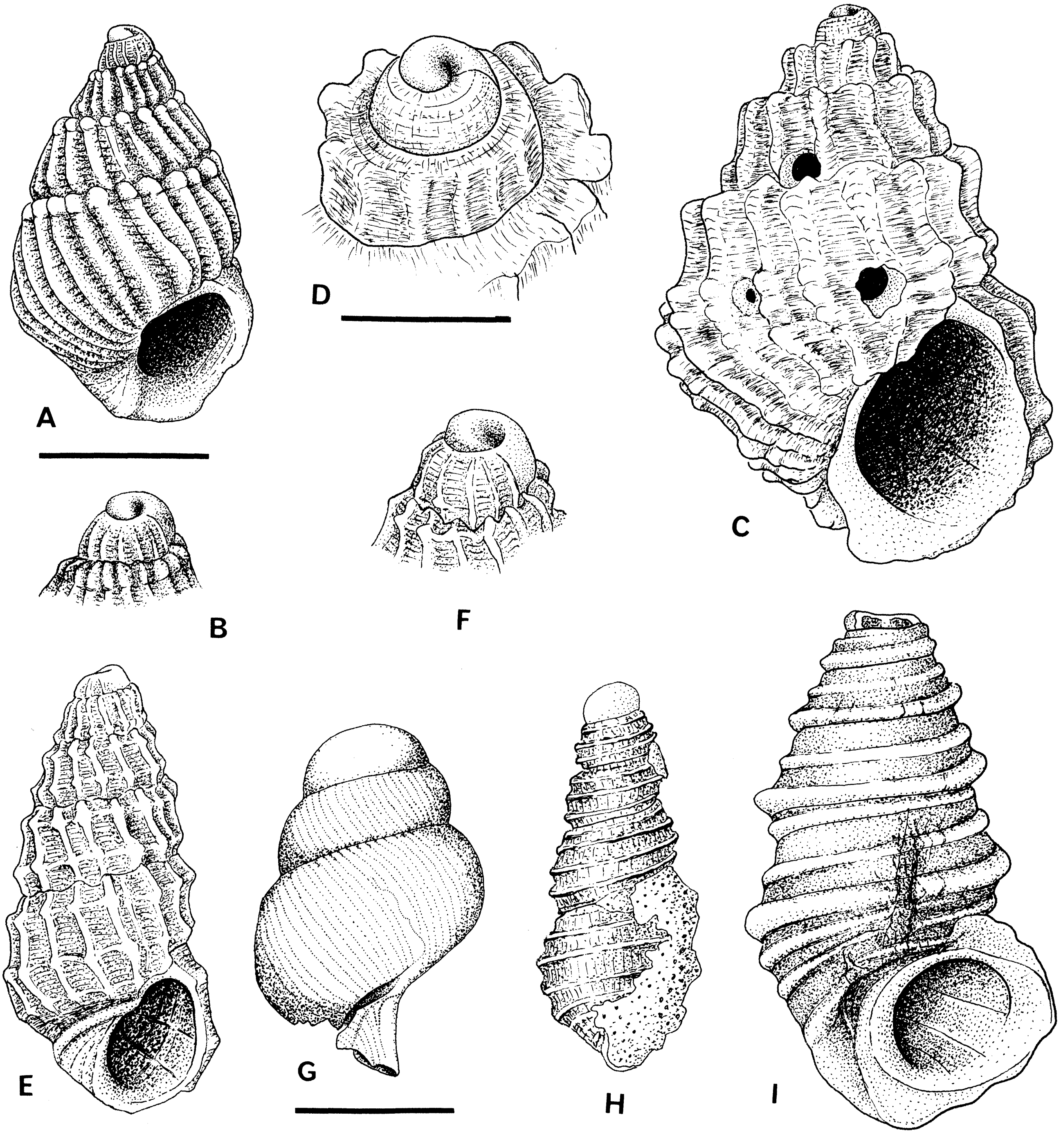

Fig. 75. A-B, *Contraxiala obliqua* Laseron; type-species of *Contraxiala* Laseron; holotype; Michaelmas Cay, Queensland (AMS, C.102453). **C-D**, *Costabieta horrida* (Garrett); holotype of *Costabieta paucina* Laseron, type-species of *Costabieta* Laseron; Michaelmas Cay Queensland (AMS, C.102465). **E-F**, *Herewardia kesteveni* (Hedley); type-species of *Herewardia* Iredale; holotype, 31-36 m, Masthead Reef, Queensland (AMS, C.19539). **G**, *Corena tuberculifera* A. Adams; type-species of *Corena* A. Adams; presumed holotype; Gulf of Suez (University Museum, Cambridge). **H**, *Veterator quadricincta* (Marwick); type-species of *Veterator* Laws; holotype; Miocene, Waikura Stream, Patutahi, New Zealand (NZGS, TM1342). **I**, *Pyramidelloides* (*Chrystella*) *islandica* (Laseron); type-species of *Chrystella* Laseron; holotype; Christmas Island, Indian Ocean (AMS, C.102464). **Scale:** A, C, E, H all same scale - 1 mm; B, D, F, I all same scale - 0.5 mm; G - 1 mm.

pulmonate; Streptaxidae, Pupillidae, or Enidae being the most likely families to which it could belong. It is unlikely that the fragmentary specimen will ever be satisfactory determined.

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References

Aartsen, J.J. Van, 1976. European marine Mollusca: notes on less well-known species. 1. *Alvania* (*Alcidiella*) *spinosa* Monterosato, 1890. Basteria 40: 127-132.

——— 1982. European marine Mollusca: notes on less well-known species. V. *Cingula* (*Setia*) *macilenta* (Monterosato, 1880) and *Rissoa concinnata* Jeffreys, 1883. Basteria 46: 127-128.

——— 1982a. Synoptic tables of Mediterranean and European Conchology. Gen. *Alvania*. Tav. 18. La Conchiglia 14 (158-159): 4-5.

——— 1982b. Synoptic tables of Mediterranean and European Conchology. Gen. *Alvania*. Tav. 19. La Conchiglia 14(160-161): 16-17.

——— 1982c. Synoptic tables of Medit. & Europ. Conchology. Genus *Alvania* (subg. *Alvinia* & *Galeodina*). Tav. 20. La Conchiglia 14 (162-163): 8-9.

Aartsen, J.J. Van & I. Nofroni, 1982. Synoptic tables of Mediterranean and European Conchology. Gen. *Alvania,* subgen. *Turbona*. Tav. 17. La Conchiglia 14(156-157): 20-21.

Aartsen, J.J. Van & A. Verduin, 1978. On the conchological identifications of *Cingula* (*Setia*) *fusca* (Philippi, 1841), *C.* (*S.*) *turriculata* (Monterosato, 1884), and *C.* (*S.*) *inflata* (Monterosato, 1884), marine gastropods from the Mediterranean. Basteria 42: 27-47.

Adams, A., 1863. On *Microstelma* and *Onoba*, two forms of rissoid gasteropods, with notices of new species of the latter from Japan. Annals and Magazine of Natural History (3)11: 347-349.

——— 1867. Descriptions of new species of shells from Japan. Proceedings of the Zoological Society of London 1867: 309-315.

——— 1870. On some genera and species of gasteropodous Mollusca collected by Mr McAndrew in the Gulf of Suez. Annals and Magazine of Natural History (4)6: 121-129.

Adams, H., 1868. Descriptions of some new species of shells collected by Geoffrey Nevill at Mauritius, the Isle of Bourbon, and the Seychelles. Proceedings of the Zoological Society of London 1868: 288-292.

Adams, H. & A. Adams, 1852. On a new arrangement of British Rissoae. Annals and Magazine of Natural History (2)10: 358-359.

Aldrich, T.H., 1910. New Eocene fossils from the southern States. The Nautilus 24(7): 73-75.

Babio, C.R. & Thiriot-Quiévreux, C., 1974. Gastéropodes de la région de Roscoff. Etude particulière de la protoconque. Cahiers de Biologie marine 15: 531-549.

Bavay, A., 1922. Coquilles des sables marins de l'Indo-Pacifique. Genres *Sansonia* Jousseaume, *Pickworthia* Iredale, *Mecoliotia* Hedley. Journal de Conchyliologie, Paris 66(2): 155-161.

Bayan, J.F., 1870-1873. Etudes faites dans la collection de L'Ecole des Mines sur des fossiles nouveaux ou mal connus 1: 1-80 (1870), 2: 81-164 (1873).

Berry, S.S. 1958a. Notices of new eastern Pacific Mollusca. II. Leaflets in Malacology 1(15): 83-90.

——— 1958b. West American molluscan miscellany. - II. 1. Proposal of five new generic taxons. Leaflets in Malacology 1(16): 91-95.

Bivona (E. Bernardi), A., 1838. Generi e specie di Molluschi descritti dal Barone Antonio Bivona E Bernardi (Published posthumously by F. Andrea). Giornale de' Letterati Sicilia 61: 211-227 (not seen).

Blainville, H.M., 1827. Rissoaire, *Rissoaria* (Conchyl.).

Dictionnaire des Sciences Naturelles 45: 477-480.

Boettger, O., 1887. Die Rissoidengattung *Stossichia*, Brus., ihre Synonymie u. ihre lebenden u. fossilen Vertreter. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 14: 136-147.

——— 1893. Die marine Mollusken der Philippinen, nach den Sammulungen des Herrn José Florencio Quadras in Manila. 1. Die Rissoiden. Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft 25: 97-115.

Bouchet, P., 1976. Mise en évidence de stades larvaires planctoniques chez des Gasteropodes Prosobranches des étages bathyal et abyssal. Bulletin du Muséum National d'Histoire Naturelle. 3. série, 400, zoologie 277: 947-971.

Brusina, S., 1870. Bibliotheca malacologica. II. Ipsa Chiereghinii Conchylia. Pisa 280pp.

Bucquoy, E., P. Dautzenberg & G. Dollfus, 1882-1886. Les Mollusques Marins du Roussillon. Tome I. Gastropodes, 565 pp, 66 pls; *Rissoina* and *Rissoa,* pp. 260-314 (1884)

Clark, W., 1852. On some undescribed animals of the British Rissoae. Annals and Magazine of Natural History 10: 254-264.

——— 1857. On *Rissoa pulcherrima*, Annals and Magazine of Natural History, 2nd Ser. 20: 262-263.

Climo, F.M., 1974. Description and affinities of the subterranean molluscan fauna of New Zealand. New Zealand Journal of Zoology 1(3): 247-284.

Coan, E., 1964. A proposed revision of the rissoacean families Rissoidae, Rissoinidae, and Cingulopsidae (Mollusca: Gastropoda). Veliger 6(3): 164-171.

Conrad, T.A., 1865a. Catalogue of the Eocene and Oligocene Testacea of the United States. American Journal of Conchology 1: 1-35.

——— 1865b. Descriptions of new Eocene shells of the United States. American Journal of Conchology 1: 142-149, pl. 10.

Cossmann, M., 1888, 1896. Catalogue illustré des coquilles Fossiles de l'Eocène des environs de Paris. Annales de la Société royale malacologique de Belgique 23(1888): 1-328, pls 1-12; 31(1896): 1-94, pls 1-3.

——— 1893. Notes complémentaires sur la faune Eocène de l'Alabama. Annales de géologie et de paléontologie. Palermo 12: 1-52.

——— 1909, 1921. Essais de Paléoconchologie Comparée, 9(1909): 1-248, pls 1-4; 12(1921): 1-336, plts 1-11; Paris.

Cotton, B.C., 1944. Recent Australian species of Rissoidae. Transactions of the Royal Society of South Australia 68: 286-314.

——— 1959. South Australian Mollusca. Archaeogastropoda. Handbook of the Flora and Fauna of South Australia. Government Printer, Adelaide, 449 pp.

Creek, G.A., 1951. The reproductive system and embryology of the snail *Pomatias elegans* (Müller). Proceedings of the Zoological Society of London 121: 599-640.

Crosse, H., 1868. Les Méléagrinicoles. Espéces nouvelles, par L. de Folin (1). Journal de Conchyliologie, Paris 16: 217-219.

——— 1885. Bibliographie. Journal de Conchyliologie, Paris 33: 137-160.

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. Bulletin of the Museum of Comparative Zoology, Harvard 18: 1-492, pls 10-40.

Dautzenburg, P. & Fischer, P.H., 1897. Campagnes scientifiques de S.A. le Prince Albert ler de Monaco. Diagnoses d'espèces nouvelles de gastéropodes. Bulletin de la Société zoologique de France 22: 37-45.

Davis, G.M., 1979. The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. Academy of Natural Sciences of Philadelphia, Monograph 20: 1-120.

——— 1980. Snail hosts of Asian *Schistosoma* infecting man: evolution and coevolution. In: The Mekong Schistosome; Malacological Review, supplement 2: 195-238.

Davis, G.M., V. Kitikoon & P. Temcharoen, 1976. Monograph on '*Lithoglyphopsis*' *aperta*, the snail host of Mekong River schistosomiasis. Malacologia 15(2): 241-287.

Davis, G.M., M. Mazurkiewicz & M. Mandracchia, 1982. *Spurwinkia*: morphology, systematics, and ecology of a new genus of North American marshland Hydrobiidae (Mollusca : Gastropoda). Proceedings of the Academy of Natural Sciences of Philadelphia 134: 143-177.

Dell, R.K., 1952. New marine mollusca from the Cook Strait area and southern New Zealand. Transactions of the Royal Society of New Zealand 79: 412-418.

Delphy, J. & A. Magne, 1938. Phototropisme, phototactisme et locomotion de *Rissoa parva* (da Costa). Procés verbaux de la Société linnéenne de Bordeaux 90: 31-32.

Deshayes, G.-P., 1839-53. Traité élémentaire de Conchyliologie avec les applications de cette science à la géologie. Explication des planches 1-80. Paris.

Desmarest, A.G., 1814. Description des coquilles univalves du genre *Rissoa* de M. de Freminville. Bulletin de la Société. philomathique de Paris (1814): 7-9 (Note: Author's name misspelt Desmarets on title page).

Finlay, H.J., 1924. New Zealand Tertiary rissoids. Transactions and Proceedings of the New Zealand Institute 55: 480-494.

——— 1926. New shells from New Zealand Tertiary beds: Part 2. Transactions and Proceedings of the New Zealand Institute 56: 227-258.

——— 1927. A further commentary on New Zealand molluscan systematics. Transactions and Proceedings of the New Zealand Institute 57: 320-385.

——— 1930. Invalid molluscan names, No. 1. Transactions and Proceedings of the New Zealand Institute 61: 37-48.

Fischer, J.- C., 1969. Géologie, paléontologie et paléoécologie du Bathonien au sud-ouest du Massif Ardennais. Mémoires du Muséum National d'Histoire Naturelle, Série C, 20: 1-319, pls 1-21.

Fischer, P., 1880-1887. Manuel de Conchyliologie et de Paléontologie conchyliologique ou Histoire Naturelle des Mollusques vivants et fossiles. Paris, L.F. Savy, XXIV + 1369 pp, 23 pls.

Fleming, C.A., 1966. Marwick's illustrations of New Zealand shells, with a checklist of New Zealand Cenozoic Mollusca. New Zealand Department of Scientific and Industrial Research, Bulletin 173, 456 pp.

Fleming, J., 1818. Conchology. - In: Supplement to the fourth and fifth edition of the Encyclopedia Britannica III(1): 313.

Folin, L. de & L. Périer, 1867-1886. Les fonds de la mer, étude internationale sur les particularités nouvelles des régions sous-marines. 4 volumes, Paris.

Fretter, V., 1956. The anatomy of the prosobranch *Circulus striatus* (Philippi) and a review of its systematic position. Proceedings of the Zoological Society of London 129: 369-381.

Fretter, V. & A. Graham, 1962. British prosobranch molluscs, their functional anatomy and ecology. Ray Society, London XVI + 755 pp.

——————— 1978. The prosobranch molluscs of Britain and Denmark. Part 4 - Marine Rissoacea. Journal of Molluscan Studies, Supplement 6: 151-241.

Fretter, V. & R. Manly, 1979. Observations on the biology of some sublittoral prosobranchs. Journal of Molluscan Studies 45: 209-218.

Fretter, V. & A.M. Patil, 1958. A revision of the systematic position of the prosobranch gastropod *Cingulopsis* (= *Cingula*) *fulgida* (J. Adams). Proceedings of the Malacological Society of London 33: 114-126.

——————— 1961. Observations on some British rissoaceans and a record of *Setia inflata* Monterosato, new to British waters. Proceedings of the Malacological Society of London 34: 212-233.

Fretter, V. & M.C. Pilkington, 1970. Prosobranchia - Veliger larvae of Taenioglossa and Stenoglossa. Fiches d'Identification. Zooplankton 129-132.

——————— 1971. The larval shell of some prosobranch gastropods. Journal of the Marine Biological Association of the United Kingdom 51: 49-62.

Gabb, W.M., 1873. Description of some new genera of Mollusca. Proceedings of the Academy of Natural Sciences of Philadelphia 24: 270-274.

Gistel, J., 1848. Naturgeschichte des Thierreichs für höhere Schulen bearbeitet. Stuttgart (not seen).

Gofas, S. & A. Warén, 1982. Taxonomie de quelques espèces du genre *Alvania* (Mollusca, gastropoda) des côtes Iberiques et Marocaines. Bollettino Malacologico 18(1-4): 1-16.

Golikov, A.N. & O.G. Kussakin, 1967. Molluscs of the Possiet Bay (the Sea of Japan) and their ecology (in Russian). Transactions of the Zoological Institute, Leningrad 42: 5-154, 14 pls.

——————— 1974. Additions to the fauna of shell-bearing gastropods from the intertidal zone of the Kuril Islands (in Russian). Sbornik Rabot Instituta Biologyi Morya 1: 289-299.

Golikov, A.N. & O.A. Scarlato, 1972. The Class Gastropoda. In: Definition of the fauna of the Black and Azov Seas (in Russian) 3: 65-166.

Golikov, A.N. & Y.I. Starobogatov, 1975. Systematics of prosobranch gastropods. Malacologia 15(1): 185-232.

Gordon, M., 1939. A new subgenus and species of West Coast '*Alvania*'. The Nautilus 53: 29-33.

Gougerot, L. & J. Le Renard, 1977. Clefs de détermination des petites espèces de Gastéropodes de l'Eocène du Bassin Parisien. X - Le genre *Rissoina*. Cahiers des Naturalistes. Bulletin des Naturalistes Parisiens, N.S. 33: 29-44.

Gould, A.A., 1860-1. Descriptions of shells collected by the North Pacific Exploring Expedition. Proceedings of the Boston Society of Natural History 7: 138-142, 161-167, 323-340, 382-389, 400-409 (additional parts published in 1859 and 1862).

Gray, J.E., 1847a (Oct.). The classification of the British Mollusca. By W.E. Leach, M.D. Annals and Magazine of Natural History 20: 267-273.

——————— 1847b (Nov.). A list of the genera of Recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London 1847: 129-242.

Guppy, J.L., 1867. Notes on West Indian geology, with remarks on the existence of an Atlantis in the early Tertiary period and descriptions of some new fossils from the Caribbean Miocene. Geological Magazine 4: 496-501.

Habe, T., 1958. The fauna of Akkeshi Bay XXV. Gastropoda. Publications from the Akkeshi Marine Biological Station 8: 1-39, pls I-V.

Hedley, C., 1903. Scientific results of the trawling expedition of H.M.C.S. 'Thetis'. Mollusca. Part II, Scaphopoda and Gastropoda. Australian Museum Memoir 4: 325-402, pls 36-38.

——————— 1904. Studies on Australian Mollusca. Part 8. Proceedings of the Linnean Society of New South Wales 29: 182-212, pls 8-10.

——————— 1918. A checklist of the marine fauna of New South Wales. Part 1. Mollusca. Journal and Proceedings of the Royal Society of New South Wales 51: M1-M120.

Hershler, R. & G.M. Davis, 1980. The morphology of *Hydrobia truncata* (Gastropoda : Hydrobiidae): relevance to systematics of *Hydrobia*. Biological Bulletin 158: 195-219.

Iredale, T., 1915. A commentary on Suter's 'Manual of the New Zealand Mollusca'. Transactions and Proceedings of the New Zealand Institute 47: 417-497.

——————— 1917. On some new species of marine Mollusca from Christmas Island, Indian Ocean. Proceedings of the Malacological Society of London 12: 331-334, pl. 13.

——————— 1924. Results from Roy Bell's molluscan collections. Proceedings of the Linnean Society of New South Wales 49: 179-278, pls 33-34.

——————— 1955. Rissoid sectional names. Proceedings of the Royal Zoological Society of New South Wales 1953-4: 81.

Jablonski, D. & R.A. Lutz, 1980. Molluscan larval shell morphology. Ecological and paleontological applications. In: Skeletal Growth of Aquatic Organisms. Edit. Rhoads, D.C. & R.A. Lutz, Plenum Publishing Corporation, pp. 323-377.

Janssen, A.W., 1967. Beiträge zur kenntnis des Miocäns von Dingden und seiner Mollusken fauna 1. Geologica et Palaeontologica 1: 115-173.

Jeffreys, J.G., 1867, 1869. The Mollusca. Marine shells. British Conchology, London IV (1867): 1-486, pls 1-4; V(1869): 1-258, pls 1-102.

——————— 1870. Mediterranean Mollusca. Annals and Magazine of Natural History (4)6: 65-86, 457-458.

——————— 1884. On the Mollusca procured during the 'Lightning' and 'Porcupine' expeditions, 1868-70 (Part 7). Proceedings of the Zoological Society of London 1884: 111-149, 2 pls.

Johansson J., 1939. Anatomische studien über die Gastropoden familien Rissoidae und Littorinidae. Zoologiska bidrag från Uppsala 18: 289-296.

——————— 1948. Uber die Geschlechtsorgane der Hydrobiiden und Rissoiden und den ursprünglichen Hermaphroditismus der Prosobranchier. Arkiv für Zoologi 40A(15): 1-13.

——————— 1950. Über die weiblichen Geschlechtsorgane von *Hyala vitrea*, einer von dem *Rissoa*-Typus stark abweichenden Form der Gruppe Rissoacea. Arkiv für Zoologi 42A(7): 1-6.

——————— 1953. On the genital organs of some mesogastropods: *Cerithium vulgatum* Brug., *Triphora perversa* (L.) and *Melanella* (*Eulima*) *intermedia* (Cantr.). Zoologiska bidrag från Uppsala 30: 1-23.

——————— 1956. Genital organs of two *Alvania* species, and a comparison with related families (Moll. Pros.). Arkiv für Zoologi, A.S. 9: 377-387.

Kay, E.A., 1979. Hawaiian marine shells. Reef and shore fauna of Hawaii. Section 4: Mollusca. Bishop Museum Press Honolulu. XVIII + 652 pp.

Keen, A.M., 1971. Seashells of tropical West America. Marine molluscs from Baja California to Peru. 2nd edit. Stanford University Press, Stanford. 1064 pp.

Kobelt, W., 1878. Illustrirtes Conchylienbuch 1(5): I-XVI, 105-144.

Kosuge, S., 1964. Anatomical study of *Diala goniochila* (A. Adams) (Gastropoda). Bulletin of the National Science Museum, Tokyo 7: 33-36.

——— 1965a. Descriptions of new genera and species of the family Rissoidae. Venus, Japanese Journal of Malacology 24: 108-112, pl. 15.

——— 1965b. Anatomical study on Japanese Rissoacea (I). On the family Rissoidae (I). Venus, Japanese Journal of Malacology 24(2): 130-151, pl. 15.

——— 1969. Anatomical study of Japanese Rissoidea (Gastropoda, Prosobranchia) II. On the family Stenothyridae. Bulletin of the National Science Museum, Tokyo 12(2): 217-239.

Kuroda, T., 1960. A catalogue of molluscan fauna of the Okinawa Islands. ? privately printed. 104 pp, 3 pls.

Ladd, H.S., 1966. Chitons and gastropods (Haliotidae through Adeorbidae) from the Western Pacific Islands. United States Geological Survey Professional Paper 531: I-IV, 1-98, 16 pls.

Laseron, C.F., 1950. Review of the Rissoidae of New South Wales, Records of the Australian Museum 22(3): 257-287.

——— 1956. The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian Zoogeographical Provinces. Australian Journal of Marine and Freshwater Research 7(3): 384-484.

Laws, C.R., 1944. The molluscan faunule at Pakaurangi Point, Kaipara, No. 3. Transactions and Proceedings of the Royal Society of New Zealand 76: 537-541.

Lazareva, A.I., 1971. A contribution to the taxonomy of gastropoda from the genus *Falsicingula* Habe (Prosobranchia, Rissoidea) (In Russian). Zoologicheskii Zhurnal 50(5): 768-770.

Leach, W.E., 1852. Molluscorum Britanniae synopsis. A synopsis of the Mollusca of Great Britain arranged according to their natural affinities and anatomical structure. Edit. by J.E. Gray. J. van Voorst, London.

Lebour, M.V., 1934. Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth rissoides. Journal of the marine biological Association of the United Kingdom 19(n.s.): 523-539.

Locard, A., 1897. Expédition scientifique du Travailleur et du Talisman pendant les années 1880, 1881, 1882 et 1883. Mollusques testacés 1. Paris. 516 pp, 22 pls.

Ludbrook, N.H., 1941. Gastropoda from the Abattoirs Bore, Adelaide, South Australia together with a list of some miscellaneous fossils from the bore. Transactions of the Royal Society of South Australia 65: 79-102, pls 4, 5.

Marcus, E. & E. Marcus, 1963. Mesogastropoden von der Küste São Paulos. Akademie der Wissenschaften und der Literatur. Abhandlungen der Mathematisch - Naturwissenshaft - lichen Klasse 1: 1-105.

——— 1964. On *Rissoina chesneli* (Michaud, 1830). Proceedings of the Malacological Society of London 36: 163-172.

Martens, E. von, 1878, Mollusca. The Zoological Record for 1876. 62 pp.

Marwick, J., 1931. The Tertiary Mollusca of the Gisborne District. New Zealand Geological Survey palaeontological Bulletin 13: 1-177, 18 pls.

Melvill, J.C., 1918. Descriptions of thirty-four species of marine Mollusca from the Persian Gulf, Gulf of Oman, and Arabian Sea, collected by Mr F.W. Townsend. The Annals and Magazine of Natural History 1(9th series): 137-158, pls 4-5.

Monterosato, T.A. Di,1878. Enumerazione e sinonimia delle conchiglie Mediterranee. Giornale di scienze naturali ed economiche di Palermo 13: 61-115.

——— 1884a (1884-1885). Conchiglie littorali Mediterranee. Naturalista Siciliano 3(1884): 87-91, 102-111, 137-140, 159-163, 227-231, 277-281; 4(1884-5): 21-25, 60-63, 80-84, 200-204.

——— 1884b. Nomenclatura generica e specifica di alcune conchiglie Mediterranee. Palermo. 152 pp.

——— 1890. Conchiglie delle profundita del Mare di Palermo. Naturalista Siciliano 9: 140-151.

——— 1891. Molluschi Fossili Quaternari di S. Flavia. Naturalista Siciliano 10(5): 1-14.

——— 1917. Molluschi viventi e quaternari raccolti lungo le coste della Tripolitania. Bollettino della societa' zoologica Italiana 4: 1-25, 2 pls.

Moore, D.R., 1969. Systematics, distribution, and abundance of the West Indian micromollusk *Rissoina catesbyana* d'Orbigny. Transactions-Gulf Coast Association of Geological Societies 19: 425-6.

Mörch, O.A.L., 1876 (1875-77). Synopsis molluscorum marinorum Indianum occidentalium inprimis insularum danicarum. Malakozoologische Blätter 22 (1875): 142-184; 23 (1876): 45-58, 87-143; 24 (1877); 14-66, 93-123.

Mohrenstern, S.V., 1858-1864. Die family der Rissoiden I (1858) *Rissoina*: 1-120, 11 pls; II (1864) *Rissoa*: 1-58, 4 pls. Wein.

Nevill, G., 1881. New or little known Mollusca of the Indo-Malayan fauna. Journal of the Asiatic Society of Bengal 50: 125-167.

——— 1885. Hand list of Mollusca in the Indian Museum, Calcutta. Part II. Gastropoda. Prosobranchia-Neurobranchia (contd.). Government Printer, Calcutta. X + 306 pp.

Newton, R.B., 1891. Systematic list of the F.E. Edwards collection of British Oligocene and Eocene Mollusca in the British Museum (Natural History), with references to the type-specimens from similar horizons contained in other collections belonging to the Geological Department of the Museum. British Museum (Natural History), London. XXVIII + 365 pp.

Nordsieck F., 1972. Die europäischen Meeresschnecken (Opisthobranchia mit Pyramidellidae; Rissoacea). Gustav Fischer, Stuttgart. 327 pp.

Oyama, K., 1962. New gastropods from Japan. Venus, Japanese Journal of Malacology 22(1): 56-58.

——— 1973. Revision of Matajiro Yokoyama's type Mollusca from the Tertiary and Quaternary of the Kanto area. Palaeontological Society of Japan, Special Papers 17: 1-148, 57 pls.

Palmer, K.V.W., 1937. The Clairbornian Scaphopoda, Gastropoda and Dibranchiate Cephalopoda of the southern United States. Bulletin of American Paleontology 7(32)1: 1-548; 2: 549-730, 90 pls.

Pchelintsev, V.F. & I.A. Korobkov, 1960. Mollyuski-Bryukhonogie. Osnovy Paleontologii. Gosoudarstvennoye, Nauch-tekhno izdatelstvo po geologii i okhrane nedr, Moscow 4: 1-360.

Philippi, R.A., 1836. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit. Berlin. I-XIV, 1-268, 28 pls. (Part 2 published in Halle, 1844).

Piani, P., 1979. Rissoacea Mediterranei. Digesta I. Le specie Mediterranee del genere *Galeodina* Monterosato, 1884.

Bollettino Malacologico 15(3-4): 67-73.

——— 1980. Catalogo dei Molluschi conchifera viventi nel Mediterraneo. Bollettino Malacologico 16: 113-224.

Pilsbry, H.A., 1922. Revision of W.M. Gabb's Tertiary Mollusca of Santo Domingo. Proceedings of the Academy of Natural Sciences of Philadelphia 73: 305-435, pls 16-47.

Pilsbry, H.A. & T.L. McGinty, 1949. New marine mollusks of Florida and the Bahamas. Nautilus 63: 9-15.

Ponder, W.F., 1965a. The family Eatoniellidae in New Zealand. Records of the Auckland Institute and Museum 6: 47-99.

——— 1965b. A revision of the New Zealand Recent species previously known as *Notosetia* Iredale, 1915 (Rissoidae, Gastropoda). Records of the Auckland Institute and Museum 6: 101-130.

——— 1966a. The New Zealand species previously known as *Zelaxitas* Finlay, 1927 (Mollusca: Gastropoda). Records of the Dominion Museum, Wellington 5: 163-176.

——— A new family of the Rissoacea from New Zealand. Records of the Dominion Museum, Wellington 5: 177-184.

——— 1967. The classification of the Rissoidae and Orbitestellidae with descriptions of some new taxa. Transactions of the Royal Society of New Zealand, Zoology 9: 193-224.

——— 1968. The morphology of some small New Zealand prosobranchs. Records of the Dominion Museum, Wellington 6: 61-95.

——— 1974. A review of the Australian species assigned to *Rissopsis* Garrett with a description of a new species of *Rissopsetia* (Mollusca: Gastropoda). Journal of the Malacological Society of Australia 3: 25-35.

——— 1982a. Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). Australian Journal of Marine and Freshwater Research 33: 89-159.

——— 1982b. The anatomy and relationships of *Hydrococcus brazieri* (T. Woods) (Mollusca: Gastropoda: Rissoacea). Journal of Molluscan Studies 48: 64-79.

——— 1983a. Review of the genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea). Records of the Australian Museum, 35: 231-281.

——— 1983b. Rissoaform gastropods from the Antarctic and sub-Antarctic. Eatoniellidae, Rissoidae, Barleeidae, Cingulopsidae, Orbitestellidae and Rissoellidae (Mollusca: Gastropoda) of Signy Island, South Orkney Islands, with a review of the Antarctic and sub-Antarctic species. British Antarctic Survey Scientific Reports 108: 1-96.

——— 1984. A review of the genera of the Iravadiidae (Mollusca: Gastropoda: Rissoacea) with an assessment of the relationships of the family. Malacologia 25: 21-71.

——— (in press). The relationships of *Elachisina* Dall (Mollusca: Gastropoda: Rissoacea).

——— (in press). A revision of the genus *Botelloides* (Mollusca: Gastropoda: Trochacea).

Ponder, W.F. & S.J. Hall, 1983. Pelycidiidae, a new family of archaeogastropod molluscs. Nautilus 97(1): 30-35.

Ponder, W.F. & E.K. Yoo, 1976. A revision of the Australian and Tropical Indo-Pacific Tertiary and Recent species of *Pisinna* (= *Estea*) (Mollusca: Gastropoda: Rissoidae). Records of the Australian Museum 30: 150-247.

——— 1980. A review of the genera of the Cingulopsidae with a revision of the Australian and tropical Indo-Pacific species (Mollusca: Gastropoda: Prosobranchia). Records of the Australian Museum 33(1): 1-88.

Powell, A.W.B., 1926. Descriptions of six new species and a new genus of gastropod Mollusca from northern New Zealand. Transactions and Proceedings of the New Zealand Institute 56: 591-596.

——— 1927a. The genetic relationships of Australasian rissoids. Transactions and Proceedings of the New Zealand Institute 57: 534-548.

——— 1927b. Deep-water Mollusca from south-west Otago. Records of the Canterbury Museum, Christchurch 3: 113-124.

——— 1930. New species of New Zealand Mollusca from shallow-water dredgings. Transactions and Proceedings of the New Zealand Institute 60: 532-543.

——— 1937. New species of marine Mollusca from New Zealand. Discovery Reports 15: 153-222, pls 45-56.

——— 1979. New Zealand Mollusca. Marine, land and freshwater shells. Collins, Auckland. XIV + 500 pp.

Quintaret, G., 1904. Sur la disposition générale du système nerveux chez la *Rissoa elata* var *oblonga* (Desmarest). Compte rendu de l'Académie des Sciences 139: 301-2.

Radoman, P., 1973. New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. Prosebna Izdanja. Museum d'Histoire Naturelle de Beograd. Editions hors serie 32: 1-30.

Rassmussen, E., 1951. Faunistic and biological notes on marine invertebrates. II. The eggs and larvae of some Danish marine gastropods. Videnskabelige Meddelelser fra Dansk natur-historisk Forening i. KjØbenhavn 113:201-249.

——— 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1-495.

Rehder, H.A., 1980. The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gómez. Smithsonian Contributions to Zoology 289: 1-167.

Rex, M.A., C.A.V. Unmersen, & R.D. Turner, 1979. Reproductive pattern in the abyssal snail *Benthonella tenella* (Jeffreys). In: Reproductive ecology of marine invertebrates, ed. S.E. Stanwyck. University of South Carolina Press, Columbia. pp. 137-188.

Risso, A, 1813 a (Aug.). Sur la presqu'île de Saint-Hospice aux environs de Nice, département des Alpes-Maritimes. Journal des Mines 200: 81-98.

——— 1813b (Sept.). Observations géologiques sur la presqu'île de St. Hospice, département des Alpes-Maritimes. Nouveau Bulletin des Sciences, par la Société Philomatique de Paris 3(5): 339-342.

——— 1826. Des principales productions de l'Europe Méridionale. Histoire Naturelle 4: 1-439, pls 1-12. Paris.

Sacco, F., 1895, 1904. I Molluschi dei Terreni Terziarii del Piemonte e Della Liguria Part 18 (1895): 1-51, pls 1-129; part 30 (1904): 1-203, pls 1-31.

Sars, G.O., 1878. Mollusca regionis Arcticae Norvegiae. Bidrag til Kundskaben om Norges Arktiske Fauna 1: I-XIII, 1-466, 18 pls.

Schmeltz, J.D.E., 1874. Catalog V der Zum Verkauf stehenden Doubletten aus den naturhistorischen Expedition der Herren J.C. Godeffroy & Sohn in Hamburg. XXXVI + 215 pp. Hamburg.

Schütt, H., 1968. Verwandtschaftliche Beziehungen höhlenbewohneneder Rissoaceen Dalmatiens. Archiv für Molluskenkunde 98(3-4): 103-111.

Seguenza, L.Fu G., 1903. Rissoidi neogenici della provincia di Messina. Palaeontographia Italica 9: 35-60, pl. 11.

Sherborn, C.D., 1902-1933. Index animalium. 10 volumes. London.

Skavoshevskaya, L.V., 1975a. Peculiarities of the reproductive system of the Rissoacea and their importance for taxonomy in this superfamily (in Russian). In: Likharev, I.M. (Editor), Molluscs, their system, evolution and significance in nature. Theses in communications. Academy of Sciences, U.S.S.R. Institute of Zoology. Izdatel'stvo 'Nauka', Leningrad: 117-120.

———— 1975b. Morphological peculiarities of the reproductive system in *Falsicingula athera* and the systematic status of the genus *Falsicingula* Habe (Gastropoda, Rissoacea) (in Russian). Zoologicheskii Zhurnal 54: 510-516.

———— 1979. Organisation, reproduction and systematic position of *'Thapsiella' plicosa* (Smith) from the Sea of Japan. In: Morphology, systematics and phylogeny of molluscs. Zoological Institute, Leningrad: 93-101.

———— 1982. Organization, reproduction, habitat of *Falsicingula athera* and systematic position of the Falsicingulidae (Gastropoda, Prosobranchia) (in Russian). Zoologicheskii Zhurnal 61: 1297-1308.

———— 1983. Organization and systematic position of Rissoacea (Gastropoda, Pectinibranchia) (in Russian). In: Molluscs, their systematics, ecology and distribution. Seventh meeting on the investigation of molluscs. The USSR Academy of Sciences Zoological Institute: 15-18.

Smith, S.M., 1971. *Rissoa violacea* Desmarest, *Rissoa lilacina* Récluz, *Rissoa rufilabrum* Alder and *Rissoa porifera* Lovén and their distribution in British and Irish Waters. Journal of Conchology 27: 235-241.

Sohl, N.F., 1960. Archaeogastropoda, Mesogastropoda and Stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations. United States Geological Survey, Professional Paper 331-A: 1-151, 18 pls.

Starmühlner, F., 1970. Die Mollusken der Neukaledonischen Binnengewässer. Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer (Hydrobio) 4: 3-127, 110 pls.

Stoliczka, F., 1867-1868. Cretaceous fauna of Southern India. 2. The Gastropoda. Memoirs of the Geological Survey of India. Palaeontologia indica, Series V, 2: I-XIII + 1-500 pp., 28 pls.

Strand, E., 1928. Miscellanea nomenclatorica zoologica et Palaeontologica. Archiv für Naturgeschichte 92, A.8: 30-75.

Taki, I. & K. Oyama, 1954. Matajiro Yokoyama's Pliocene and later faunas from the Kwanto region in Japan. Palaeontological Society of Japan, Special Papers, No. 2: 1-67, pls 1-49.

Taviani, M., 1975. Osservazioni sull *Alvania heraelaciniae* Ruggieri. Conchiglie, Milano 11: 205-210.

Thiele, J., 1929(-1935). Handbuch der systematischen Weichtierkunde. Jena. 1:1-376 (1929).

Thiriot-Quiévreux, C., & C.R. Babio, 1975. Etude des protoconques de quelques prosobranches de la région de Roscoff. Cahiers de Biologie Marine 16: 135-148.

Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. Meddelelser FRA Kommissionen for Danmarks Fiskeri - og HavundersØgelser, serie: Plankton 4(1): 1-523.

Tomlin, J.R. le B., 1938. The genus *Nevillia*. Journal of Conchology, London 21: 79.

Tomlin, J.R. le B., & L.J. Shackleford, 1915. The marine Mollusca of São Thomé, II. Descriptions of a new genus and five new species. Journal of Conchology, London 14: 307-309.

Tryon, G.W., 1887. Solariidae, Ianthinidae, Trichotropidae, Scalariidae, Cerithiidae, Rissoidae, Littorinidae. Manual of Conchology 9: 1-488, pls 1-71.

Verduin, A., 1976. On the systematics of recent *Rissoa* of the subgenus *Turboella* Gray, 1847, from the Mediterranean and European Atlantic coasts. Basteria 40: 21-73.

———— 1979. *Rissoa* (*Turgidina*) *testudae* subg.nov., sp.nov., a marine gastropod from the Straits of Gibraltar. Basteria 43: 47-50.

———— 1982. On the taxonomy and variability of Recent European and North African marine species of the subgenus *Rissostomia* Sars, 1878, of the genus *Rissoa* Desmarest, 1814 (Mollusca, Gastropoda, Prosobranchia). Basteria 45: 143-166.

———— 1983. On the taxonomy of Recent Mediterranean species of the subgenus *Loxostoma* of the genus *Rissoa* (Mollusca, Gastropoda, Prosobranchia). Basteria 47: 61-66.

Viader, R., 1938. Description of nine marine shells from Mauritius and its dependencies. Bulletin of the Mauritius Institute 1: 3-8, 2 pls.

Villa A., 1941. Dispositio systematica conchyliorum terrestrium et fluviatilium, quae adservantur in collectione fratrum Ant. et Joh. Villa plurium academiarum scientiarum sodalium conspectu abnormitatun novarumque specierum descriptionibus adjectis. 64 pp. Milano.

Vokes, H.E., 1948. Cretaceous molluscs from depths of 4875-4885 feet in the Maryland Esso well. In: Anderson, J.L., *et al.*, Cretaceous and Tertiary subsurface geology (Maryland). Maryland Department Geology, Mines and Water Resources, Bulletin 2: 126-151, pls 3-4.

Voorwinde, J., 1966. A reclassification of some Rissoacea from the Western Pacific. Journal of the Malacological Society of Australia 10: 41-46.

Warén, A., 1974. Revision of the Arctic-Atlantic Rissoidae (Gastropoda, Prosobranchia). Zoologica Scripta 3: 121-135.

———— 1980. Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material. Conchological Society of Great Britain and Ireland, Special Publication 1: 1-60, 8 pls.

———— 1984. An anatomical description of *Eulima bilineata* Alder with remarks on and a revision of *Pyramidelloides* Nevill (Mollusca, Prosobranchia, Eulimidae). Zoologica Scripta 12:273-294.

Weinkauff, H.C., (1878, 1881) 1877-85. Die Gattungen *Rissoina* und *Rissoa*. Systematisches Conchylien-Cabinet von Martini und Chemnitz 1(22): 1-16 (1877), 17-40 (1880), 41-80 (1881), 81-120 (1884), 129-206 (1885), 28 pls.

Wenz, W., 1938-1944. Gastropoda. Handbuch der Paläozoologie 6(1), Lief 1-7. 1639 pp.

Wigham, G.D., 1975. The biology and ecology of *Rissoa parva* (Da Costa) (Gastropoda: Prosobranchia). Journal of the Marine Biological Association of the United Kingdom 55: 45-67.

Woodring, W.P., 1928. Miocene mollusks from Bowden, Jamaica. Part II, Gastropods and discussion of results. Carnegie Institution of Washington, Publication 385: 1-564.

———— 1957. Geology and Paleontology of Canal Zone and Adjoining parts of Panama - Geology and description of Tertiary mollusks (Gastropods: Trochidae to Turritellidae). United States Geological Survey, Professional Paper 306-A: 1-145, 23 pls.

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APPENDIX 1

Materials and Methods

Material suitable for Scanning Electron Microscope (SEM) examination of the teleoconch and protoconch, as well as the operculum and the radula, was obtained for as many type-species of genera as possible from museums in several countries and from field collections. Anatomical information has been collated and new information on the external features and anatomy of many species has been added to that already available.

The methods used in mounting material for examination with the SEM are given by Ponder and Yoo (1976). Anatomical work was carried out by dissection in Bouin's fixative or by the examination of serial sections.

The diagnoses include information on shell morphology which is usually based on as broad a sample as possible of the species included in the genus. The information on the radula, operculum and protoconch microsculpture has usually been obtained from fewer species and these are marked under 'Material Examined' with an asterisk (radula and operculum) or a cross (protoconch microsculpture). Those examined alive and anatomically are referred to under the appropriate headings. An indication of the number of specimens examined anatomically is given. Where it is not indicated whether this examination was by dissection or sectioning, the material has been dissected only.

A list of synonyms is given under the recognized genus-group taxa along with a diagnosis and a summary of distribution. This includes lists of the type-species of the genus and synonyms, and, in most cases, additional typical species. To facilitate an assessment of the validity of these assignments, the location and status (type or non-type) of the material is given under 'Material Examined'.

It has been possible to examine a wide range of species in most of the genera and, in those cases where previous generic placements are markedly at variance with the assessments I have made, these species are listed under the appropriate genus.

APPENDIX 2

Abbreviations used in Text

AIM	Auckland Institute and Museum, New Zealand.
AMS	The Australian Museum, Sydney.
ANSP	The Academy of Natural Sciences of Philadelphia, USA.
auct.	*auctorum* (of authors).
AUG	Auckland University, Geology Department, Palaeontology collection, New Zealand.
BMNH	British Museum (Natural History), London.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii.
CAS	California Academy of Sciences, San Francisco, USA.
GML	Rijksmuseum van Geologie en Mineralogie, Leiden, Holland.
HUM	Museum für Naturkunde, Humboldt-Universitat, E. Berlin, D.D.R.
IRSB	Institut Royal des Sciences Naturelles de Belgique, Brussels.
LACM	Los Angeles County Museum of Natural History, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA.
MOM	Musée Océanographique de Monaco.
ms	Manuscript.
NHMG	Museo Civvico di Storia Naturale 'G. Doria', Genoa, Italy.
NHMP	Muséum National d'Histoire Naturelle, Paris, France.
NHMS	Naturhistoriska Riksmuseet, Stockholm, Sweden.
NHMV	Naturhistorisches Museum Wien, Austria.
NMNZ	National Museum of New Zealand, Wellington.
NMV	Museum of Victoria, Melbourne, Australia.
NMW	National Museum of Wales, Cardiff, UK.
NSMT	National Science Museum, Tokyo, Japan.
NZGS	New Zealand Geological Survey, Lower Hutt.
OM	The University Museum, Oxford, UK.
PCB	University of California, Paleontology collection, Berkeley, USA.
RSM	Royal Scottish Museum, Edinburgh, UK.
SAM	South Australian Museum, Adelaide.
SEM	Scanning electron microscope.
SMF	Forschungsinstitut Senckenberg, Frankfurt, W. Germany.
TGM	Instituto di Geologia, Paleontologia e Geograffia Fisica, Universita di Torino, Italy.
TM	Tasmanian Museum, Hobart, Australia.
UC	University Museum, Cambridge, UK.
UMC	Université Pierre et Marie Curie, Collection de Paléontologie, Paris, France.
USNM	National Museum of Natural History, Washington, D.C. USA.
WAM	Western Australian Museum, Perth.
ZMC	Zoologisk Museum, Copenhagen, Denmark.

APPENDIX 3

By W.F.Ponder and D.Beechy.

The characters and their states listed in Tables 3 to 6 have been analysed using the TAXON Numerical Taxonomy Package, running on the CYBER76 of the CSIRONET computing system. The program MCAN was used to create a matrix of inter-individual distances, using a combination of unweighted numeric, binary and multistate variables as appropriate. The inter-individual distance is the Canberra metric;

$$\frac{x_ik - x_jk}{x_ik + x_jk},$$

where x_ik is the value of attribute k for individual i (Lance & Williams, 1967).

The dendrograms were produced by the program SAHN (Sequential Agglomerative Hierarchial Non-overlapping Clustering Program) using a flexible sort strategy (Lance & Williams, 1966).

Several different classifications were generated using combinations of data primarily to test the hypothesis that only two subfamilies can be recognised within the Rissoidae. These analyses were carried out after the revision was completed and a summary of the results is appended as an example of a semi-objective, unweighted analysis of the available data.

The program gives the percentage contribution of each character towards each branch. The results are briefly outlined below and three examples of the classifications are shown in figs 151–153.

1. **Shell Characters Only** (Fig. 151). Most of the early classifications have relied almost entirely on shell characters. The results show a division into the *Rissoina*-like genera and the remainder of the family. The only exception is that *Rissoa* and *Mohrensternia* are grouped with *Rissoina*. The non-*Rissoina*-like genera are not divided into sculptural groups, suggesting that other shell features are more important. In fact at the primary branch the following characters were the most important: umbilicus (12.6%), posterior apertural notch (12.1%), the type of protoconch (11.5%), and the apertural varix (10.7%). The second branch utilized, as the most important characters, the peristome (18.3%), the posterior apertural notch (12.3%), and the outer lip (10.1%). Three groups were created at the next level with the aperture (14.9%), the outer lip (13%), and the teleoconch sculpture being the major components. Perhaps surprisingly the classification adopted using shell characters agrees rather well with the classifications adopted using other data, even when shell characters are excluded.

2. **Shell, Opercular and Radular Characters.** A very similar classification to the above is generated. In both, the genera *Lironoba*, *Merelina* and *Attenuata* group together with *Manzonia*. The first and second branches involved the same shell characters as in the above classification but at the third level (three branches) the major character was the denticles on the lateral margins of the central teeth of the radula (12.5%), followed by four shell characters.

3. **Shell, Opercular, Radula and Head-foot Characters.** This classification was also similar to the shell classification and the first division again used the same shell characters as the major attributes.The second and third branching levels used, however, as their major character the metapodial tentacle (10.2% and 9% respectively) with the umbilicus (8.7%), the varix (8.6%) and the posterior pedal gland (6%) being the other main characters at the second level.

Rissoa and *Pusillina* are located together in this classification and these genera fall within the major group containing the *Rissoina*-like genera (Rissoininae). *Merelina*, *Lironoba* and *Attenuata* form a subgroup which, unlike the previous classifications, excludes *Manzonia*.

4. **Anatomical Characters.** Using this data set the genera related to *Rissoina* separate out very clearly. *Merelina* and *Rissoa* form a subgroup at the fourth level of branching and *Lucidestea*, *Voorwindea* and *Obtusella* form a group at the second level of branching. The characters making the greatest contribution to the first branch, and therefore separating off the *Rissoina* group, are the genital characters. These include the capsule gland (13.5%), the vestibule (10.2%), and whether the penial duct is open or closed (9.1%). Other penial characters follow in importance.

The second level of branching (separating the group including *Lucidestea* from the remainder of the non-*Rissoina*-like rissoids) uses the ctenidial filaments (18.1%), the nature of the vestibule (16.8%), and the seminal receptacle (14.6%) as the major charcters. The remainder of the genera are broken into two main groups separated by the nature of the prostate gland (14.6%), the capsule gland (14.6%) and the bursa copulatrix (10.3%).

5. **All Non-shell Characters** (Fig. 152). Again the *Rissoina*-like genera (Rissoininae) are separated out on the first branch. The primary characters involved are the same as those in the last classification, but with slightly lower percentage contributions. The next branching level separates *Rissoa* together with *Lucidestea* and *Voorwindea*, *Obtusella* being well separated in another group. The main characters are the metapodial tentacle (8.5%), the prostate (7.4%) and the ctenidial filaments (6.8%). The remainder of the genera fall into two main groups separated by the posterior pedal gland (7.4%), the degree of separation of the cerebral ganglia (7.4%) and the capsule gland (6.9%).

6. **All Characters** (Fig. 153). In this, the most important of the classifications, the *Rissoina*-like genera again grouped well but, as in two other classifications, *Rissoa* and *Mohrensternia* were included in this group. This group of genera was separated at the first branch and characters of importance included the capsule gland (7.58%), the vestibule (4.1%), the penial duct (3.9%), the shell aperture (3.7%) and the protoconch sculpture (3.6%). The second branch divided the remaining genera into two groups using the vestibule (6.3%), the nature of the distal end of the penis (5.7%), the ctenidial filaments (5.6%) and the metapodial tentacles (4.4%).

