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Review of the Genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea)

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ABSTRACT. The Barleeidae, a family of minute, marine rissoacean gastropods, is diagnosed and distinguished from the Rissoidae, with which it has usually been associated and with which it is convergent, particularly in shell form. Two subfamilies are recognized, the Barleeinae, containing five genera, two of which are new, and the Anabathrinae, containing 8 genera, one of which is new. The anatomy of several species in both subfamilies is described and the evolution of the female genitalia, in particular, is discussed. The shells, radulae, opercula and, where known, features of the head-foot and anatomy are described for each genus and typical species listed. The Barleeinae is centred in the warm-temperate and tropical eastern Pacific and the Anabathrinae in Australasia. The relationship of the Barleeidae to other families in the lower mesogastropods is briefly discussed.

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The Barleeidae encompasses a compact group of small rissoacean gastropods found mainly in shallow marine habitats in tropical to temperate regions worldwide. They have been included in the Rissoidae by most workers although, since Thiele (1925), *Barleeia* has been regarded as belonging in a separate subfamily. Fretter & Graham (1962) suggested that *Barleeia* might require a separate family on the basis of the anatomical information presented by Fretter & Patil (1961). Nordsieck (1972) and Fretter & Graham (1978) have used Barleeidae as a family, but without adequate discussion. Coan (1964) and Ponder (1967) used both Barleeinae and Anabathrinae, the latter group including several genera previously regarded as typical Rissoidae, as subfamilies of the Rissoidae.

Barleeids, as here recognized, are centred in temperate and subtropical Australasia (the subfamily Anabathrinae) and in western North and Central America (subfamily Barleeinae). They frequently occur in very large numbers on algae in the lower littoral and sublittoral but, despite this, little is known of their taxonomy, biology or ecology. Southgate (1982) has provided some biological and ecological data on *Barleeia unifasciata* (Montagu), the European type species of the family. Fretter & Patil (1961) provided some anatomical information about the same species and Ponder (1968) gave an account of the anatomy of three New Zealand species in the Anabathrinae. Lebour (1934) and Fretter & Graham (1962, 1978) gave a description of the egg capsules and the direct development of *Barleeia unifasciata*.

Judging from their protoconch morphology, all Barleeidae have direct development. The lack of a planktotrophic larval life may have contributed to the relatively high diversity in the two centres of speciation. Their assumed poor dispersal capability may account, at least in part, for the relatively small numbers of species found in areas outside these centres.

The Barleeidae do not have a known fossil record before the Eocene but are presumably Mesozoic in origin. Barleeids are not common as fossils, probably because of their preference for hard-bottom, shallow-water habitats.

There have been only four attempts to group genera in a subfamily around *Barleeia* on a world-wide basis: Thiele (1925, 1929), Wenz (1939), Coan (1964) and Ponder (1967). Thiele (1929) included only two genera (*Anabathron* and *Barleeia*, with *Nodulus* as a subgenus of *Barleeia*). Wenz (1939) added several genera which Ponder (1965a, 1965b) later showed to be eatoniellids and cingulopsids. *Anabathron* was given subfamily status by Coan (1964) and the validity of a subfamily based on this genus (but of considerably different composition from that envisaged by Coan) was supported by evidence given by Ponder (1967). Coan (1964) included 36 genera and subgenera in his Barleeinae but Ponder (1967) reassigned most of these to other families and some to other subfamilies of the Rissoidae, *Nodulus* being the only genus tentatively included in the Barleeinae apart from *Barleeia*.

Slavoshevskaya (1975) proposed a new family, Ansolidae, on the basis of the female reproductive system of *Ansola* (= *Barleeia* herein) *augustata* (Pilsbry). This family name is here regarded as a synonym of Barleeidae (see below).

The Anabathrinae, together with the Barleeinae, form a cohesive grouping which can be regarded as a family. Some of the important characters typifying this family are the pitted protoconch microsculpture, single oviduct gland, and the presence of a chitinous inner shell layer (Ponder & Yoo, 1976, fig. 12c,d) and a penis. Table 1 lists some of the important characters used to distinguish the subfamilies of the Barleeidae and, for comparison, the Rissoidae. Figure 9 outlines the major characters and character states separating the Barleeidae from several rissoacean and littorinacean families. The relationships of the Barleeidae are more fully explored in the Discussion.

Materials and Methods

The Scanning Electron Microscope (SEM) was used to examine shells, radulae and opercula using the methods given by Ponder & Yoo (1976). Anatomical work was carried out by dissection and by the examination of serial sections stained with Mallory's Triple Stain.

The majority of species described in the family have been examined and these are listed in their original names under each genus together with an indication of the status of the material examined. Species that have had their radula and operculum examined are marked under 'Material Examined' with an asterisk. Material examined alive for head-foot details and preserved material examined for anatomical details referred to under the appropriate headings. Shell descriptions are based on a synopsis of the shell features of the genus but, because of limited suitable material, the examination of protoconch microsculpture has been confined to a few species in each group. These are marked with a dagger in the list of material examined.