The major groups recognisable subjectively are (1) the *Rissoina*-group of genera, (2) the *Lucidestea*-group (also including *Obtusella* and *Voorwindea*) and (3) the *Merelina*-group (also including *Lironoba* and *Attenuata*). The computer analysis, using non-weighted characters, gives the following results:

(1) *Rissoina*-group. This group clustered and separated well in all the classifications. Some genera (*Rissoa* and *Mohrensternia* or *Pusillina*) are included in this group in all the classifications involving shell characters, presumably due to convergence in shell-features. When shell-characters are excluded the group separates cleanly at the first branch. In summary, the computer analysis appears to confirm that the Rissoidae

should be divided into two subfamilies, Rissoininae and Rissoinae.

(2) *Lucidestea*-group. This group was definitively separated using only anatomical characters. In all of the other classifications they are either separated or have additional genera included in the same group.

(3) *Merelina*-group. This group separated, using shell characters, along with *Manzonia*, on the fifth branching level. It formed a small subgroup in the classifications not involving anatomical characters but, in the classification using only anatomical characters, *Lironoba* and *Merelina* did not group (there is no anatomical data for *Attenuata*). With all non-shell characters the three genera formed part of a larger subgroup, and with all characters they formed a separate subgroup. The results suggest that, while they share a number of characters in common, there is no justification for creating higher categories for groups 2 and 3 on the available data. Similarily, there is no justification whatsoever for recognising family-groups based on *Onoba*, *Alvania* and *Cingula*.

References

Lance, G.N. & W.T. Williams, 1966. A generalised sorting strategy for computing classifications. Nature, 212:218.

——————— 1967. Mixed data classificatory programs. 1. Agglomerative systems. Australian Computer Journal, 1:15–20.

Primitive state in Rissoacea-Littorinacea	Primitive state in Rissoidae	Derived state in Rissoidae
Shell		
Inner chitinous layer present	Inner chitinous layer absent	—
Multispiral protoconch (planktotrophic larva)	—	Paucispiral protoconch (direct development)
Simple peristome	—	Duplicated peristome
Operculum		
Peg present, operculum thick	—	Peg absent, operculum thin
Nucleus eccentric	—	Nucleus subcentral
Radula		
Central teeth with one pair of basal processes	—	Central teeth with 2 pairs of basal processes
Central teeth with simple lateral margins	—	Central teeth with denticles developed from lateral margins
Few, large cusps	Small, numerous cusps	—
Cusps on both sides of marginal teeth	Cusps on outer side of inner marginal teeth and on both sides of outer marginal teeth	Cusps only on outer side of inner marginal teeth and on inner side of outer marginal teeth
Head-foot		
Pallial tentacles absent	A right and left pallial tentacle present	Pallial tentacles lost
Metapodial tentacle present	Metapodial tentacle triangular	Metapodial tentacle subdivided, a single filament, or lost
Posterior pedal mucous gland absent	—	Posterior pedal mucous gland present
Alimentary Canal		
Salivary glands pass through nerve ring	Salivary glands pass over nerve ring	—
Oesophageal pouches and gland present	Oesophageal pouches and gland lost	—
Style sac without crystalline style	Style sac with crystalline style	—
Stomach short and ovoid	—	Stomach elongate
Nervous System		
Circum-oesophageal ganglia loosely connected, supra and suboesophageal connectives long	—	Circum-oesophageal ganglia concentrated with cerebrals abutting, cerebrals and pleurals fused and suboesophageal and supraoesophageal ganglia with very short connectives

Table 1. Assumed primitive states of selected non-genital characters in the Rissoacea and their states in the Rissoidae. A dash indicates no change from the previous column. For further explanation see text.

Primitive state in Rissoacea-Littorinacea	Primitive state in Rissoidae	Derived state in Rissoidae
Male Genital System		
Penis absent	Penis present, with open duct	Penis present, with closed duct
	Penis with accessory glandular tissue	Penis lacking accessory glands
Prostate open	—	Prostate closed or absent (if absent, penis has prostatic tissue)
Prostate pallial (ie. within wall of pallial cavity)	—	Prostate partly or entirely visceral
Female Genital System		
Pallial glandular oviduct open	—	Pallial oviduct gland closed
Oviduct gland single	Oviduct gland divided into upper and lower glands. Upper gland coiled or U-shaped	— Upper gland a single ovoid mass
One sperm sac present	Two sperm sacs (bursa copulatrix and seminal receptacle) present	One or both lost or replaced with new structures
No anterior sperm-storing structure	—	Anterior sperm storage in modified vestibule

Table 2. Assumed primitive states of male and female genital characters in the Rissoacea and their states in the Rissoidae. A dash indicates no change from the previous column. For further explanation see text.

	Central teeth: cutting edges less than 3 × wider than height of tooth	Number of pairs of basal denticles	Denticles from lateral margins present and shorter than basal cusps (1), longer than basal cusps (2), absent (3)	U-shaped ventral extension poorly-developed (1), moderately-developed (2), well-developed (3)	Number of cusps on either side of primary cusps	*Lateral teeth:* Number of cusps on inner side of primary cusp	Number of cusps on outer side of primary cusp	Cusps on outer side of outer marginal teeth	*Operculum:* subcentral with nucleus	With peg
Rissoa	+	1	1	2	1–3	0–4	2–7	–	–	–
Pusillina	+	1	1,3	1–3	1–5	0–5	2–12	–	–	–
Setia	+	1	1,3	2–3	2–3	2–4	4–12	–	–	–
Alvania	+	1	1,3	1–2	2–6	3–6	4–12	–	–	–
Manzonia	+	1	3	1–2	2–4	5–7	5–7	–	–	–
Frigidoalvania	+	1	3	1	3–5	7–8	5–7	–	–	–
Parashiela	+	1	3	3	4	5–6	12–13	–	–	–
Cingula	+	1	1	1–2	2–4	3–5	3–9	–	–	–
Onoba	+	1	1	2–3	2–7	3–9	3–10	–	–	–
Powellisetia	+	1	1	2–3	4–6	6–8	10–20	–	–	–
Peringiella	+	1	1,3	2–3	2–4	3–5	3–6	–	–	–
Benthonella	+	1	1,3	1–2	5–9	3–6	3–8	–	+	–
Boreocingula	+	1	1	3	4–7	3–10	6–12	–	–	–
Lucidestea	+	2	1	1	3–5	6–11	10–16	–	–	–
Obtusella	+	2	3	2	4–6	6–8	14–15	–	–	–
Voorwindia	+	2	2	1	3	2–6	13–16	–	–	–
Striatestea	+	1	3	?	2	0	10	–	–	–
Merelina	+	2	3	1	2–4	4–6	7–9	–	+	–
Lironoba	+	2	3	1–2	4–6	3–7	8–9	–	±	(±)
Attenuata	–	0–(1)	3	1	6–21	0?–5	0?–19	–	±	+
Rissoina	+	1	1,3	1–3	2–5	4–7	2–9	±	–	–
Zebina	+	1	1,3	2–3	2–6	4–9	5–11	±	–	–
Schwartziella	+	1	1	2–3	3–5	5–9	4–7	–	–	–
Folinia	+	1	1	2	3–5	4–6	4–5	–	–	–
Stosicia	+	1	3	2	2–6	3–4	5–10	–	–	–
Lapsigyrys	+	1	1	2	(4–5)	0	0	–	–	–

Table 3. Radular and opercular characters and character-states in the genera of the Rissoidae. + character or state present; – character or state not present; (+) character or state present but weakly-developed or rarely-developed; (–) character or state rarely-absent; ? character or state not known.

	Protoconch: of two whorls or more	Sculpture of: smooth spiral ridges (1), gemmate spiral ridges (2), weak spiral threads (3), raised dots or dashes (4), axial threads (5), punctate (6), smooth (7)	*Teleoconch;* ovate (1), conic to ovate-conic (2), elongate-ovate to elongate-conic (3)	Umbilicate	*Sculpture:* predominately axial (1), predominately spiral (2), clathrate (3), very weak or smooth (4)	Base with distinctly different sculpture	*Aperture;* with anterior channel (1), angulation only (2), with broad excavation (3), rounded (4)	With posterior notch or indentation	With duplicated peristome	With varix on outer lip	With denticles inside outer lip	Outer lip opisthocline (1), orthocline (2), prosocline (3)	Outer lip reflected	Periostracum calcified (1), horny (2), very thin (or absent?) (3)	Minute (< 2mm) (1), small (2–5mm) (2), medium (5–10mm) (3), large (> 10mm) (4)
Rissoa	+	3,(4),7	2,3	–	1,(4)	±	4	+	–	(±)	–	1,2,3	±	3	2–3
Pusillina	±	3,(4),7	1,2	±	1,(4)	±	3,4	+	–	(±)	–	1,2,3	–	3	1–2
Mohrensternia	+	7?	2	–	1	(+)	4	+	–	–	–	1	–	?	3
Setia	–	1,2	1,2	–	(2),4	–	4	–	–	(±)	–	3	–	3	1
Alvania	±	1,3,4,(5)	1,2,3	(±)	(2),3	(+)	4	(±)	–	(±)	±	1,2,3	–	3	1–2
Manzonia	±	1,2,4	2,3	–	1,3	+	4	(±)	+	+	–	1	–	1,3	1–2
Frigidoalvania	–	3	1,2	–	(1),2,(3)	+	(2),4	+	–	+	–	1,(2)	–	2	2
Parashiela	±	3,4,7	2	–	1,(3)	–	4	–	+	+	–	2	–	3	1
Cingula	–	1,3,5	2,3	–	2,(4)	–	4	(±)	–	(±)	–	2,3	–	3	1–2
Onoba	–	1,3,4,7	2,3	(±)	(1),2,(3),4	(±)	4	+	–	–	–	1	–	2,3	1–2
Powellisetia	–	4	1,2	±	(2),4	–	4	+	–	(±)	–	(1),2	–	3	1–2
Peringiella	–	6,7	3	–	4	–	4	+	–	+	±	2	–	3	1–2
Benthonella	+	1,3,4	2	+	1,4	(±)	(2),4	–	–	–	–	2,(3)	–	3	2–3
Boreocingula	–	6	1	–	2,4	–	4	(+)	–	(±)	–	(3)	–	2	2
Lucidestea	–	(3),7	2	±	(2),4	–	4	(+)	–	+	–	2	–	3	1
Obtusella	+	3,4	1,2	(±)	(2),4	–	4	–	–	(±)	–	1,2	–	3	1
Voorwindia	+	3,7	1	+	4	–	4	–	–	–	–	2	–	3	2
Striatestea	–	7	3	–	(2),4	+	4	–	–	(+)	–	2	±	3	1
Amphirissoa	–	3	1	(+)	(2),4	–	4	–	+	–	–	2	+	3	1
Merelina	–	2	3	–	2,3	+	4	–	+	+	–	1	–	3	2
Lironoba	–	(1),3,4,6	2,3	–	2	–	4	(+)	+	+	–	1	–	3	1–2
Attenuata	–	1,4	2,3	–	2	(±)	4	–	(±)	+	–	1	–	3	1–2
Rissoina	±	3,4,6,7	3	–	1,2,3,4	±	1	+	–	+	–	1	–	1,3	2–4
Zebina	±	7	(2),3	–	(1),2,4	–	4	+	–	+	±	1	–	3	2–4
Schwartziella	±	4,6,7	3	–	1	±	4	+	–	+	–	1	–	1,3	1–2
Folinia	+	3	3	–	1,(4)	+	1	+	+	+	–	1	–	3	2
Cossmannia	+	7	3	–	4,(3)	–	(2)	–	–	+	–	3	–	?	3
Stosicia	±	7	3	–	2,3	–	1	+	–	+	–	(1),2	±	3	2
Lapsigyrus	+	7	2	–	2,(3)	–	4	+	–	+	–	(1)	–	3	2
Pseudotaphrus	+	7	3	(±)	2	–	(1)	+	–	+	–	2	–	?	3
Microstelma	±	?7	2,3	(±)	1,4	(±)	1	+	–	+	–	1	–	3	2–3

Table 4. Shell characters and character-states in the genera of Rissoidae. + character or state present; – character or state not present; (+) character or state present but weakly developed or rarely developed; (–) character or state rarely absent.

	Male *Penis.* With terminal filament (1), pointed end (2), rounded end (3)	Parallel-sided (1), tapering (2), swollen distally (3)	With accessory glands or papillae	Duct open	Duct marginal or submarginal	*Prostate Gland.* Entirely pallial (1), pallial + visceral (2), entirely visceral (3), penial (4), absent (5)	Open ventrally along entire length	With internal muscular papilla	*Female* Vestibule modified for sperm storage.	Capsule gland with simple ventral channel only (1), ventral channel and sperm tube and/or groove (2), lateral flap outside ventral channel (3), open ventrally with sperm groove (4)	Bursa copulatrix approx. equal in size or larger than upper oviduct gland (1), smaller than upper oviduct gland (2), absent (3)	Seminal receptacle small relative to bursa (1), approximately equal in size (2), absent (3)	Upper oviduct gland with sperm-storing lobes	Upper oviduct gland coiled or U-shaped	Accessory sperm sac(s) at posterior end of long, non-glandular duct to upper oviduct gland (1), long non-glandular duct present but no sperm sacs (2), no duct or sperm sacs (3)
Rissoa	1	1	–	–	+	4	–	–	–	3	1	1	+	–	3
Pusillina	1,2,3	(1),2	(±)	–	+	1,2	–	–	±	1	1,2,3	1,3	±	±	3
Setia	2	2	–	–	+	1	–	–	–	1?	2	3	–	+	3
Alvania	2	2,3	(±)	–	+	1,2	–	–	–	1	(1),2	1,3	–	+	1
Manzonia	1,2	(1),2	–	–	+	2	–	–	–	1?	1,2	1	–	±	3
Frigidoalvania	2	1	–	–	+	2	–	–	–	1	2	3	–	+	2
Parashiela	1	2	–	–	±	?	–	–	?	?	?	?	?	?	?
Cingula	2	2	(+?)	–	(±)	1	–	+	–	1	1,2	3	–	+	1
Onoba	2	1,2	–	–	+	1,(2)	–	–	–	1	2	1	–	(±)	3
Powellisetia	2	2	–	–	+	2	–	–	–	1?	2	1	–	–	3
Benthonella	1	1	–	–	+	2	–	–	–	1	2	1	–	–	3
Boreocingula	2	2	–	–	+	2	–	–	–	1	2	1	–	–	3
Lucidestea	1	1	–	–	–	1	–	–	+	1	2	2	–	+	3
Obtusella	1	1	–	–	+	2	–	–	+	4	2	1-2	–	–	3
Voorwindia	1,2	(3)	–	–	+	3	–	–	+	1	3	–	–	–	3
Merelina	2	1-2	–	+	–	1	+	–	–	4	1	1	–	+	3
Lironoba	1	1-2	–	+	+	(2)	–	–	–	(4?)	2	?	–?	?	3
Rissoina	1,2	(2),3	(±)	±	+	1,(2)	(–)	–	+	2	1	1	–	+	3
Zebina	1?	3	–?	+	+	1	+	–	+	2	2	2	–	?	3
Schwartziella	2	2,(3)	+	+	+	3,5	+	–	+	2	1,2	1	–	+?	3
Stosicia	(1)	3	+	+	+	1	–	–	+	2	1	1	–	–?	3

Table 5. Reproductive characters and character-states in the genera of the Rissoidae. Genera for which these characters are not known are excluded from the table. + character or state present; – character or state not present; (+) character or state present but weakly-developed or rarely-developed; (–) character or state rarely-absent; ? character or state not known.

	Head-foot characters Pigment present (other than white)	Left pallial tentacle present	Right pallial tentacle present	Metapodial tentacle triangular (1), narrow (2), triangular base and narrow distally (3), multiple (4), absent (5)	Posterior pedal gland present	*Anatomical characters* Ctenidial filaments triangular (1), finger-like (2), vestigial (3), absent (4)	Stomach-style sac ratio	Stomach length-width ratio	Cerebral ganglia separated by connective	Length of supraoesophageal connective/ length of supraoesophageal ganglion	Length of suboesophageal connective/ length of suboesophageal ganglion
Rissoa	+	–	+	2,3	+	1-2	2.5-4.4	1.6-3.3	+	1.1	0.5
Pusillina	±	±	+	2,(5?)	+	2	2.2-3.7	1.7-2.2	+	0.7	0.5
Setia	±	±	±	2,5	+	2	2.7-3.1	1.6-2.1	±	?	?
Alvania	±	+	+	4	±	2	1.7-3	1.4-2.1	±	1.5-2.3	0 – 0.2
Manzonia	–	+	+	1,3,5	±	2	2.6-3	1.5-2	?	?	?
Frigidoalvania	–	+	+	1	?	2	3.6-3.7	1.8-2	+	2	0
Parashiela	–	–	+	1	–	2	3.3	1.8	?	?	?
Cingula	–	–	+	1	(+)	2	1.3-2.4	1.7-2.2	?	?	?
Onoba	–	(±)	(±)	1	(±?)	2	2.3 – 4	1.4-2.2	?	?	?
Powellisetia	–	±	±	5	+	2	2.8	1.9	?	?	?
Benthonella	–	–	–	5?	?	2	2.8	1.7	?	?	?
Boreocingula	–	–	–	5	?	2	2.3	1.6	?	?	?
Lucidestea	(+)	–	(±)	2	+	3	2.8	1.6	?	?	?
Obtusella	–	–	±	2,5?	– ?	4	2.2-2.9	1.4-1.9	?	?	?
Voorwindia	–	–	+	2	–	3	3.1	2.1	?	?	?
Merelina	–	–	–	5	–	2	4.3	2.5	–	0.7	0.5
Lironoba	–	–	–	1	–	2	3.1 – 5.5	2-2.7	?	?	?
Rissoina	–	+	+	1,(5)	–	1-2	4.5-5.6	3-4	±	1-3	0-1.5
Zebina	–	+	+	1	–	2	2.4	1.7	?	?	?
Schwartziella	–	+	+	1	–	1,2	2.3	2	+	?	?
Stosicia	–	–	+	5	–	2	1.7	1.5	?	?	?

Table 6. Head-foot and non-reproductive characters and character states in the genera of the Rissoidae. Genera for which these characters are not known are excluded from the table. + character or state present; – character or state not present; (+) character or state present but weakly-developed or rarely-developed; (–) character or state rarely-absent; ? character or state not known.

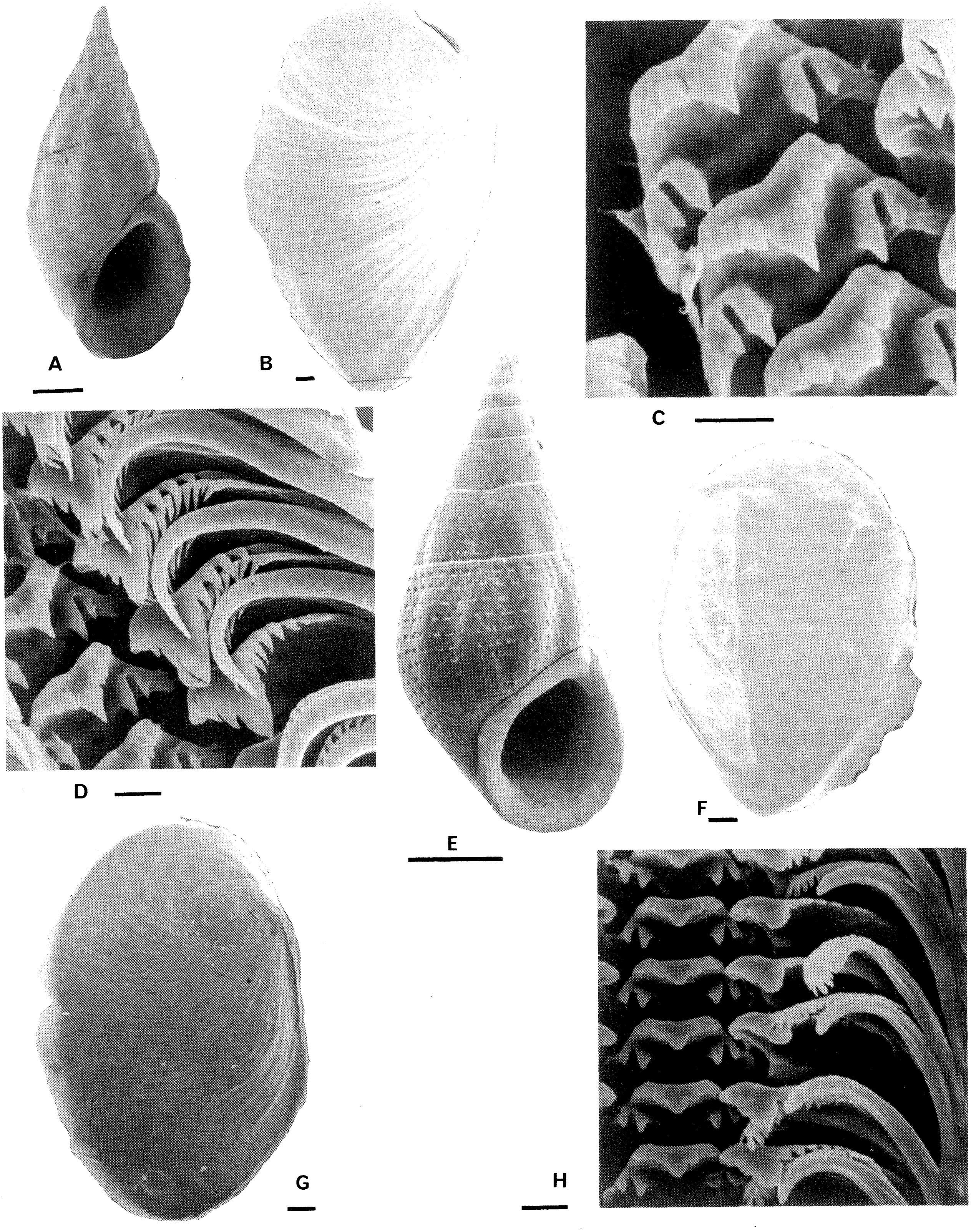

Fig. 76. **A-D**, *Rissoa ventricosa* Desmarest; type-species of *Rissoa* Desmarest: **A**, shell; **B**, operculum (outer side); **C-D**, radula, **C**, central teeth (A-B, Palermo Sicily, BMNH, 1911.10.26. 19894-19903; C-D, Nizza, Sicily, AMS, C.43239). **E-H**, *Rissoa violacea* Desmarest: **E**, shell; **F-G**, operculum, **F**, inner side, **G**, outer side; **H**, radula (Villafranca, France, AMS, C.43232). **Scale:** shells - 1 mm; opercula - 0.1 mm; radulae - 0.01 mm.

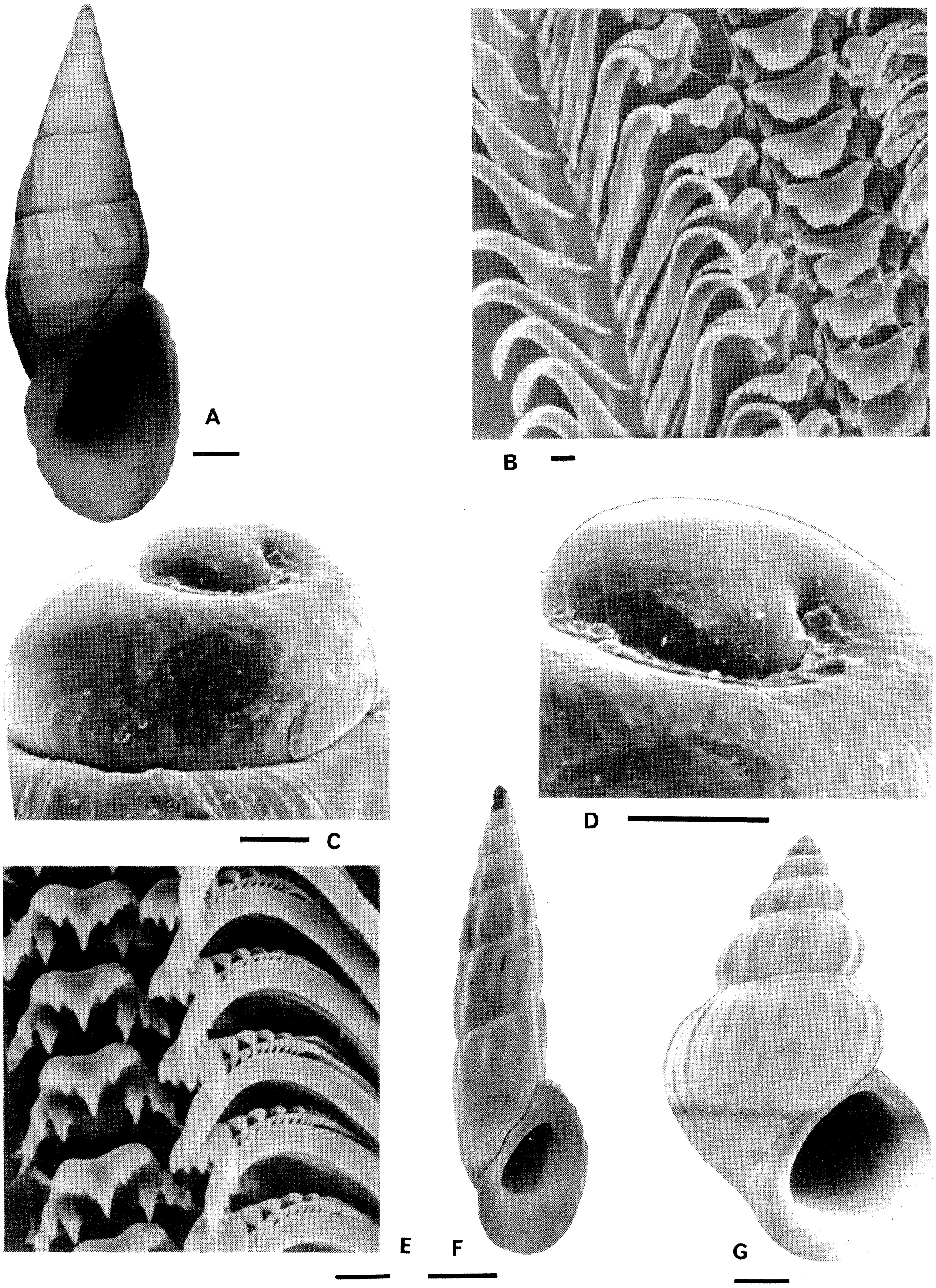

Fig. 77. **A-D**, *Rissoa membranacea* (J. Adams), type-species of *Rissostomia* Sars: **A**, shell; **B**, radula; **C-D**, protoconch (Lamlash Bay, Arran Island, Scotland, BMNH, 1911.10.26.19612-19631). **E-F**, *Rissoa auriscalpium* (Linné), type-species of *Goniostoma* Villa and *Zippora* Leach: **E**, radula; **F**, shell (Cannes, France, IRSB). **G**, *Mohrensternia inflata* (Andrzejowski); shell (Mussdorf, Vienna, Austria, lowermost Sarmation (Miocene), AMS, C.134865). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

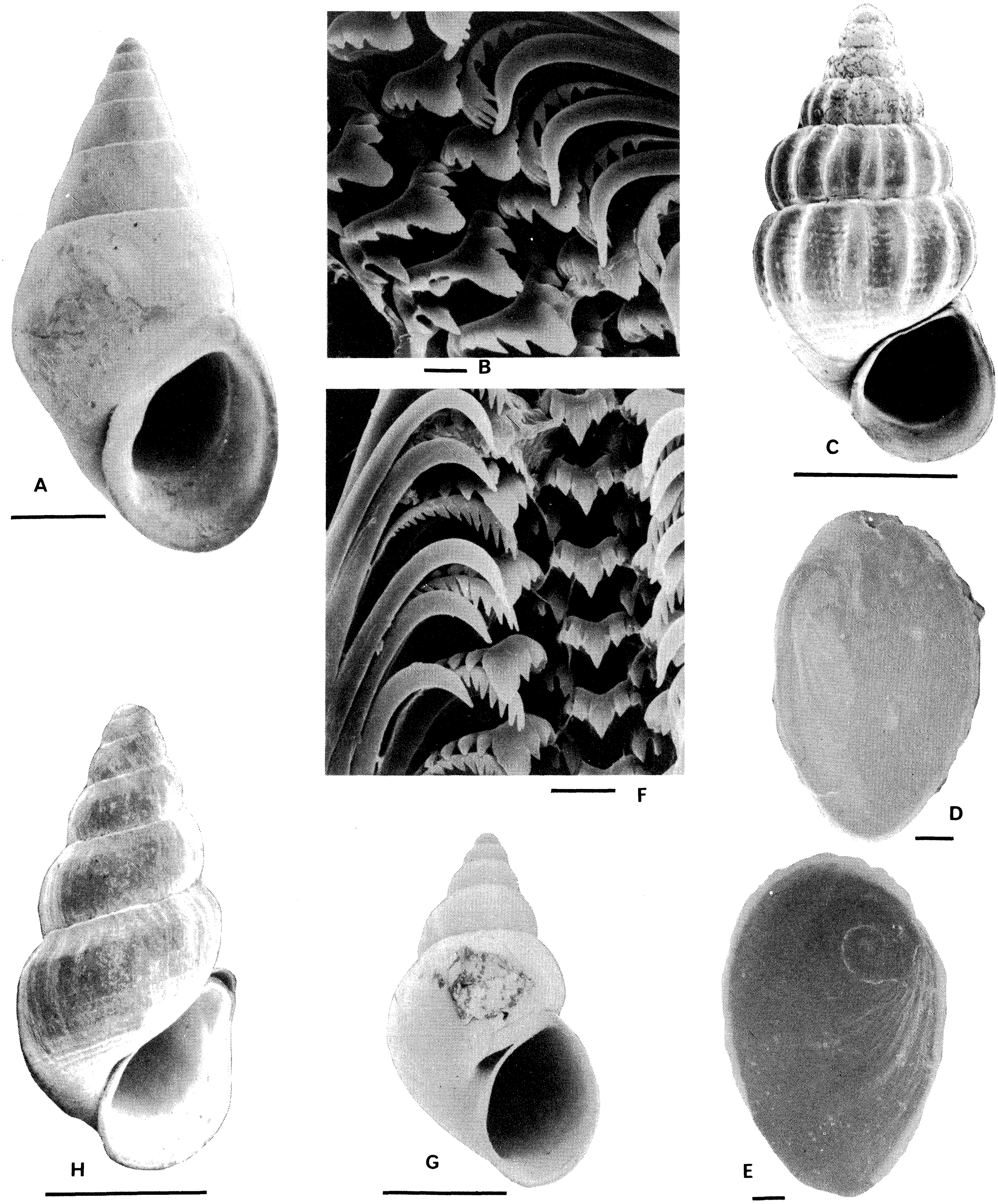

Fig. 78. **A-B**, *Rissoa monodonta* Philippi, type-species of *Loxostoma* Bivona-Bernardi and *Schwartzia* Bucquoy, Dautzenberg & Dollfus: **A**, shell; **B**, radula (France, AMS, C.134866). **C-F**, *Rissoa similis* Scacchi, type-species of *Apicularia* Monterosato: **C**, shell; **D-E**, operculum, **D**, inner and **E**, outer sides; **F**, radula (Messina, Sicily, AMS, C.43202). **G**, *Pusillina* (*Pusillina*) *benzi* Aradas & Maggiore, type-species of *Benzia* Nordsieck; shell (Sicily, ex Aradas BMNH, 1911.10.26.20783-20790). **H**, *Pusillina* (*Pusillina*) *janusi* (Nordsieck), type-species of *Auriconoba* Nordsieck; shell (Porto Santo, Madeira, paratype, AMS, C.108981). **Scale:** shells - 1 mm; opercula - 0.1 mm; radulae - 0.01 mm.

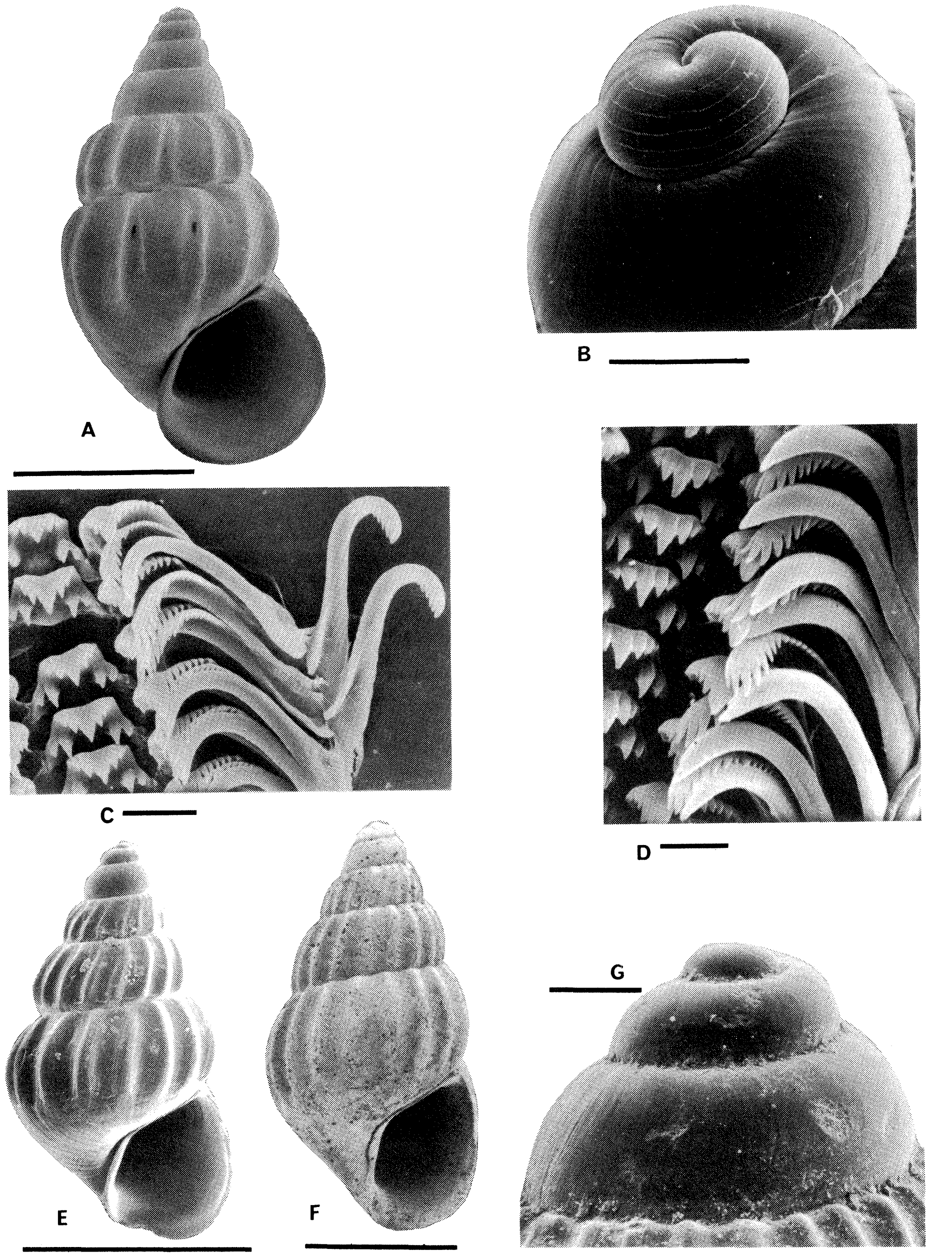

Fig. 79. **A-C**, *Rissoa parva* (Da Costa), type-species of *Turboella* Gray: **A**, shell; **B**, protoconch; **C**, radula (A, Plymouth, England, BMNH, acc. no. 1838; B,C, Cowsand, near Plymouth, AMS, C.134867). **D-E**, *Pusillina* (*Pusillina*) *dolium* Nyst, type-species of *Pusillina* Monterosato: **D**, radula; **E**, shell (Palermo, Sicily, AMS, C.134871). **F-G**, *Pusillina* (*Pusillina*) *nana* (Lamarck): **F**, shell; **G**, protoconch (Grignon, near Paris, France, Lutétian (Middle Eocene); AMS, C.134868). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

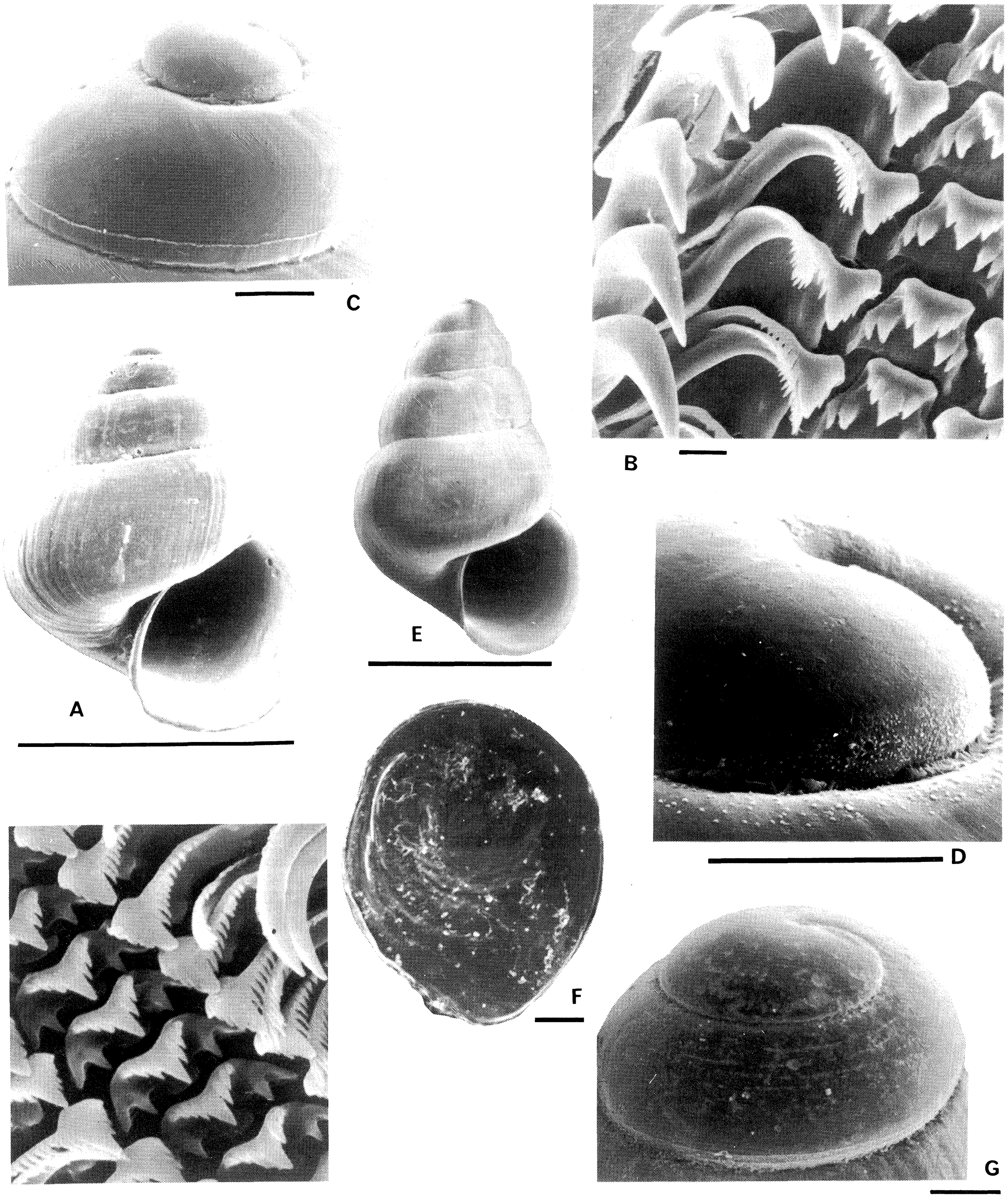

Fig. 80. **A-D**, *Pusillina* (*Pusillina*) *inconspicua* (Alder), type-species of *Mutiturboella* Nordsieck: **A**, shell; **B**, radula; **C-D**, protoconch, **D**, initial whorl (A, Bergen, Norway, BMNH, 1911.10.26. 24472-24491; B, Cumbrae, Scotland, BMNH, 1911.10.26. 21643-21662; C-D, 9-15 m, Plymouth Sound, England, AMS, C.134869). **E-H**, *Setia* (*Pseudosetia*) *turgida* (Jeffreys), type-species of *Pseudosetia* Monterosato: **E**, shell; **F**, operculum (inner side); **G**, protoconch; **H**, radula (off Korsfjorden, W. Norway, 320 m, AMS, C.134870). **Scale:** shells - 1 mm, protoconchs and operculum - 0.1 mm; radulae -0.01 mm.

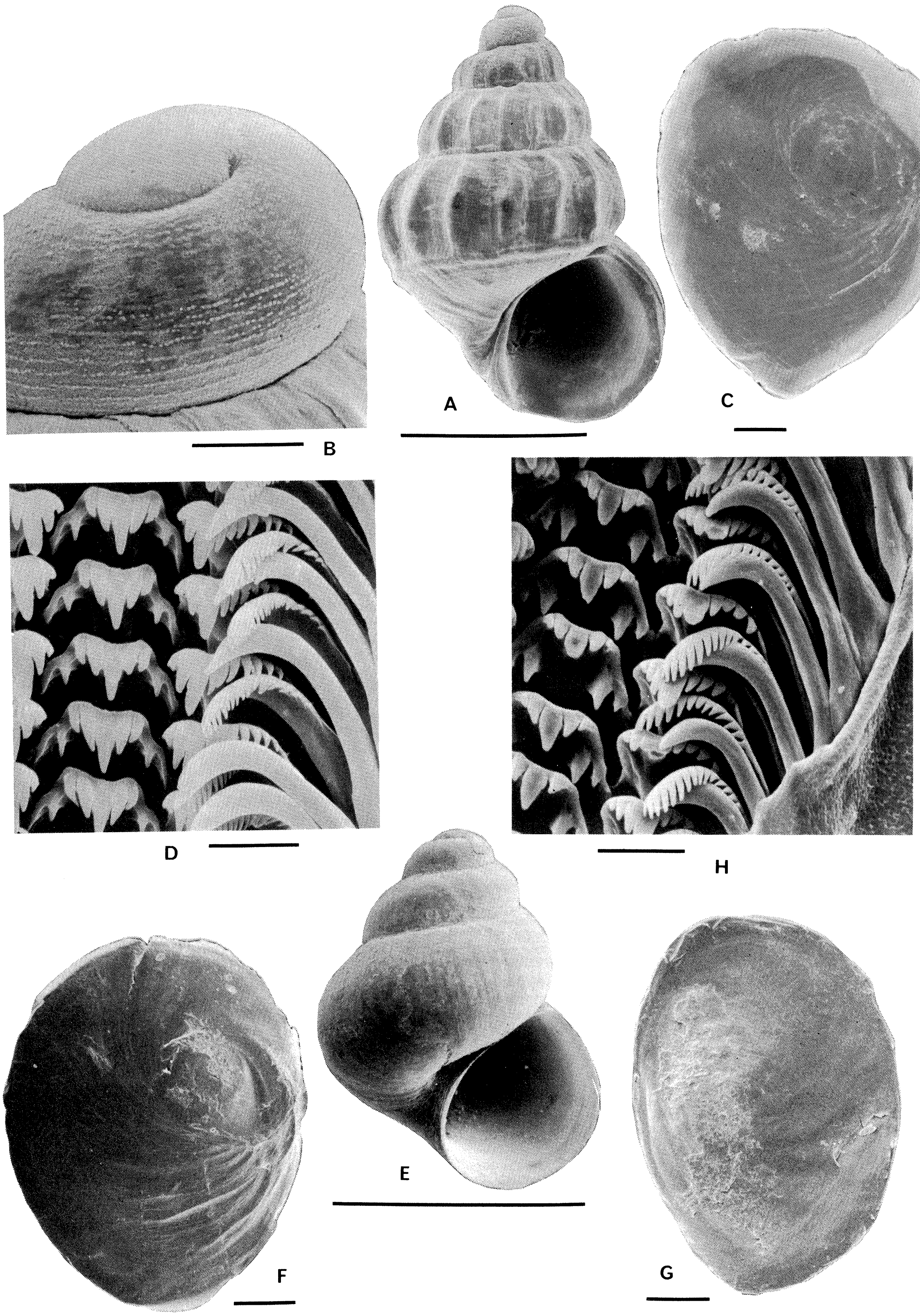

Fig. 81. **A-D**, *Pusillina* (*Haurakia*) *hamiltoni* (Suter), type-species of *Haurakia* Iredale: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D**, radula (Haughton Bay, Wellington, New Zealand, AMS, C.67055). **E-H**, *Setia* (*Setia*) *pulcherrima* (Jeffreys), type-species of *Setia* H. & A. Adams: **E**, shell; **F-G**, operculum, **F**, outer side, **G**, inner side; **H**, radula (Guernsey, Channel Islands, England, probable syntype, USNM, 183153). **Scale:** shells - 1 mm; protoconch and opercula - 0.1 mm; radulae - 0.01 mm.

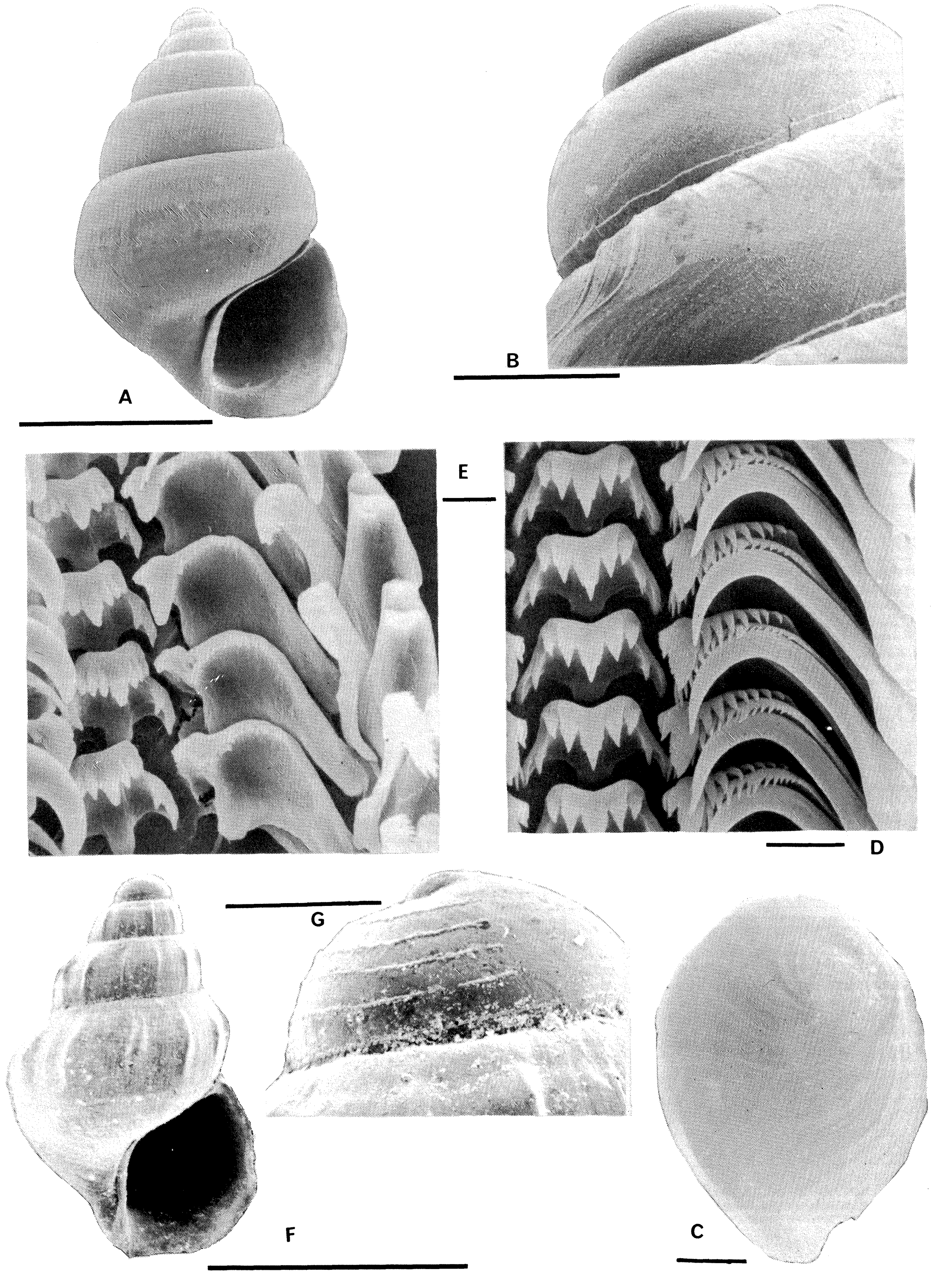

Fig. 82. **A-E**, *Pusillina* (*Haurakia*) *marmorata* (Hedley), type-species of *Vitricithna* Laseron: **A**, shell; **B**, protoconch; **C**, operculum (outer side); **D-E**, radula (A,B,D, Honolulu, Hawaii, AMS, C.134873; C,E, Lizard Island, Queensland, Australia, AMS, C.134874). **F-G**, *Pusillina* (*Haurakia*) *pellucida* (Powell), type-species of *Haurakiopsis* Powell: **F**, shell; **G**, protoconch (92 m, off Three Kings Islands, New Zealand, *Discovery* Stn 934, paratype, AMS, C.134872). **Scale:** shells -1 mm; protoconch and operculum - 0.1 mm; radulae - 0.01 mm.

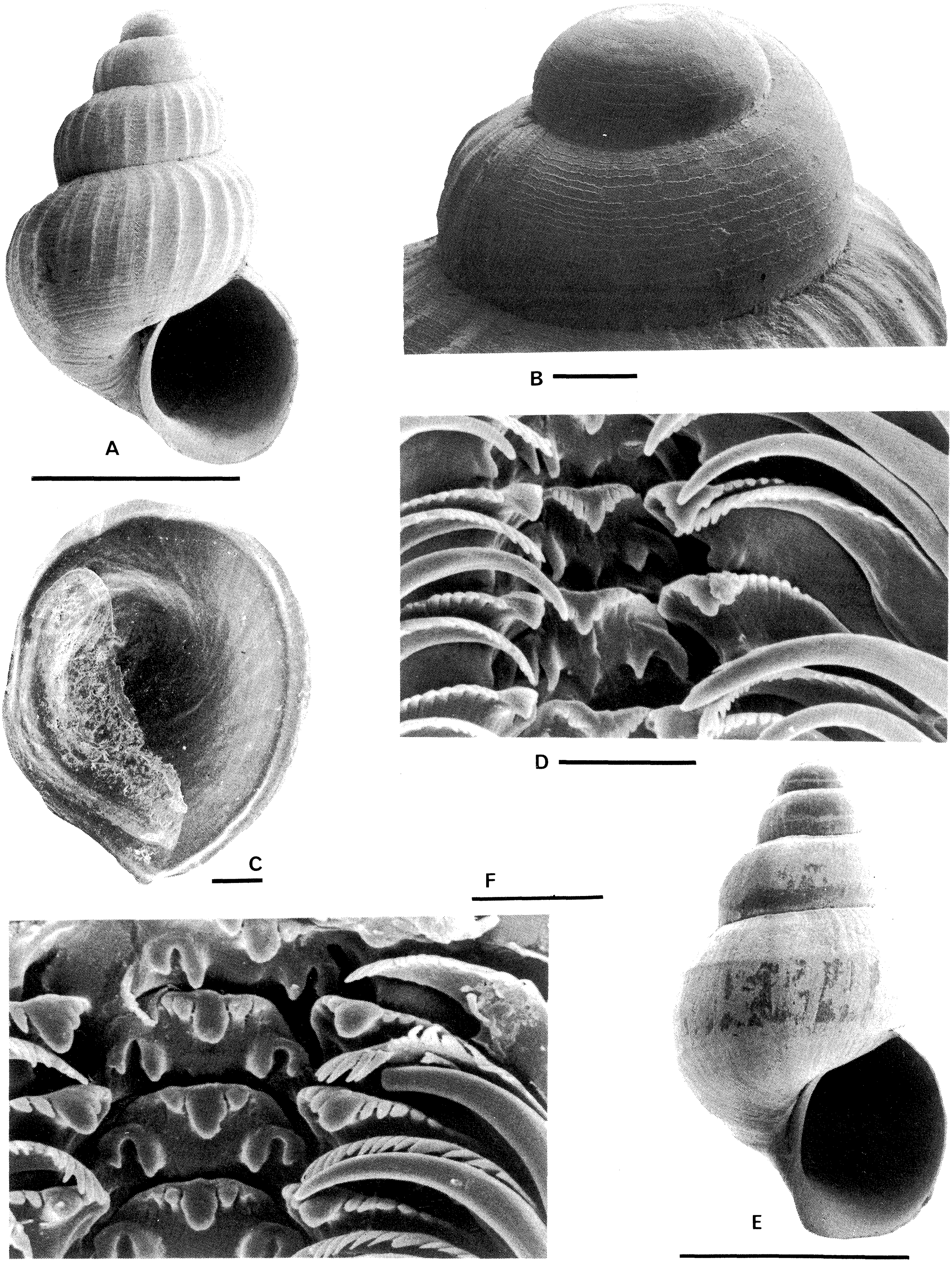

Fig. 83. **A-D**, *Pusillina* (*Vicinirissoa*) *harpa* (Verrill), type-species of *Vicinirissoa* n.subgen.: **A**, shell; **B**, protoconch; **C**, operculum (inner side): **D**, radula (530m, S. of Martha's Vineyard, Mass., U.S.A., USNM, 151903). **E-F**, *Pusillina* (*Ameririssoa*) c.f. *pseudoareolata* (Warén): **E**, shell; **F**, radula (808 m, off New York, U.S.A., AMS). **Scale:** shells — 1 mm; protoconch and operculum - 0.1 mm; radulae - 0.01 mm.

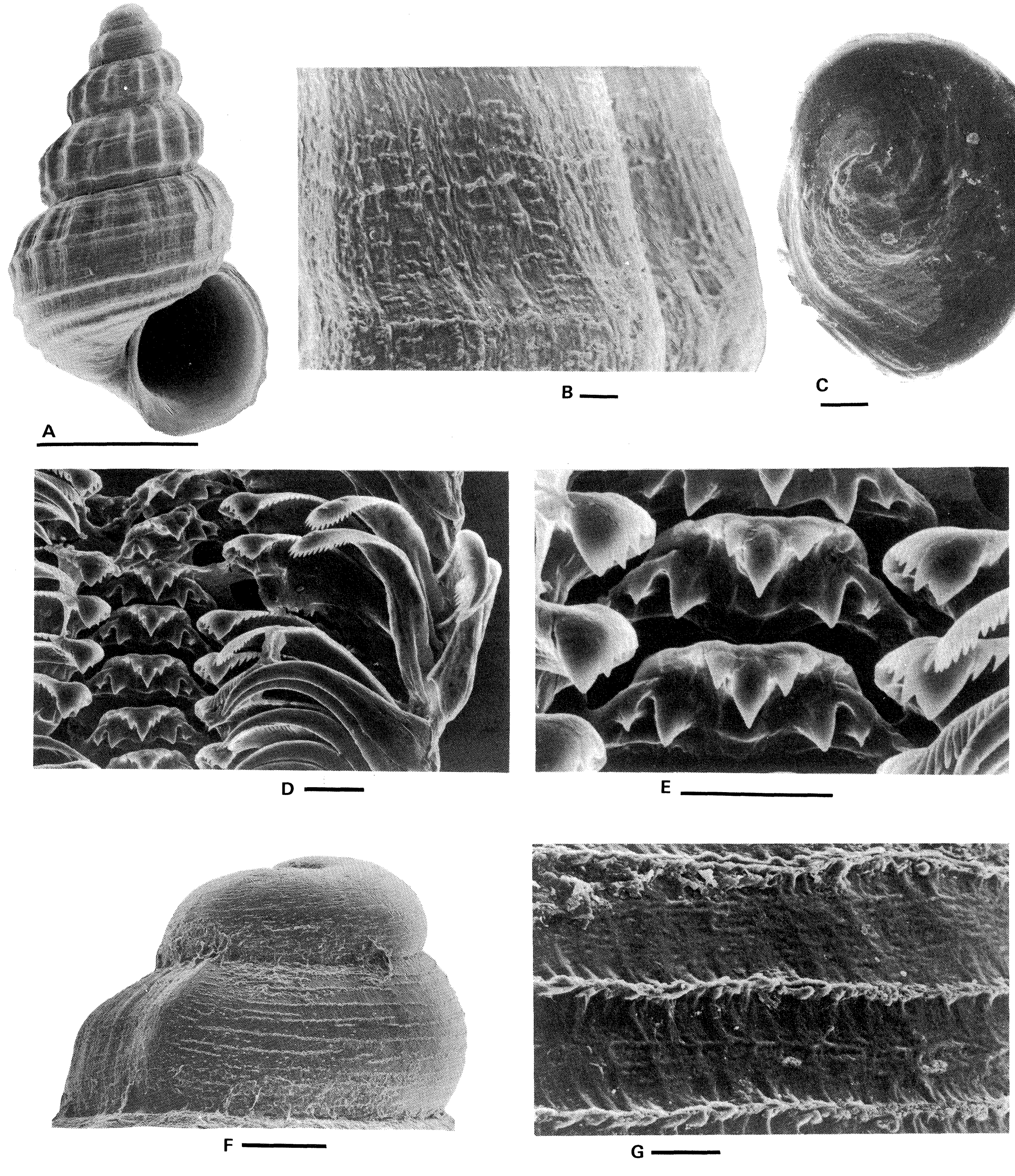

Fig. 84. *Pusillina* (*Ameririssoa*) *pseudoareolata* (Warén); type-species of *Ameririssoa* n.subgen.: **A**, shell; **B**, teleoconch microsculpture; **C**, operculum (inner side); **D-E**, radula, **E**, detail of central teeth; **F-G**, protoconch, **G**, microsculpture on last half whorl of protoconch (paratype, Frenchman's Bay, Maine, U.S.A., USNM, 184952). **Scale:** shell - 1 mm; protoconch and operculum - 0.1 mm; radula and microsculpture (B, G) - 0.01 mm.

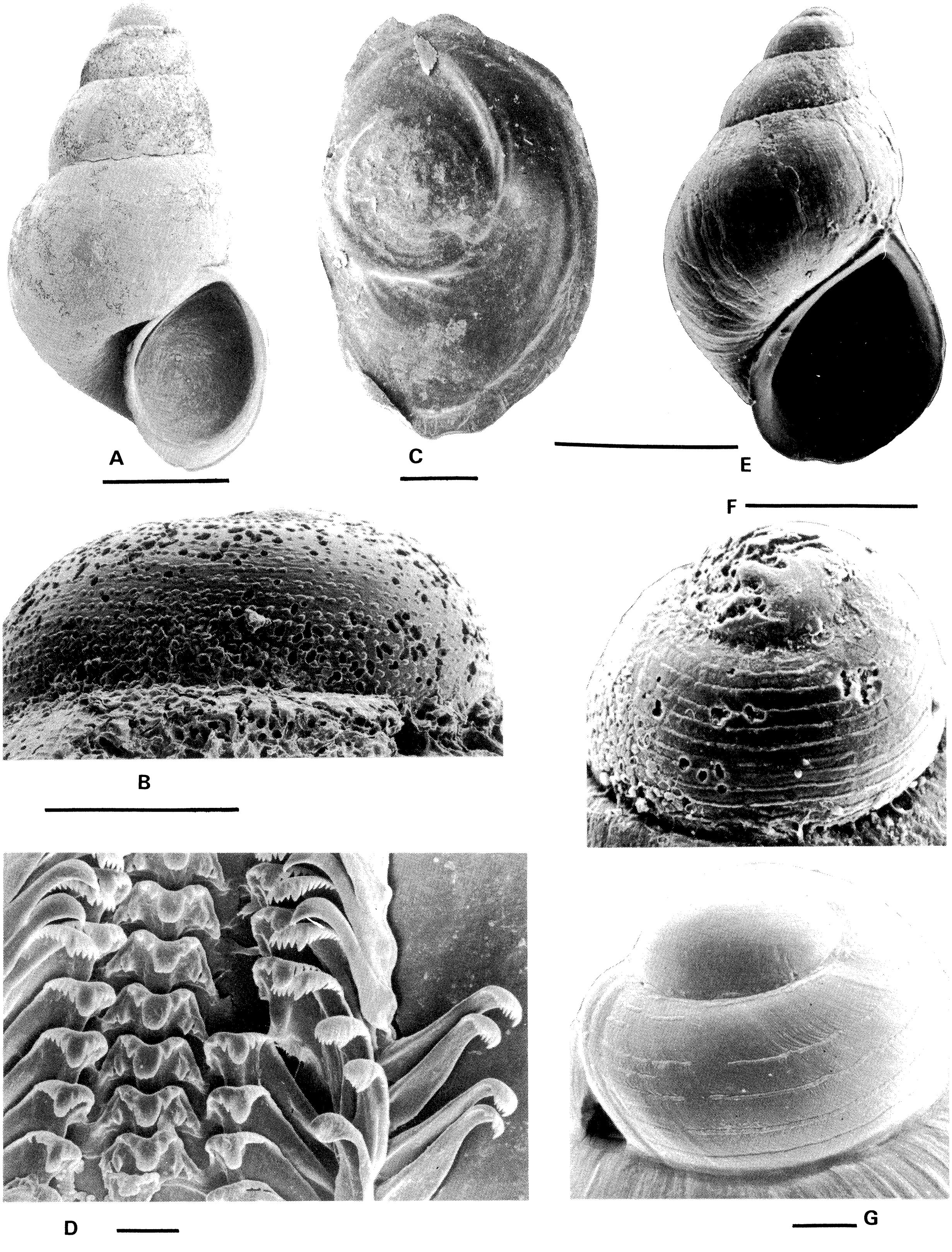

Fig. 85. **A-D**, *Setia* (*Setia*) *fusca* (Philippi), type-species of *Rudolphosetia* Monterosato: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D**, radula (Palermo, Sicily, ex Monterosato, USNM, 332303). **E-F**, *Setia* (*Setia*) *perminima* (Manzoni): **E**, shell; **F**, protoconch (Madeira, AMS, C.134875). **G**, *Setia* (*Setia*) *pulcherrima* (Jeffreys); type-species of *Setia* H. & A. Adams: protoconch (Guernsey, Channel Islands, England probable syntype, USNM, 183153). **Scale:** shells - 0.5 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

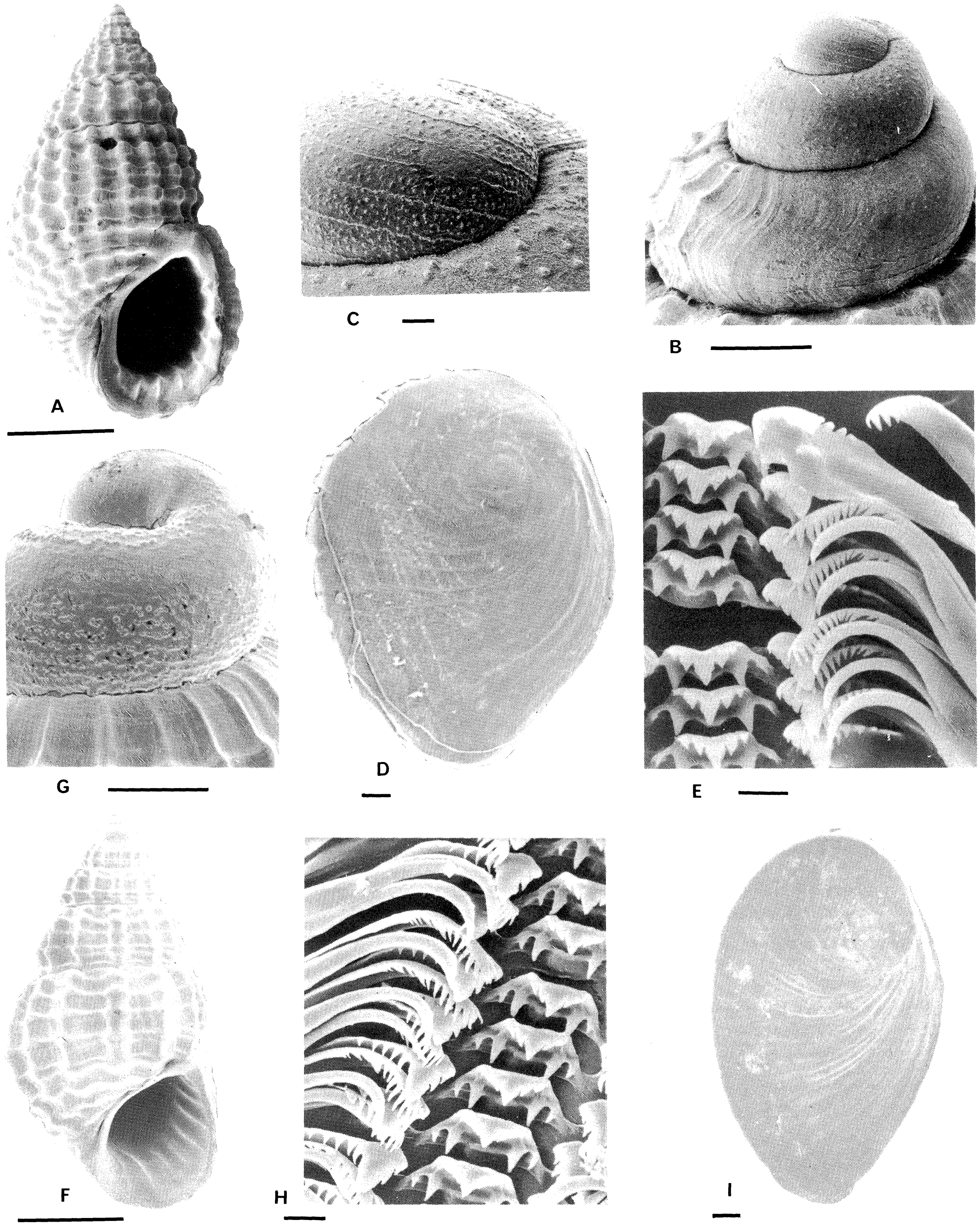

Fig. 86. **A-E**, *Alvania* (*Alvania*) *cimex* (Linné), type-species of *Alvania* Risso and *Acinus* Monterosato: **A**, shell; **B-C**, protoconch, **C**, detail of initial whorl; **D**, operculum (outer side); **E**, radula (A-C, Calvi, Corsica, AMS, C.134876; D-E, Melilla, Morocco, AMS, C.134877). **F-I**, *Alvania* (*Alvania*) *lineata* Risso, type-species of *Alvanolira* Nordsieck: **F**, shell; **G**, protoconch; **H**, radula; **I**, operculum (outer side) (Barcelona, Spain, AMS, C.134878). **Scale:** shells - 1 mm; protoconchs B, G and opercula - 0.1 mm; protoconch C and radulae - 0.01 mm.

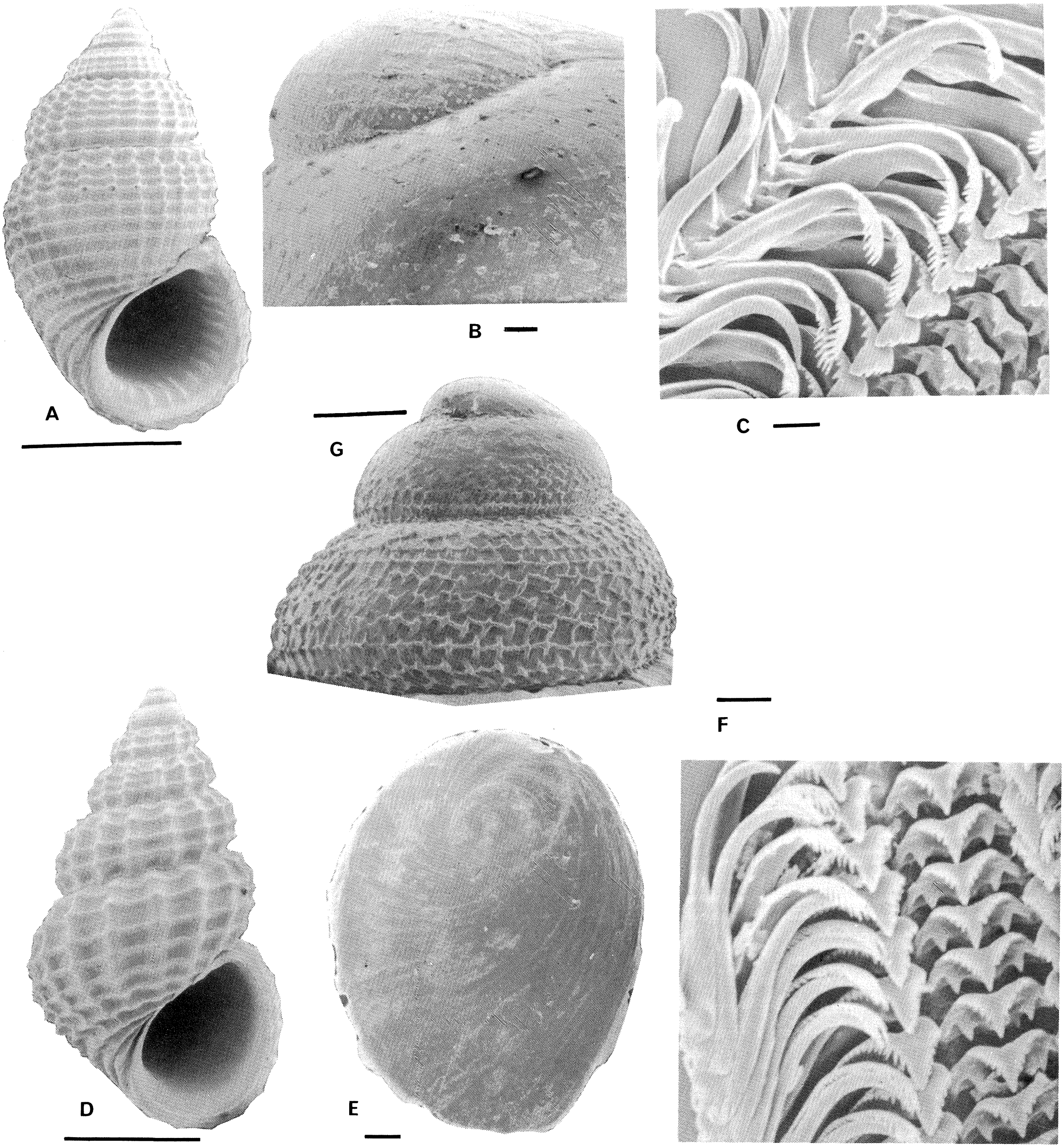

Fig. 87. **A-C**, *Alvania* (*Alvania*) *beanii* (Hanley), type-species of *Turbona* Leach in Gray and *Zacanthusa* Leach: **A**, shell; **B**, protoconch (detail of initial whorl); **C**, radula (Loch Fyne, Argyll, Scotland, BMNH, 47.9.13.66-69). **D-G**, *Alvania* (*Alvania*) *cimicoides* (Forbes), type-species of *Acinulus* Seguenza: **D**, shell; **E**, operculum (outer side); **F**, radula; **G**, protoconch (D-F, 274 m, Trondheimsfjord, Norway, BMNH, 1911.10.26.22217-22230; G, 168 m, Adventure Bank, Mediterranean Sea, AMS, C.24053). **Scale:** shells - 1 mm; protoconch G – 0.1 mm; protoconch B and radulae – 0.01 mm.

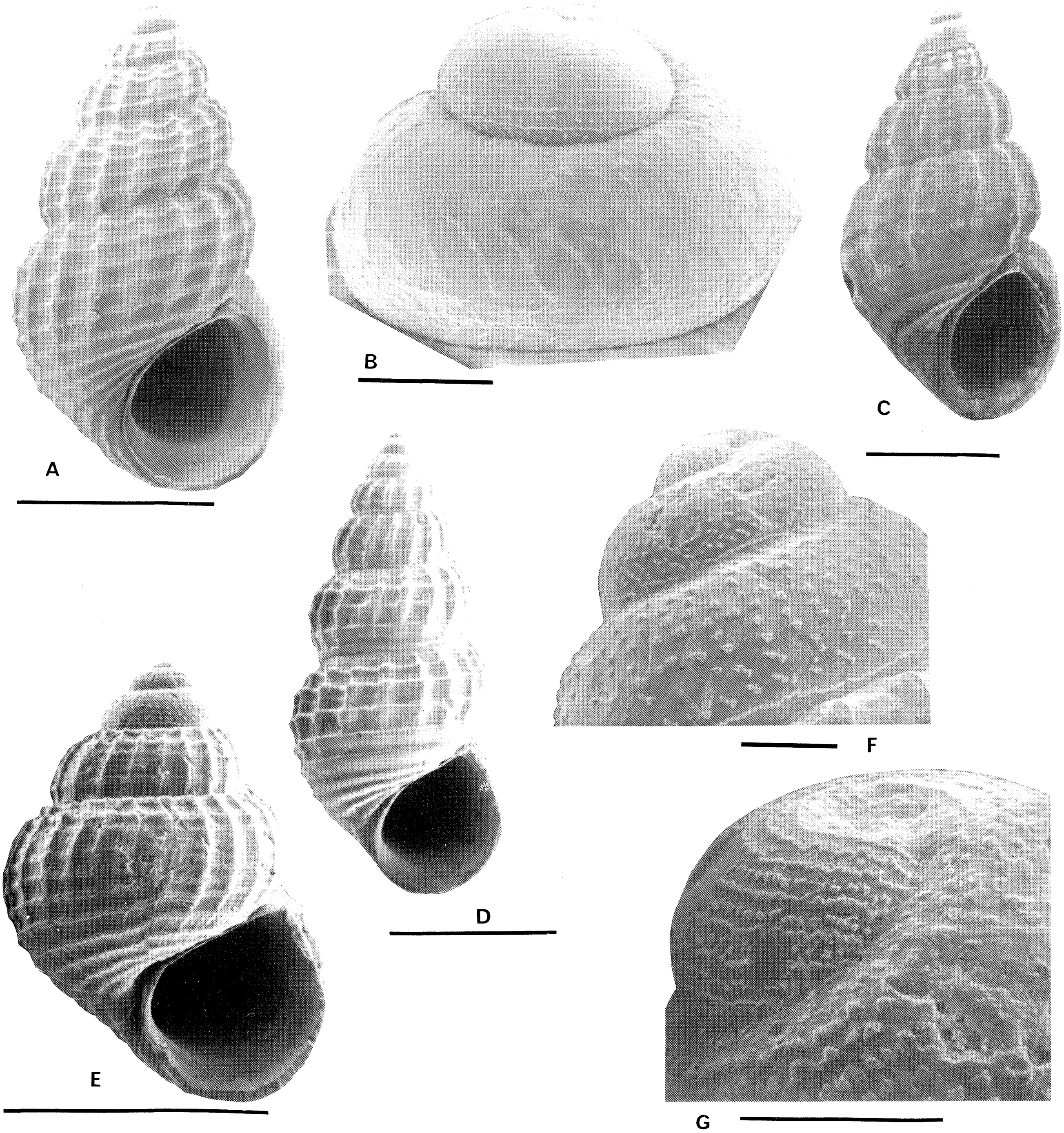

Fig. 88. **A-B**, *Alvania* (*Alvania*) *testae* (Aradas and Maggiore), type-species of *Actonia* Monterosato: **A**, shell; **B**, protoconch (12-102 m, Cape Tenez, Algeria, AMS, C.24100). **C**, *Alvania* (*Alvania*) *lanciae* (Calcara), type-species of *Lanciella* Nordsieck: shell (St. Raphael, France, BMNH, 1926.8.24.637-656). **D**, *Alvania* (*Alvania*) *rudis* (Philippi), type-species of *Thapsiella* Fischer: shell (Algiers, BMNH). **E-G**, *Alvania* (*Alvania*) *dingdensis* (Janssen), type-species of *Pseudalvania* Janssen: **E**, shell; **F-G**, protoconch, **G**, detail of first whorl (Dingden, W. Germany, Miocene, AMS, C.96090). **Scale:** shells - 1 mm; protoconchs - 0.1 mm.

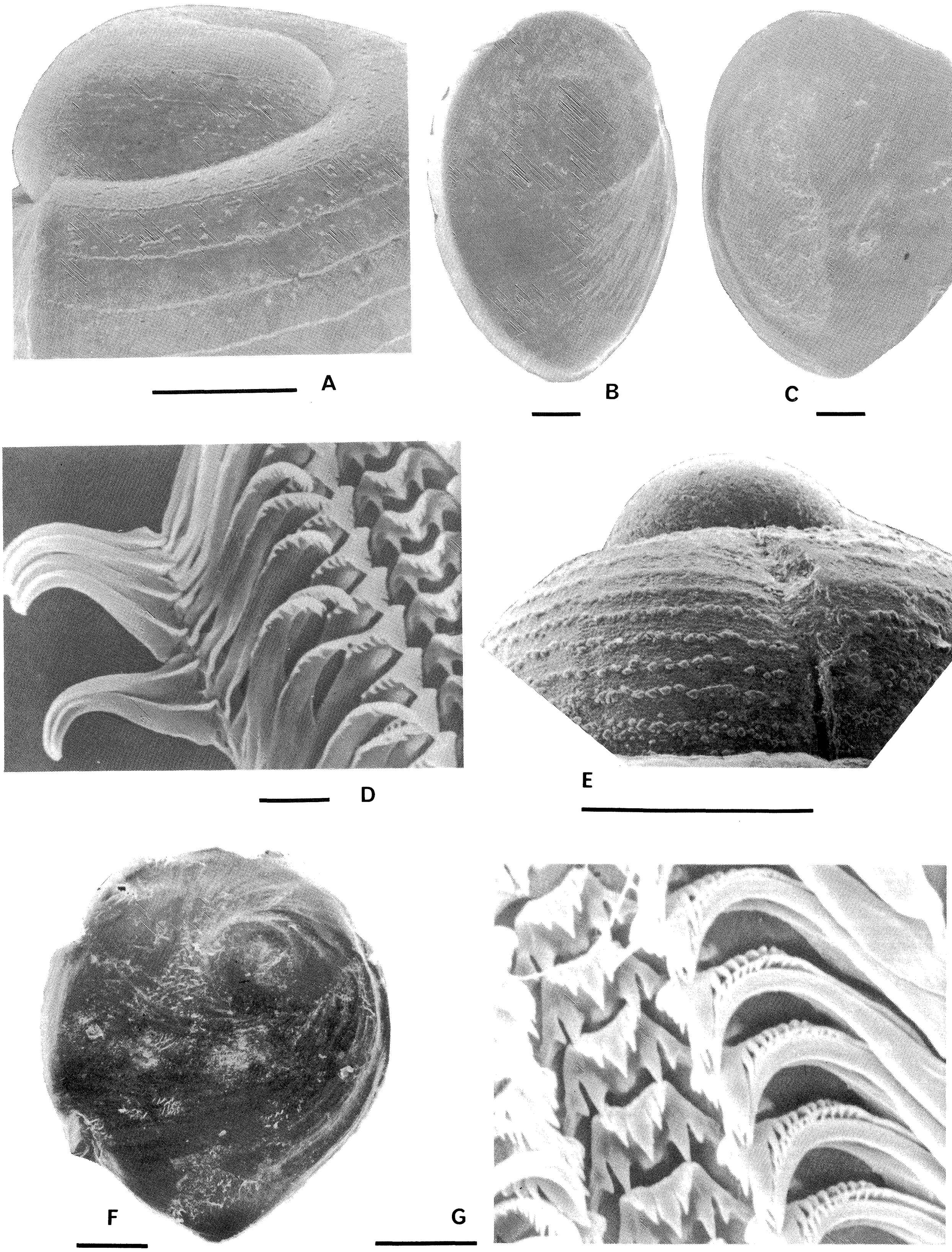

Fig. 89. **A-D**, *Alvania* (*Alvania*) *macandrewi* (Manzoni), type-species of *Andrewiella* Nordsieck: **A**, protoconch; **B-C**, operculum (**B**, outer and **C**, inner side); **D**, radula (Madeira, BMNH, 1911.10.26.22001-22020). **E-G**, *Alvania* (*Alvania*) *scabra* (Philippi), type-species of *Alvaniella* Sacco: **E**, protoconch; **F**, operculum (outer side); **G**, radula (Madeira, BMNH, 1911.10.26.21789-21808). **Scale:** protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

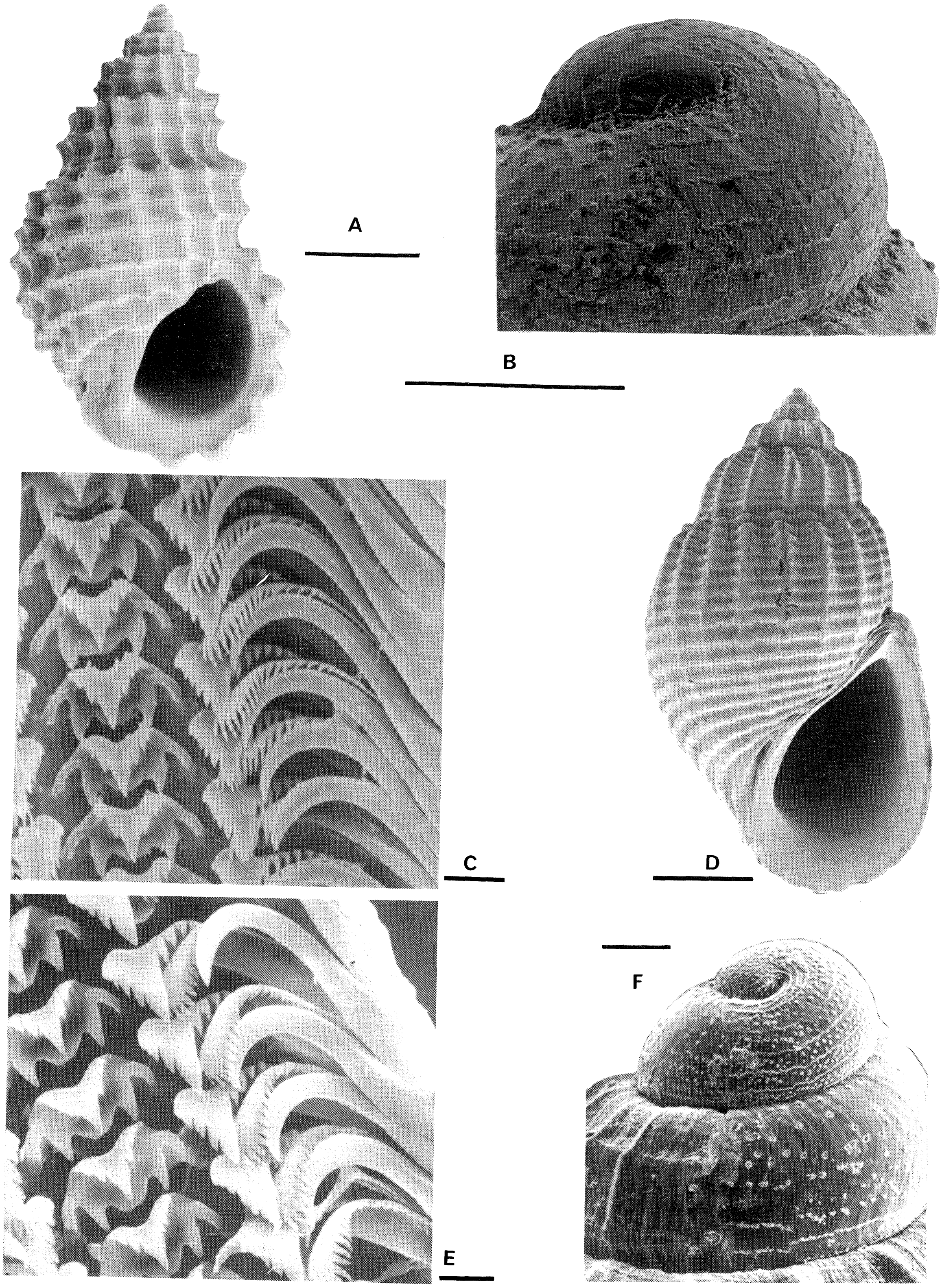

Fig. 90. **A-C**, *Alvania* (*Alvania*) *cancellata* (Da Costa), type-species of *Acinopsis* Monterosato: **A**, shell; **B**, protoconch; **C**, radula (A-B, Calvi, Corsica, AMS, C.138986; C, Herm, Channel Islands, England, BMNH, acc. no. 1480). **D-F**, *Alvania* (*Alvania*) *lactea* (Michaud), type-species of *Massotia* Bucquoy, Dautzenberg & Dollfus: **D**, shell; **E**, radula; **F**, protoconch (D-F, Fort National, ?Algeria, IRSB; E, Jersey, England, BMNH,1911.10.26.22802-22820).
Scale: shells - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

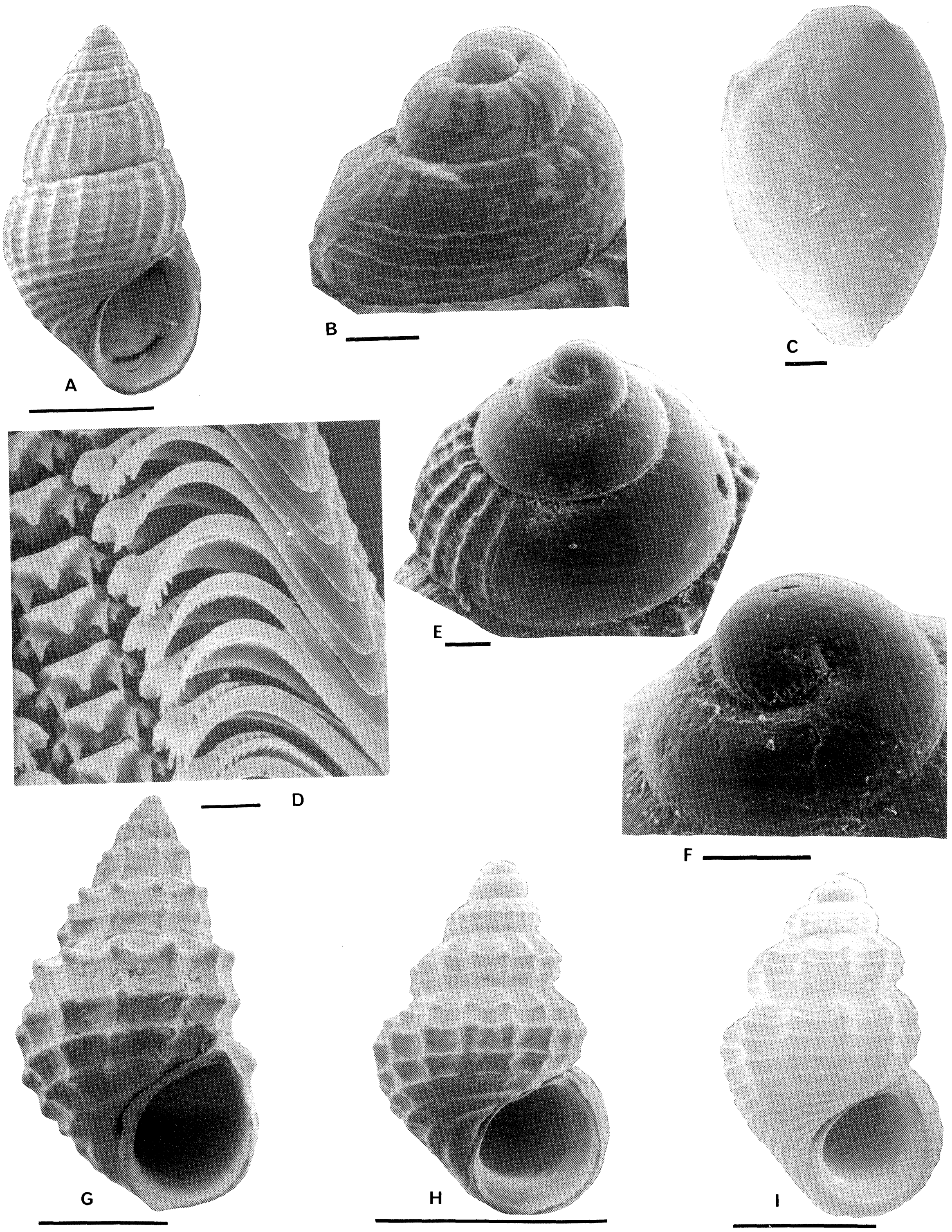

Fig. 91. **A-D**, *Alvania* (*Alvania*) *novarensis* (Frauenfeld), type-species of *Conalvinia* Ponder: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D**, radula (A-B, Ship Rock, Port Hacking, New South Wales, Australia, AMS, C.138155; C-D, Dunwich, N. Stradbroke Island, Queensland, Australia, AMS). **E-F**, *Alvania* (*Alvania*) *houdasi* (Cossmann), protoconch: **F**, detail of initial whorl (Thionville-sur-Opton, Yvelines, France, Lutétien (Eocene), AMS, C.138977). **G**, *Alvania* (*Alvania*) *heraelaciniae* Ruggieri, type-species of *Profundialvania* Taviani, shell (Macerata, Marche, Italy, Lower Pliocene, AMS, C.134879). **H**, *Alvania* (*Alvania*) *scabra* (Philippi), type-species of *Alvaniella* Sacco, shell (Madeira, BMNH, 1911.10.26.21789-21808). **I**, *Alvania* (*Alvania*) *macandrewi* (Manzoni) type-species of *Andrewiella* Nordsieck, shell (Madeira, BMNH, 1911.10.26.22001-22020). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

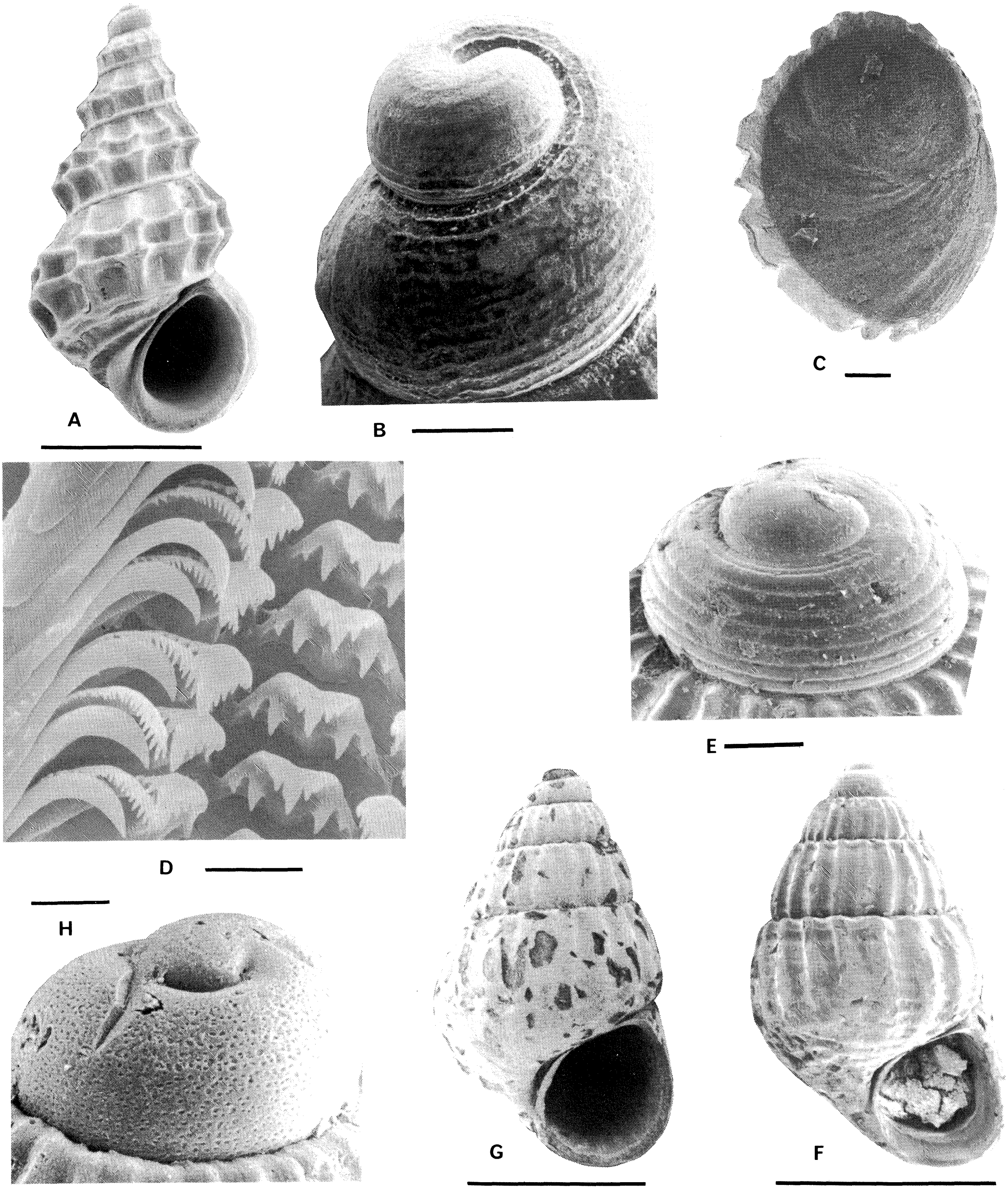

Fig. 92. **A-D**, *Alvania* (*Alvania*) *pagodula* (Bucquoy, Dautzenberg & Dollfus): **A**, shell; **B**, protoconch; **C**, operculum (outer side); **D**, radula (A-B, Roussillon, France, IRSB; C-D, Playa El Palmer, near Almeria, Spain, AMS, C.134880). **E-F**, *Alvania* (s.l.) *tallahatchiensis* (Sohl): **E**, protoconch; **F**, shell (Tabannee Creek, Mercers Mill, Tennessee, U.S.A., Ripley Formation, Upper Cretaceous, USNM). **G-H**, *Alvania* (s.l.) *crebricostata* (Sohl): **G**, shell; **H**, protoconch (locality as last, USNM). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

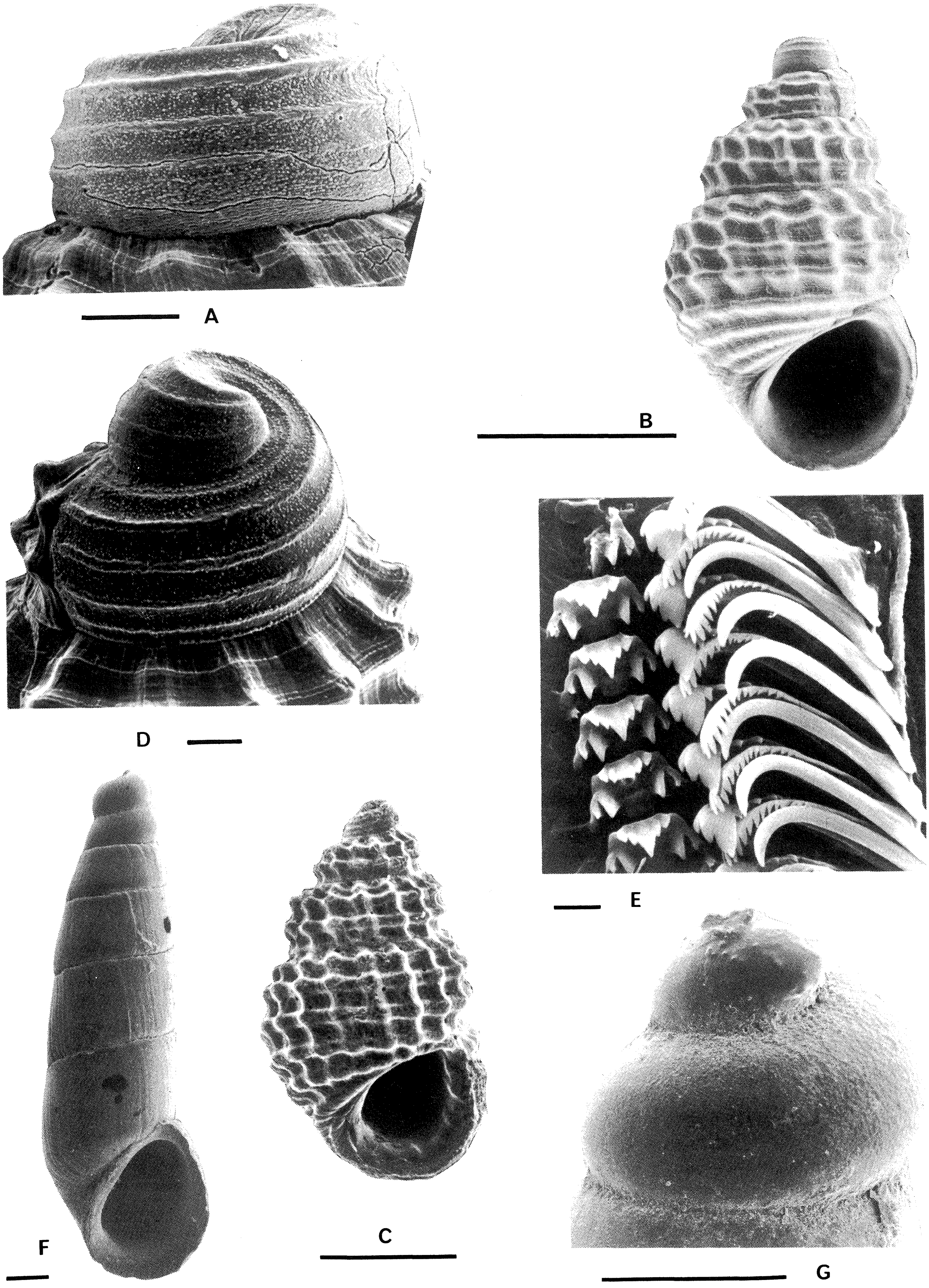

Fig. 93. **A-B**, *Alvania* (*Alvania*) *isolata* (Laseron): **A**, protoconch; **B**, shell (27 m, Christmas Island, Indian Ocean, AMS, C.134881). **C-E**, *Alvania* (*Alvania*) sp.: **C**, shell; **D**, protoconch; **E**, radula (Flic en Flac, W. coast Mauritius, AMS, C.134882). **F-G**, *Striatestea* sp.: **F**, shell; **G**, protoconch (20 m, Whangaroa Harbour entrance, NMNZ, M.41170). **Scale:** shells (B, C) - 1 mm; protoconchs and shell (F) - 0.1 mm; radula - 0.01 mm.

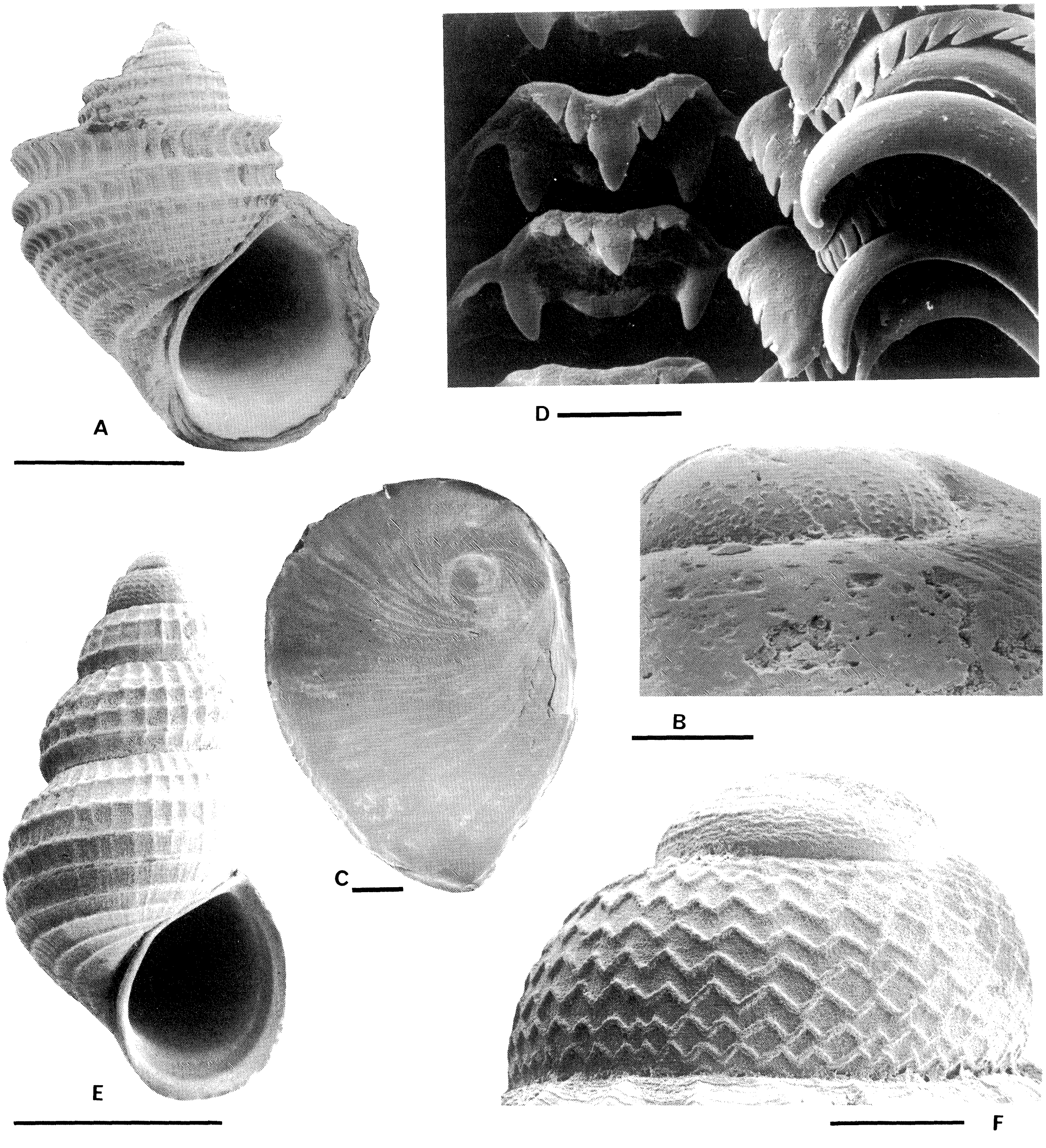

Fig. 94. **A-D**, *Alvania* (*Galeodina*) *carinata* (Da Costa), type-species of *Galeodina* Monterosato: **A**, shell, **B**, protoconch (detail of initial whorl); **C**, operculum (outer side); **D**, radula (Jersey, Channel Islands, England, BMNH, 1911.10.26.22839-22858). **E-F**, *Alvania* (*Alvania*) *jeffreysi* (Waller): **E**, shell; **F**, protoconch (450–500 m, off Krossfjord, Norway, MCZ, 277846). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

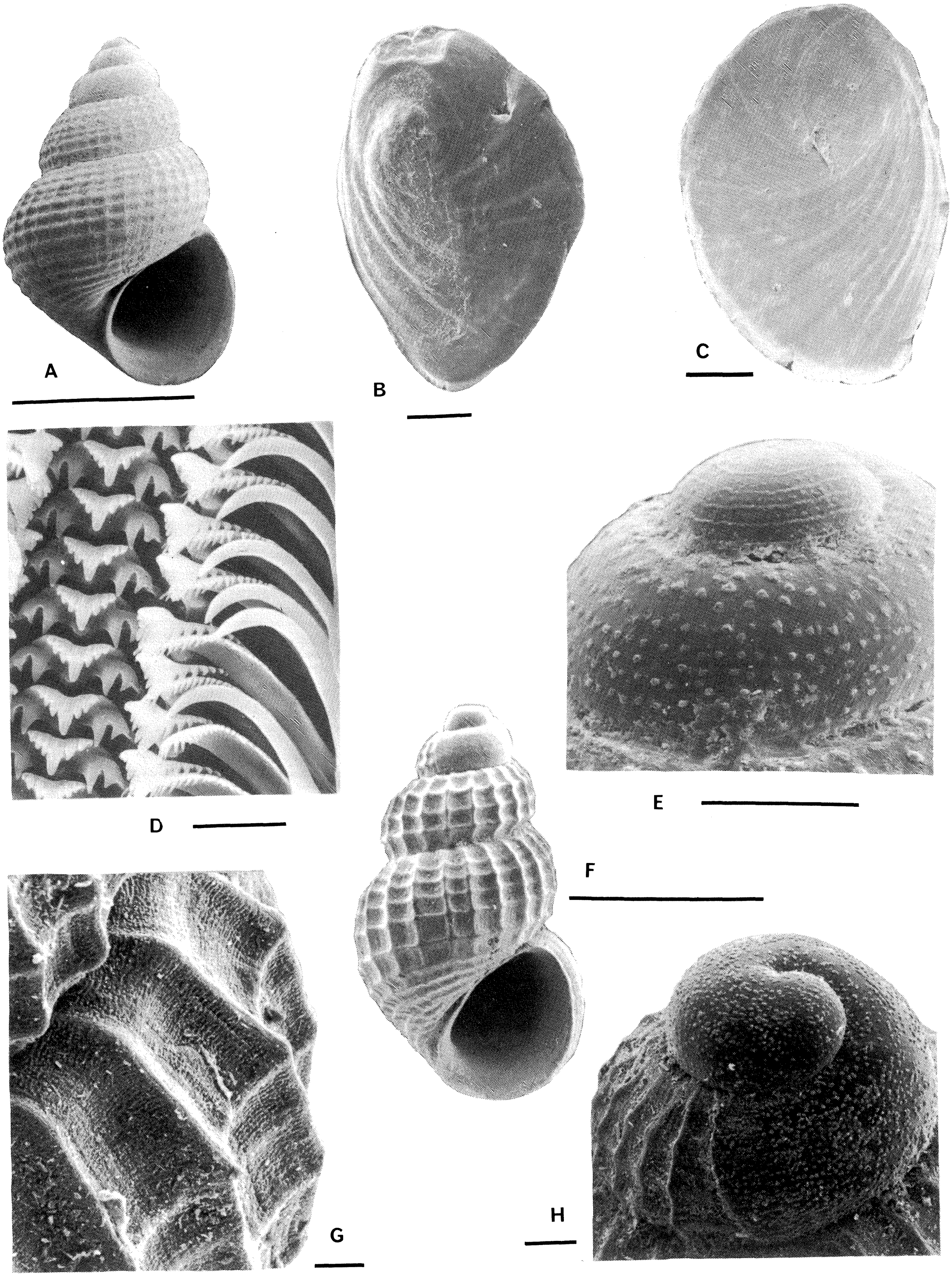

Fig. 95. **A-E**, *Alvania* (*Alvania*) *punctura* (Montagu), type-species of *Arsenia* Monterosato: **A**, shell; **B-C**, operculum (**B**, inner side; **C**, outer side); **D**, radula; **E**, protoconch (Isle of Cumbrae, Firth of Clyde, Scotland, BMNH, 1911.10.26.22642-22661). **F-H**, *Alvania* (*Alvania*?) *bonneti* (Cossmann): **F**, shell; **G**, detail of teleoconch sculpture; **H**, protoconch (Thionville - sur- Opton, Yvelines, France, Lutétien (Eocene), AMS, C.138978). **Scale:** shells - 1 mm; protoconchs, microsculpture and opercula - 0.1 mm; radula - 0.01 mm.