Abbreviations Used

AIM:	Auckland Institute and Museum, New Zealand.

AMS:	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.
BPC:	University of California, Paleontology collection, Berkeley, USA.
CAS:	California Academy of Sciences, San Francisco, USA.
HUM:	Museum für Naturkunde, Humboldt-Universität, E. Berlin, DDR.
LACM:	Los Angeles County Museum of Natural History, USA.
MCZ:	Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA.
MS:	manuscript.
NHMB:	Institute Royal des Sciences Naturelles de Belgique, Brussels.
NHMV:	Naturhistorisches Museum, Wien, Austria.
NM:	Natal Museum, Pietermaritzburg, Natal, South Africa.
NMNZ:	National Museum of New Zealand, Wellington.
NMV:	National Museum of Victoria, Melbourne.
NMW:	National Museum of Wales, Cardiff, UK.
OUM:	The University Museum, Oxford, UK.
RSM:	Royal Scottish Museum, Edinburgh, UK.
SAM:	The South Australian Museum, Adelaide.
TGM:	Instituto di Geologia, Paleontologia e Geografia Fisica, Universitá di Torino, Italy.
TM:	Tasmanian Museum, Hobart.
USNM:	National Museum of Natural History, Washington, DC, USA.

Taxonomy

Family BARLEEIDAE Gray, 1857

(*ex* Barleeiadae Gray, 1857)

Diagnosis. *Shell:* Small to minute (less than 5 mm in length), broadley-ovate to elongately-conical, umbilicate or non-umbilicate, solid, with inner chitinous layer, smooth or varously sculptured. Aperture with or without varix, rounded to weakly channelled anteriorly and posteriorly. Protoconch paucispiral, dome-shaped, microsculpture of minute pits. Periostracum thin.

Head-foot: Snout short, bilobed; cephalic tentacles long and tapering to short and paddle-shaped, conspicuously or inconspicuously ciliated, eyes in bulges at their outer bases. Pallial tentacles and metapodial tentacles typically absent (posterior pallial tentacle and short, triangular metapodial tentacle present in one genus). Foot short, simple, with or without posterior mucous gland opening by a longitudinal slit reaching to posterior end of foot. Anterior mucous gland present.

Anatomy: Pallial cavity with ctenidium about half the length of, to nearly equal in length to osphradium, ctenidial filaments finger-shaped, their bases narrower than osphradium. Jaws present or absent, odontophore well developed; salivary glands simple, tubular, not passing through nerve ring. Oesophagus lacking oesophageal gland; oesophageal pouches present in some Barleeinae. Stomach with style sac containing crystalline style. Male with penis attached to midline of head behind eyes, or behind right eye; with or without penial prostatic tissue; prostate gland pallial or partly visceral, usually well-developed, closed in most species. Seminal vesicle coiled over inner (ventral) side of stomach. Female with monaulic or diaulic genital duct; if diaulic, spermathecal opening at posterior end of pallial cavity. Capsule gland well-developed, pallial; albumen gland continuous with capsule gland and embedded in kidney. Ventral channel thin-walled, with sperm channel on left or with separated sperm duct which opens at common aperture with capsule gland at small anterior vestibule, or, in diaulic species, absent. Bursa copulatrix, if present, lying on left side of glandular oviduct. Seminal receptacle typically on left side of albumen gland, lying horizontally (i.e. latero-ventrally) and opening near or at junction of upper oviduct with oviduct gland. Upper oviduct simple, narrow. Nervous system with circumoesophageal ganglia concentrated; pedal ganglia abutting against cerebro-pedal ganglia. Renal organ with or without nephridial gland.

Operculum: Oval, pseudoconcentric or concentric with eccentric nucleus, corneous, with or without 1-2 internal pegs or internal ridge.

Radula: Taenioglossate, with few to numerous cusps on teeth. Central teeth with one pair of small basal denticles, lateral margins usually thickened, lateral teeth with short cutting edge (approximately ½-⅓ length of tooth).

Remarks. The Barleeidae is convergent with the Rissoidae, the Eatoniellidae and the Cingulopsidae. The major characters separating the Rissoidae and Barleeidae are listed in Table 1. The opercular characters (pseudoconcentric with a peg in the Barleeinae, double-layered in the Anabathrinae), the inner chitinous shell layer and pitted protoconch microsculpture are all diagnostic of the Barleeidae. This family differs from the Eatoniellidae (Ponder, 1965a, Ponder & Yoo, 1978) in having a penis as well as in many other characters. Species of the Cingulopsidae (Ponder, 1965c, Ponder & Yoo, 1980) also lack a penis and those of the Cingulopsidae and Eatoniellidae lack punctate protoconch microsculpture, have readily distinguishable radulae and differ anatomically. A more detailed discussion of the relationships of the family is given below, and summarized in Fig. 9.

Recognized Genera and Subgenera

The 13 barleeid genera listed below are arranged in the order in which they appear in the text.