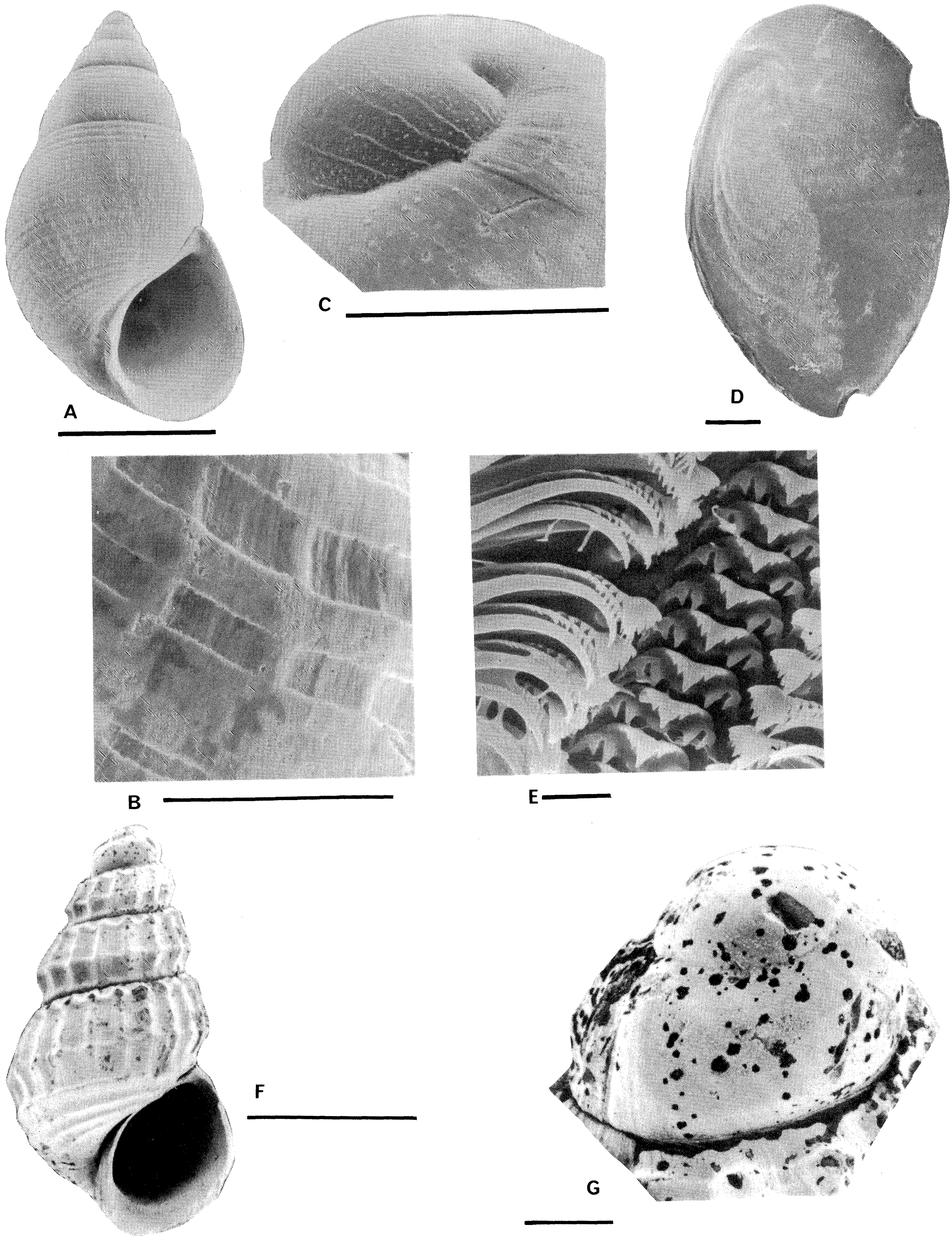

Fig. 96. **A-E**, *Alvania* (*Crisilla*) *semistriata* (Montagu), type-species of *Crisilla* Monterosato: **A**, shell; **B**, microsculpture of teleoconch; **C**, protoconch showing detail of first whorl; **D**, operculum (inner side); **E**, radula (Tenby, Wales, BMNH, 1911.10.26.2308-23099). **F-G**, *Alvania* (*?Linemera*) cf. *monileata* (Marwick): **F**, shell; **G**, protoconch (Gladstone, North Island, New Zealand, Plio-Pleistocene, NMNZ, M42876). **Scale:** shells - 1 mm; protoconchs, microsculpture and operculum - 0.1 mm; radula - 0.01 mm.

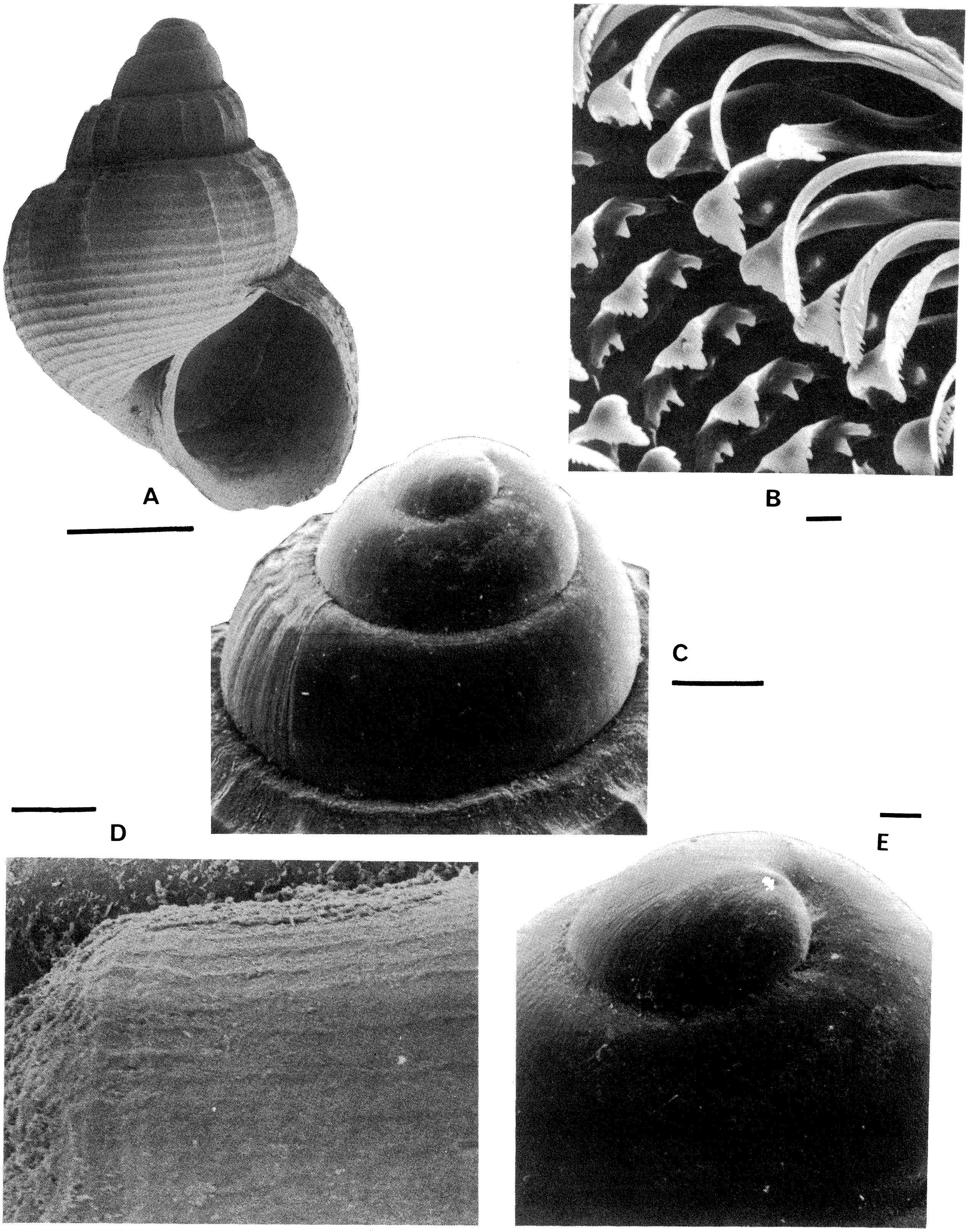

Fig. 97. **A-E**, *Alvania* (*Punctulum*) *wyvillethomsoni* (Friele), type-species of *Punctulum* Jeffreys: **A**, shell; **B**, radula; **C-E**, protoconch (**D**, detail of microsculpture on last whorl; **E**, detail of apex) (1322 m, north of Faeroes Islands, North Atlantic Ocean, ZMC). **Scale:** shell - 1 mm; protoconch - 0.1 mm; microsculpture and radula - 0.01 mm.

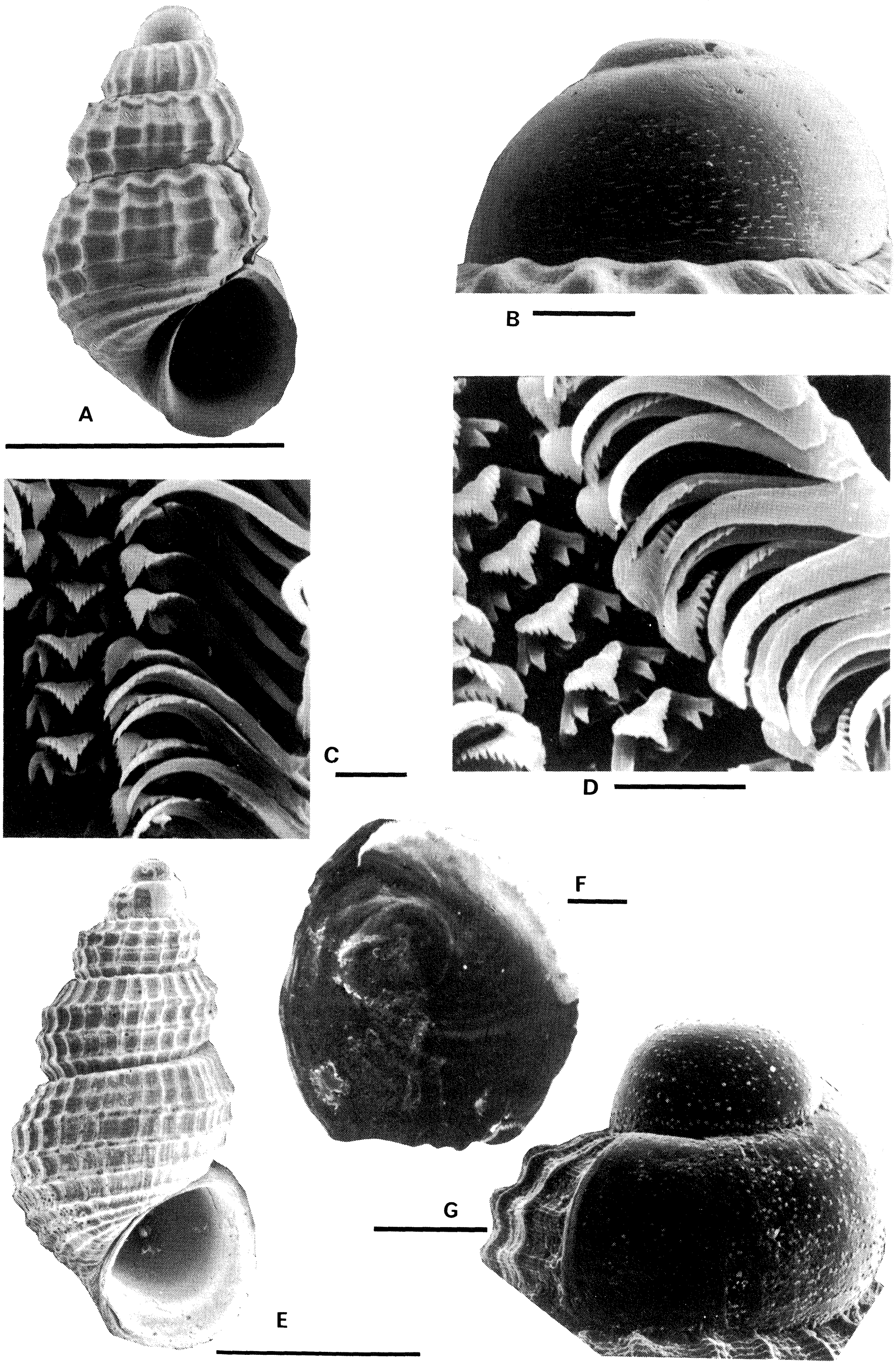

Fig. 98. **A-C**, *Alvania* (*Linemera*) *interrupta gratatoides* (Finlay): **A**, shell; **B**, protoconch; **C**, radula (110 m, off Stephens Island, Cook Strait, New Zealand, NMNZ, M53152). **D-G**, *Alvania* (*Linemera*) *suprasculpta* (May): **D**, radula; **E**, shell; **F**, operculum (inner side); **G**, protoconch (Middle Harbour, Sydney, New South Wales, Australia (AMS, C.32471). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

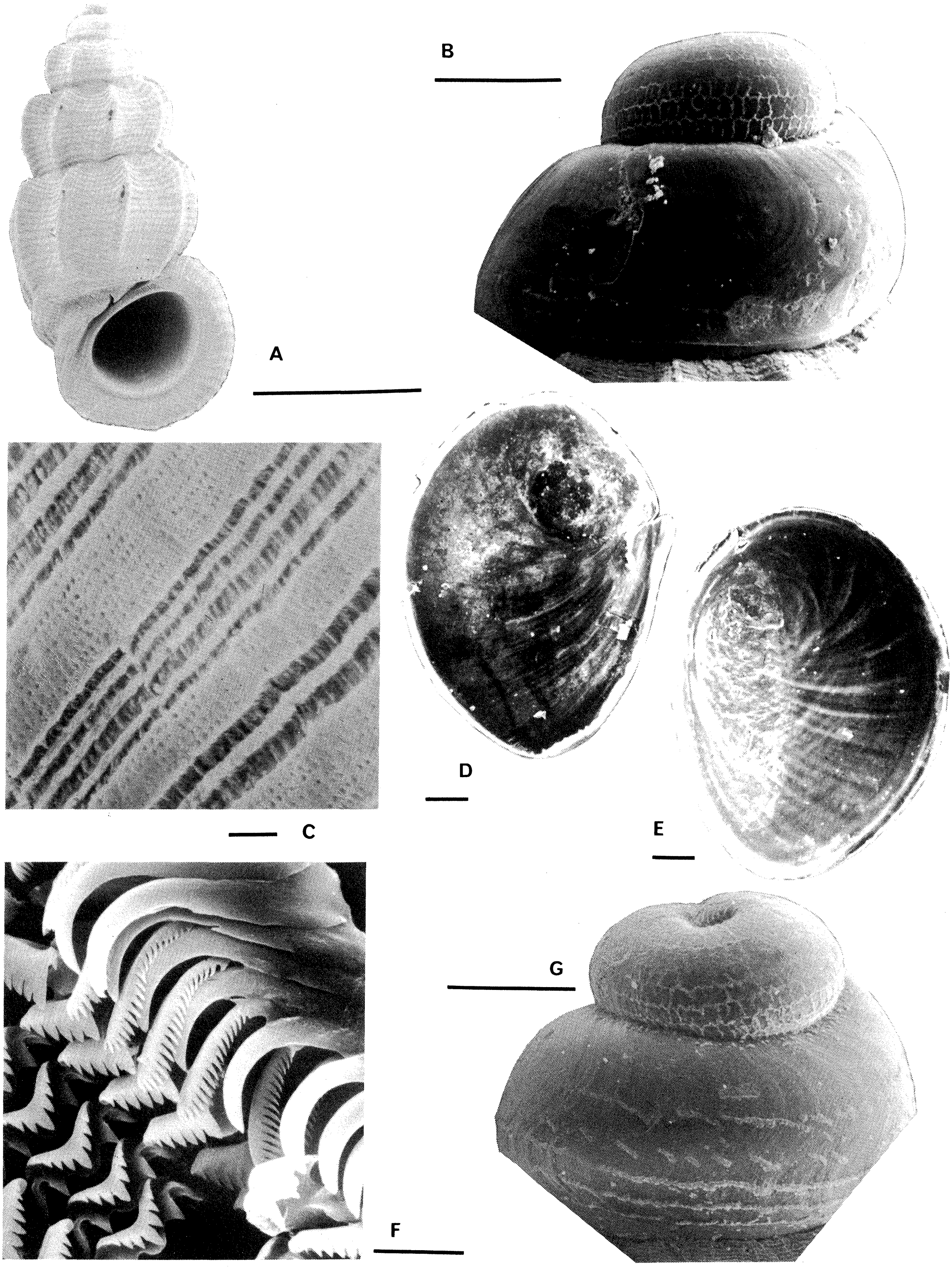

Fig. 99. **A-F**, *Manzonia* (*Manzonia*) *crassa* (Kanmacker in Adams), type-species of *Manzonia* Brusina: **A**, shell; **B**, protoconch; **C**, microsculpture of teleoconch; **D-E**, operculum (**D**, outer side, **E**, inner side); **F**, radula (A,C, Dellys, Algeria, AMS, C.550; B,D-F, Pt de la Corbiere, Jersey Is., England, IRSB). **G**, *Manzonia* (*Alvinia*) *zetlandica* (Montagu), type-species of *Flemellia* Nordsieck; protoconch (200 m, Korsfjord, Norway, AMS, C.134883). **Scale:** shell - 1 mm; protoconchs and opercula - 0.1 mm; microsculpture and radula - 0.01 mm.

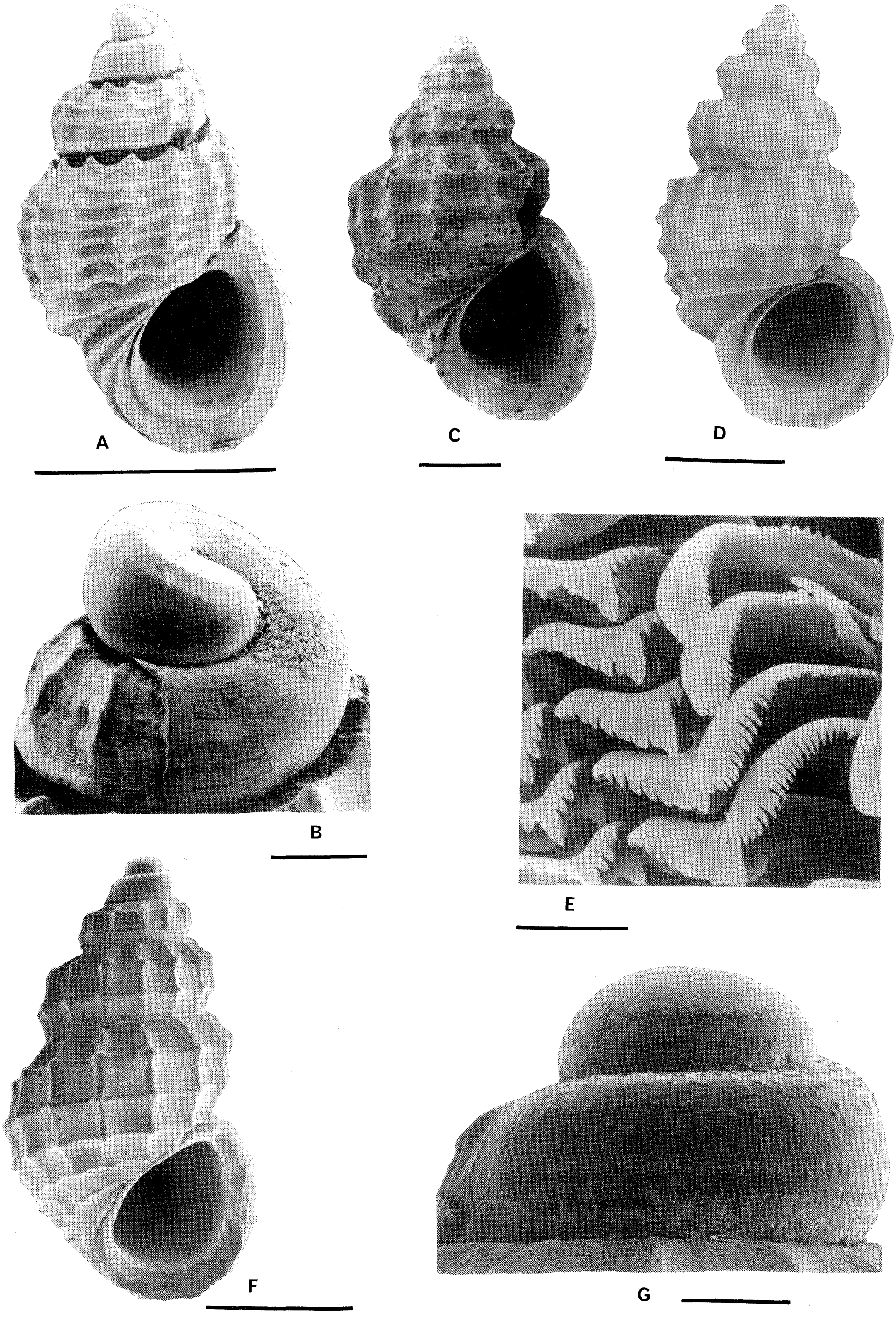

Fig. 100. **A-B**, *Manzonia* (*Manzonia*) *crispa* (Watson): **A**, shell; **B**, protoconch (Madeira, ANSP, 331432). **C**, *Manzonia* (*Manzonia*) *duboisii* (Nyst); shell (Söllingen, West Germany, Oligocene, NMV, P47882). **D-E**, *Manzonia* (*Alvinia*) *zetlandica* (Montagu), type-species of *Flemellia* Nordsieck: **D**, shell; **E**, radula (200 m, Korsfjorden, Norway, AMS, C.134883). **F-G**, *Manzonia (Alvinia) dictyophora* (Philippi): **F**, shell; **G**, protoconch (Secca del Bagno, Lipari Island, Eolie Islands, N. Sicily, S. Palazzi Colln). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radula - 0.01 mm.

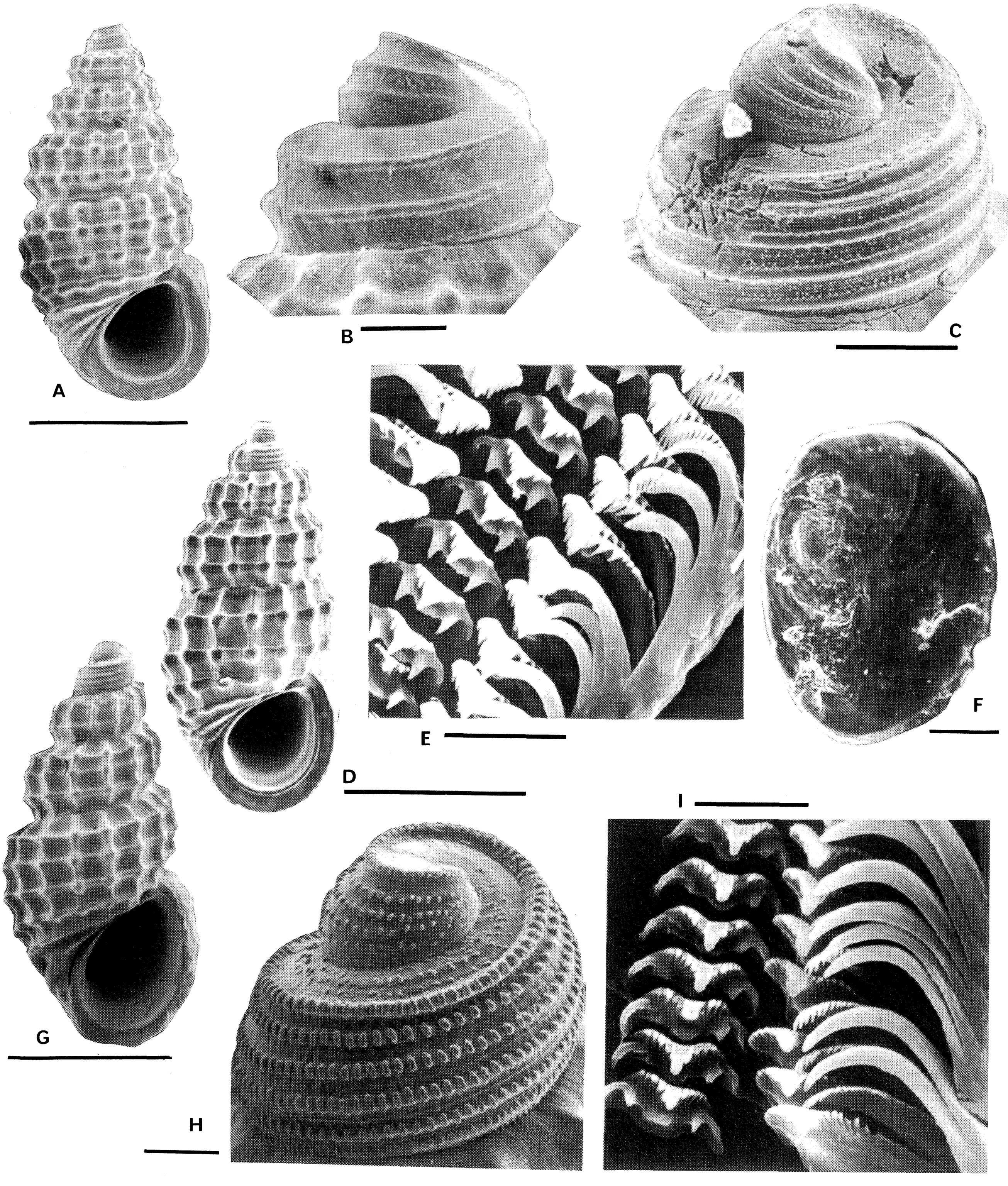

Fig. 101. A-B, *Manzonia (Simulamerelina) corruga* (Laseron), type-species of *Simulamerelina* n.subgen.: **A,** shell; **B,** protoconch (Heron Island, Queensland, AMS, C.134884). **C-F,** *Manzonia* (*Simulamerelina*) cf. *corruga* (Laseron): **C,** shell; **D,** protoconch; **E,** radula; **F,** operculum (inner side) (Lord Howe Island, Australia, AMS, C.59732). **G-I,** *Manzonia* (*Alvinia*) *aequisculpta* (Keep): **G,** shell; **H,** protoconch; **I,** radula (Piedra Colorada, Cedros Island, Baja California, AMS, C.134885). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

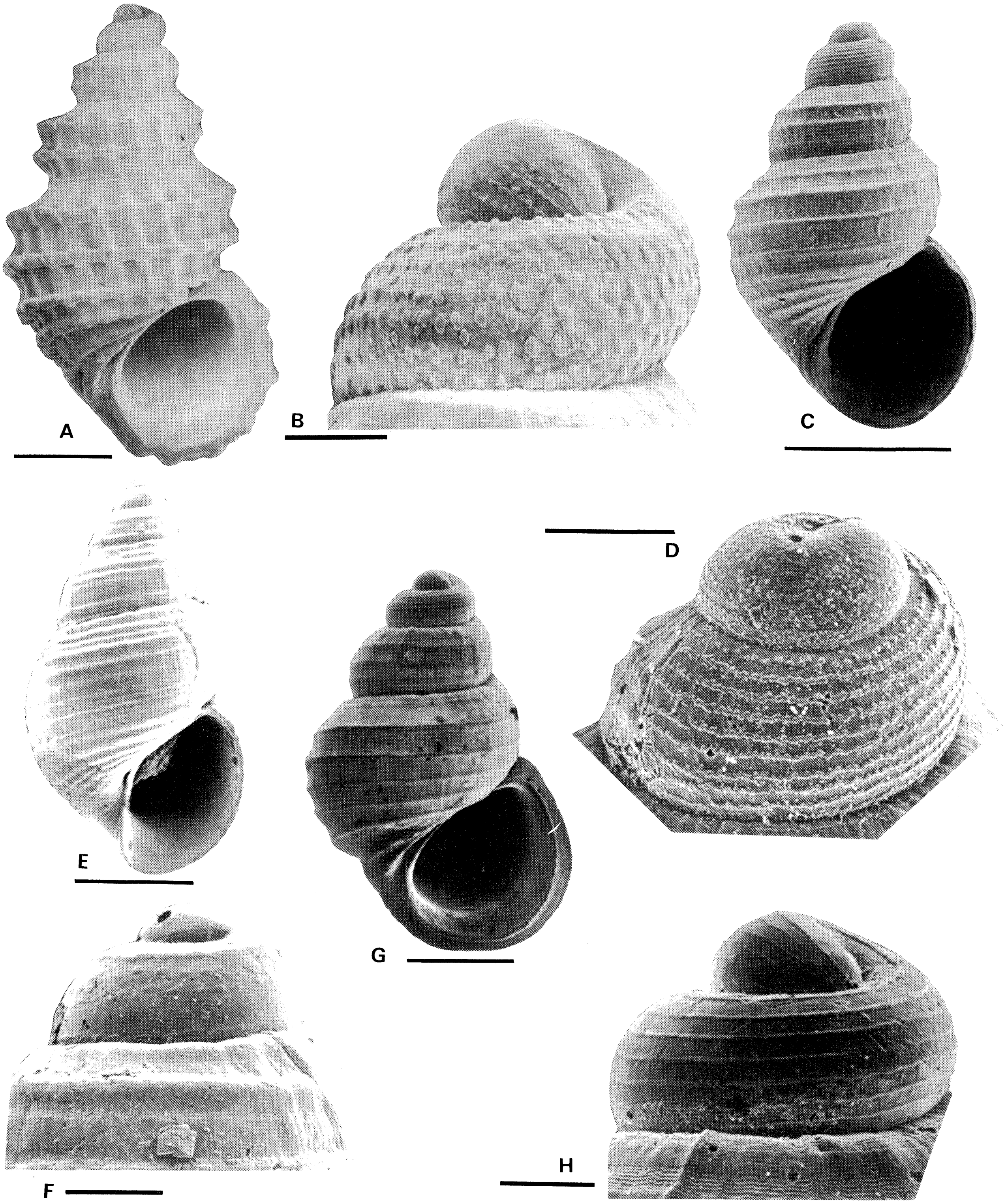

Fig. 102. **A-B**, *Manzonia* (*Alvinia*) *weinkauffi* (Monterosato), type-species of *Alvinia* Monterosato: **A**, shell; **B**, protoconch (Dellys, Algeria, AMS, C.548). **C-D**, *Alvania* (*Alvania*) *watsoni* (Watson): **C**, shell; **D**, protoconch (Madeira, BMNH, 1911.10.26.23348-23367). **E-F**, *Alvania* (*Crisilla*) *pseudocingulata* (Nordsieck), type-species of *Crisillosetia* Nordsieck: **E**, shell; **F**, protoconch (paratype; Ibiza, Balearic Is., Spain, AMS, C.108980). **G-H**, *Manzonia* (*Alvinia*) *moniziana* (Watson), type-species of *Moniziella* Nordsieck: **G**, shell; **H**, protoconch (Madeira, BMNH, 1911.10.26.23391-23402). **Scale:** shell A - 1 mm; shells C, E, G - 0.5 mm; protoconchs - 0.1 mm.

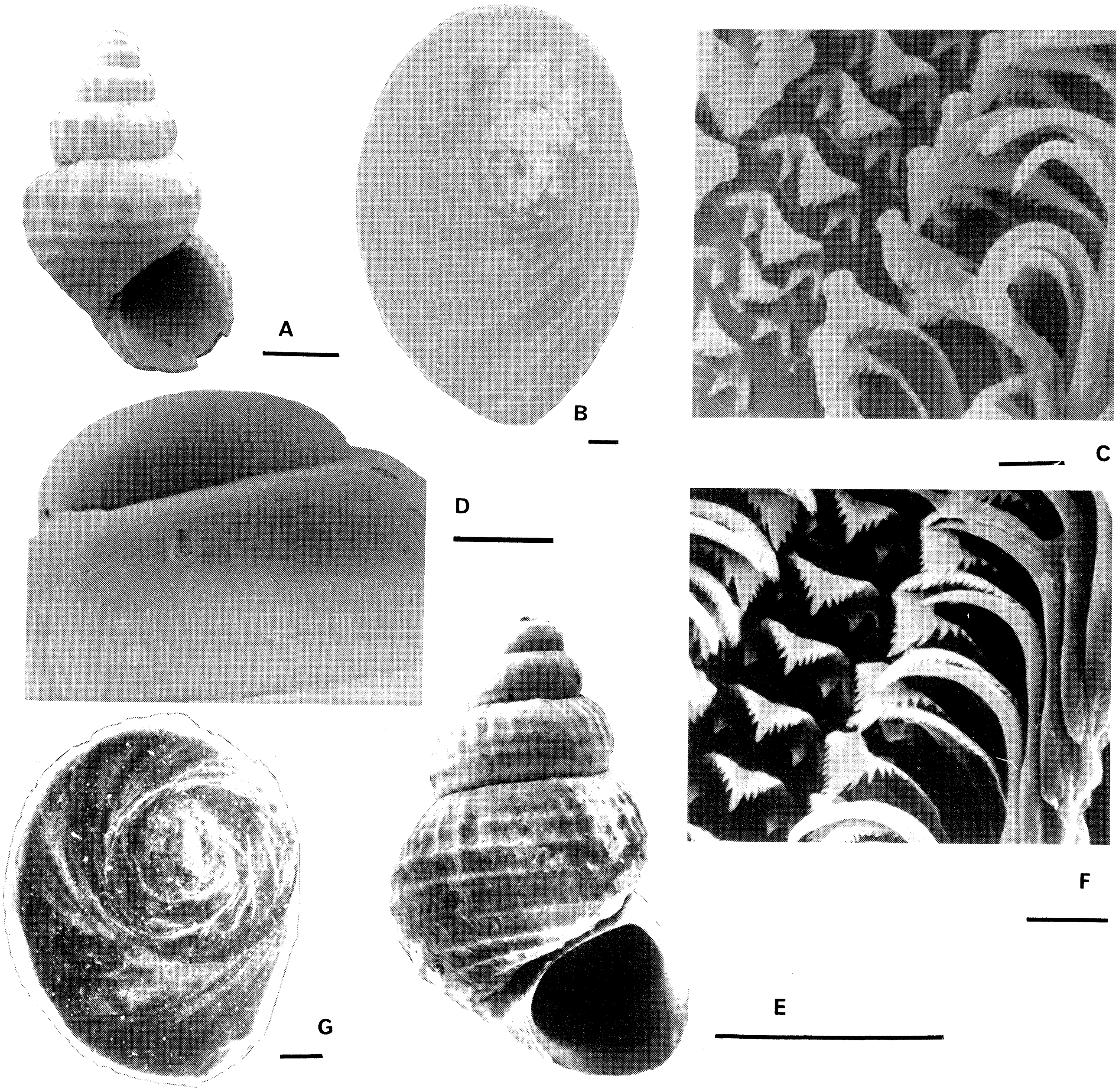

Fig. 103. **A-D**, *Frigidoalvania janmayeni* (Friele), type-species of *Frigidoalvania* Warén: **A**, shell; **B**, operculum (outer side); **C**, radula; **D**, protoconch (A, 186 m, between Hope and Edge Islands, Spitzbergen, Arctic Ocean, IRSB; B-D, 180 m, Spitsbergen, Arctic Ocean, AMS, C.134888). **E-G**, *Onoba* (*Onoba*) *pelagica* (Stimpson): **E**, shell; **F**, radula; **G**, operculum (outer side) (Eastport, Maine, USA, MCZ, 34493). **Scale:** shells - 1 mm; protoconch and opercula - 0.1 mm; radulae - 0.01 mm.

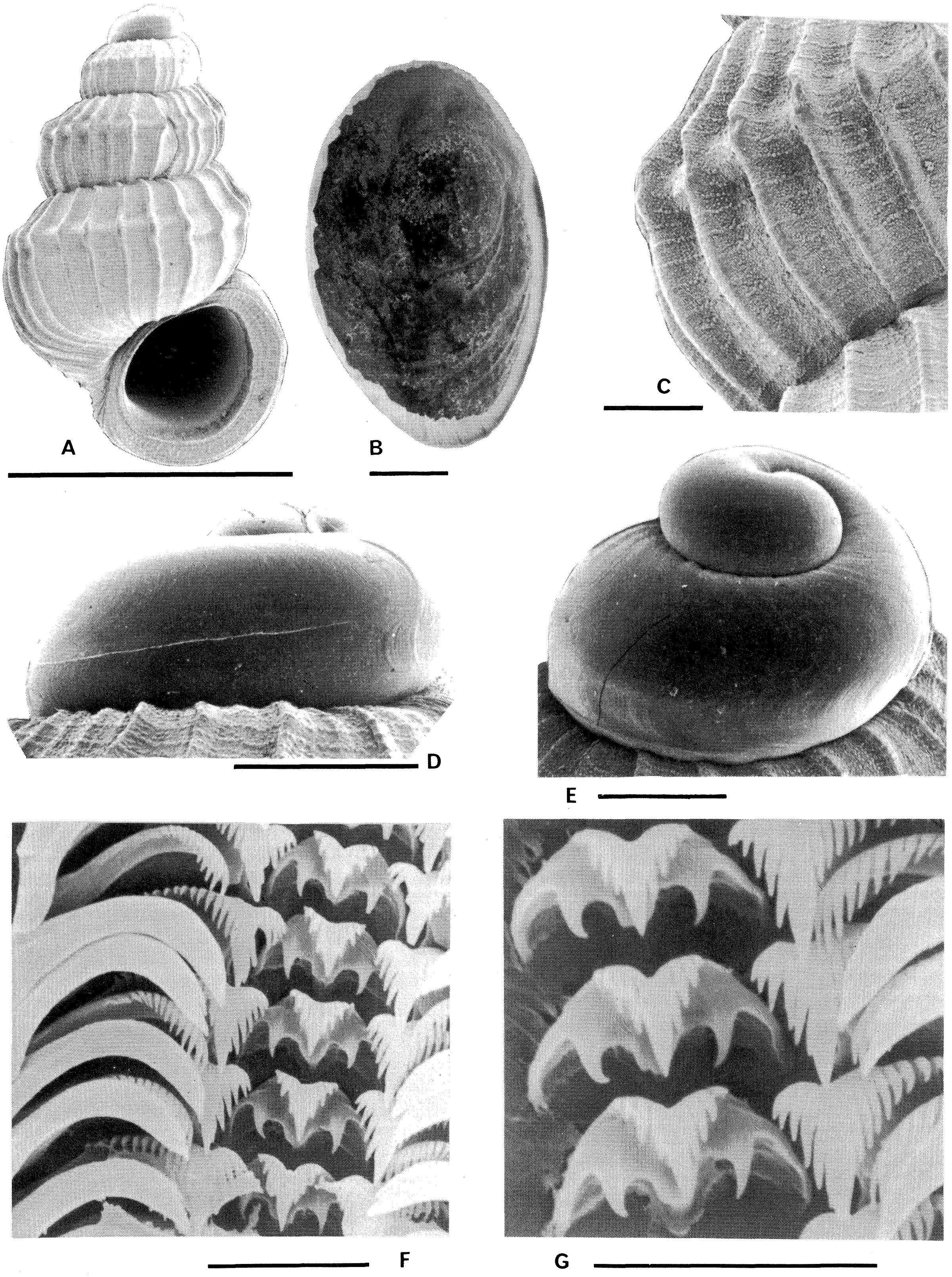

Fig. 104. **A-G**, *Parashiela ambulata* Laseron, type-species of *Parashiela* Laseron: **A**, shell; **B**, operculum (outer side); **C**, microsculpture of teleoconch; **D-E**, protoconch; **F-G**, radula (**G**, detail of central teeth) (A, C-E, Lizard Island, Queensland AMS, C.134890; B,F,G. 2 m, near Basilisk Passage, Port Moresby, Papua New Guinea, AMS, C.138979). **Scale:** shell - 1 mm; protoconchs, microsculpture and operculum - 0.1 mm; radulae - 0.01 mm.

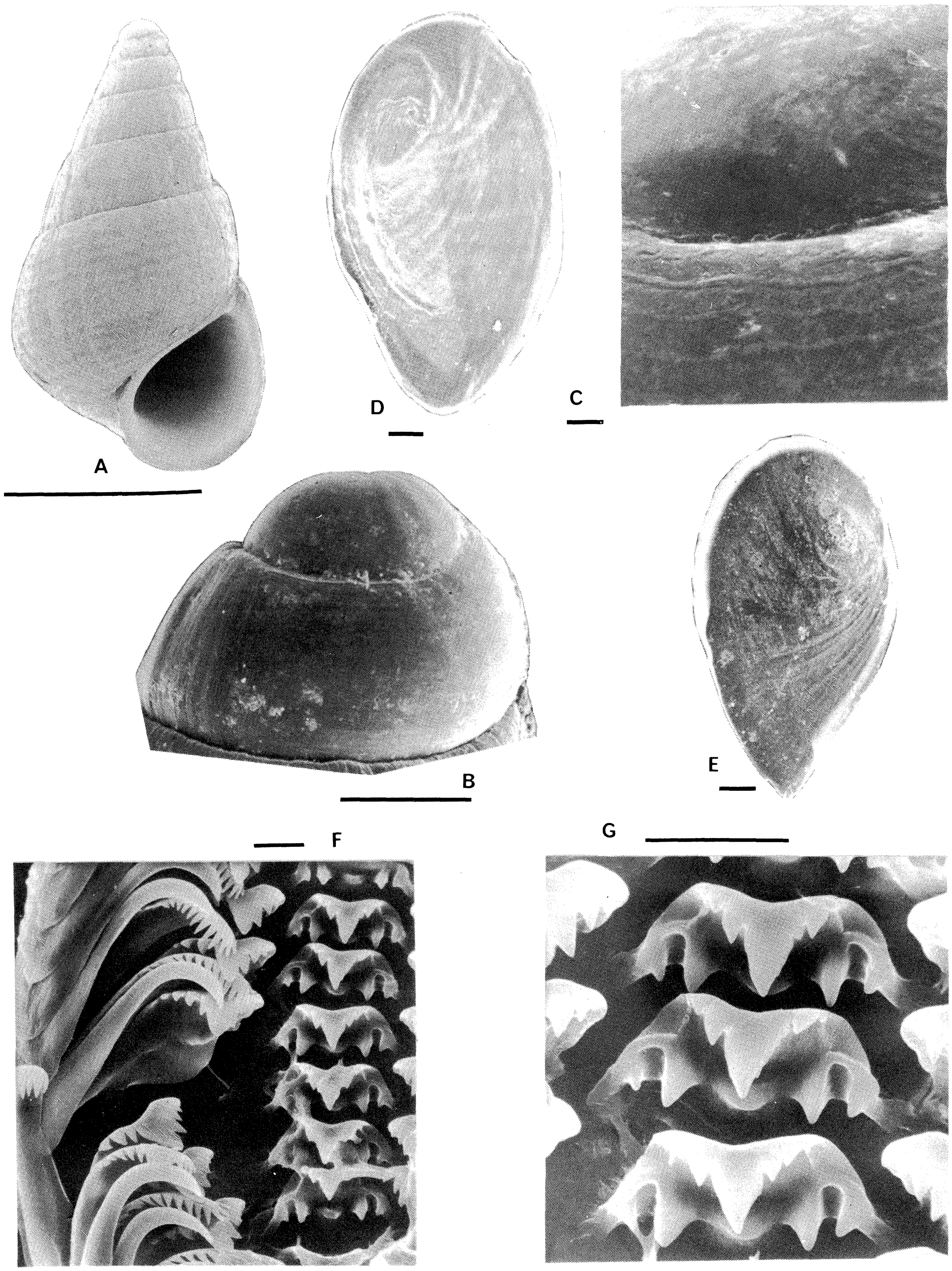

Fig. 105. **A-G**, *Cingula* (*Cingula*) *trifasciata* (J. Adams), type-species of *Cingula* Fleming: **A**, shell; **B-C**, protoconch (**C**, detail of protoconch); **D-E**, operculum (**D**, inner side, **E**, outer side); **F-G**, radula (**G**, detail of central teeth) (A, Weymouth, England, NMV, F.26612; B, Plymouth England, AMS, C.134892; C, Guernsey, England, AMS, C.134891; D-G, Scilly Isles, England, BMNH). **Scale:** shell - 1 mm; protoconch (B) and opercula - 0.1 mm; microsculpture (C) and radulae - 0.01 mm.

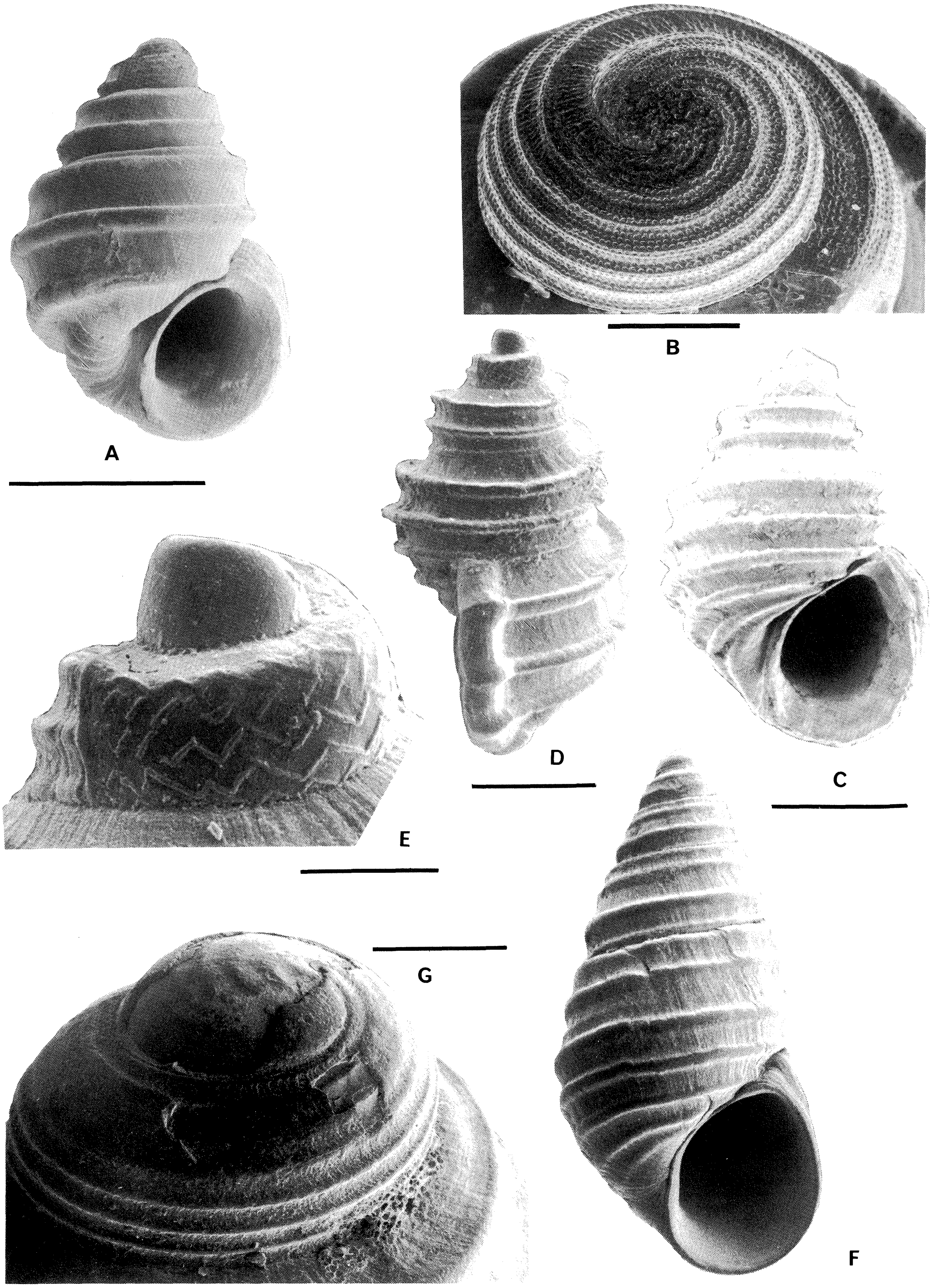

Fig. 106. A-B, *Tropidorissoia taphrodes* Tomlin & Shackleford, type-species of *Tropidorissoia* Tomlin & Shackleford: **A**, shell; **B**, protoconch (Praie das Conchas (Guadalupe), Saó Tomé, Gulf of Guinea, AMS, C. 142404). **C-E**, *Cingula* (?*Lirocingula*) *perfecta* (Smith): **C-D**, shell; **E**, protoconch (St Helena, RSM). **F-G**, *Cingula* (*Lirocingula*) *wallichi* (Smith): **F**, shell; **G**, protoconch (St Helena, USNM, 124020). **Scale:** shell F - 1 mm; shells A,C,D - 0.5 mm; protoconchs - 0.1 mm.

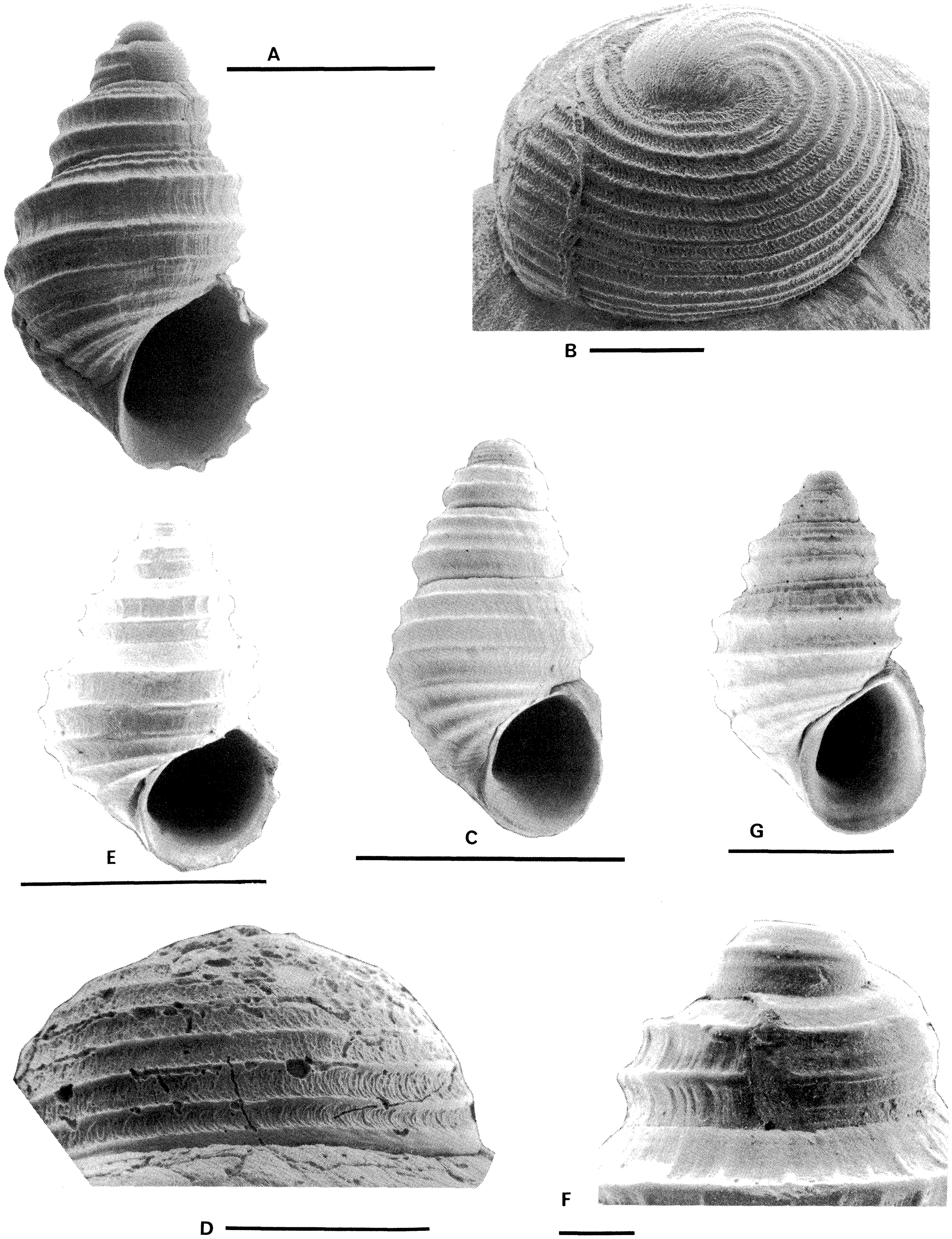

Fig. 107. **A-B**, *Cingula* (*Lirocingula*) *aequa* (Smith): **A**, shell; **B**, protoconch (St. Helena, USNM, 124025). **C-D**, *Cingula* (*Lirocingula*) *varicifera* (Smith): **C**, shell; **D**, protoconch (St. Helena, AMS, C.134893). **E-F**, *Cingula* (*Lirocingula*) sp.: **E**, shell; **F**, protoconch (Le Bois - Gouët, Loire-Atlantique, France, Eocene, AMS, C.138980). **G**, *Cingula* (*Lirocingula*) *winslowae* (Bartsch), type-species of *Lirocingula* n.subgen., shell (Kom, Table Bay, South Africa AMS, C.142403). **Scale:** shells - 1 mm; protoconchs - 0.1 mm.

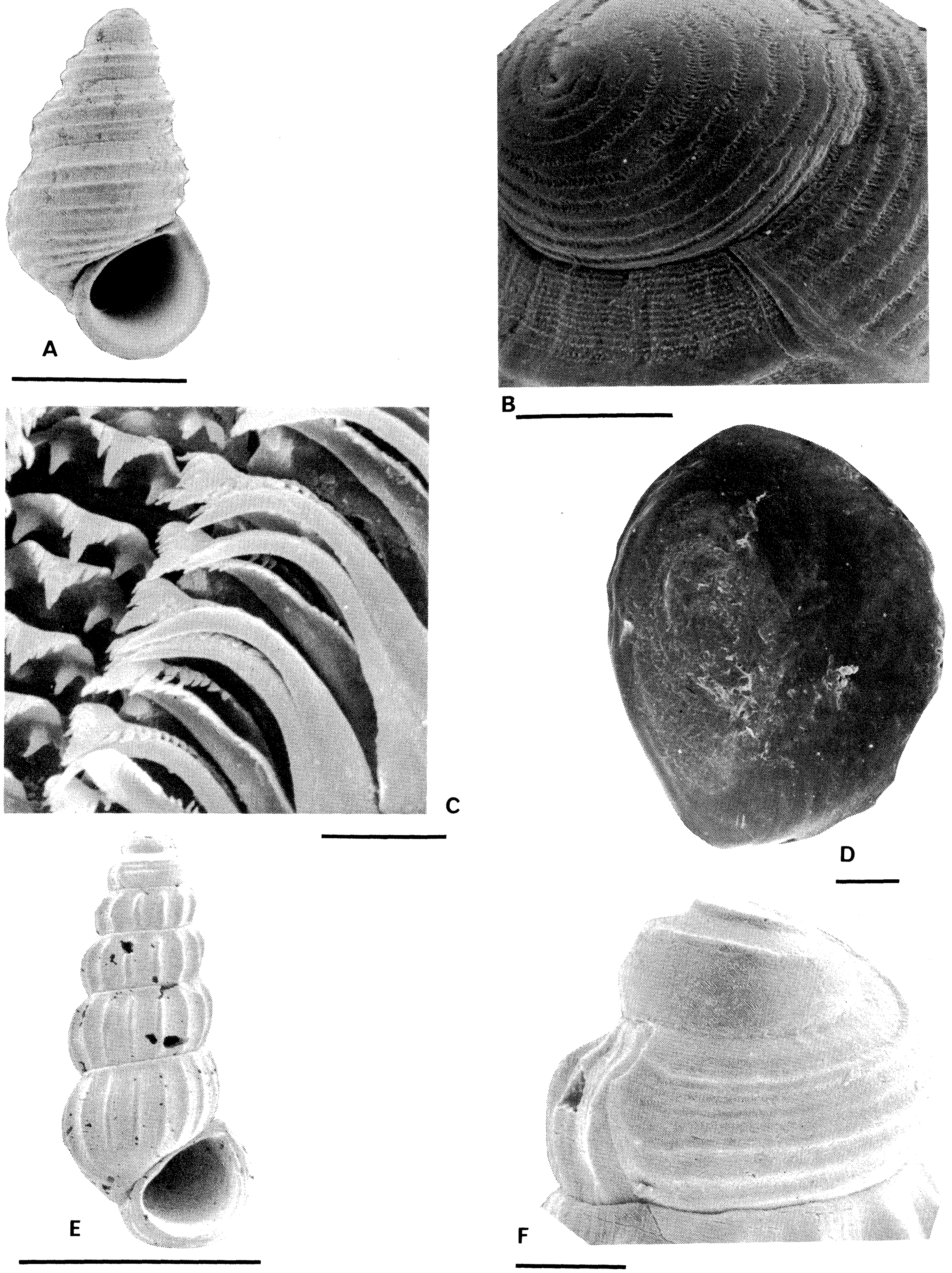

Fig. 108. **A-D**, *Cingula* (*Lirocingula*) *farquhari* (Smith): **A**, shell; **B**, protoconch; **C**, radula; **D**, operculum (inner side) (Millers Point, False Bay, South Africa, AMS, C.134894). **E-F**, *Onoba* (*Manawatawhia*) *analoga* Powell type-species of *Manawatawhia* Powell: **E**, shell; **F**, protoconch (Paratype, 92 m, off Three Kings Islands, New Zealand, AMS, C. 134895). **Scale:** Shells — 1 mm; protoconchs and opercula — 0.1 mm; radula — 0.01 mm.

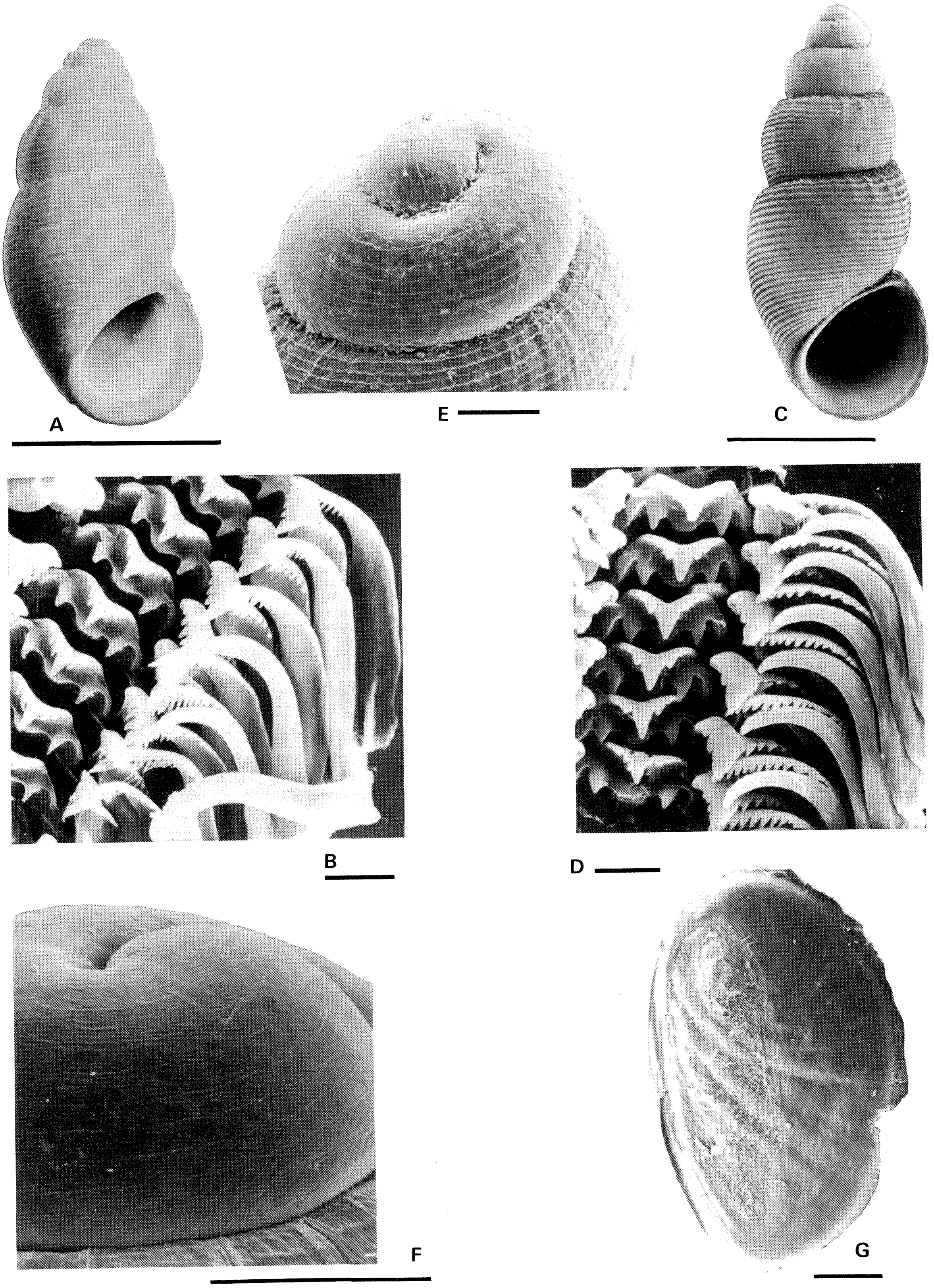

Fig. 109. A-B, *Onona (Onoba) 'semicostata* (Montagu)', type-species of *Onoba* H. & A. Adams: **A,** shell; **B,** radula (Castle Beach, Falmouth, Cornwall, England, BMNH, 303.18). **C-G,** *Onoba* (*Onoba*) *aculea* (Gould): **C,** shell; **D,** radula; **E-F,** protoconch; **G,** operculum (inner side) (C-E, Hjeltefjord, W. of Bergen, Norway, AMS, C.138156; F,G, Guernsey Is., England, BMNH, 1911.10.26.23704-23723). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

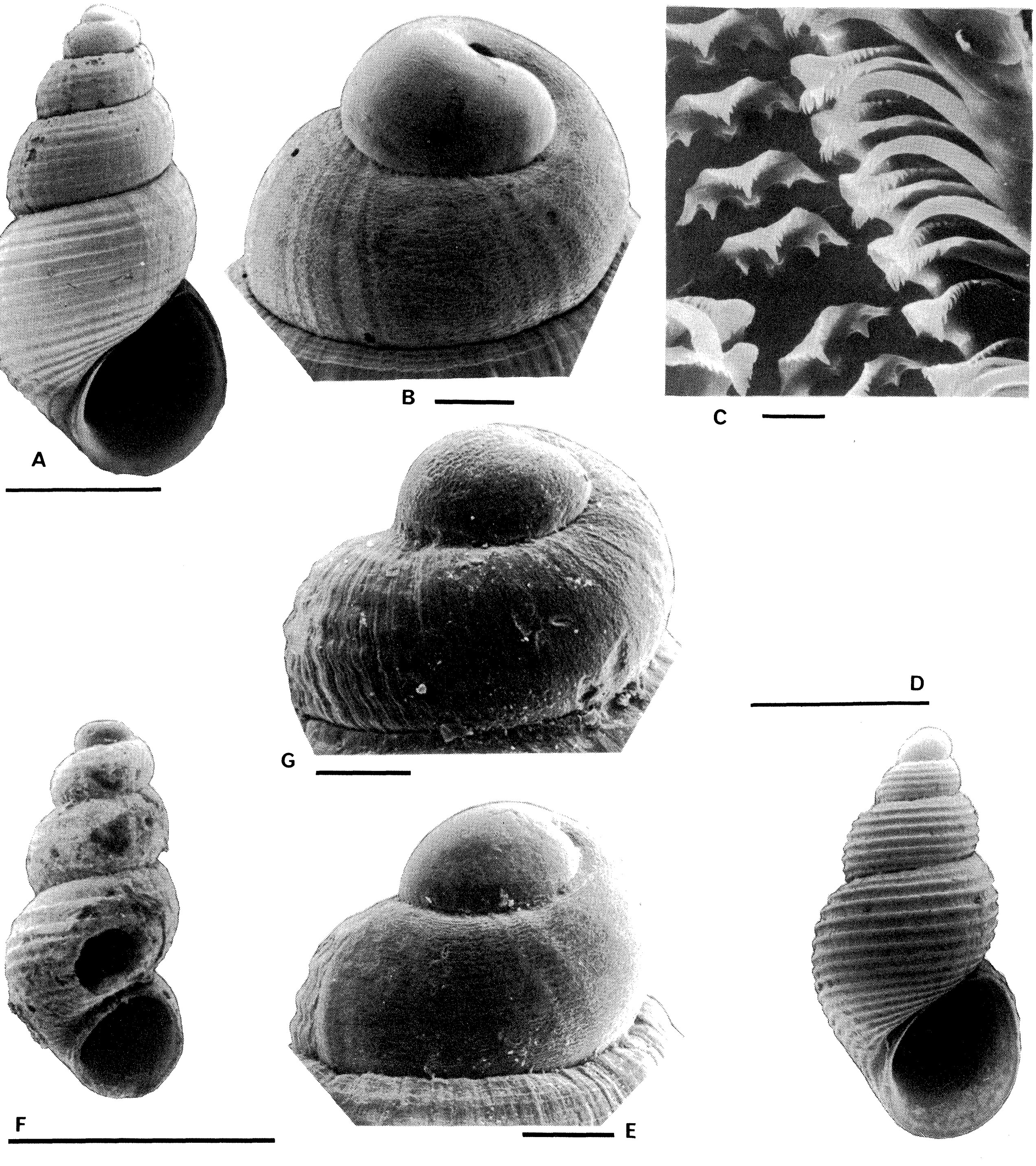

Fig. 110. **A-C**, *Onoba* (*Onoba*) *alaskana* (Dall): **A**, shell; **B**, protoconch; **C**, radula (W. end of Yukon Island, Kachemak Bay, Kenai Peninsula, Alaska, AMS, C.134896). **D-E**, *Onoba* (*Onoba*) *foveauxana* (Suter): **D**, shell; **E**, protoconch (Lyall Bay, Wellington, New Zealand, AMS, C.13572). **F-G**, *Onoba* (*Onoba*) sp.: **F**, shell; **G**, protoconch (Fresville, Manche, France, Eocene, AMS, C.134897). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radula - 0.01 mm.

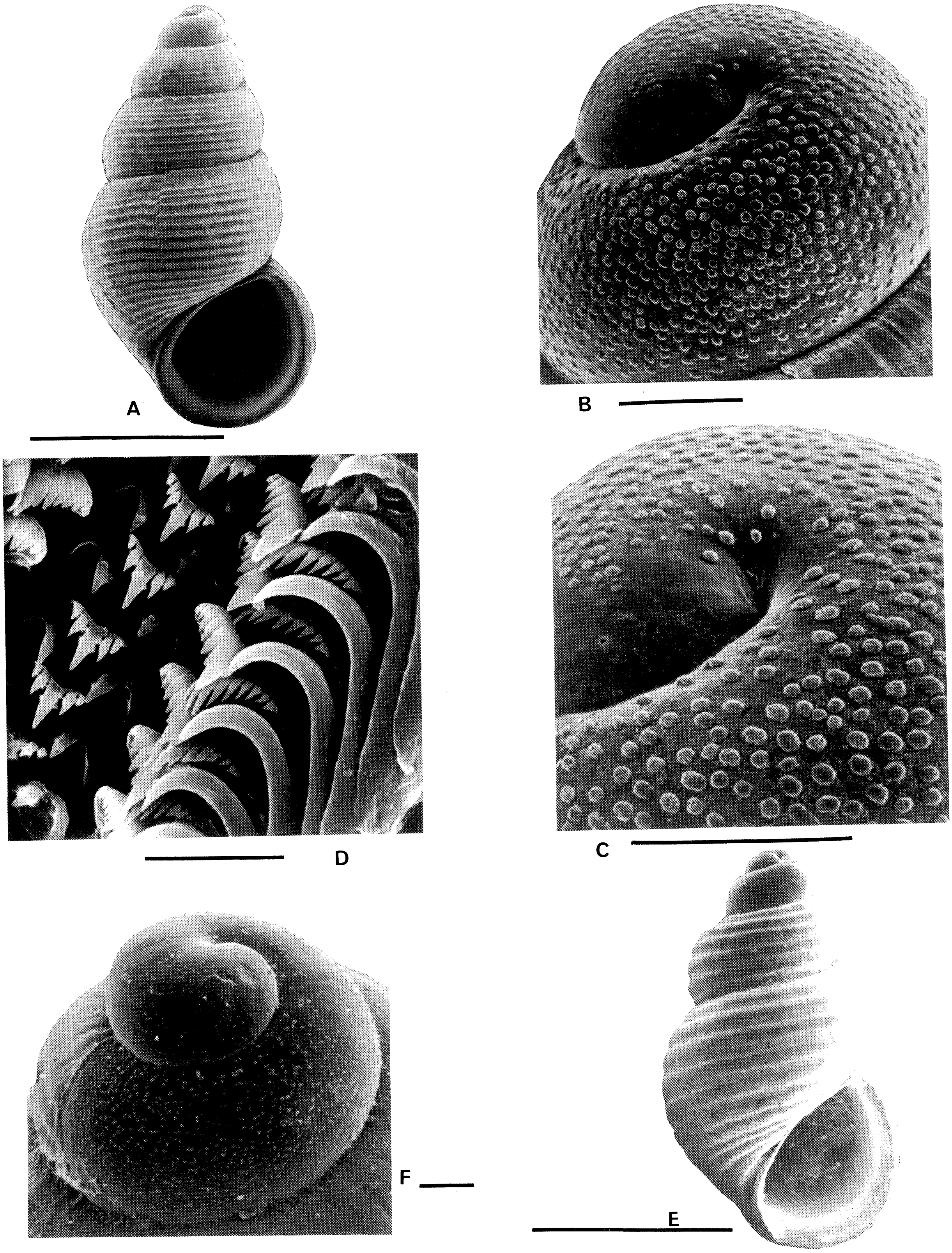

Fig. 111. **A-D**, *Onoba* (*Onoba*) *fumata* (Suter), type-species of *Subonoba* Iredale: **A**, shell; **B-C**, protoconch (**C**, detail of sculpture); **D**, radula (Lyall Bay, Wellington, New Zealand, AMS, C.134898). **E-F**, *Onoba* (*Onoba*) n.sp.: **E**, shell; **F**, protoconch (Thionville-sur-Opton, Yvelines, France, Eocene, AMS, C.138976). **Scale:** shells - 1 mm, protoconchs - 0.1 mm, radula - 0.01 mm.

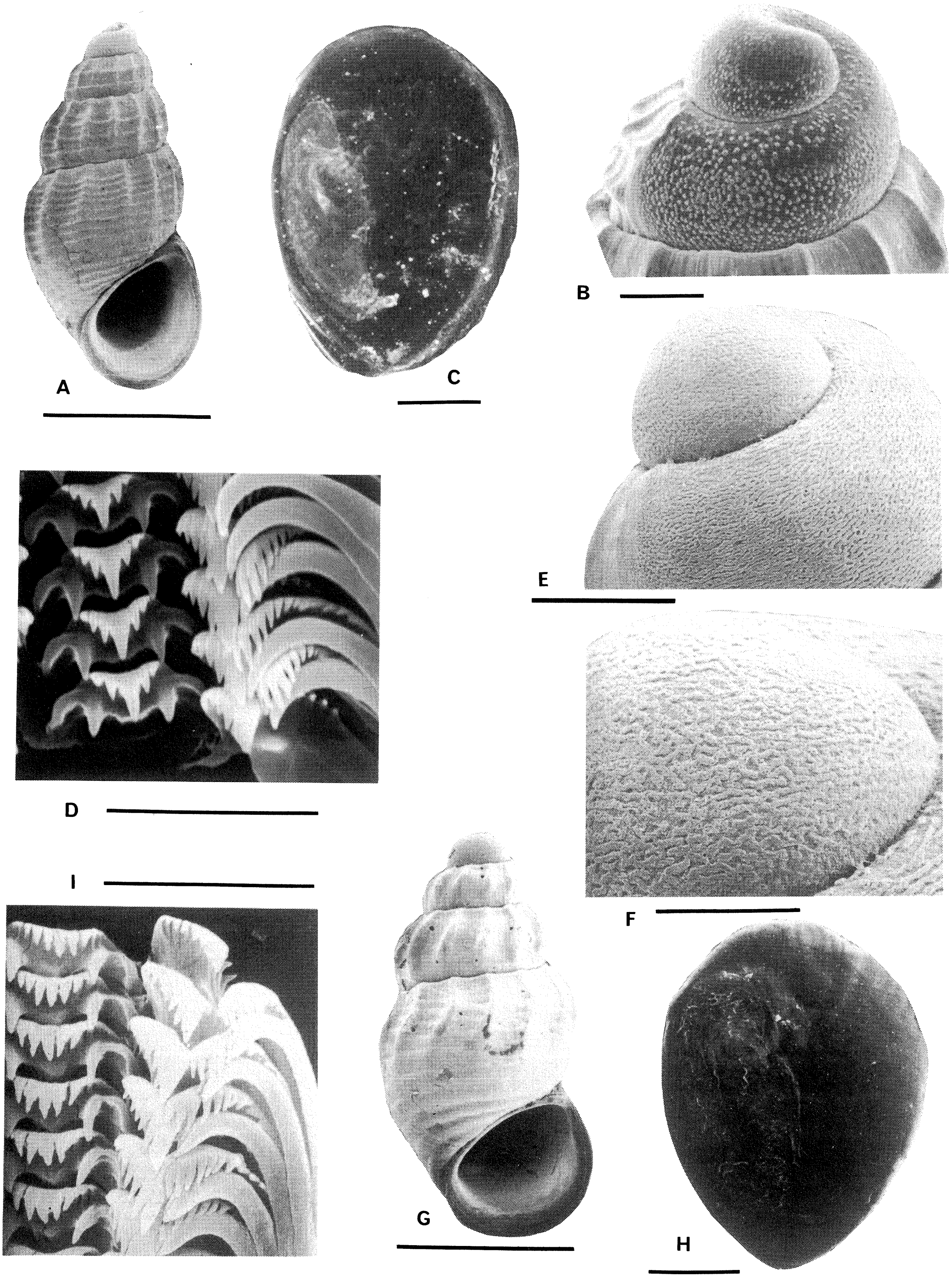

Fig. 112. **A-D**, *Onoba* (*Onoba*) *kermadecensis* (Powell): **A**, shell, **B**, protoconch; **C**, operculum (inner side); **D**, radula (Raoul Island, Kermadec Islands, AMS, C.36646). **E-I**, *Onoba* (*Onoba*) *candidissima* (Webster), type-species of *Austronoba* Powell: **E-F**, protoconch (**F**, detail of protoconch microsculpture); **G**, shell; **H**, operculum (inner side); **I**, radula (Leigh, New Zealand, AMS C.134899). **Scale:** shell A - 1 mm; shell G - 0.5 mm; protoconchs B, E and opercula - 0.1 mm; protoconch F and radulae - 0.01 mm.

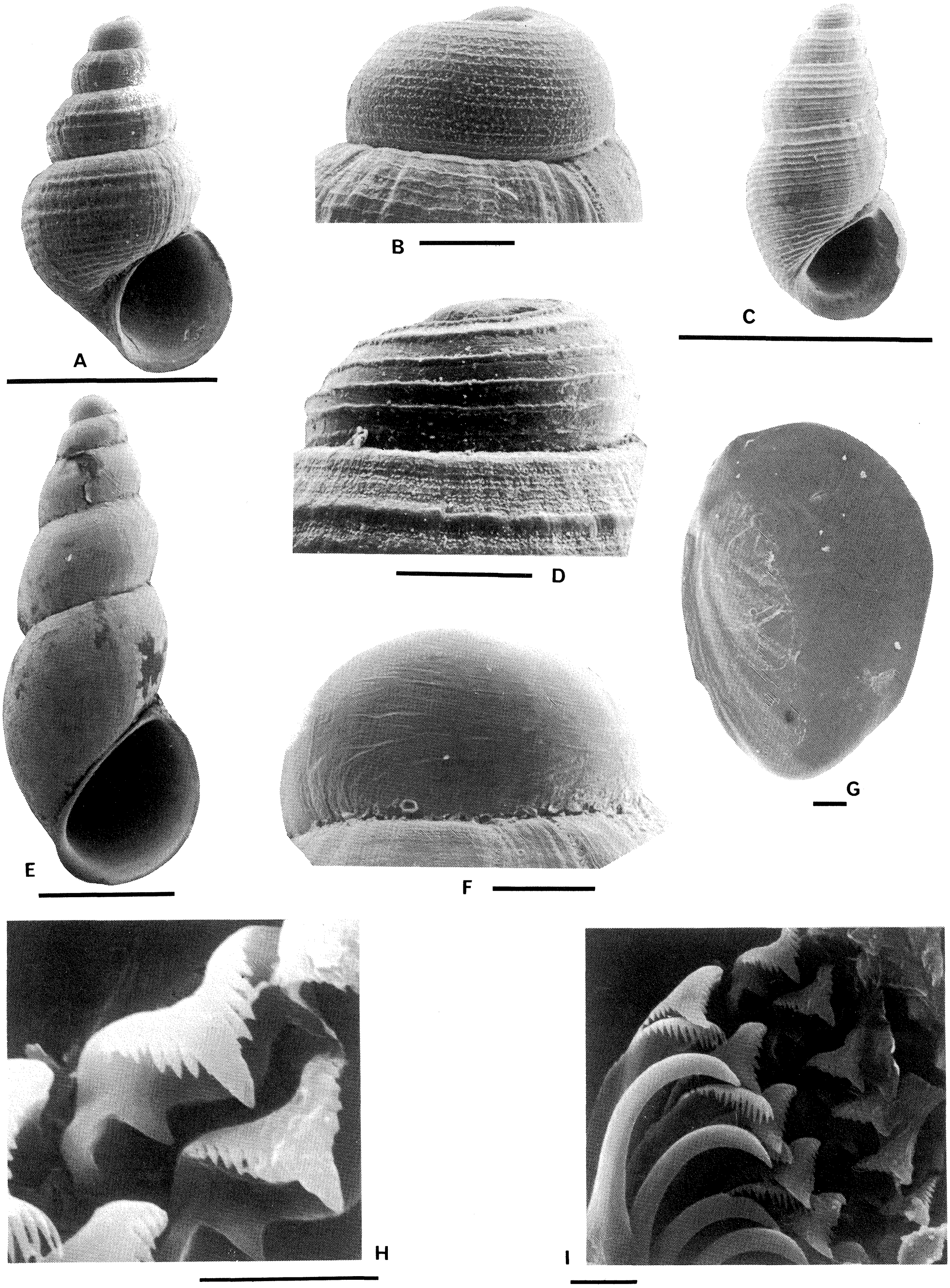

Fig. 113. A-B, *Onoba* (*Onoba*) *dinora* (Bartsch): **A**, shell; **B**, protoconch (Evans Island, Prince William Sound, Alaska, NMNZ, MF8258). **C-D**, *Onoba* (*Onoba*) *moreleti* Dautzenberg: **C**, shell; **D**, protoconch (paratype; Azores, IRSB). **E-I**, *Onoba* (*Onoba*) *cerinella* Dall: **E**, shell; **F**, protoconch; **G**, operculum (inner side); **H-I**, radula (**H**, detail of central teeth) (W. end of Yukon Island, Kachemak Bay, Kenai Peninsula, Alaska, AMS, C.138981). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

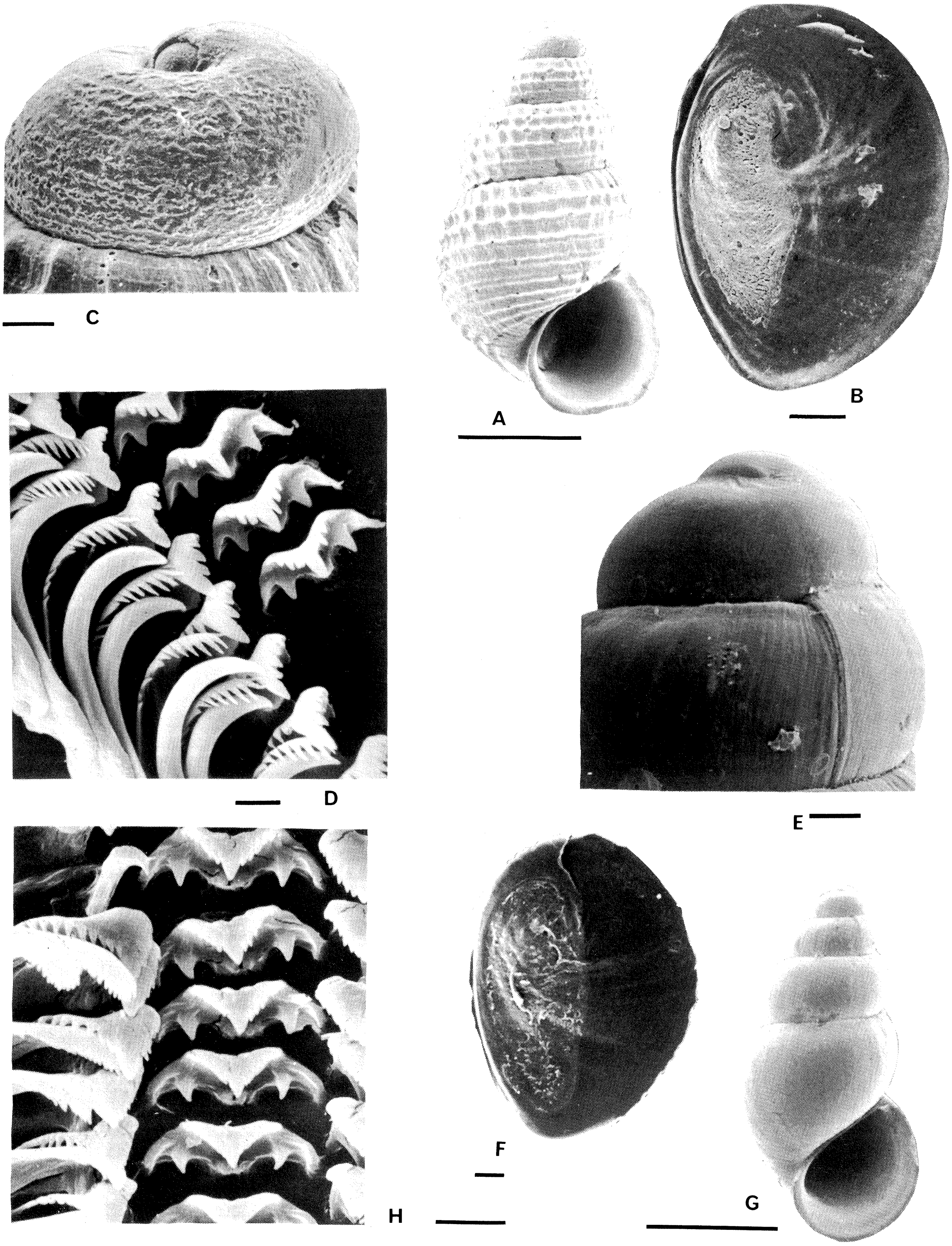

Fig. 114. A-D, *Onoba* (*Onoba*) *carpenteri* (Weinkauff), type-species of *Willettia* Gordon: **A**, shell; **B**, operculum (inner side); **C**, protoconch; **D**, radula (Franklin Point, San Mateo County, California, AMS, C.134908). **E-H**, *Onoba* (*Ovirissoa*) *kergueleni* (Smith): type-species of *Ovirissoa* Hedley: **E**, protoconch; **F**, operculum (inner side); **G**, shell; **H**, radula (46 m, Commonwealth Bay, Antarctica, AMS, C.46661). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

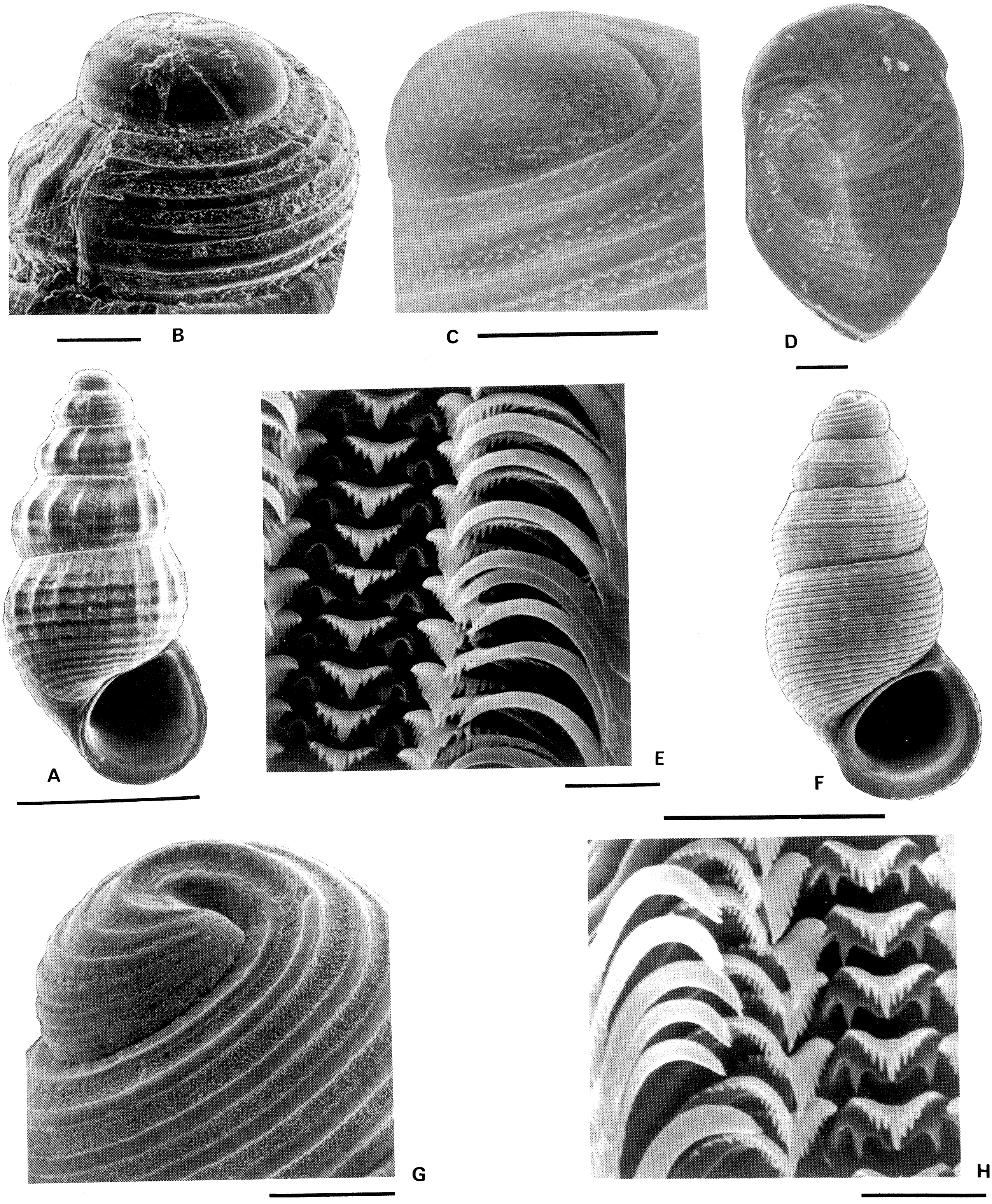

Fig. 115. **A-E**, *Onoba* (*Subestea*) *australiae* Frauenfeld, type-species of *Subestea* Cotton: **A**, shell; **B-C**, protoconch (**C**, detail of protoconch microsculpture); **D**, operculum (inner side); **E**, radula (A, 28 m, S. of Bicheno, Tasmania, AMS, C.138982; B, Honeymoon Beach, Jervis Bay, New South Wales, Australia, AMS, C.138983; D,E, Batehaven, Batemans Bay, New South Wales, AMS, C.138985). **F-H**, *Onoba* (*Subestea*) *alfredensis* (Bartsch): **F**, shell; **G**, protoconch; **H**, radula (Millers Point, False Bay, South Africa, AMS, C.134910). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

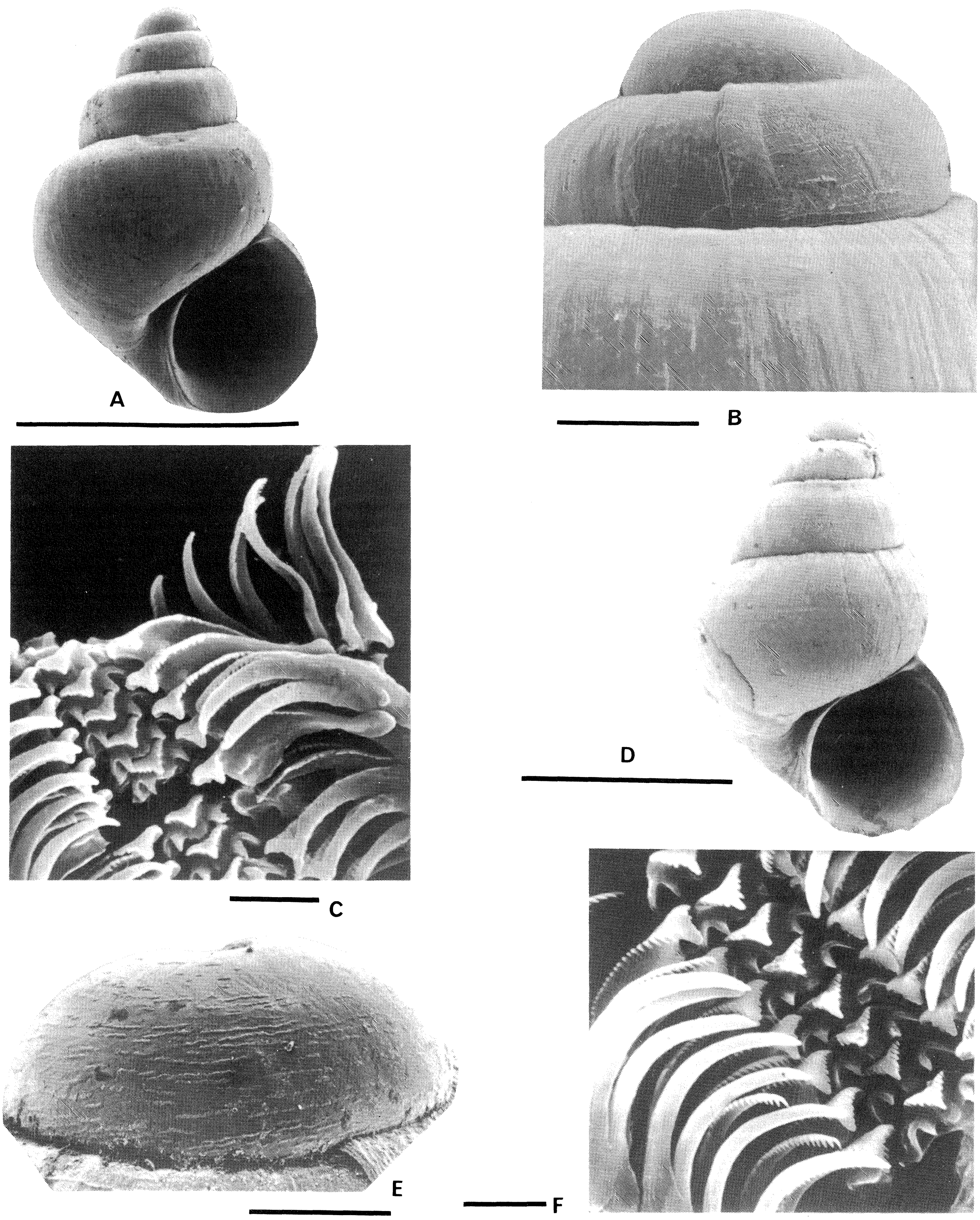

Fig. 116. **A-C**, *Powellisetia porcellana* (Suter), type-species of *Powellisetia* Ponder: **A**, shell; **B**, protoconch; **C**, radula (46-55 m, Port Adventure, Stewart Island, New Zealand, NMNZ, M42431). **D-F**, *Powellisetia subtenuis* (Powell): **D**, shell; **E**, protoconch; **F**, radula (37-44 m, Port Adventure, Stewart Island, New Zealand, AMS, C.138157). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

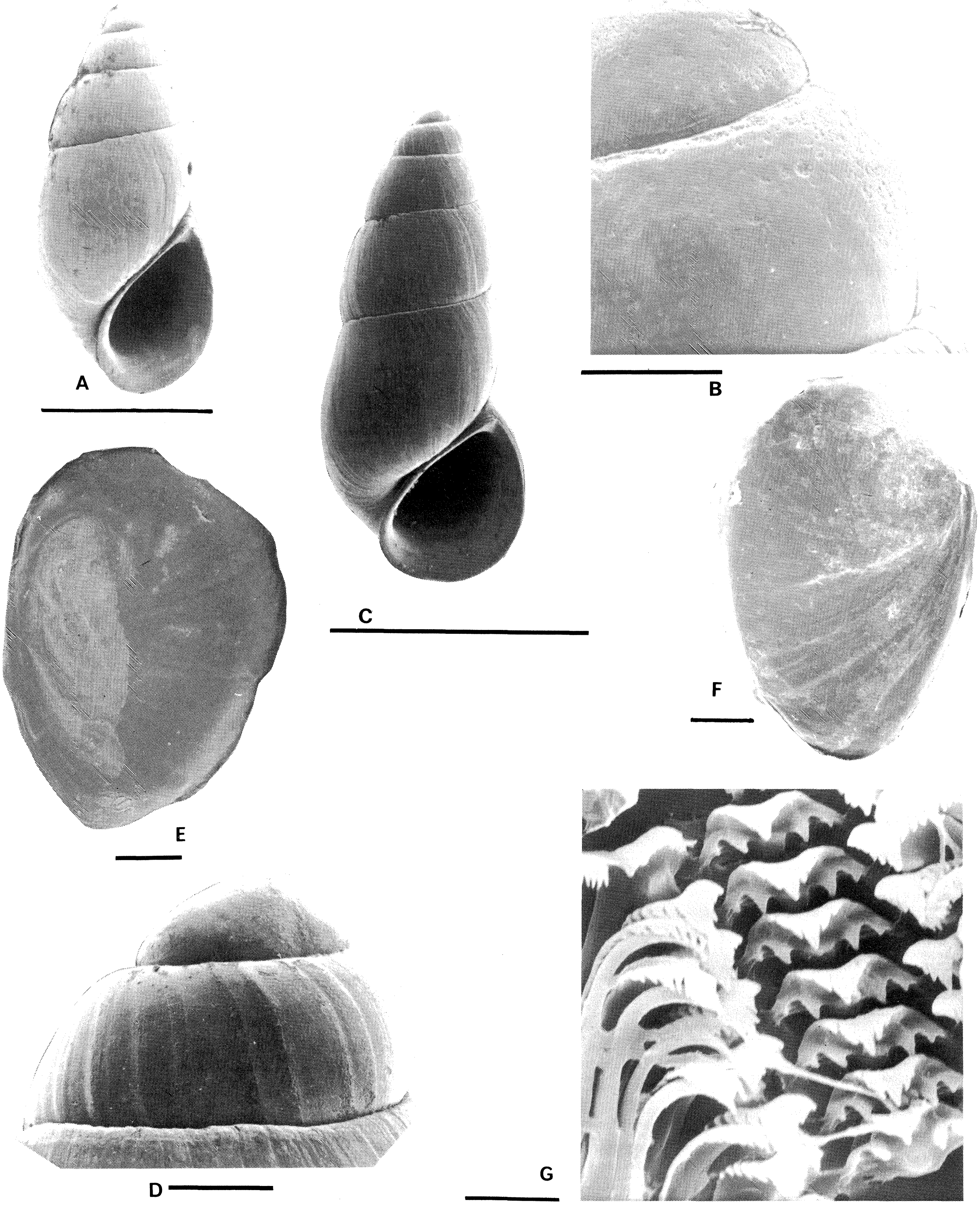

Fig. 117. **A-B**, *Peringiella denticulata nom. nov.*, type-species of *Peringiella* Monterosato; **A**, shell; **B**, protoconch (Algiers, NMW, Acc. no. 55,158). **C-G**, *Peringiella nitida* (Bucquoy, Dautzenberg & Dollfus): **C**, shell; **D**, protoconch; **E-F**, operculum (**E**, inner and **F**, outer sides); **G**, radula (Ragusa, Sicily, Italy, ex Brusina, HUM). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radula - 0.01 mm.

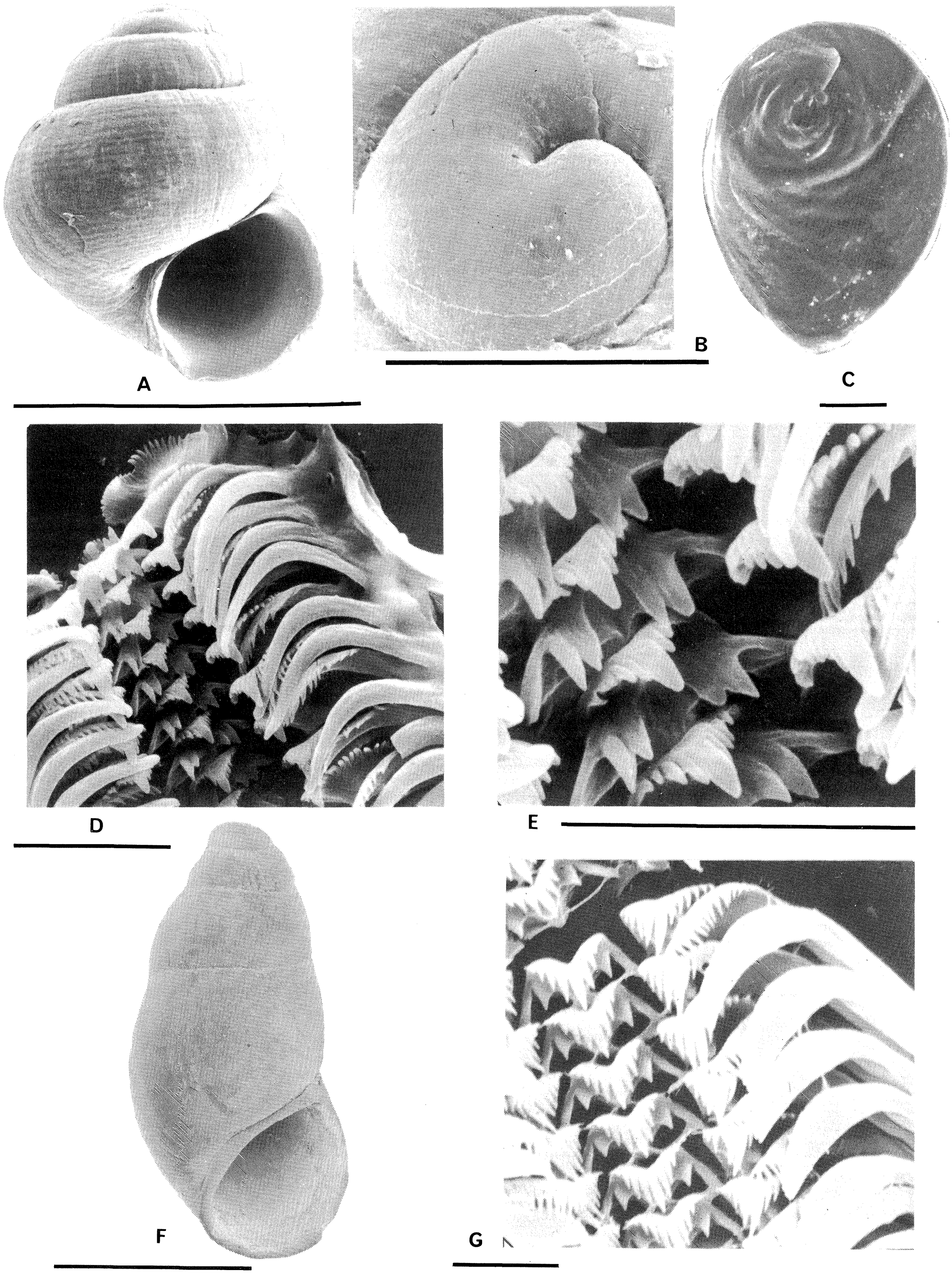

Fig. 118. **A-E**, *Obtusella intersecta* (Wood) type-species of *Obtusella* Cossmann: **A**, shell; **B**, first whorl of protoconch; **C**, operculum (inner side); **D-E**, radula (**E** detail of central teeth) (A, B, Devonshire, England, NMV; C-E, Isle of Man, England, BMNH, 1911.10.26.23323-23342). **F-G**, *Peringiella balteata* (Manzoni): **F**, shell; **G**, radula (Madeira, BMNH, 1911.10.26.24171-24190). **Scale:** shells – 1 mm; protoconch and operculum – 0.1 mm; radulae – 0.01 mm.

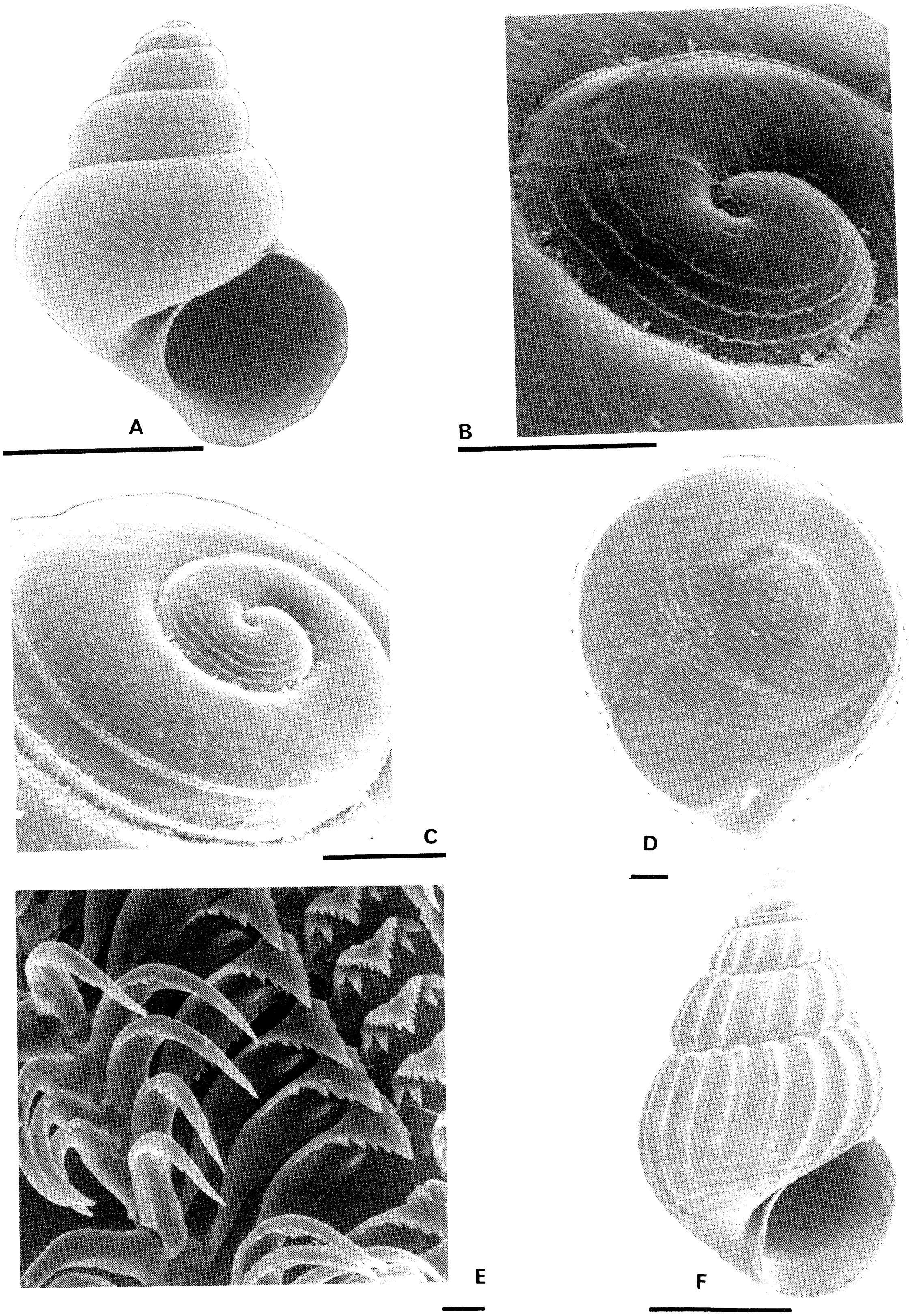

Fig. 119. A-E, *Benthonella tenella* (Jeffreys), type-species of *Hela* Jeffreys; **A**, shell; **B-C**, protoconch (**B**, detail of first whorl); **D**, operculum (inner side); **E**, radula (A, D, E, 4000 m, Bay of Biscay, AMS; B,C, 1950 m, Bay of Biscay, 44°05’N,04°19’W, NHMP). **F**, *Benthonella* sp.; shell (402-366 m, Raoul Island, Kermadec Islands, NMNZ, MF25554). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

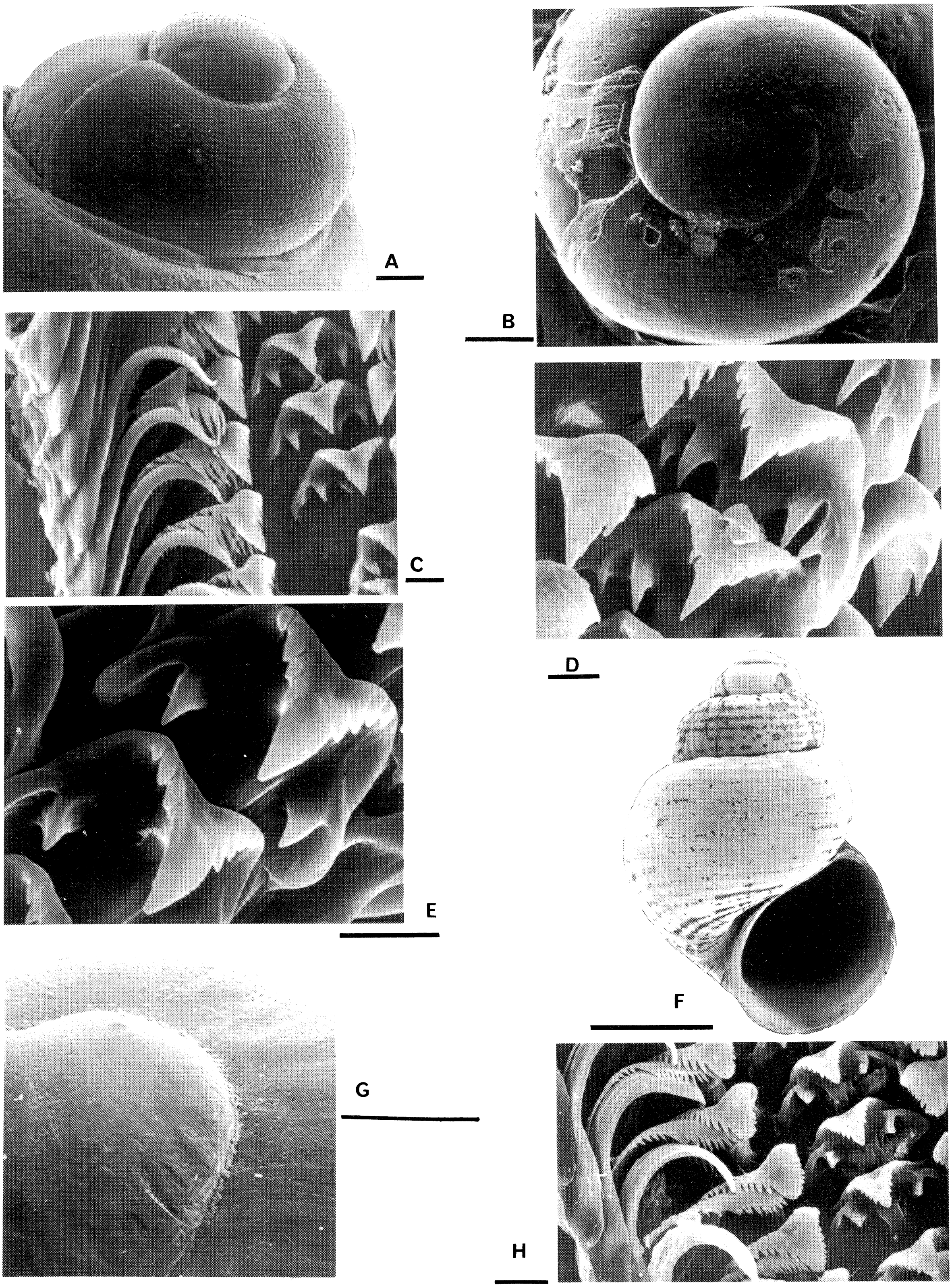

Fig. 120. **A-E**, *Boreocingula martyni* (Dall), type-species of *Boreocingula* Golikov & Kussakin: **A-B**, protoconch; **C-E**, radula (**D-E**, detail of central teeth) (A, C, 27 m, Paramushir Island, Kuril Islands, USSR, AMS, C.134901; B, D, E, Kasitsna Bay, Kenai Peninsula, Alaska, AMS, C.138984). **F-H**, *Boreocingula castanea* (Möller): **F**, shell; **G**, protoconch microsculpture; **H**, radula (10 m, Hinlopen Strait, Spitsbergen, Arctic Ocean, AMS, C.134902). **Scale:** shell - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

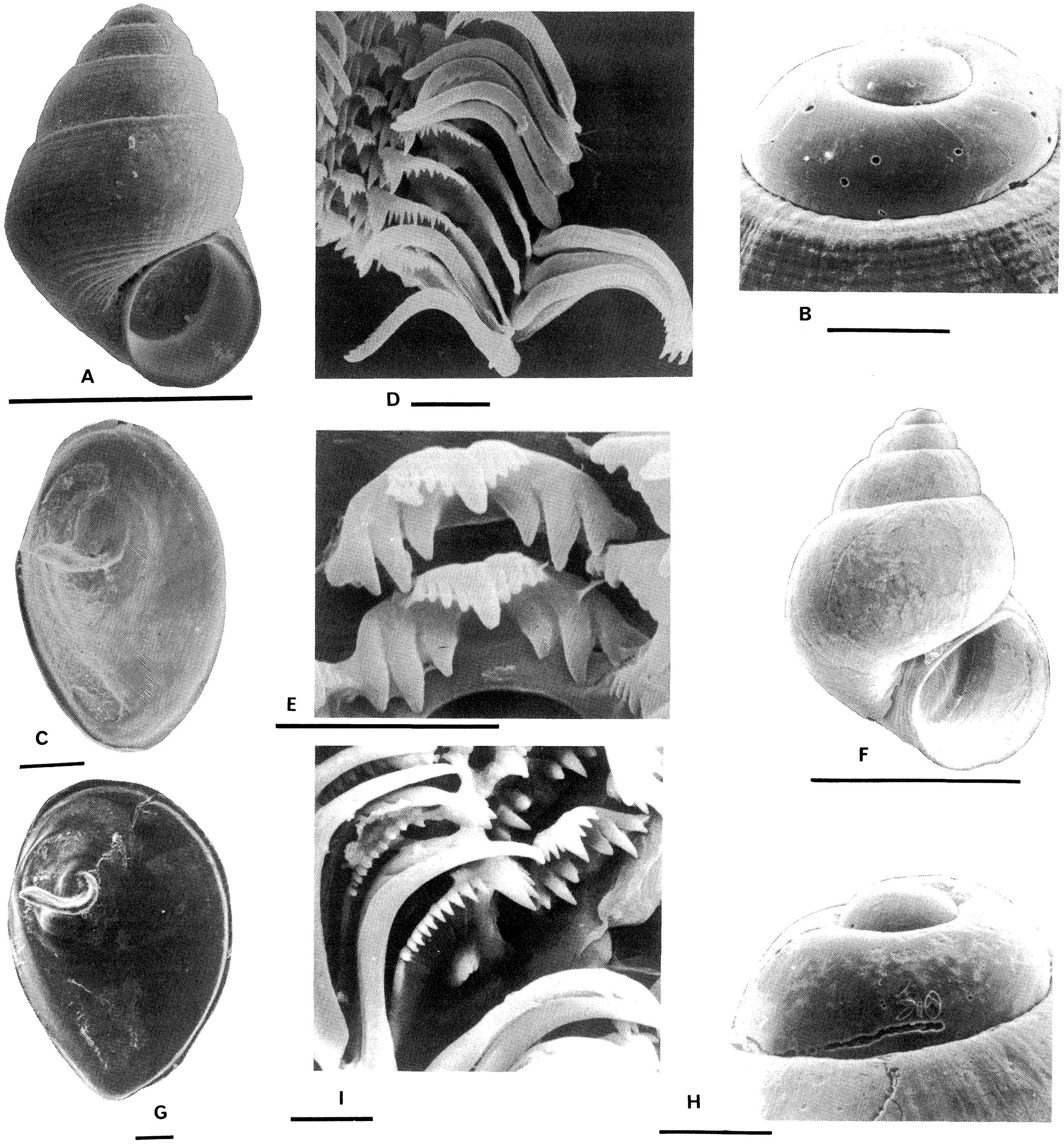

Fig. 121. **A-E**, *Lucidestea vitrea* Laseron, type-species of *Lucidestea* Laseron: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D-E**, radula (**E**, detail of central teeth) (Lizard Island, Queensland, AMS, C.134903). **F-I**, *Lucidestea ornata* (Golikov & Kussakin), type-species of *Falsisetia* Golikov & Kussakin: **F**, shell; **G**, operculum (inner side); **H**, protoconch; **I**, radula (Pos'yet Bay, Sea of Japan, USSR, ex Golikov, AMS, C.134904). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

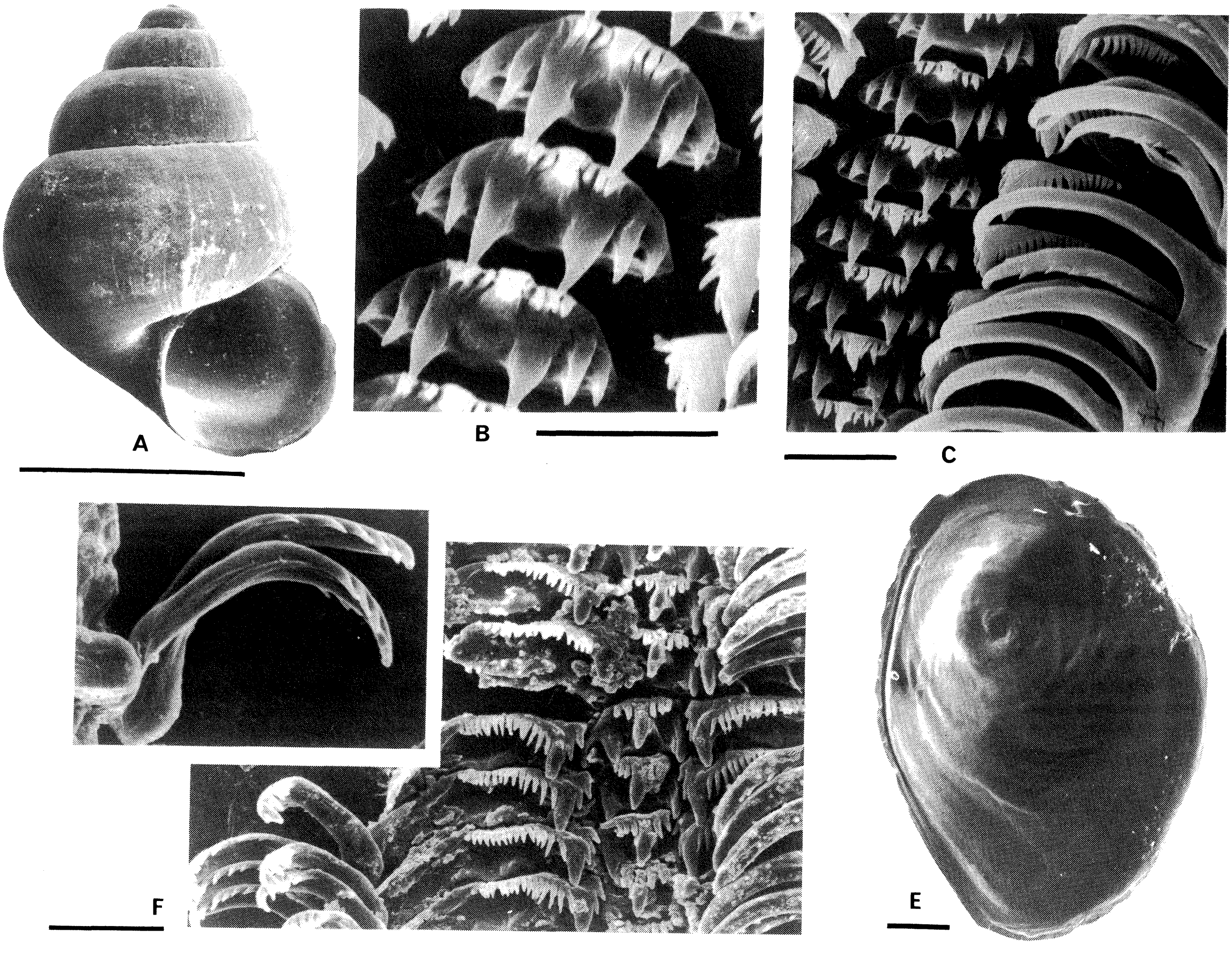

Fig. 122. **A-E**, *Voorwindia umbilicata* n.sp., type-species of *Voorwindia* n.gen.: **A**, shell; **B-D**, radula (**B**, detail of central teeth; **D**, detail of outer marginal teeth); **E**, operculum (inner side) (A, holotype, B-E, paratypes, Middle Harbour, New South Wales, Australia, AMS, C.134536, C.134537). **F**, *Voorwindia sublacuna* (Laseron); radula (topotype, 32-36 m, Masthead Island, Capricorn Group, Queensland, Australia, AMS, C.19542). **Scale:** shell - 1 mm; operculum - 0.1 mm; radulae - 0.01 mm.

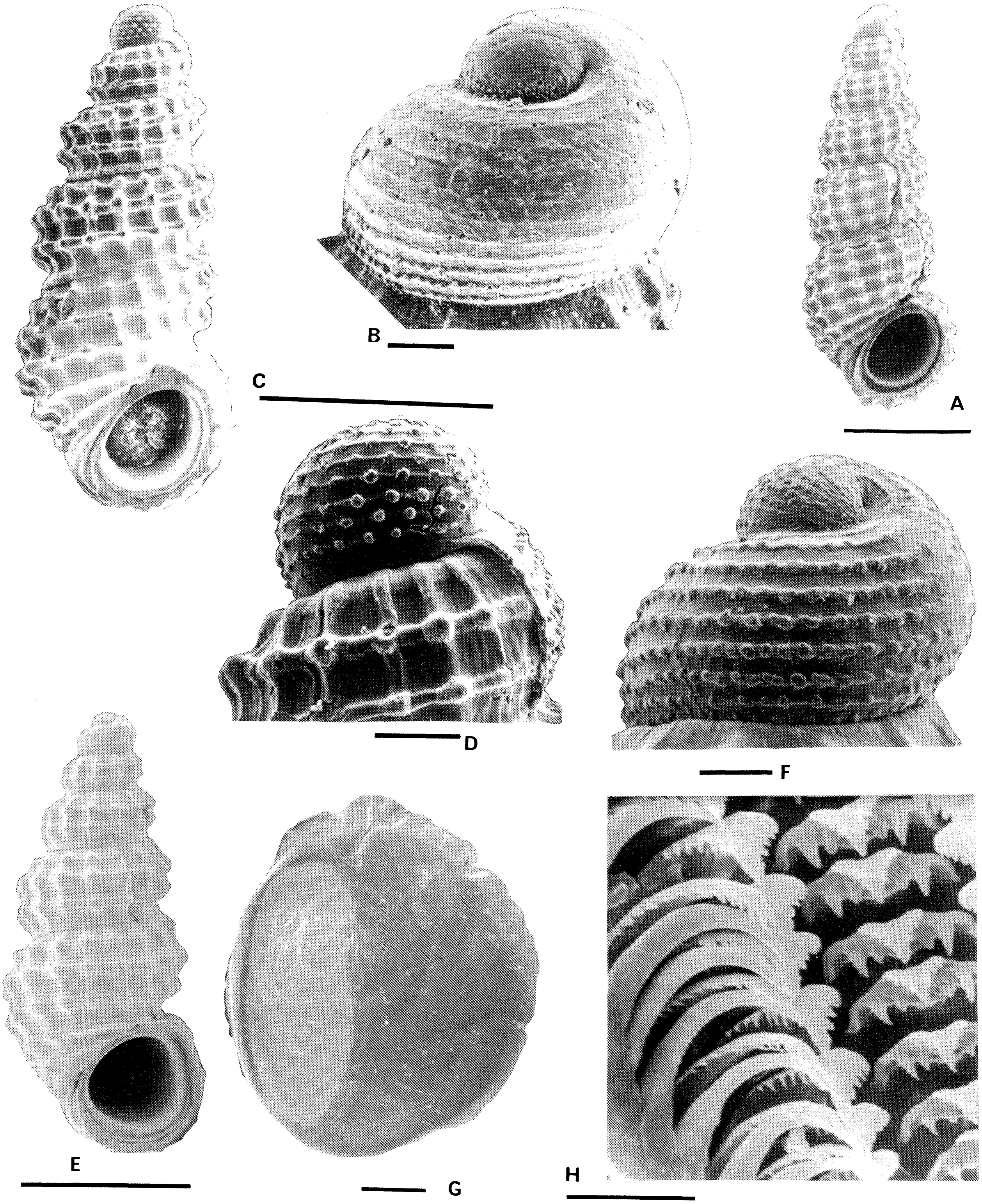

Fig. 123. **A-B**, *Merelina cheilostoma* (T. Woods), type-species of *Merelina* Iredale: **A**, shell; **B**, protoconch (88 m, S. of West Point, N.W.Tasmania, AMS, C.134906). **C-D**, *Merelina queenslandica* (Laseron), type-species of *Mereliniopsis* Ponder: **C**, shell; **D**, protoconch (Michaelmas Cay, near Cairns, Queensland, Australia, AMS, C.134905). **E-H**, *Merelina elegans* (Angas): **E**, shell, **F**, protoconch; **G**, operculum; **H**, radula (E, F, Little Coogee Bay, Sydney, New South Wales, Australia, AMS, C.138158; G, H, Balmoral, Sydney, AMS, C.138987). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 m; radula - 0.01 mm.

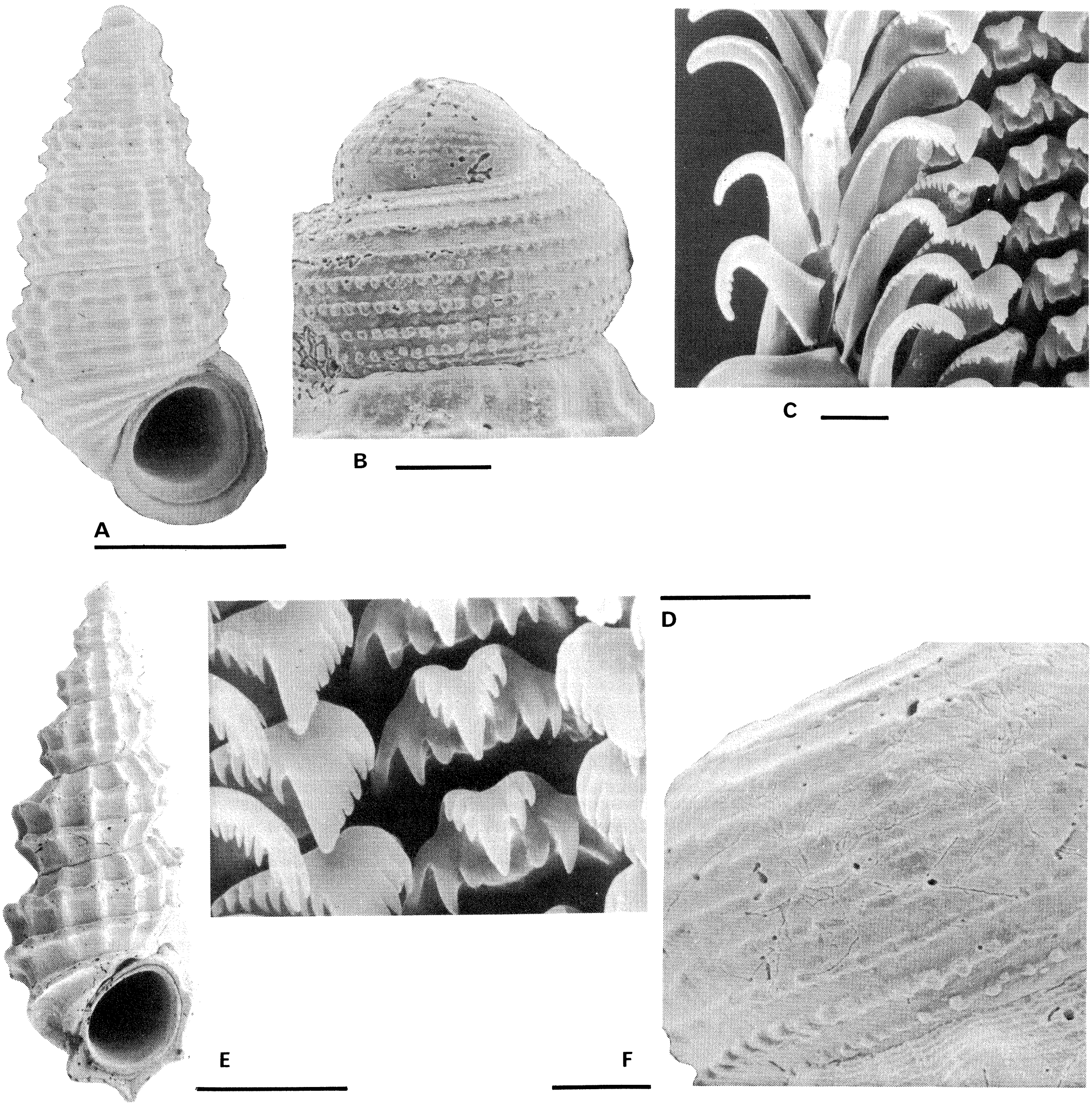

Fig. 124. **A-D**, *Merelina gracilis* (Angas): **A**, shell; **B**, protoconch; **C-D**, radula (**D**, detail of central teeth) (A, B, Bottle and Glass Rocks, Sydney, New South Wales, Australia, AMS, C.134907; C, D, Batehaven, Bateman's Bay, New South Wales, AMS, C.138988). **E-F**, *Merelina crosseaformis* (Powell), type-species of *Promerelina* Powell: **E**, shell; **F**, protoconch microsculpture (20 m, main channel,, Whangaroa Harbour, New Zealand, NMNZ, M.41142). **Scale:** shells - 1 mm; protoconchs - 0.1 mm; radulae - 0.01 mm.

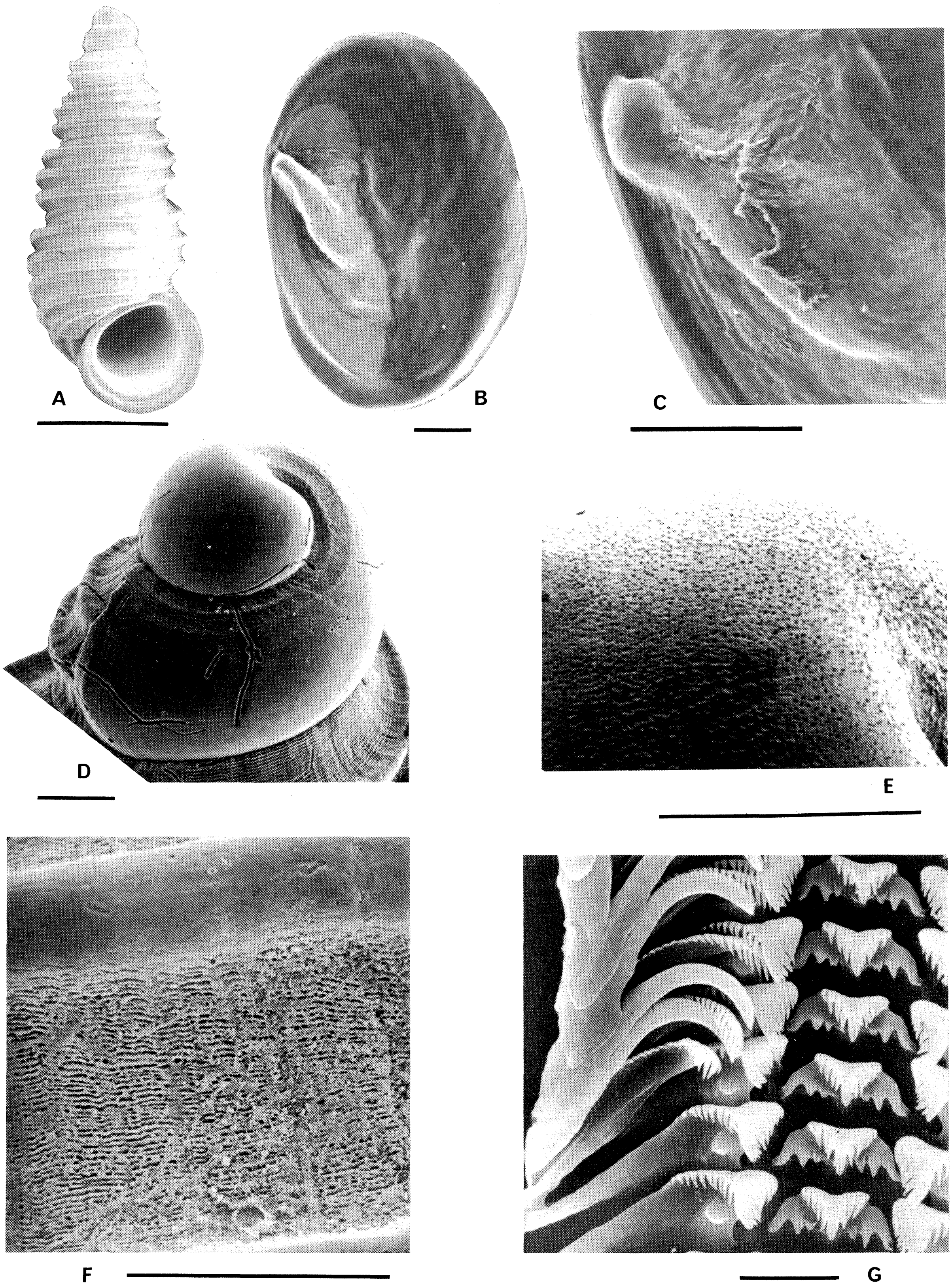

Fig. 125. **A-G**, *Lironoba australis* (T. Woods): **A**, shell; **B-C**, operculum (**B**, inner side; **C**, detail of rudimentary peg); **D-E**, protoconch (**E**, microsculpture); **F**, teleoconch microsculpture; **G**, radula (Pirates Bay, Eaglehawk Neck, Tasmania, AMS, C.138974, C.138975). **Scale:** shell - 1 mm; protoconchs, opercula and microsculpture - 0.1 mm; radula - 0.01 mm.

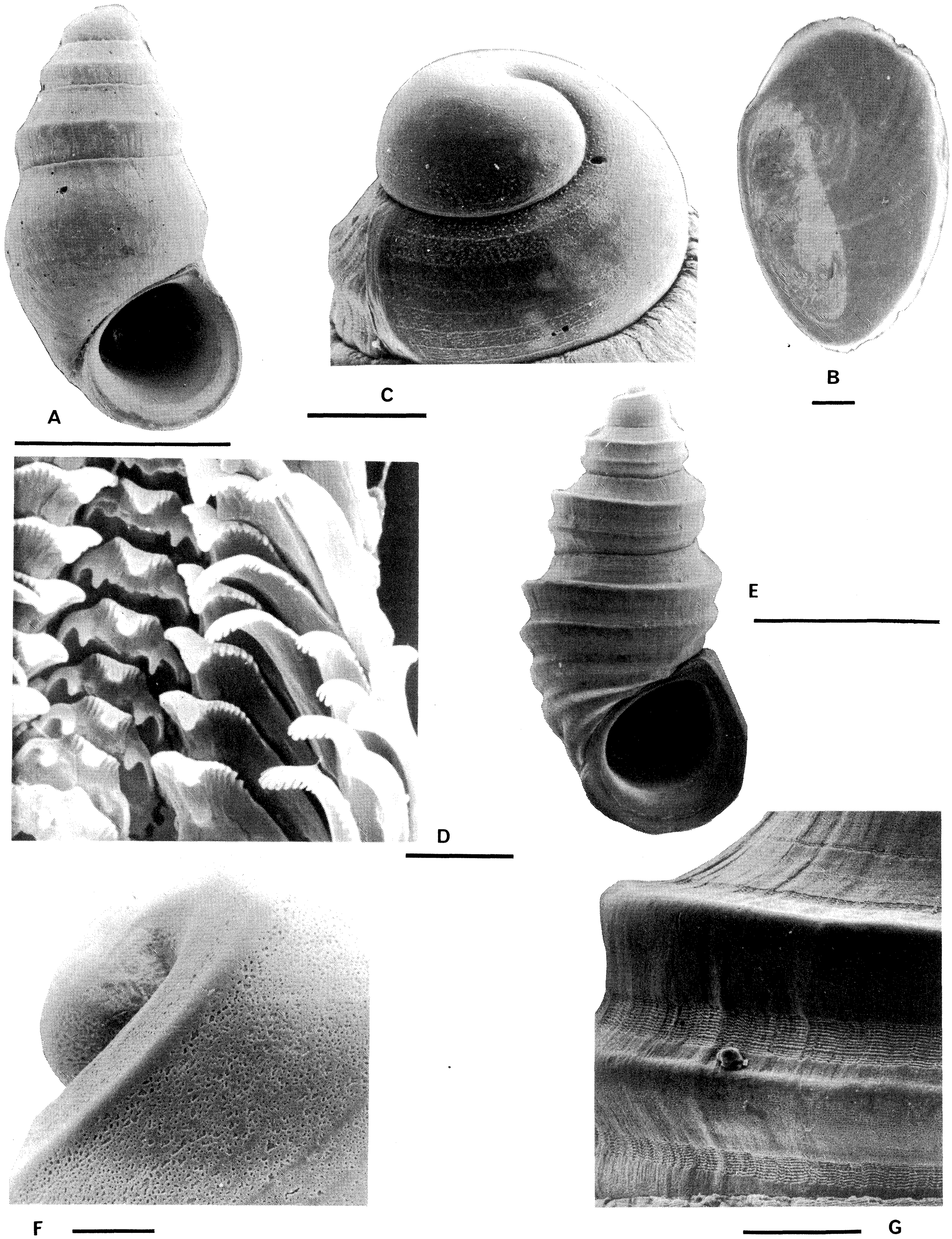

Fig. 126. **A-D**, *Lironoba unilirata* (T. Woods): **A**, shell; **B**, operculum (inner side); **C**, protoconch; **D**, radula (Pirates Bay, Eaglehawk Neck, Tasmania, AMS C.138973). **E-G**, *Lironoba suteri* (Hedley), type-species of *Lironoba* Iredale: **E**, shell; **F**, protoconch; **G**, teleoconch microsculpture (Off Poutama Island, Stewart Island, New Zealand, AMS, C.134911). **Scale:** shells - 1 mm; protoconchs, operculum and microsculpture - 0.1 mm; radula - 0.01 mm.

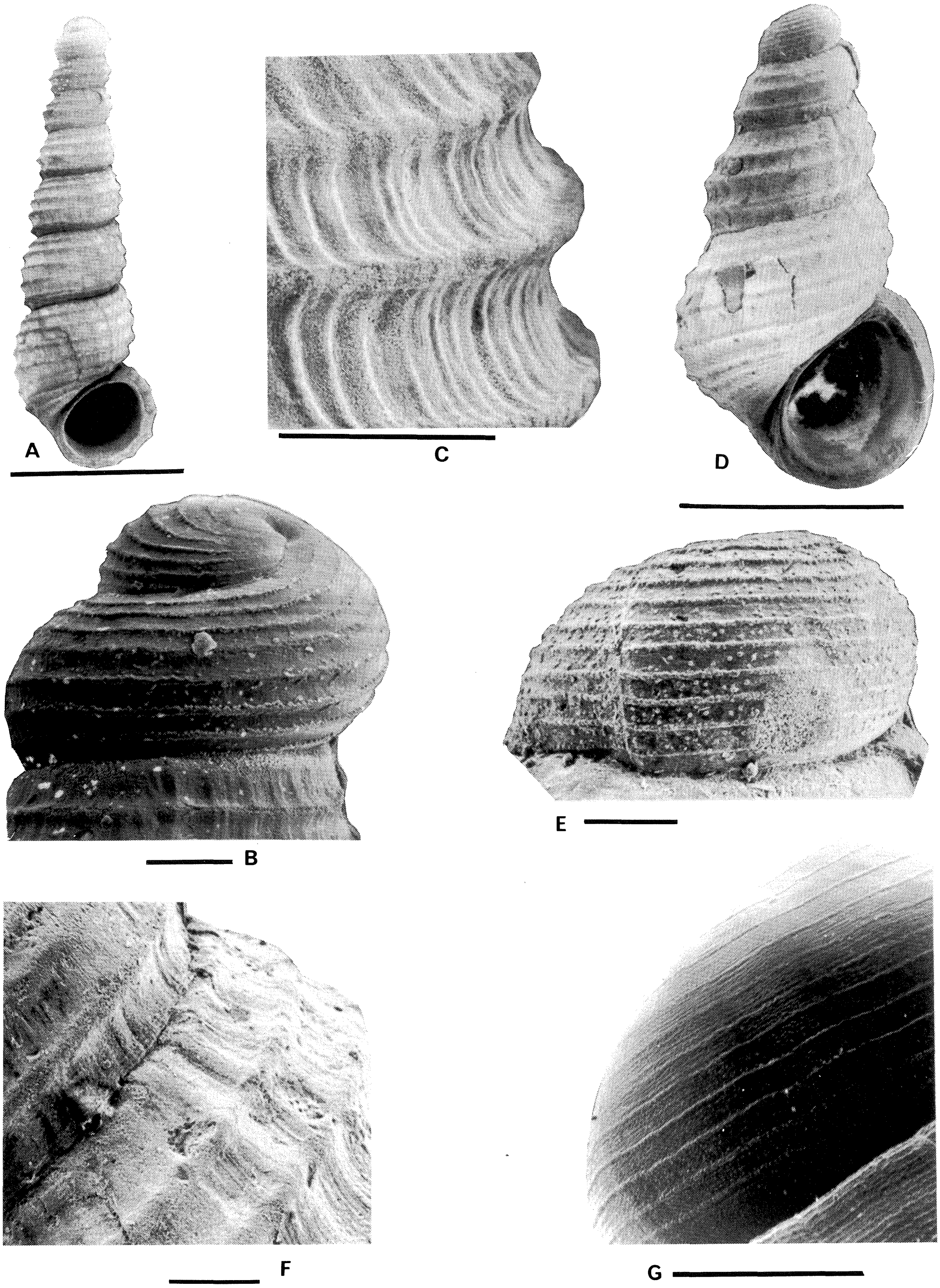

Fig. 127. **A-C**, *Attenuata integella* (Hedley), type-species of *Attenuata* Hedley: **A**, shell; **B**, protoconch; **C**, teleoconch microsculpture (146 m, 35 km E. of Narrabeen, Sydney, New South Wales, Australia, AMS, C.25915). **D-F**, *Attenuata polyvincta* (Finlay), type-species of *Nobolira* Finlay: **D**, shell; **E**, protoconch; **F**, teleoconch microsculpture (topotype, Pukeuri, N. Otago, New Zealand, Miocene, NMNZ, M27369). **G**, *Attenuata archensis* (May); protoconch microsculpture (150 m, E. of Sydney, New South Wales, Australia, AMS, C.135035). **Scale:** shells – 1 mm; protoconchs and microsculpture – 0.1 mm.

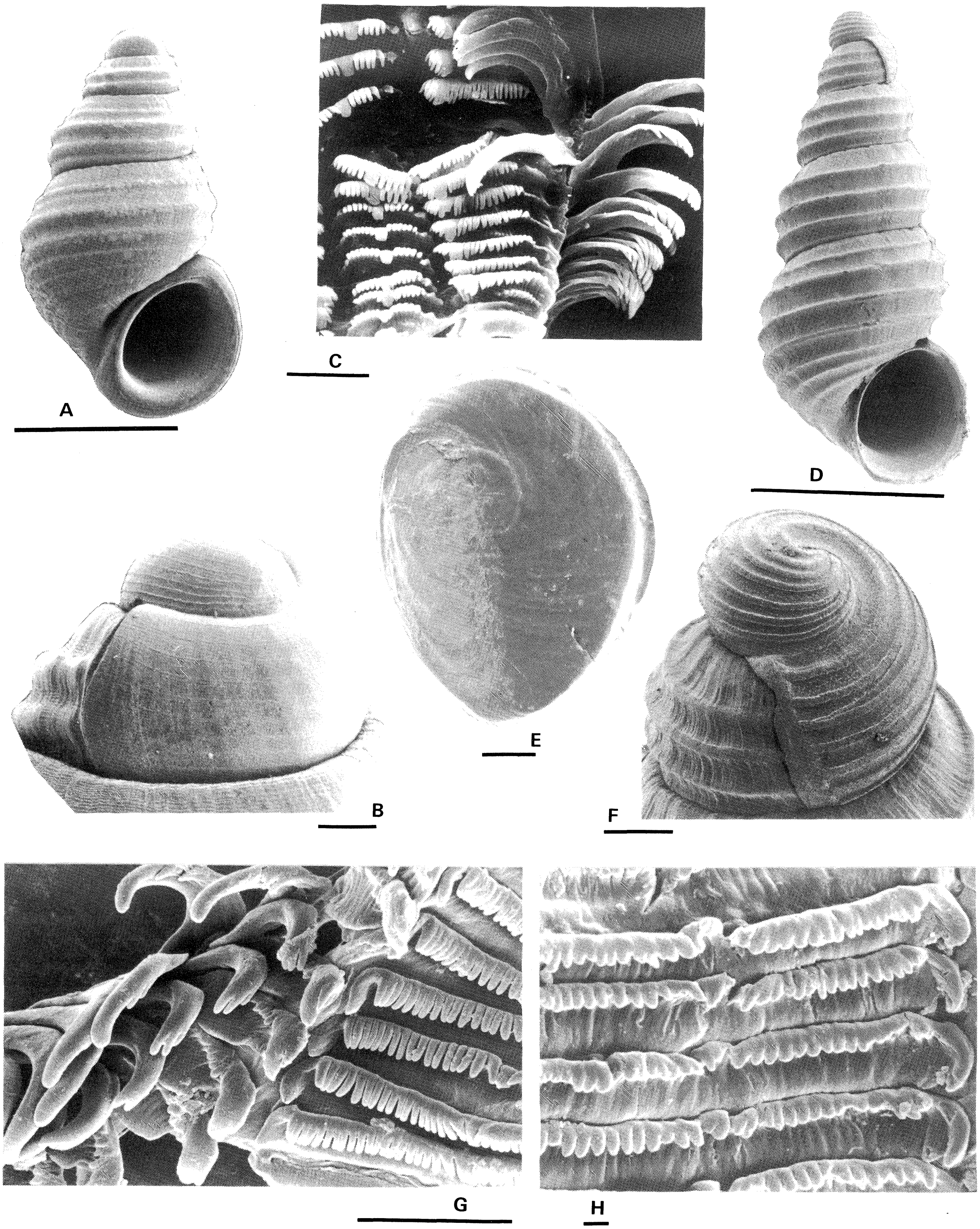

Fig. 128. **A-C**, *Attenuata archensis* (May): **A**, shell; **B**, protoconch; **C**, radula (A, off Arch Island, Tasmania, paratype, AMS, C.34115; B, C, 150 m, E. of Sydney, New South Wales, Australia, AMS, C.135035). **D-H**, *Attenuata finlayi* (Powell), type-species of *Adolphinoba* Powell: **D**, shell; **E**, operculum (inner side); **F**, protoconch; **G-H**, radula (**G**, lateral, marginal and part of central teeth; **H**, detail of central teeth) (59-74 m, E. of Major Island, New Zealand, NMNZ, M66444). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

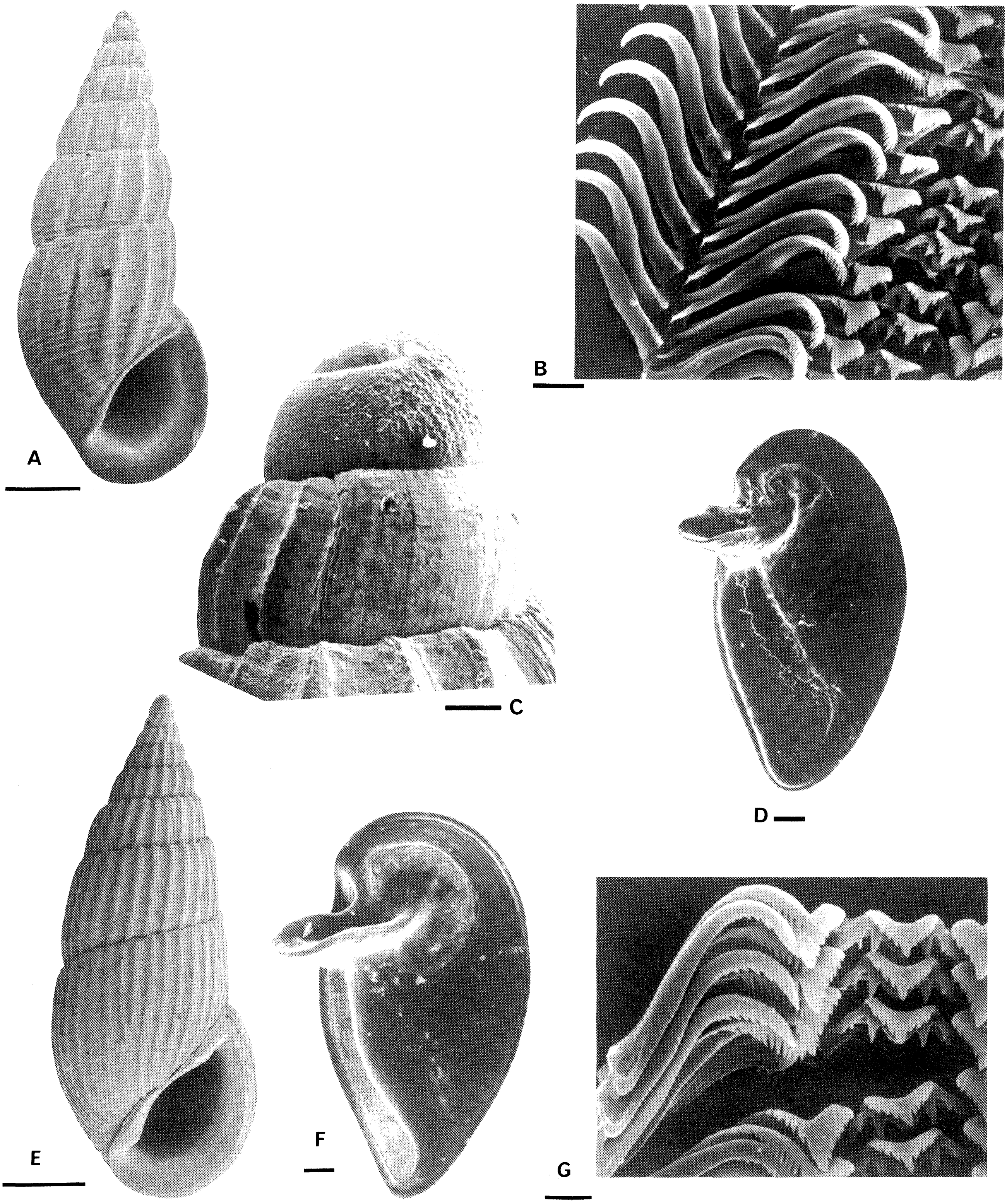

Fig. 129. **A-D**, *Rissoina* (*Rissoina*) *inca* Orbigny, type-species of *Rissoina* Orbigny: **A**, shell; **B**, radula; **C**, protoconch; **D**, operculum (inner side) (6–17 m, S. side of Bahia Herradura, S. of Coquimbo, Coquimbo Prov., Chile, AMS, C.135040). **E-G**, *Rissoina* (*Rissoina*) *ambigua* (Gould), type-species of *Peripetella* Laseron: **E**, shell; **F**, operculum (inner side); **G**, radula (E, syntype of *R. pulchella* Brazier, Barnard Island, NE. Australia, AMS, A145; F, G, Point Quobba, Western Australia, AMS, C.139686). **Scale:** shells – 1 mm; protoconch and opercula – 0.1 mm; radulae – 0.01 mm.

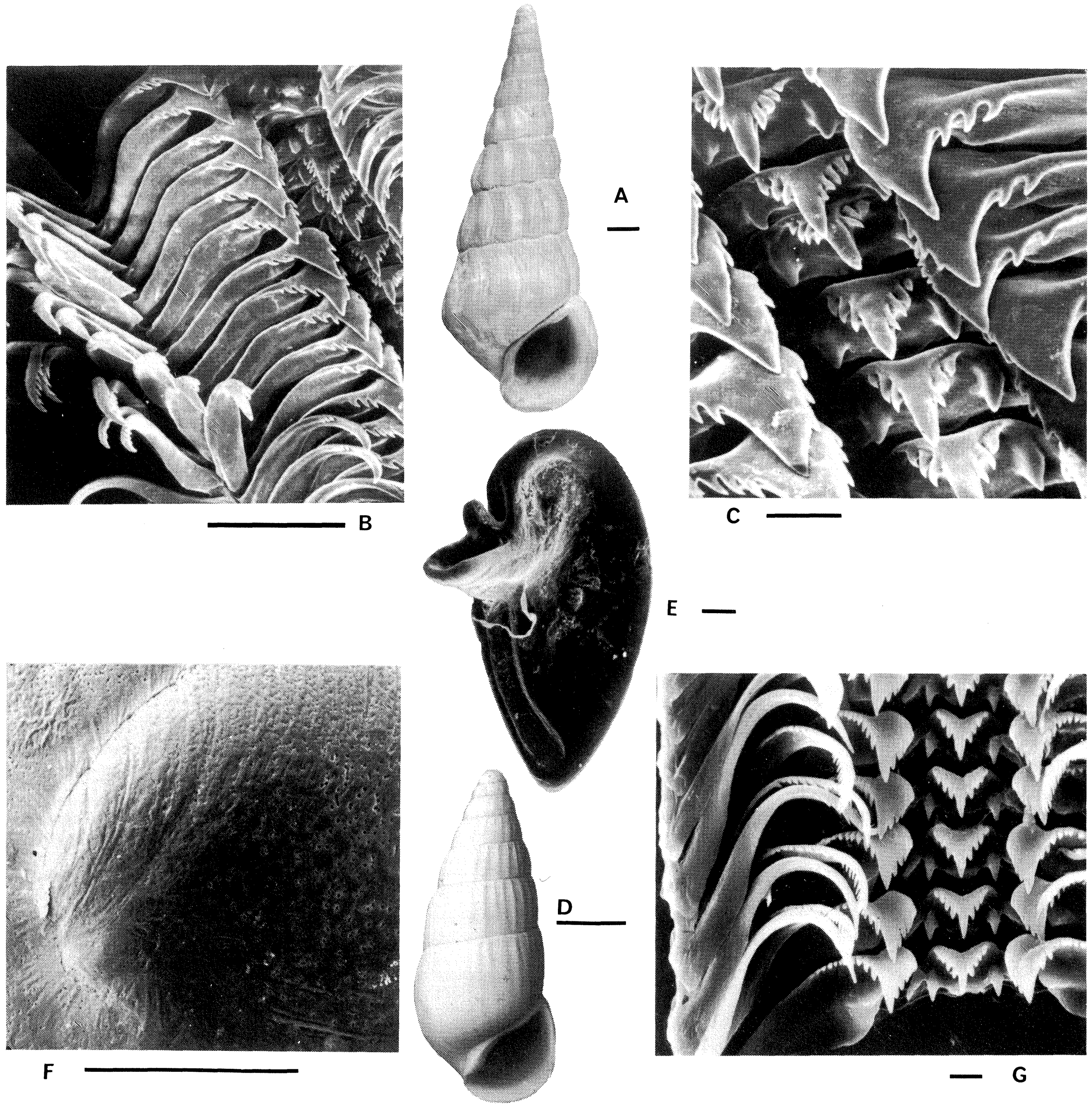

Fig. 130. **A-C**, *Rissoina* (*Rissoina*) *ferruginea* (Hedley), type-species of *Stiva* Hedley: **A**, shell; **B-C**, radula (**C**, detail of central teeth) (A, 182 m, 25 km E. of Wollongong, New South Wales, Australia, AMS, C.17862; B, C, 192-203 m, 30km E. of Malabar, Sydney, New South Wales, AMS, C.135036). **D-G**, *Rissoina* (*Rissoina*) *cretacea* T. Woods, type-species of *Laseronia* Cotton: **D**, shell; **E**, operculum (inner side); **F**, protoconch microsculpture; **G**, radula (25 m, off Gabo Island, Victoria, AMS, C.135037). **Scale:** shells - 1 mm; protoconch, operculum and radula (B) - 0.1 mm radulae (C, G) - 0.01 mm.

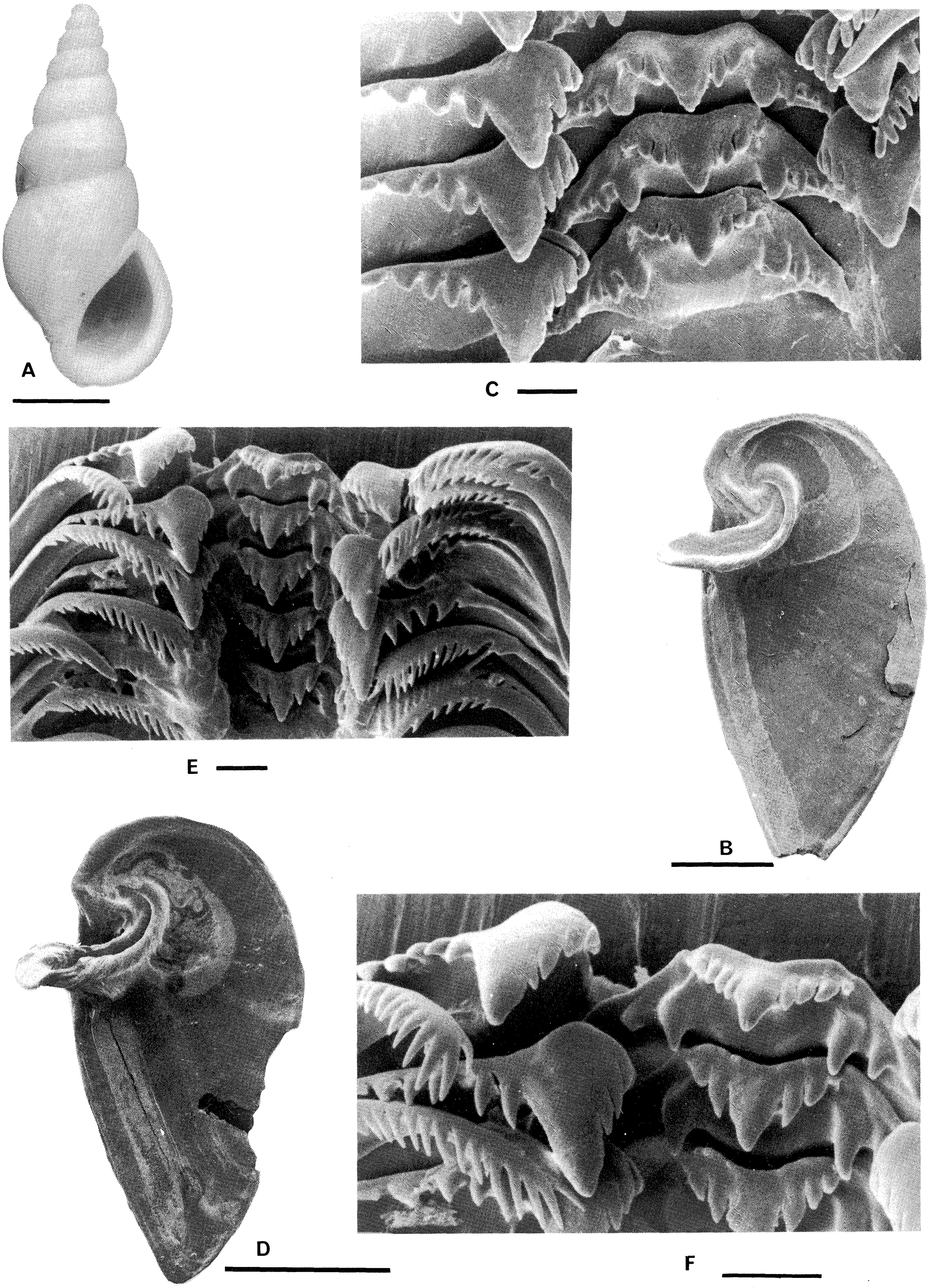

Fig. 131. **A**, *Rissoina* (*Rissoina*) *gigantea* (Deshayes), type-species of *Moerchiella* Nevill; shell (Matabungkay, Luzon, Philippines, AMS, C.139687). **B-C**, *Rissoina* (*Rissoina*) *striata* (Quoy & Gaimard): **B**, operculum (inner side); **C**, radula (E. coast, Malakula Island, Vanuatu, AMS, C.139688). **D-F**, *Rissoina* (*Rissoina*) *spirata* (Sowerby): **D**, operculum (inner side), **E-F**, radula (**F**, detail of central teeth) (Somerset Bay, Cape York Peninsula, N. Queensland, Australia, AMS, C.139691). **Scale:** shell - 5 mm; opercula - 1 mm; radulae - 0.01 mm.

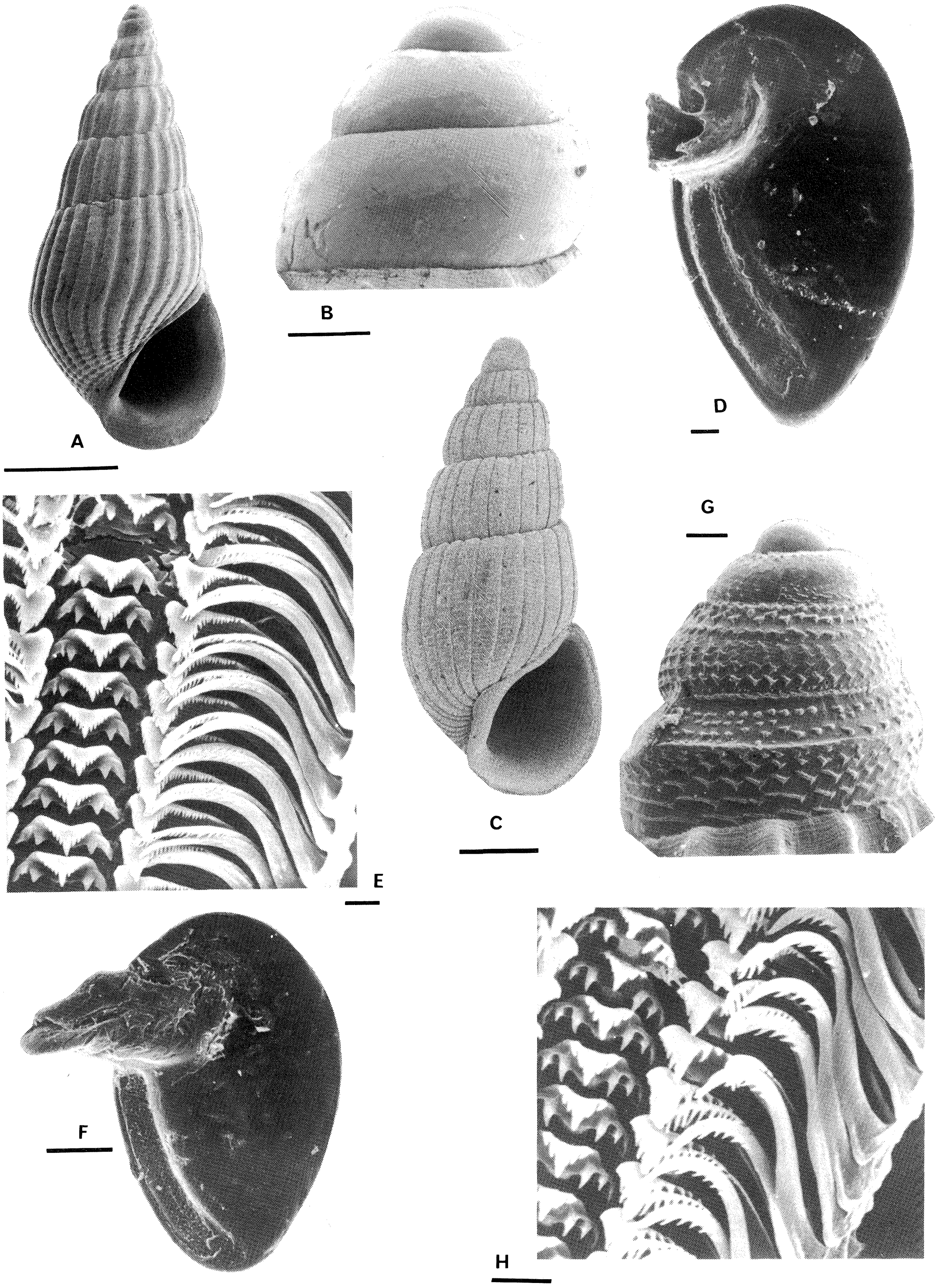

Fig. 132. **A-B**, *Rissoina* (*Rissoina*) *angulata* (Laseron), type-species of *Pleneconea* Laseron: **A**, shell; **B**, protoconch (paratypes, Lindeman Island, N. of Mackay, Queensland, Australia, AMS, C.108893). **C-E**, *Rissoina* (*Rissoina*) *iredalei* Laseron, type-species of *Caporista* Iredale: **C**, shell; **D**, operculum; **E**, radula (syntype, 27 m, Sydney Harbour Heads, New South Wales, Australia, AMS, C.102375). **F-H**, *Rissoina* (*Apataxia*) *miltozona* Tomlin, type-species of *Apataxia* Laseron: **F**, operculum; **G**, protoconch; **H**, radula (Heron Island, Queensland, AMS, C.135038). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

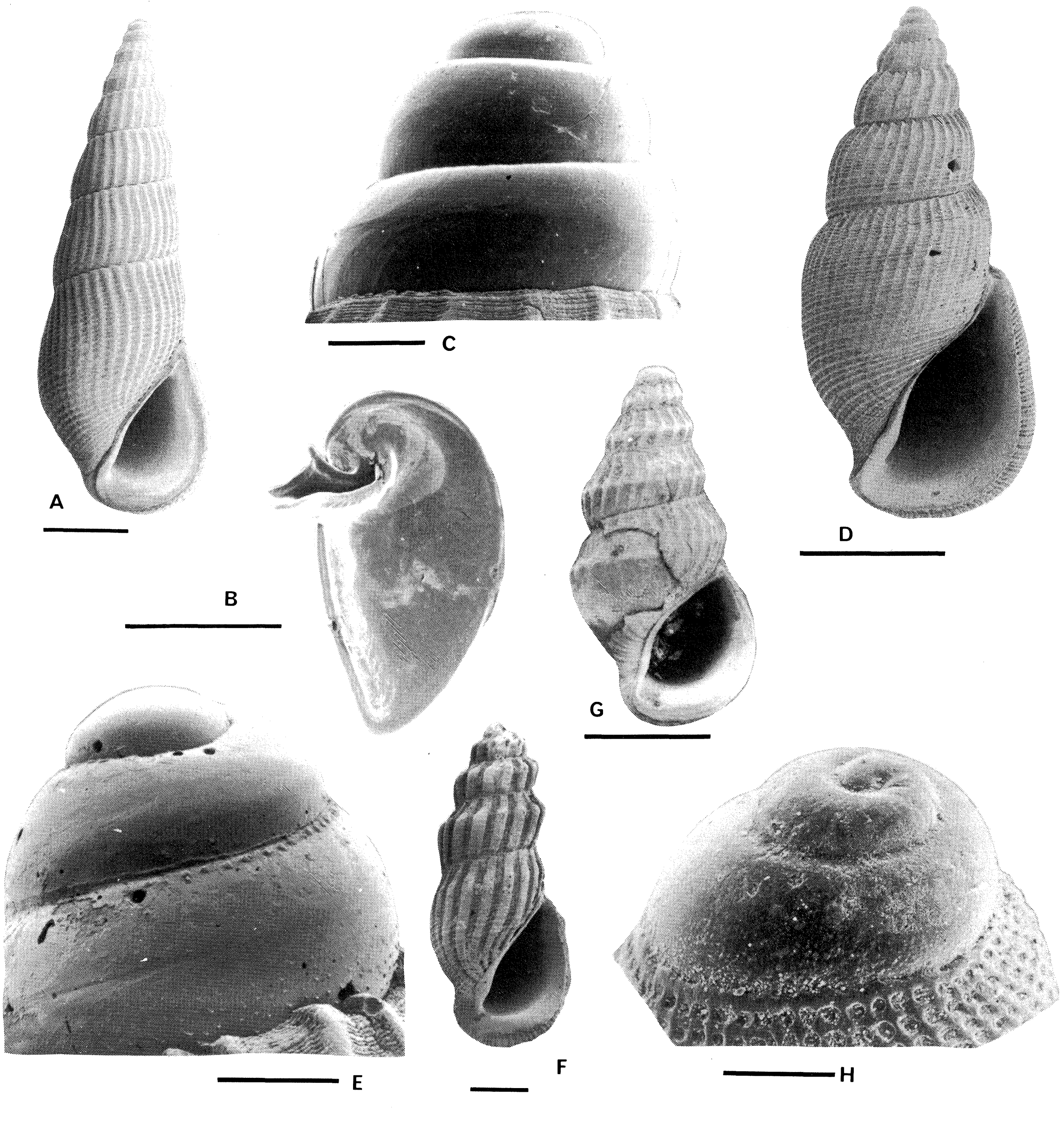

Fig. 133. **A-C**, *Rissoina* (*Rissoina*) *decussata* (Montagu), type-species of *Zebinella* Mörch: **A**, shell; **B**, operculum (inner side); **C**, protoconch (4 m, Marco Is., Florida, U.S.A., USNM, 53960). **D-E**, *Rissoina* (*Rissoina*) *concinna* (Laseron), type-species of *Zymalata* Laseron: **D**, shell; **E**, protoconch (paratype, Michaelmas Cay, Queensland, Australia, AMS, C.108892). **F**, *Rissoina* (*Rissoina*) *crenilabris* Boettger, type-species of *Parazebinella* Boettger; shell (Milne Bay, Papua New Guinea, AMS, C.8612). **G**, *Rissoina* (*Buvignieria*) *duplicata* (Sowerby), shell (Ancliffe, England, Upper Jurassic, WAM, 78.3703). **H**, *Cossmannia expansa* (Deshayes), type-species of *Cossmannia* Newton; protoconch (Thionville-sur-Opton, Yvelines, France, Eocene, Cossmann Collection, UMC). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm.

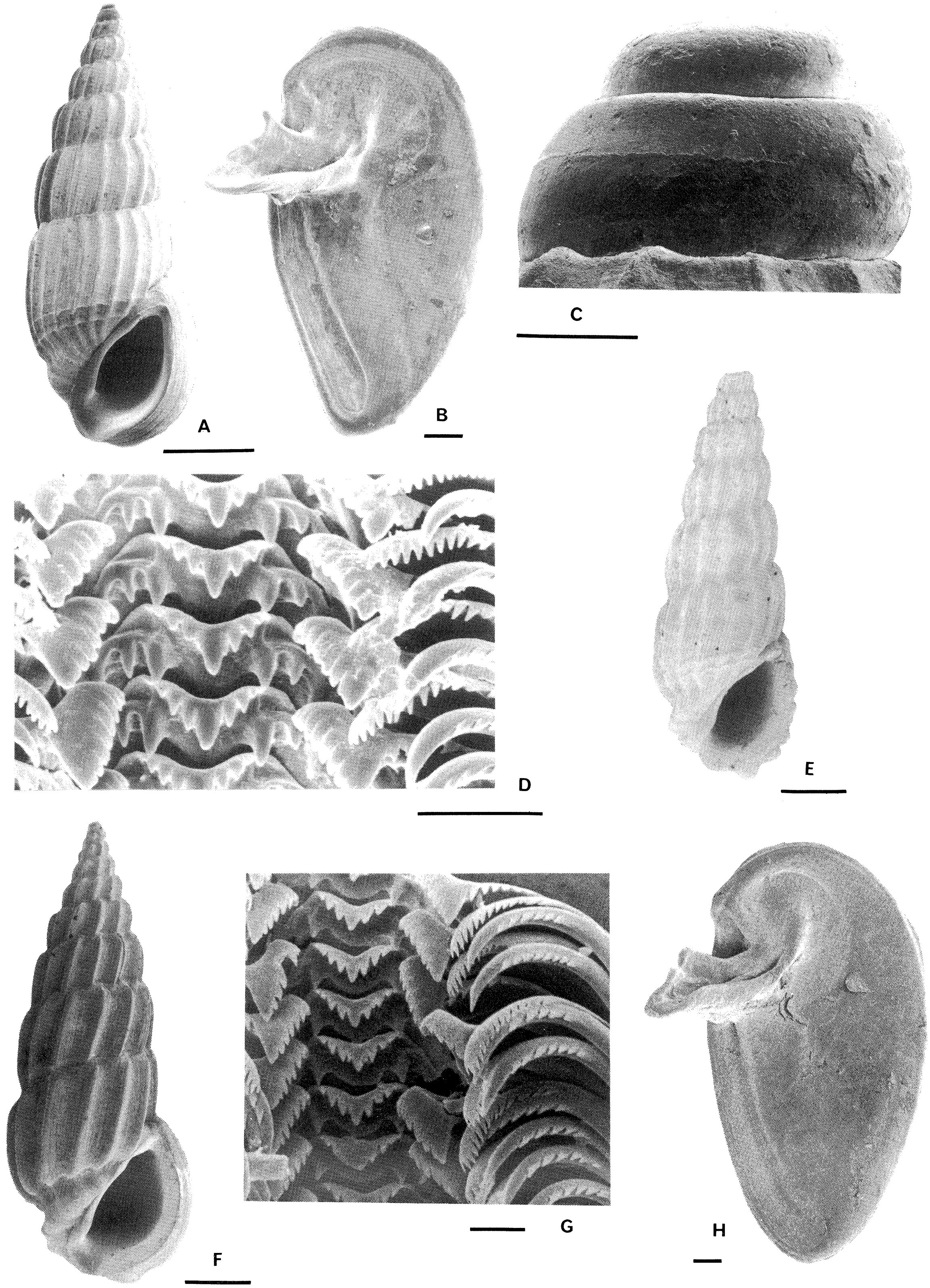

Fig. 134. **A-D**, *Rissoina* (*Rissolina*) *plicatula* Gould, type-species of *Rissolina* Gould: **A**, shell; **B**, operculum (inner side); **C**, protoconch; **D**, radula (Fukura, Awaji, Japan, USNM, 342177). **E**, *Rissoina* (*Rissolina*) *cardinalis* Brazier, type-species of *Costalynia* Laseron; shell (syntype, Katow, Papua New Guinea, AMS, A.141 ii). **F-H**, *Rissoina* (*Rissolina*) *crassa* Angas: **F**, shell; **G**, radula; **H**, operculum (Wooli, New South Wales, Australia, AMS, C.138249). **Scale:** shells - 1 mm; protoconch and operculum - 0.1 mm; radula - 0.01 mm.

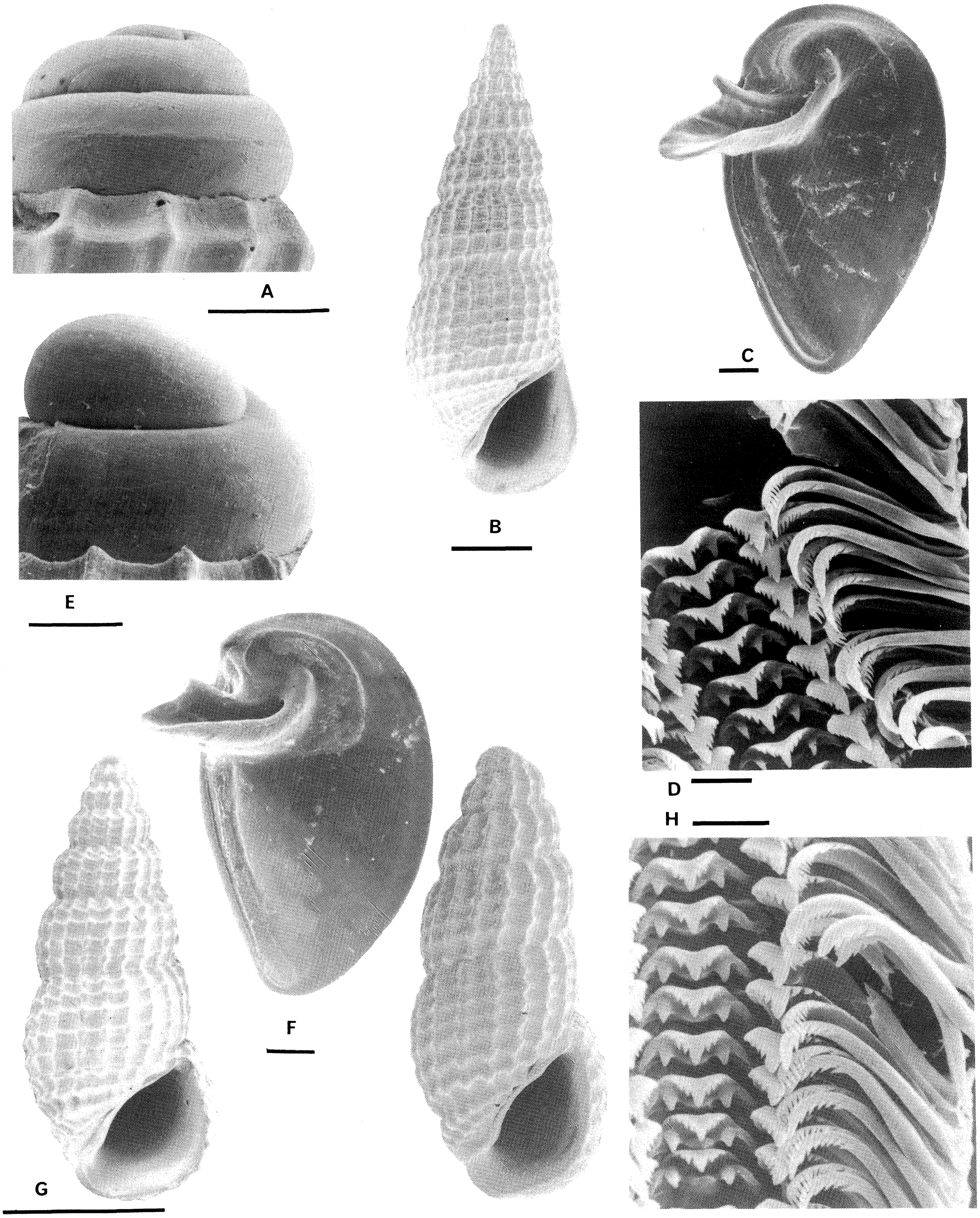

Fig. 135. **A-D**, *Rissoina* (*Phosinella*) *cancellata* Philippi, type-species of *Phosinella* Mörch: **A**, protoconch; **B**, shell; **C**, operculum (inner side); **D**, radula (5-11 m, Santa Rosa, N.W. Cuba, AMS, C.135041, ex USNM). **E-H**, *Rissoina (Phosinella) allanae* Laseron, type-species of *Phintorene* Iredale: **E**, protoconch; **F**, operculum; **G**, shell; **H**, radula (Dunwich, N. Stradbroke Island, Queensland, Australia, AMS, C.135039). **I**, *Rissoina* (*Phosinella*) *fractura* (Laseron), type-species of *Planapexia* Laseron; shell (paratype, Darwin, Northern Territory, Australia, AMS, C.108920). **Scale:** shells – 1 mm; protoconchs and opercula – 0.1 mm; radulae – 0.01 mm.

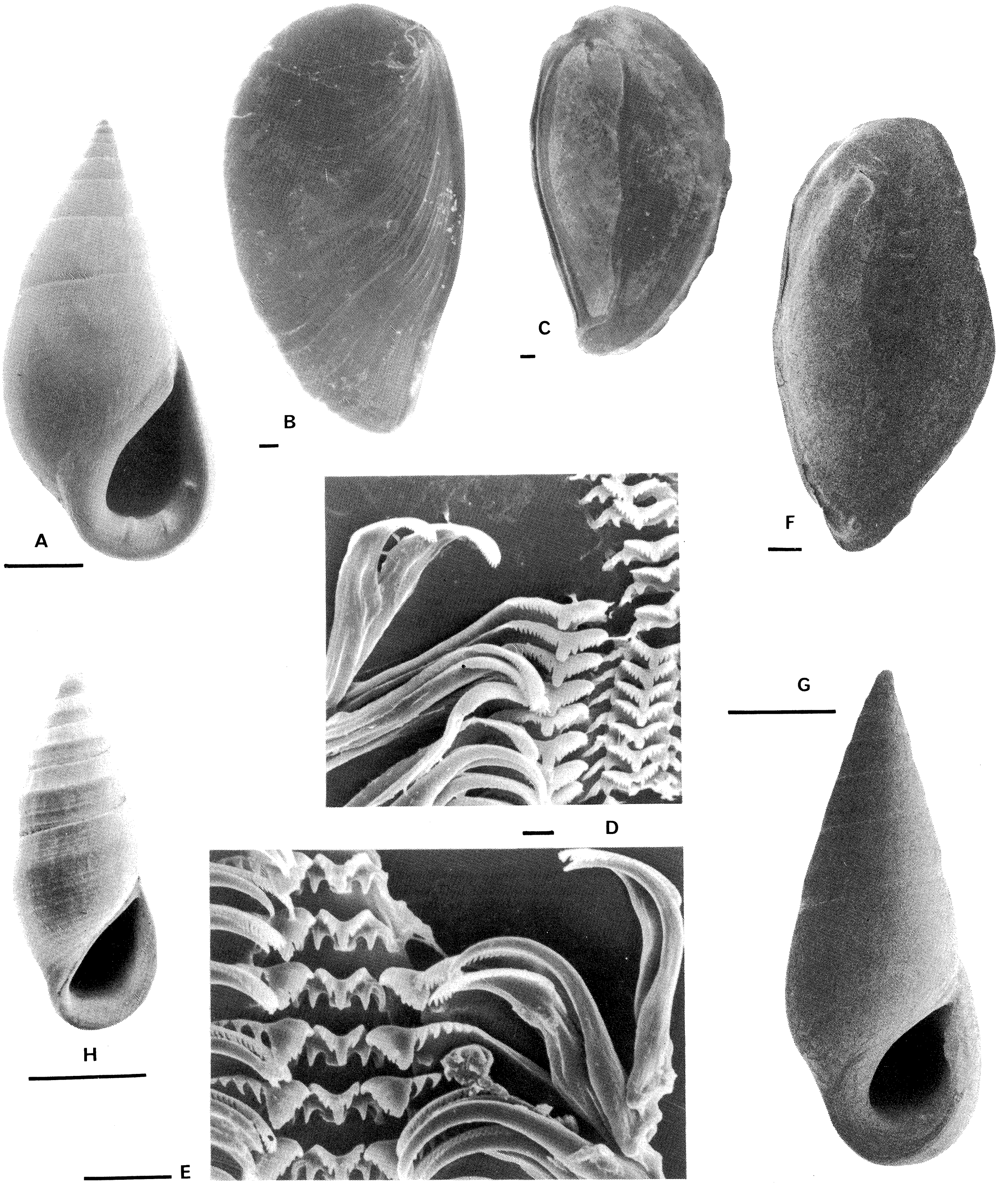

Fig. 136. A-D, *Zebina* (*Zebina*) *tridentata* Michaud: **A**, shell; **B-C**, operculum (**B**, outer side; **C**, inner side); **D**, radula (A, Waikiki, Oahu, Hawaii, BPBM, Acc. no. 666; **B-D**, Cebu, Philippines, RSM). **E-G**, *Zebina* (*Zebina*) *browniana* (Orbigny), type-species of *Cibdezebina* Woodring: **E**, radula; **F**, operculum; **G**, shell (E, Missouri Key, Florida, U.S.A., AMS, C.138250; F-G, Bahia Honda, Cuba, AMS, C.138251). **H**, *Zebina* (*Takirissoina*) *japonica* (Weinkauff), type-species of *Takirissoina* Oyama; shell (Ogokuda, Shionomisaki, Kii Peninsula, Honshu, Japan, NSMT, 56632). **Scale:** shells – 1 mm; opercula – 0.1 mm; radulae – 0.01 mm.

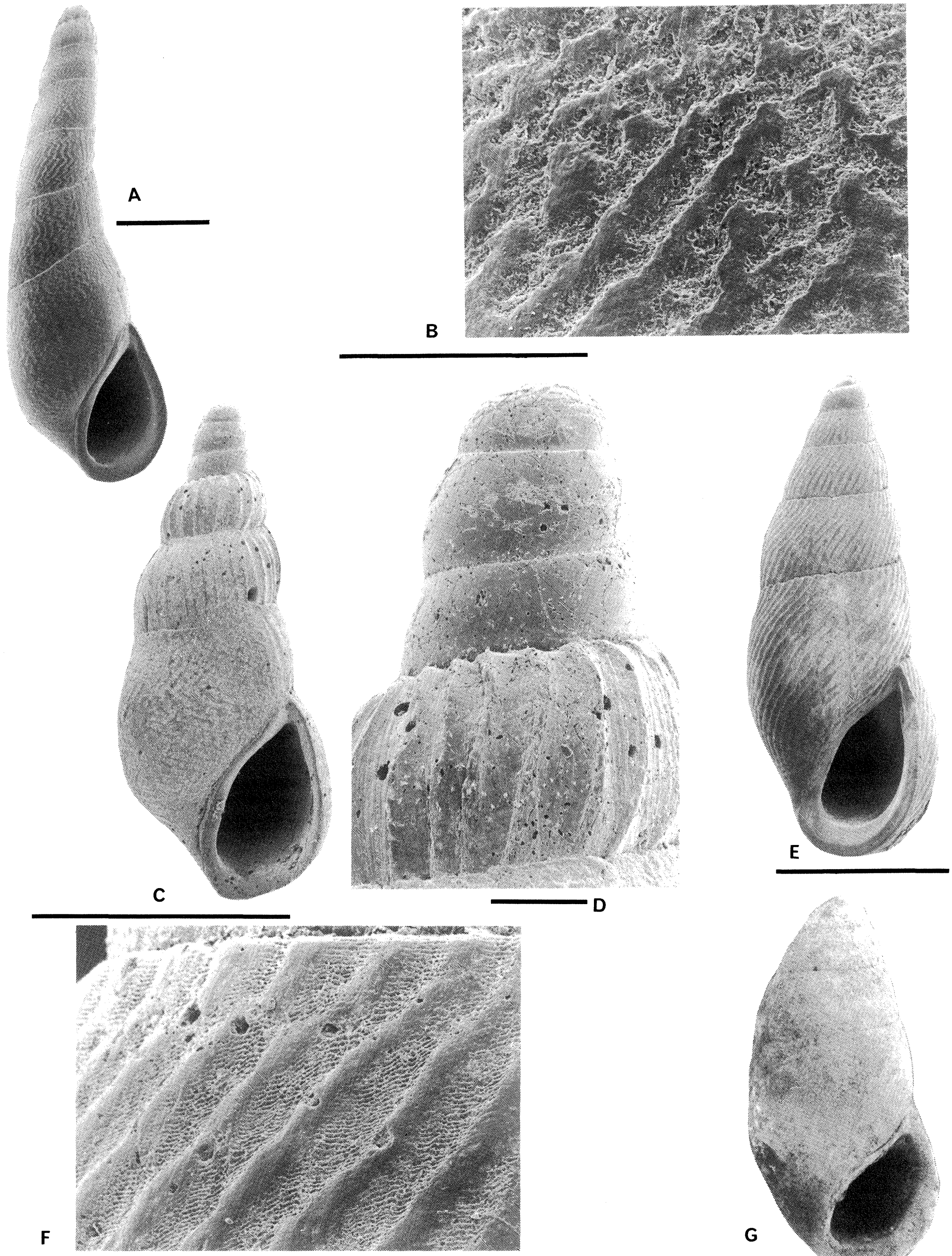

Fig. 137. A-D, *Zebina* (*Tiphyocerma*) *preposterum* (Berry), type-species of *Tiphyocerma* Berry: **A-C**, shell; **B**, detail of teleoconch sculpture; **D**, protoconch (A, B, 2-15 m, Head of Gulfo de Dulce, Costa Rica, LACM, 72-71; C, D, 18-36 m, between Rancho el Tule & Rancho Palmilla, Baja California, Mexico, LACM, 66-17). **E-F**, *Schwartziella* (*Schwartziella*) *zeltenerioides* (Yokoyama), type-species of *Rissoinella* Oyama: **E**, shell; **F**, detail of teleoconch microsculpture (Kominato, Chiba, Honshu, Japan, ANSP, 252429). **G**, *Zebina* (*Zebina*) *laevis* (Sowerby); shell (Ancliffe, England, Upper Jurassic, WAM, 78.3701). **Scale:** shells - 1 mm; protoconch and microsculpture - 0.1 mm.

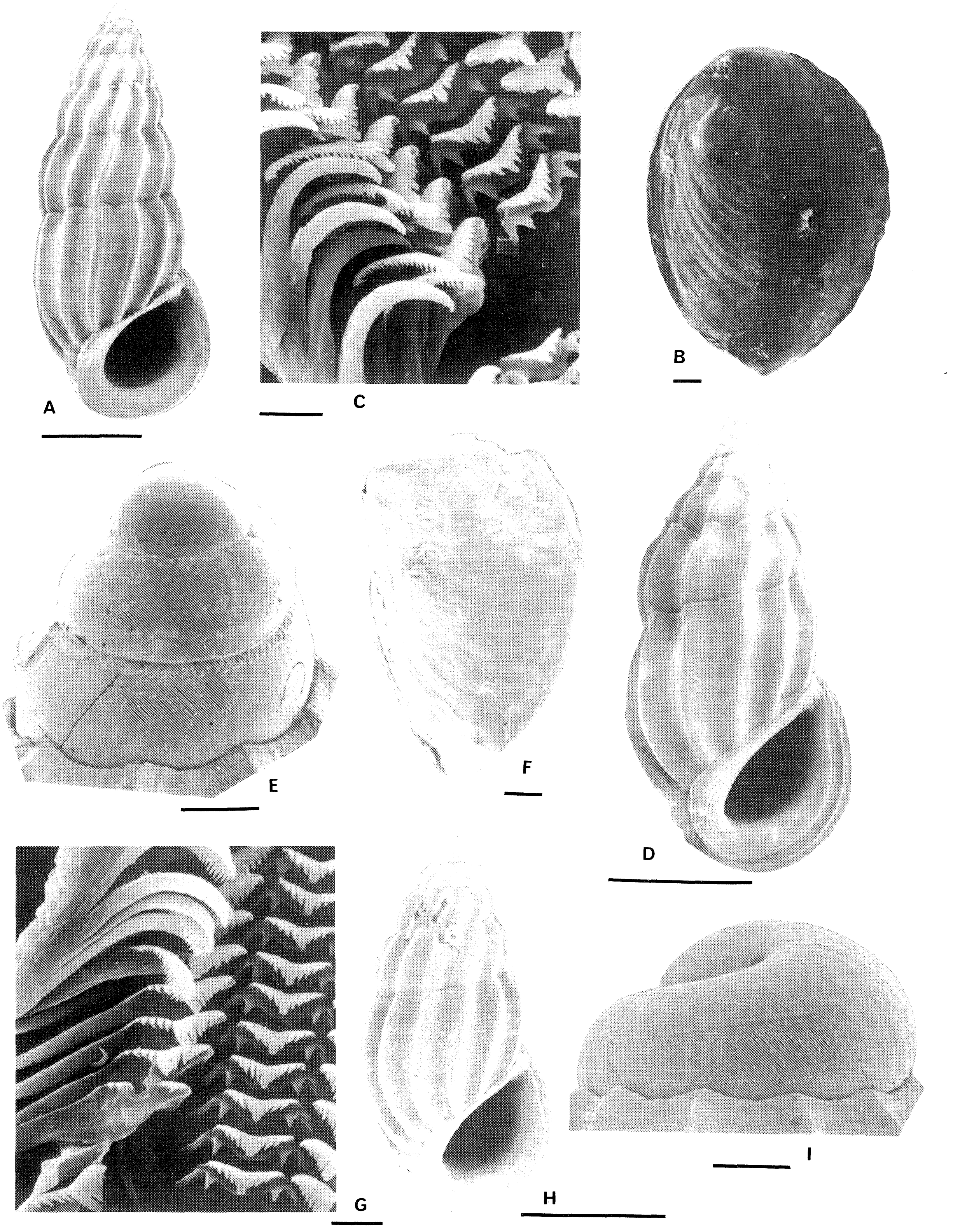

Fig. 138. **A-C**, *Schwartziella* (*Schwartziella*) *bryerea* (Montagu), type-species of *Schwartziella* Nevill (1885): **A**, shell; **B**, operculum (inner side); **C**, radula (5-11 m, Santa Rosa, N.W. Cuba, AMS, C.135042). **D-G**, *Schwartziella* (*Schwartziella*) *triticea* (Pease): **D**, shell; **E**, protoconch; **F**, operculum (inner side); **G**, radula (Mokapu Point, Kailua Bay, Oahu, Hawaii, AMS, C.135043). **H-I**, *Schwartziella* (*Schwartziella*) *inconspicua* (Brazier): **H**, shell; **I**, protoconch (Heron Island, Queensland, Australia, AMS, C.135044). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

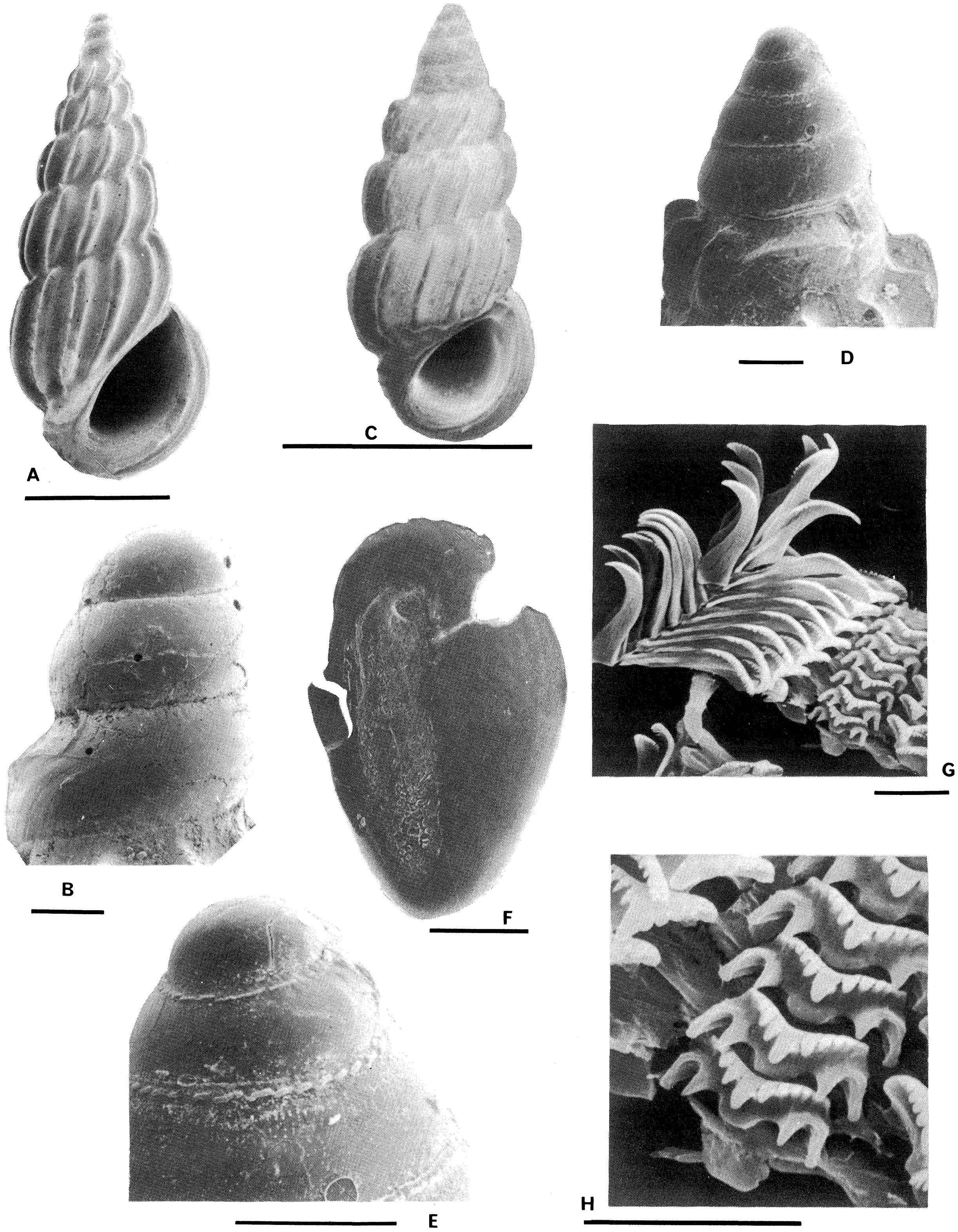

Fig. 139. **A-B**, *Schwartziella* (*Pandalosia*) *excelsis* (Laseron), type-species of *Pandalosia* Laseron: **A**, shell; **B**, protoconch (paratype, Murray Island, Queensland, Australia, AMS, C.108606). **C-H**, *Schwartziella* (*Pandalosia*) *ephamilla* (Watson): **C**, shell; **D-E**, protoconch (**E**, detail of protoconch microsculpture); **F**, operculum (inner side); **G-H**, radula (**H**, detail of central teeth) (27-30 m, N. end of Carter Reef, E. of Lizard Island, Queensland, AMS, C.135048). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radulae - 0.01 mm.

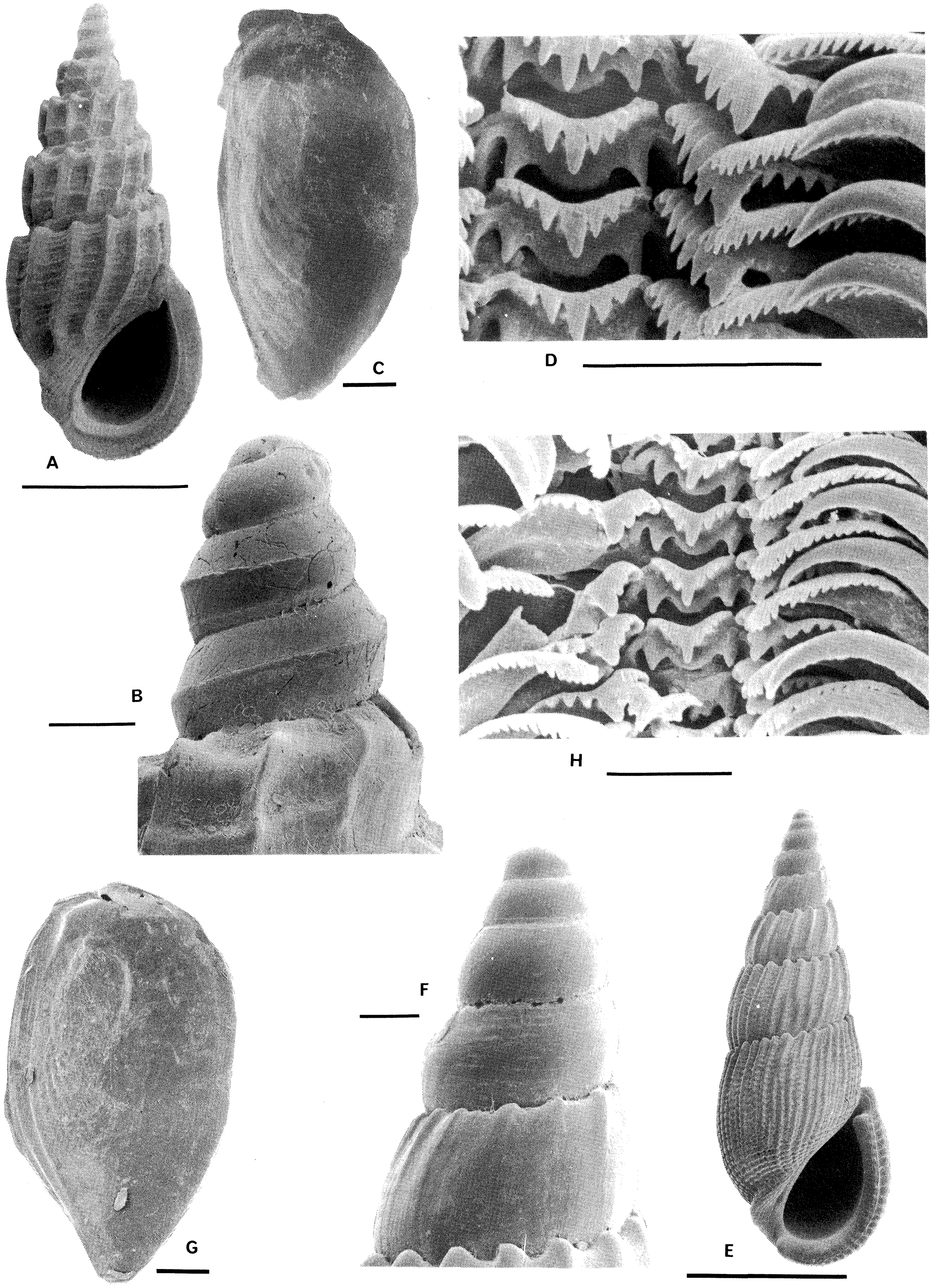

Fig. 140. **A-D**, *Folinia signae* (Bartsch), type-species of *Folinia* Crosse: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D**, radula (8-12 m, N. side Isla de Caño, Puntarenas Province, Costa Rica, LACM, 72-63). **E-H**, *Folinia ericana* (Hertlein & Strong): **E**, shell; **F**, protoconch; **G**, operculum (inner side); **H**, radula (18-36 m, between Rancho El Tule and Rancho Palmillo, Baja California, Mexico, LACM, 66-17). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; radulae - 0.01 mm.

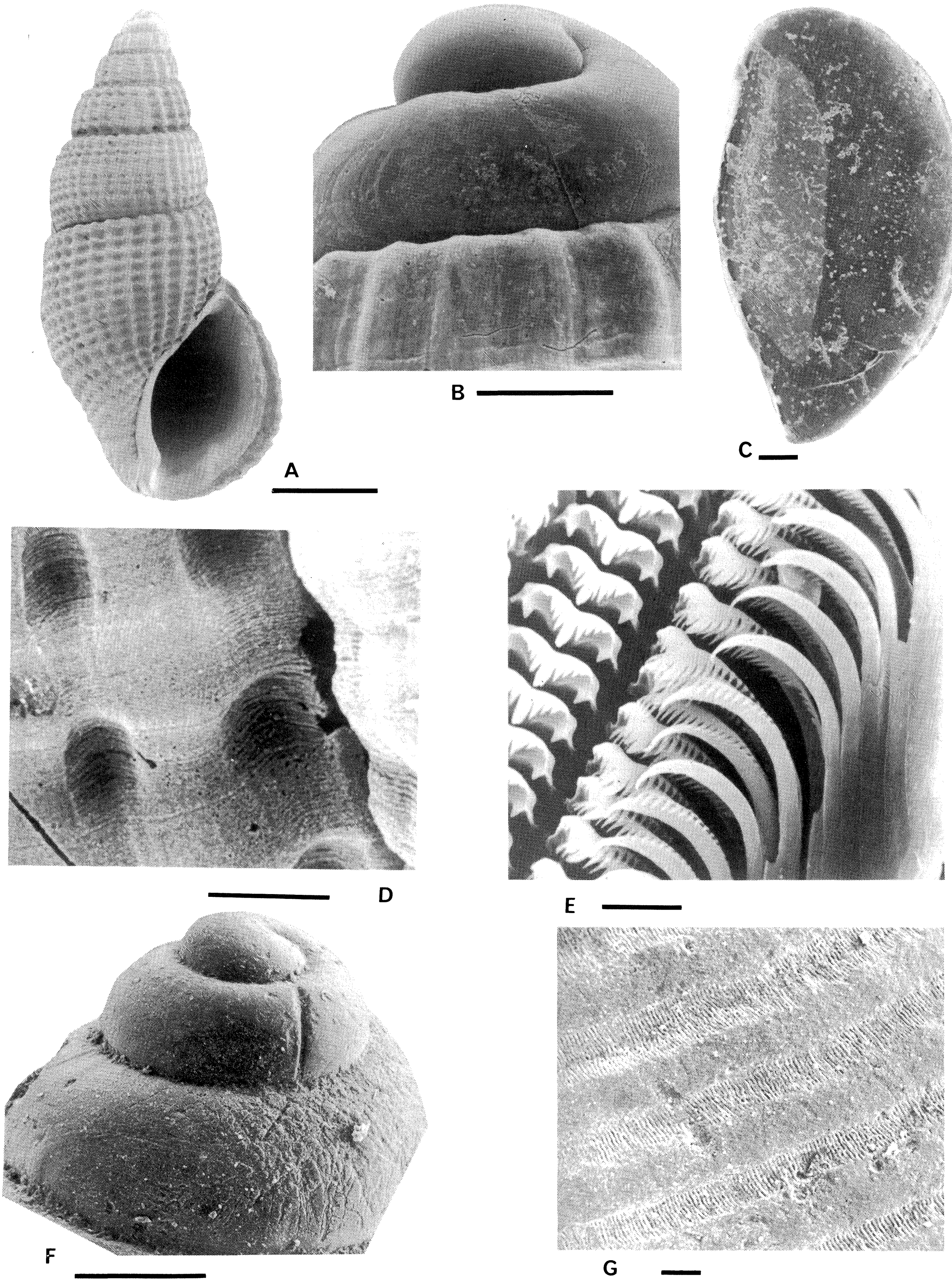

Fig. 141. **A-E**, *Stosicia* (*Isseliella*) cf. *mirabilis*: **A**, shell; **B**, protoconch; **C**, operculum (inner side); **D**, teleoconch sculpture; **E**, radula (Kapa Kapa, E. of Port Moresby, Papua New Guinea, AMS, C.135050). **F-G**, *Stosicia* (*Stosicia*) *planaxoides* (Grateloup), type-species of *Stosicia* Brusina: **F**, protoconch; **G**, teleoconch microsculpture (Steinabrunn, Austria, Miocene, BMNH, 61881). **Scale:** shell - 1 mm; protoconchs, operculum and microsculpture - 0.1 mm; radula - 0.01 mm.

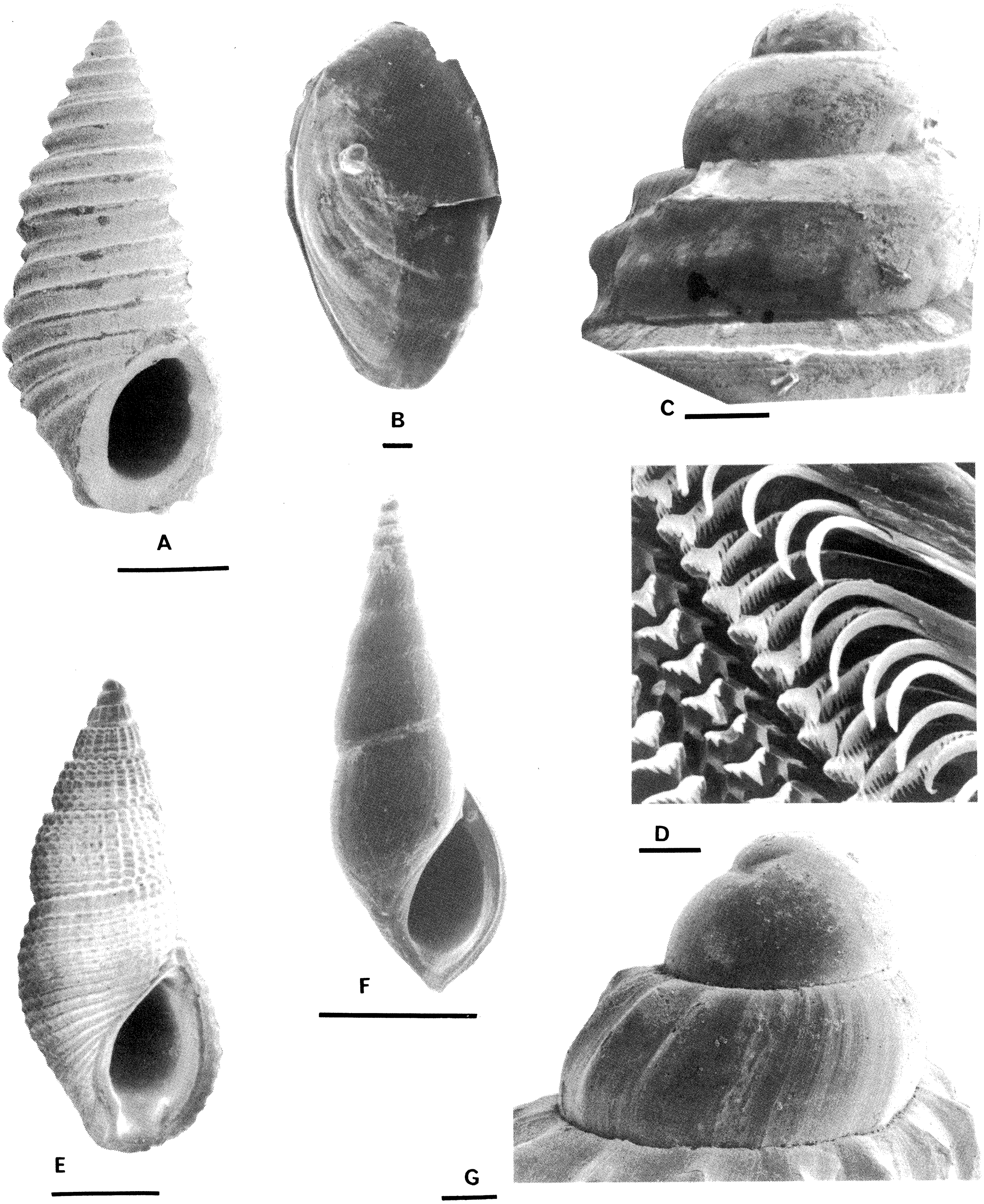

Fig. 142. **A-D**, *Stosicia* (*Stosicia*) *annulata* (Dunker): **A**, shell; **B**, operculum (inner side); **C**, protoconch; **D**, radula (Awaji, Japan, AMS, C.135049). **E**, *Stosicia* (*Isseliella*) *mirabilis*, type-species of *Isseliella* Weinkauff; shell (Upolu, West Samoa, ex Paetel, HUM). **F**, *Folinia histia* (Bartsch); shell (55 m, mouth of Bahía Conception, Baja California, Mexico, LACM, AHF2025). **G**, *Microstelma japonica* (Adams), type-species of *Amaurella* Adams; protoconch (284 m, E. of North West Island, Queensland, Australia, AMS, C.139689). **Scale:** shells - 1 mm; protoconchs and opercula - 0.1 mm; microsculpture and radulae - 0.01 mm.

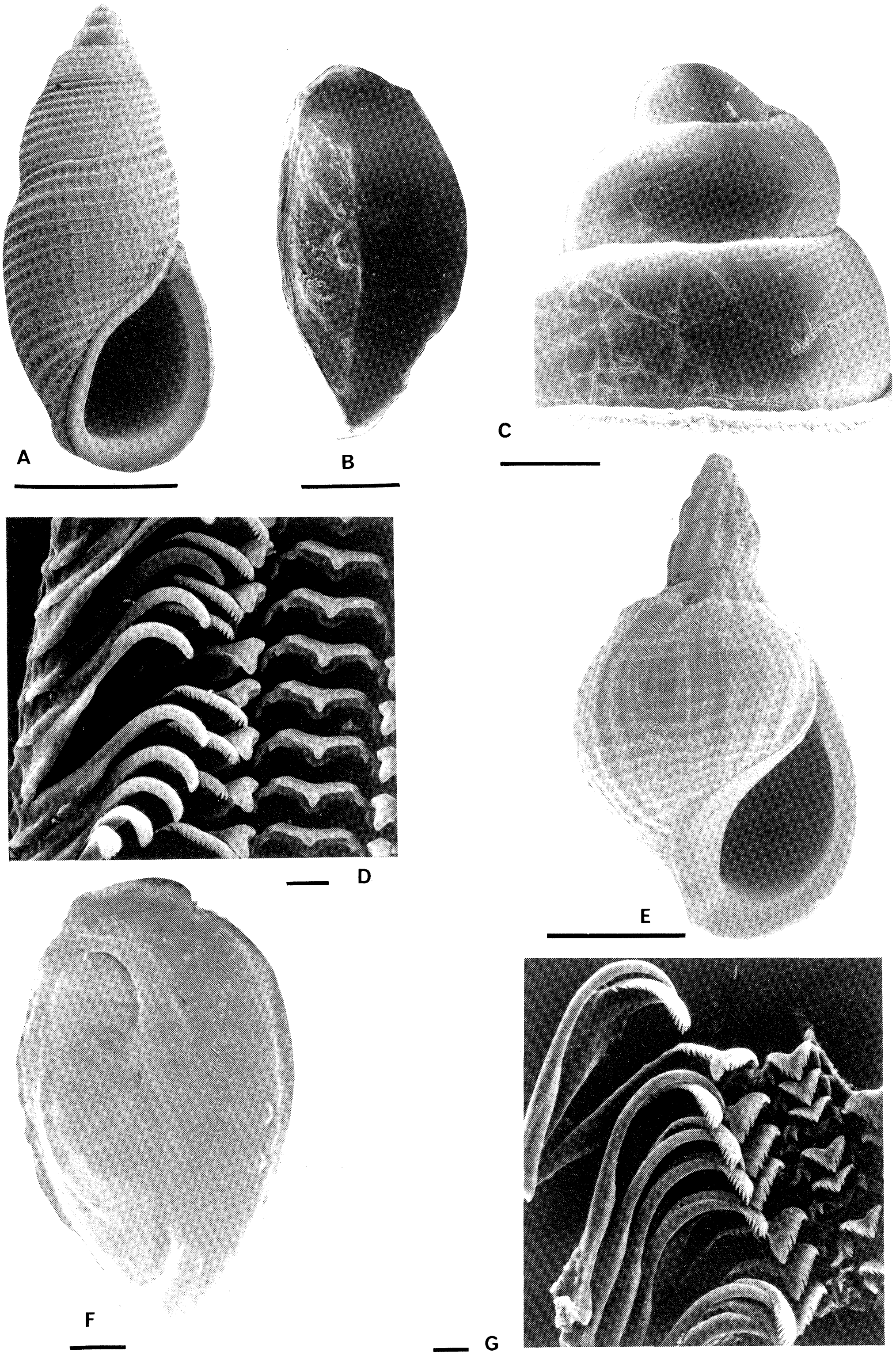

Fig. 143. **A-D**, *Lapsigyrus mutans* (Carpenter), type-species of *Lapsigyrus* Berry: **A**, shell; **B**, operculum (inner side); **C**, protoconch; **D**, radula (9-17 m, Bahía Herradura Reef, N. end of bay, Puntarenas Province, Costa Rica, LACM, 72-52). **E**, *Zebina* (*Tomlinella*) *miranda* (Viader), type-species of *Tomlinella* Viader; juvenile shell (Cocos Keeling Islands, Indian Ocean, AMS, C.134886). **F-G**, *Zebina* (*Tomlinella*) *insignis* (Adams & Reeve), type-species of *Dentrissoina* Laseron: **F**, operculum (inner side); **G**, radula (Red Sea, IRSB). **Scale:** shells - 1 mm; protoconch - 0.1 mm; opercula - 0.3 mm; radulae 0.01 mm.

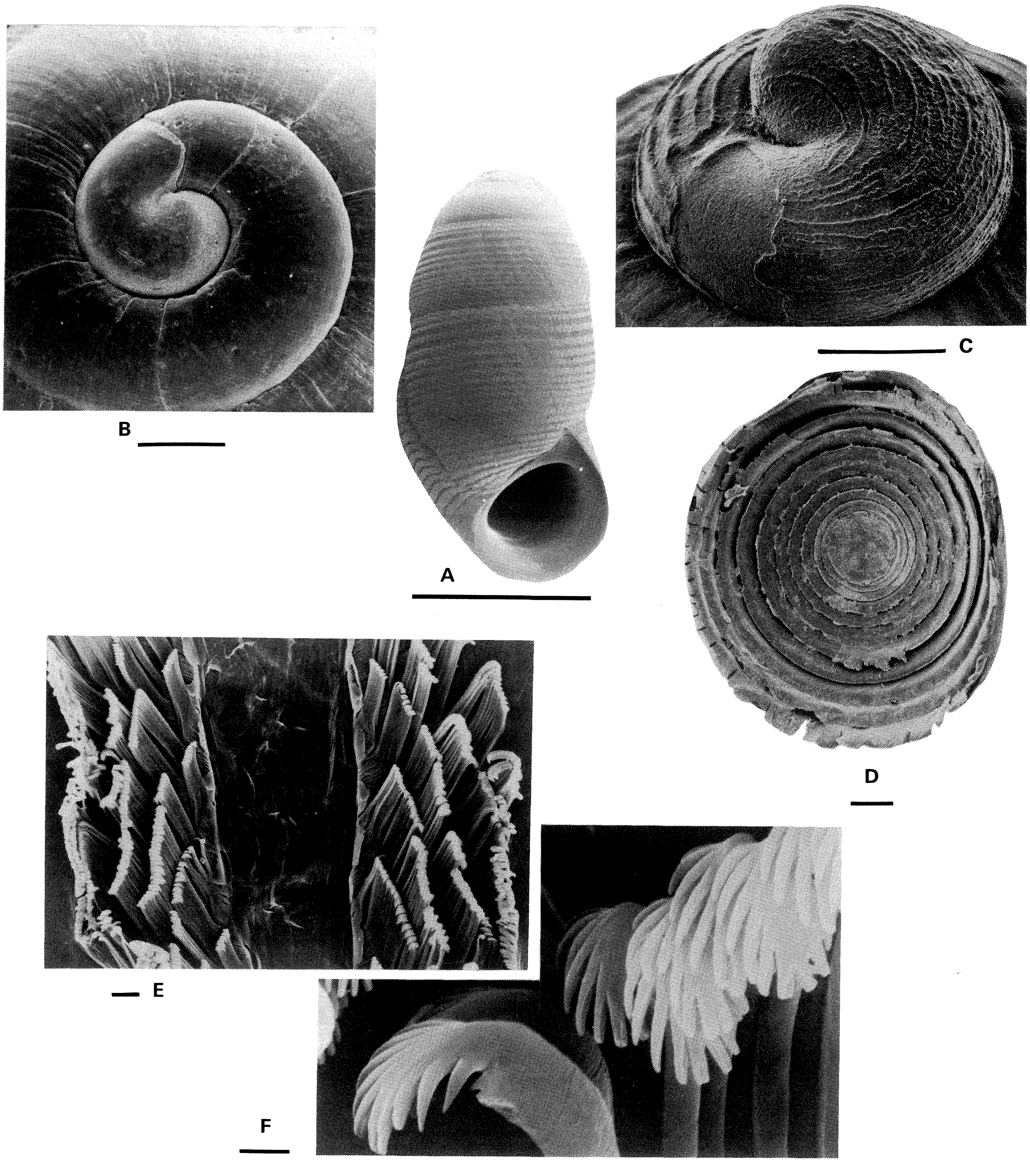

Fig. 144. **A-B**, *Botelloides glomerosus* (Hedley): **A**, shell; **B**, protoconch (paratypes, 31-36 m, Masthead Island, Queensland, AMS, C.19333). **C**, *Kaurnella denotata* Ludbrook, type-species of *Kaurnella* Ludbrook: protoconch (Weymouth's Bore, Adelaide, South Australia, Pliocene, SAM, M.518). **D-F**, *Botelloides bassianus* (Hedley), type-species of *Botelloides* Strand: **D**, operculum, (outer side); **E-F**, radula, (**F**, detail of marginal teeth) (off Beachport, South Australia, 73 m, SAM). **Scale:** shell - 1 mm; protoconchs and operculum - 0.1 mm; radula (E) - 0.01 mm; radula (F) - 0.001 mm.

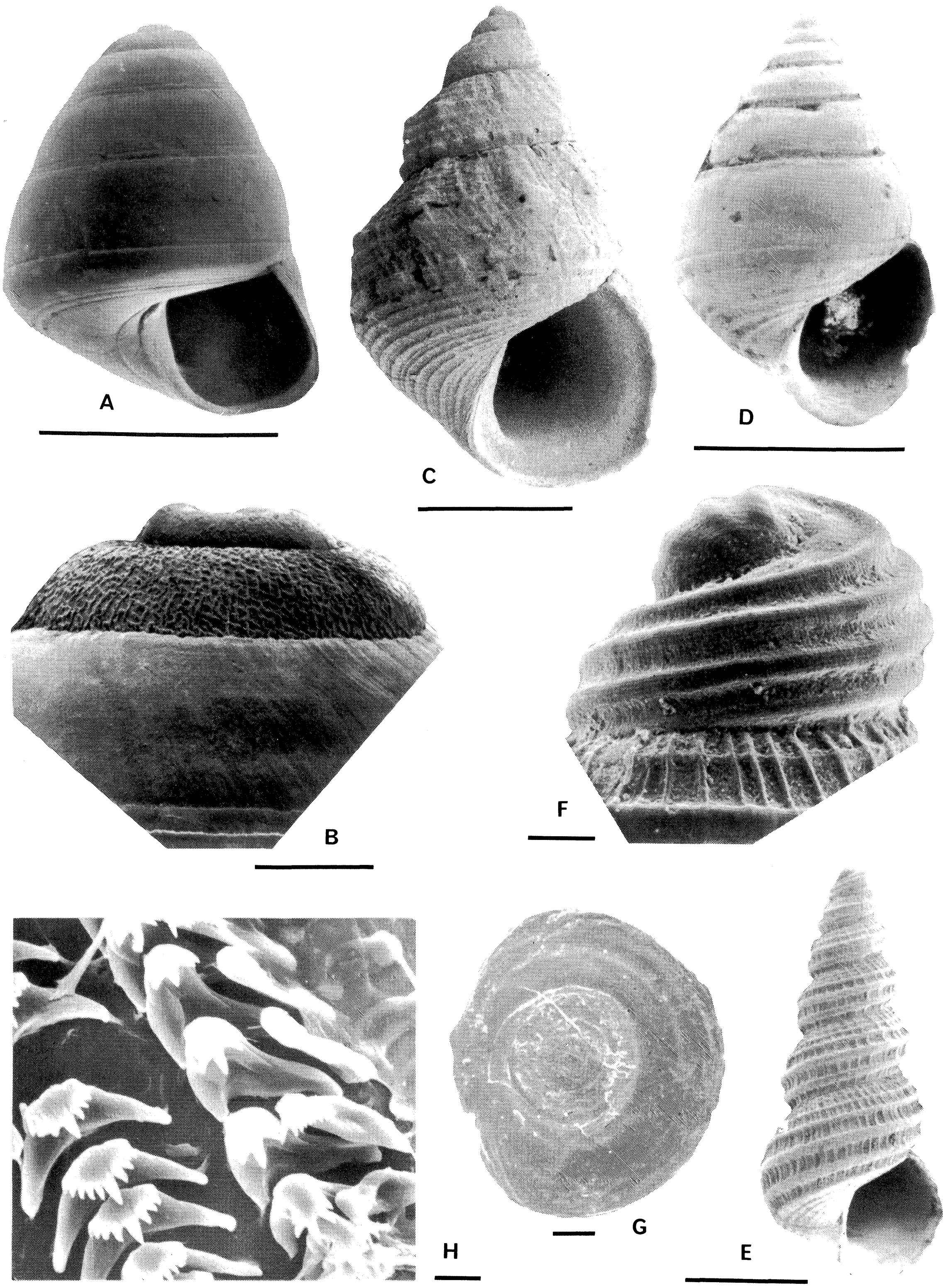

Fig. 145. **A-B**, *Anxietas perplexa* Iredale, type-species of *Anxietas* Iredale: **A**, shell; **B**, protoconch (Christmas Island, Indian Ocean, AMS, C.135051). **C**, *Kaurnella denotata* Ludbrook, type-species of *Kaurnella* Ludbrook; shell (Weymouth's Bore, Adelaide, South Australia, Pliocene, SAM, M.518). **D**, *Dialopsis semistriata* (Deshayes), type-species of *Dialopsis* Cossmann; shell (Jouy-sur-Eure, Eure, France, Eocene, AMS, C.139690). **E-H**, *Brookesena neozelanica* (Suter), type-species of *Brookesena* Finlay: **E**, shell; **F**, protoconch; **G**, operculum (inner side); **H**, radula (43 m, off Campbell Island, New Zealand, AIM). **Scale:** shells - 1 mm; protoconchs and operculum - 0.1 mm; radula - 0.01 mm.

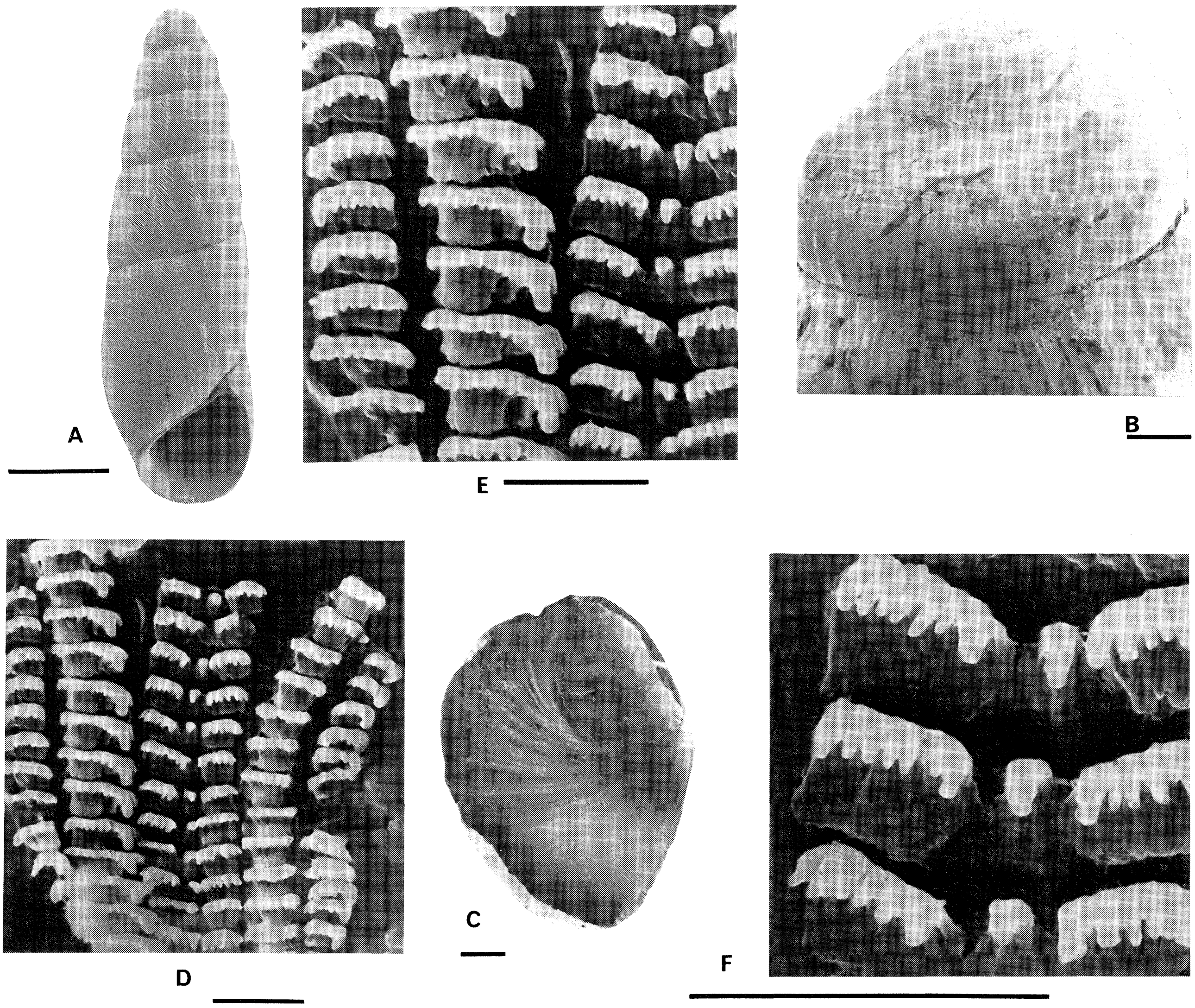

Fig. 146. **A-F**, *Epigrus cylindraceus* (T. Woods), type-species of *Epigrus* Hedley: **A**, shell; **B**, protoconch; **C**, operculum (outer side); **D-F**, radula, (F, detail of central and lateral teeth) (A, 150 m, E. of Sydney, New South Wales, Australia, AMS, C.135052; B-F, 95 m, 112 km S. of Lakes Entrance, Victoria, AMS, C.135053). **Scale:** shell - 1 mm; protoconch and operculum - 0.1 mm; radulae - 0.01 mm.

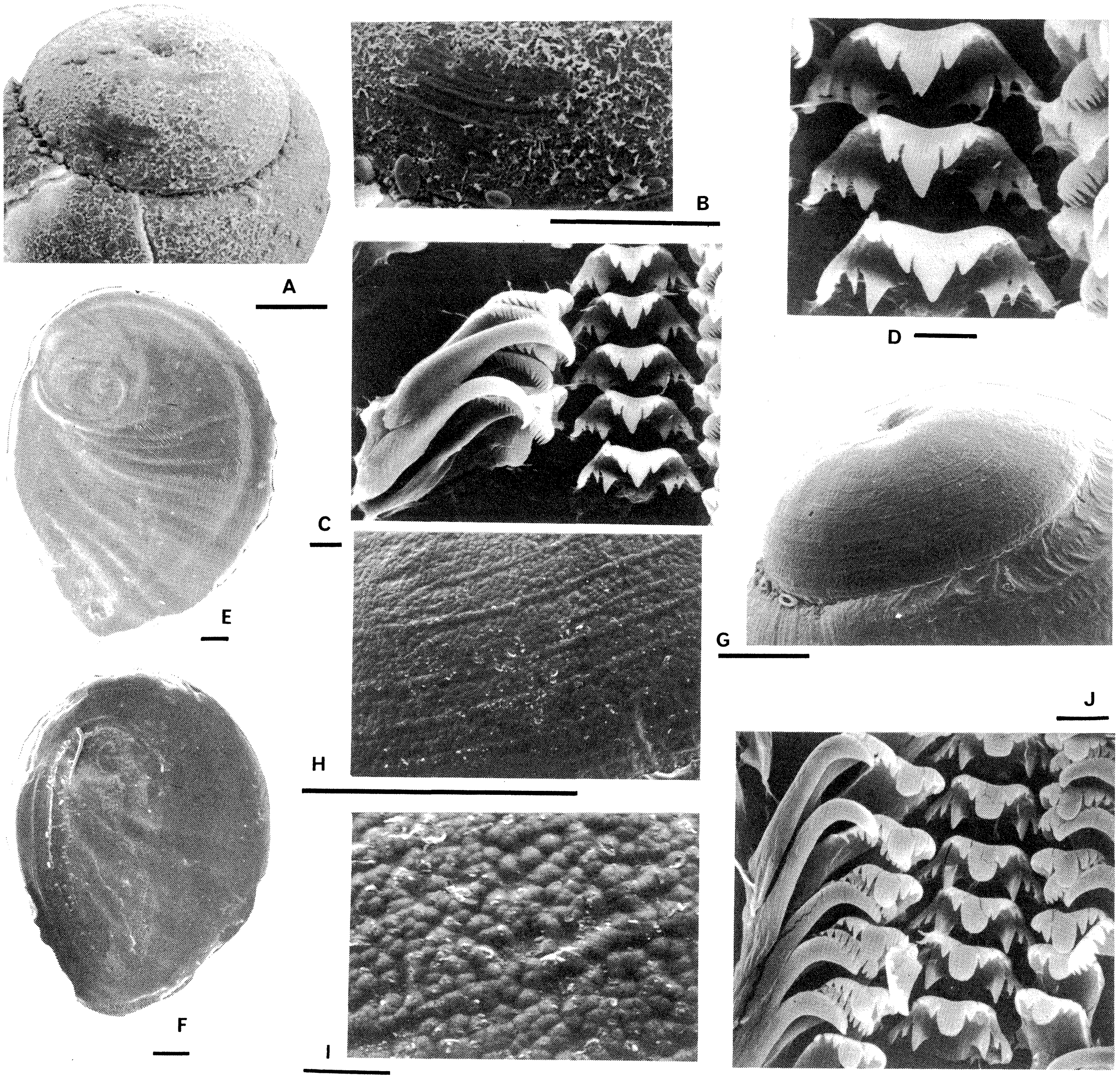

Fig. 147. **A-E**, *Falsicingula kurilensis* (Pilsbry), type-species of *Falsicingula* Habe: **A-B**, protoconch (**B**, detail of microsculpture); **C-D**, radula (**D**, detail of central teeth); **E**, operculum (inner side) (A, B, South Kuril Harbour, Kunashi Island, Kuril Islands, USSR, AMS, C.135054; C-E, Kuril Islands, USSR, AMS, C.38612). **F-J**, *Falsicingula aleutica* (Dall): **F**, operculum (inner side); **G-I**, protoconch (**H-I**, detail of microsculpture); **J**, radula (Evans Island, Prince William Sound, Alaska, USNM, 673745). **Scale:** protoconchs, opercula and microscupture (B, H) - 0.1 mm; microsculpture (I) and radulae - 0.01 mm.

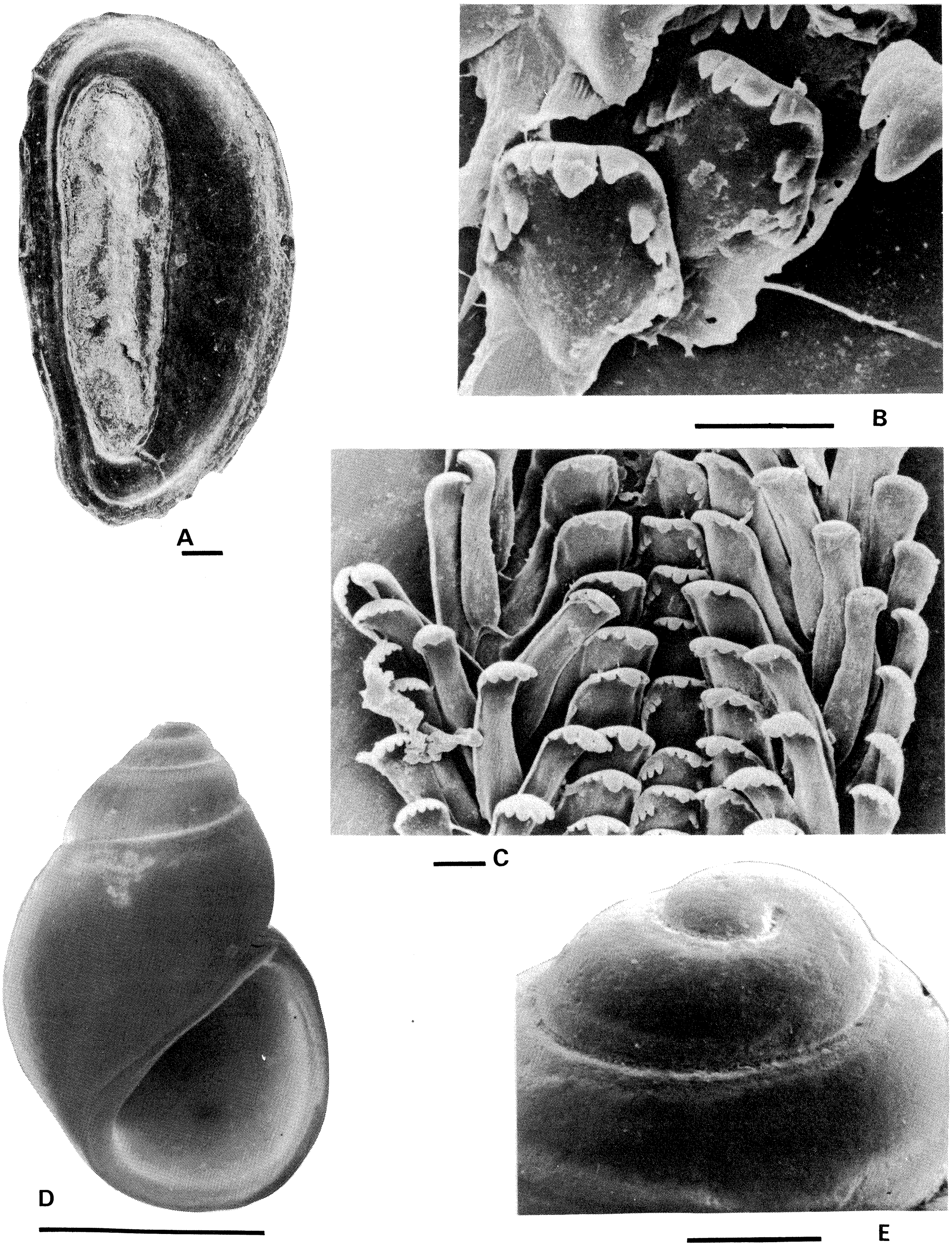

Fig. 148. **A-C**, *Floridiscrobs dysbatus* (Pilsbry & McGinty), type-species of *Floridiscrobs* Pilsbry & McGinty: **A**, operculum (inner side); **B-C**, radula, (**B**, detail of central teeth) (east end of Key West, Florida, U.S.A., LACM, 70-32). **D-E**, *Plagyostila asturiana* Fischer, type-species of *Plagyostila* Fischer: **D**, shell; **E**, protoconch (Bay of St Jean-de-Luz, France, BMNH, 1952.5.12.1-103). **Scale:** shell - 1 mm; protoconch and operculum - 0.1 mm; radulae - 0.01 mm.

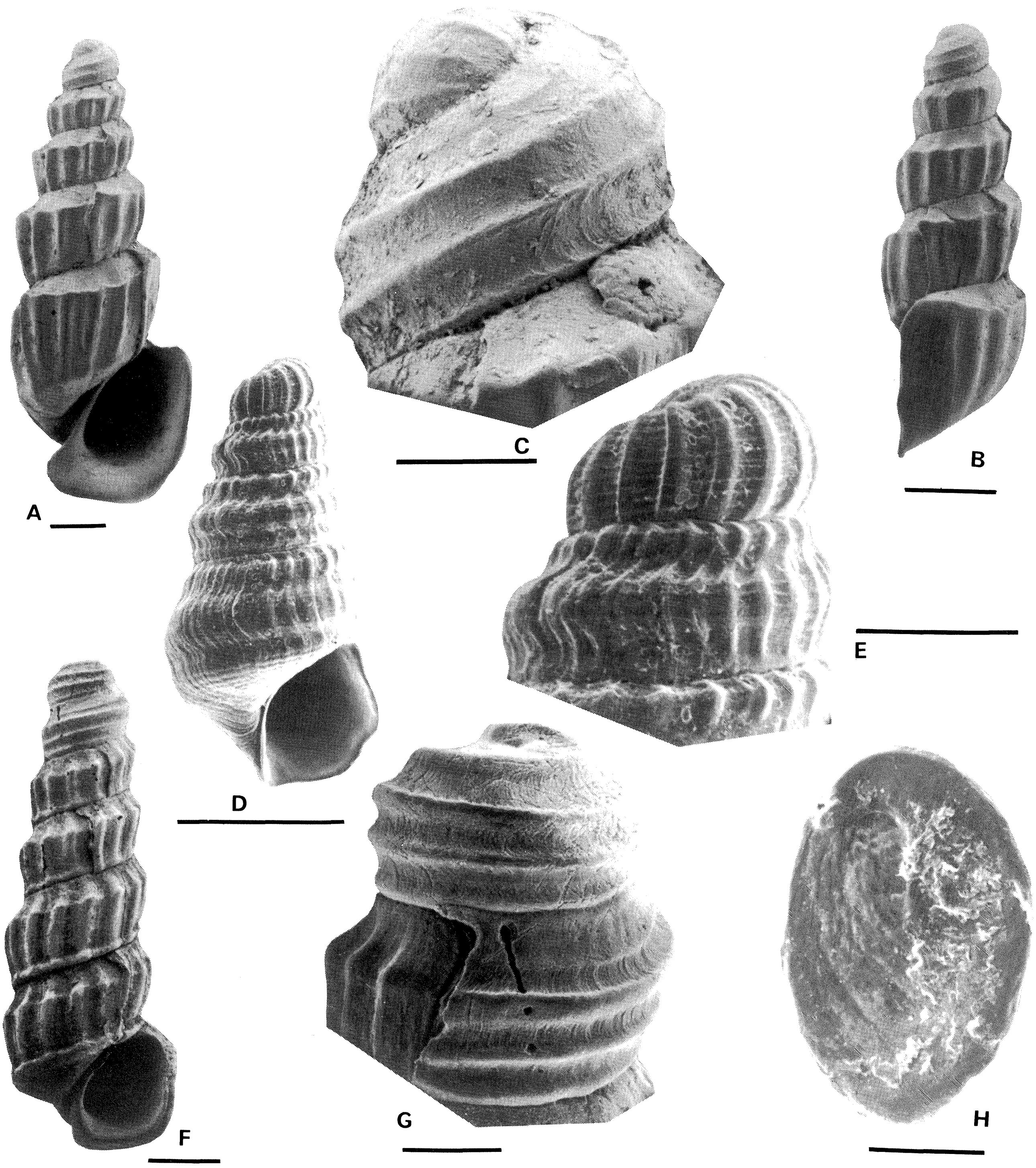

Fig. 149. **A-C**, *Awanuia porcellana* Ponder: **A-B**, shell; **C**, protoconch (Matakaoa Point, Hicks Bay, New Zealand, NMNZ, M33213). **D-E**, *Larochella toreuma* Powell, type-species of *Larochella* Powell: **D**, shell; **E**, protoconch (Titirangi Bay, Marlborough Sounds, New Zealand, NMNZ M.40710). **F-H**, *Coenaculum minutulum* (Tate & May), type-species of *Coenaculum* Iredale: **F**, shell; **G**, protoconch; **H**, operculum (inner side) (Twofold Bay, New South Wales, Australia, AMS, C.135055). **Scale:** shells - 0.3 mm; protoconchs and operculum - 0.1 mm.

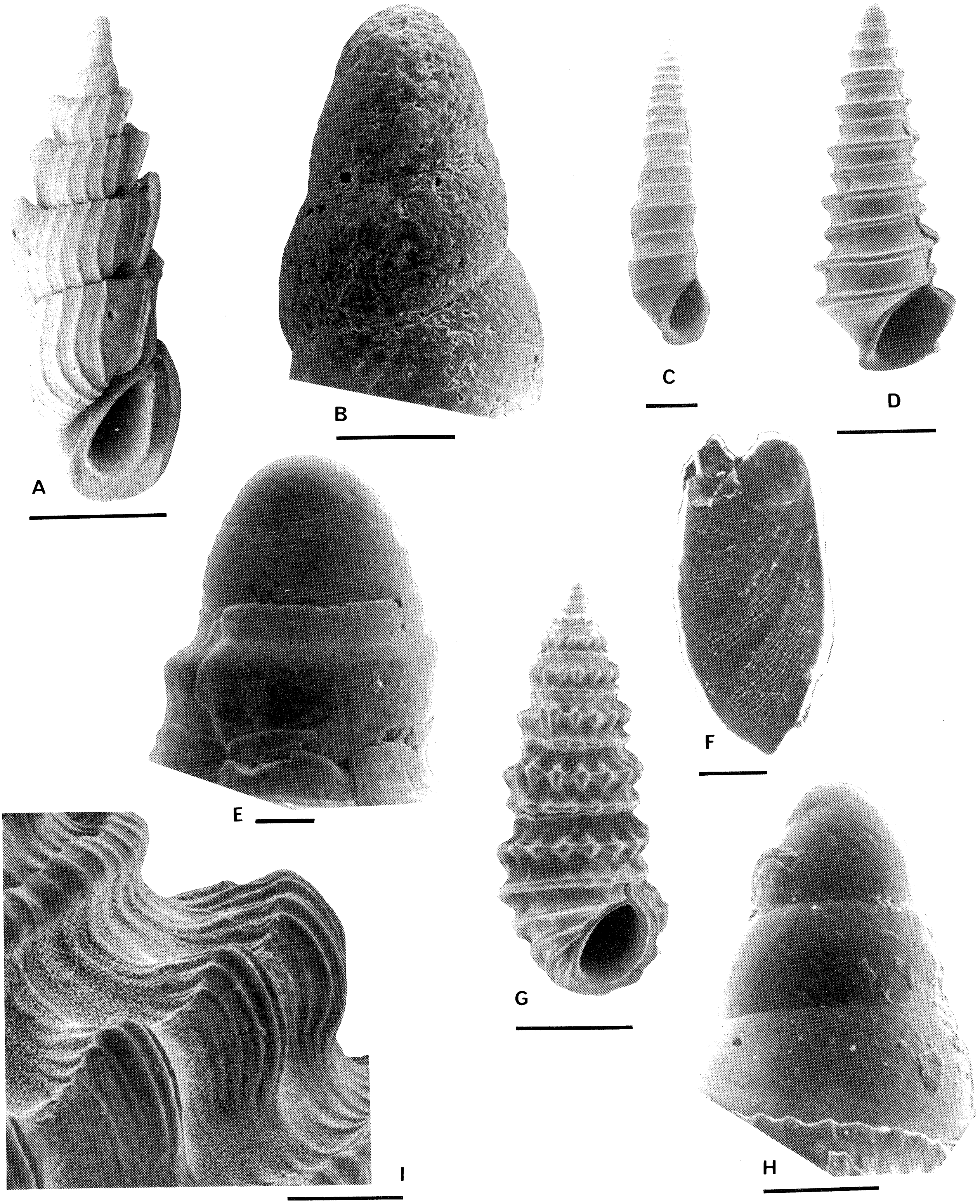

Fig. 150. **A-B**, *Palisadia subulata* Laseron, type-species of *Palisadia* Laseron: **A**, shell; **B**, protoconch (W. side of Gillett Cay, Swain Reefs, Queensland, Australia, AMS, C.138252). **C**, *Teretianax baculumpastoris* (Melvill & Standen); shell (Lifu Is., Loyalty Islands, IRSB). **D-E**, *Teretianax suteri* Oliver, type-species of *Teretianax* Iredale: **D**, shell; **E**, protoconch (Raoul Island, Kermadec Islands, AMS, C.135056). **F-I**, *Pyramidelloides miranda* A. Adams, type-species of *Pyramidelloides* Nevill: **F**, operculum; **G**, shell; **H**, protoconch; **I**, detail of teleoconch sculpture (F, Kapa Kapa, E. of Port Moresby, Papua New Guinea, AMS, C.138253; G-I, 64–73 m, W. side of Gillett Cay, Swain Reefs, Queensland, AMS, C.135057). **Scale:** shells - 1 mm; protoconchs, operculum and microsculpture - 0.1 mm.

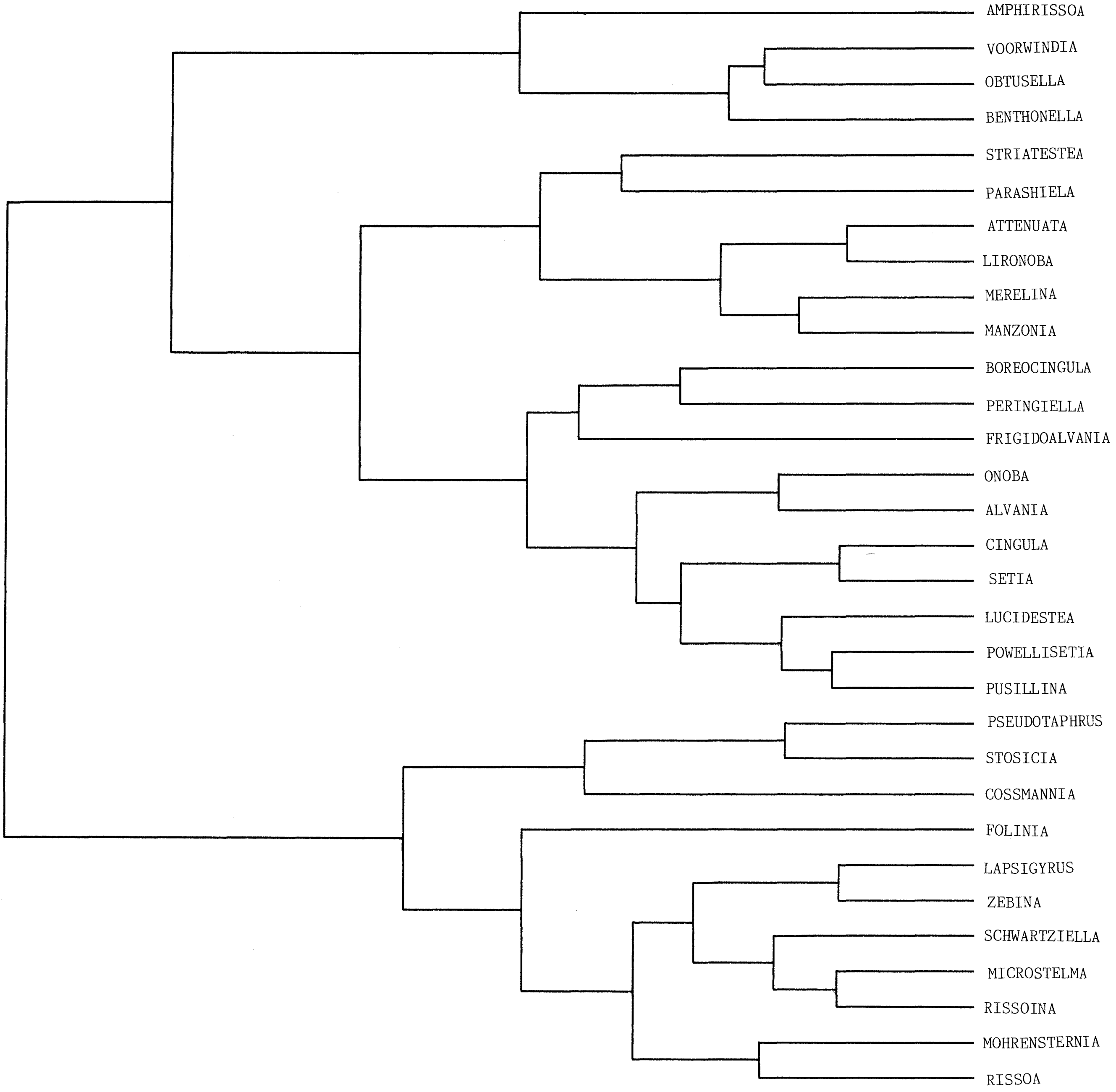

Fig. 151. Computer generated phenogram using shell characters only (for further explanation see text).

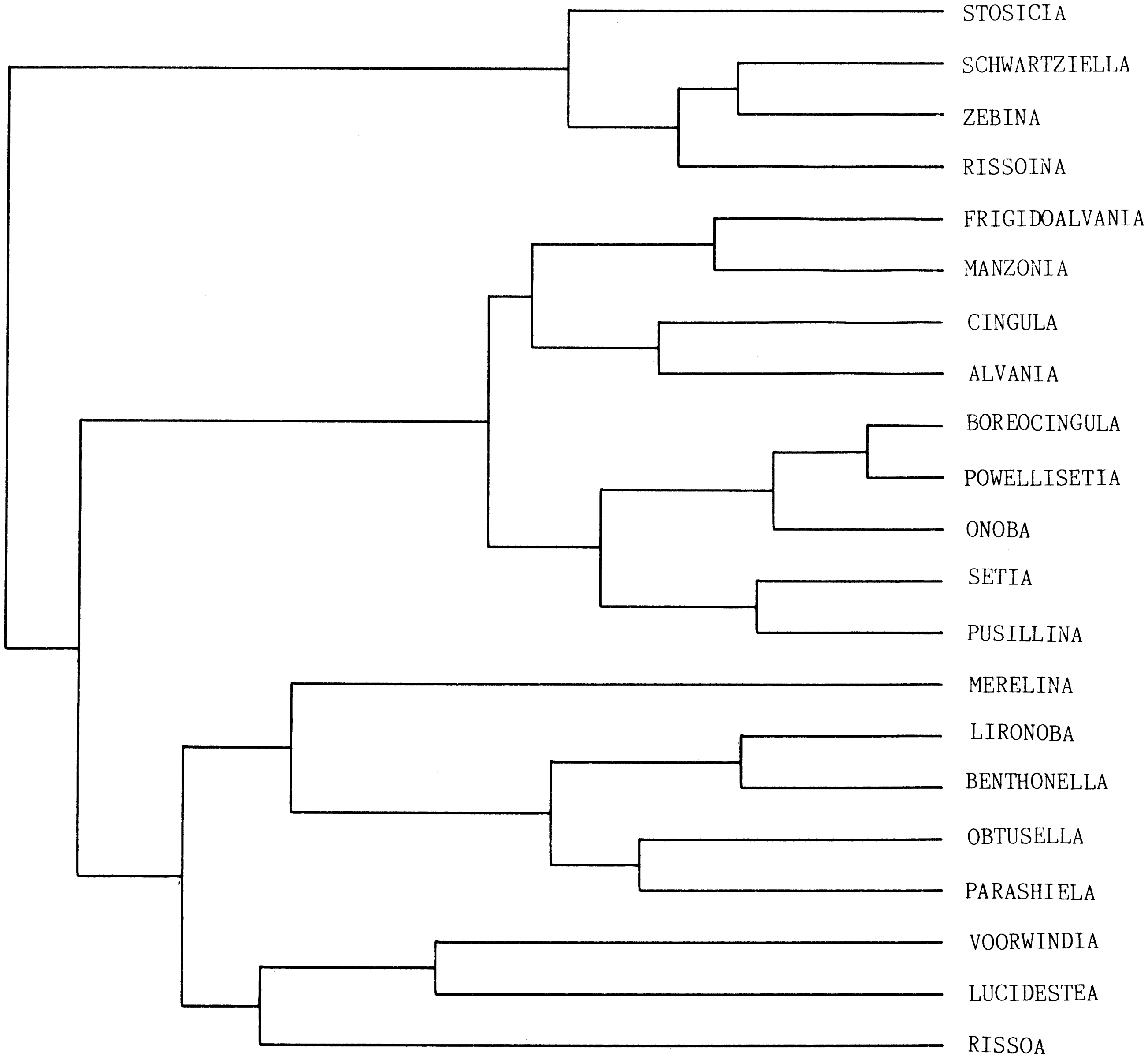

Fig. 152. Computer generated phenogram using all non-shell characters (for further explanation see text).

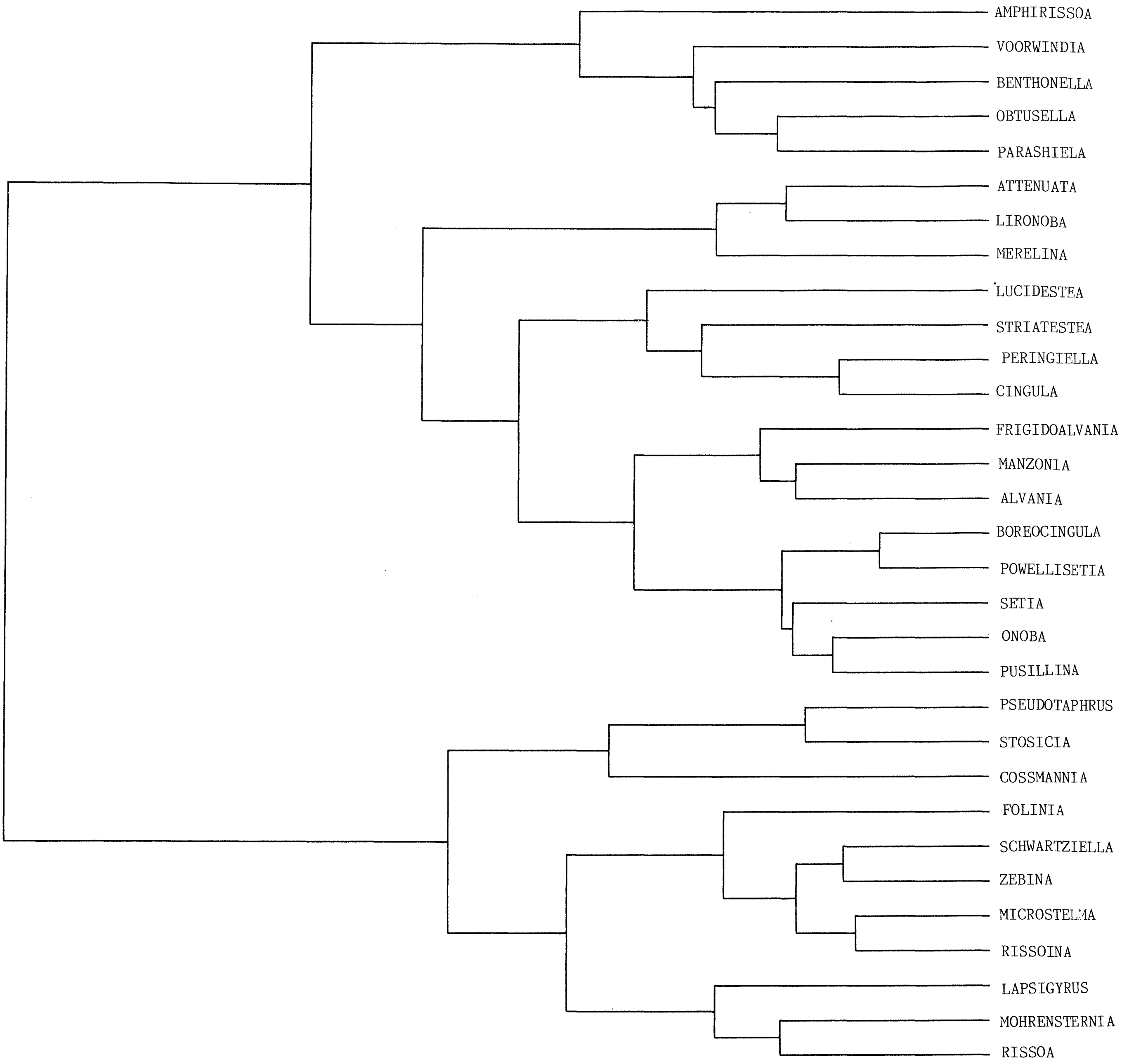

Fig. 153. Computer generated phenogram using all characters (for further explanation see text).

INDEX OF GENERIC AND FAMILY NAMES

The names listed in this index are genus-group and family- group names. The page numbers in bold type refer to major entries, those in ordinary type to minor entries.

INDEX OF SPECIES NAMES

This index contains the species-group names referred to in the text. Each name is followed by the author and date and, in most cases, by its original generic name. Proposed generic placements can be found by reference to the text. Page numbers in italics refer to illustrations.