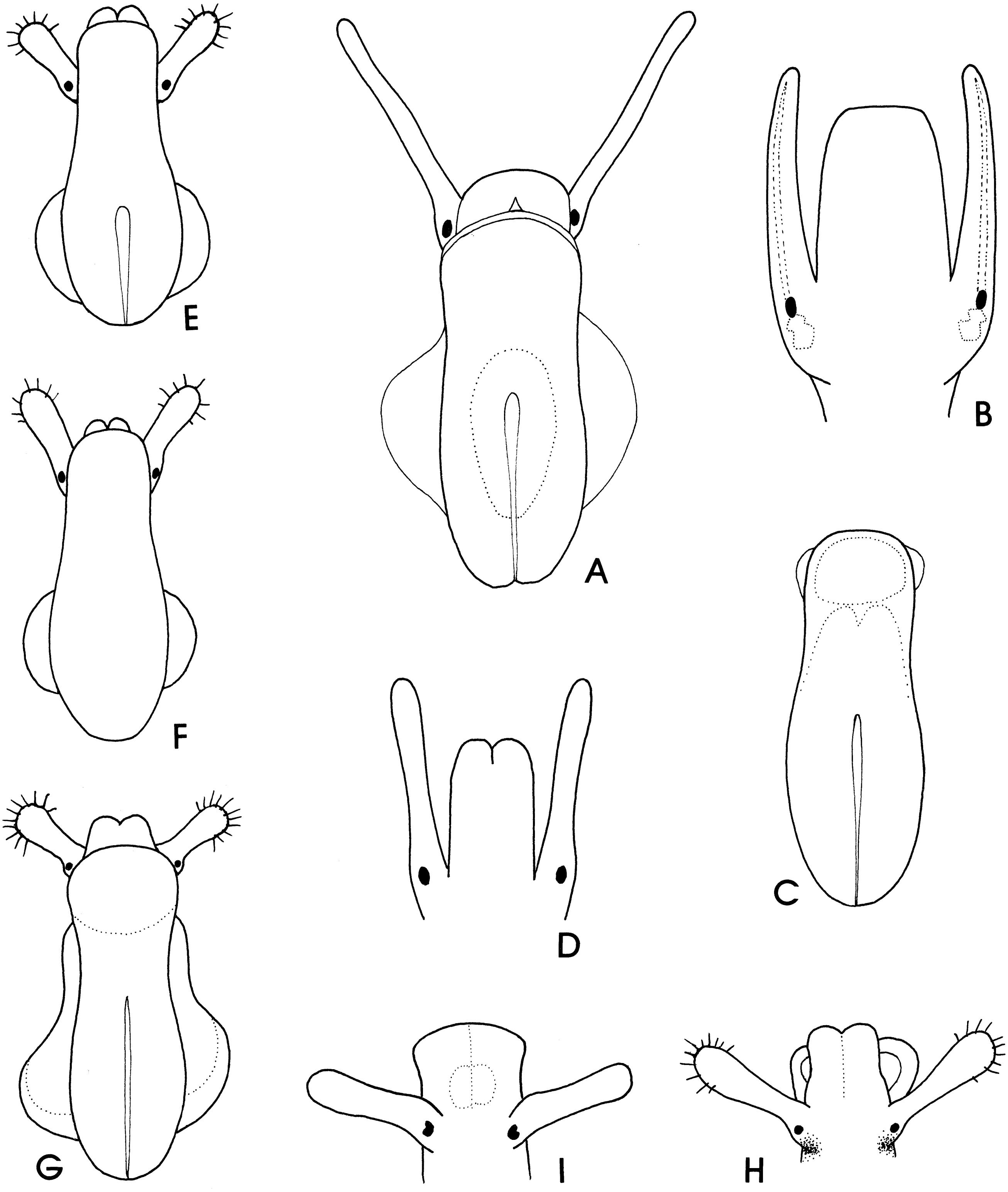

Fig. 1. **A** & **B**, Head-foot of *Barleeia unifasciata* (Montagu); Wembury, England. **A**, ventral view of head and foot; **B**, dorsal view of head. **C** & **D**, Head-foot of *Protobarleeia myersi* (Ladd); Heron Island, Queensland. **C**, ventral view of foot; **D**, dorsal view of head. **E**, Ventral view of head-foot of *Anabathron* (*Anabathron*) *contabulatum* (Frauenfeld); Boat Harbour, Cronulla, New South Wales. **F**, Ventral view of head-foot of *Anabathron* (*Scrobs*) *luteofuscus* (May); Boat Harbour, Cronulla, NSW. **G** & **H**, Head-foot of *Amphithalamus* (*Amphithalamus*) *vallei* Aguayo & Jaume; Missouri Key, Florida, USA **G**, ventral view; **H**, dorsal view. **I**, Dorsal view of head of *Badepigrus pupoides* (Adams); Port Hacking, NSW.

BARLEEINAE
- *Barleeia*
- *Protobarleeia* n.gen.
- *Lirobarleeia* n.gen.
- *Caelatura*
- *Fictonoba*

ANABATHRINAE
- *Anabathron*
  - *Anabathron* s.s.
  - *Scrobs*
- *Amphithalamus*
  - *Amphithalamus* s.s.
  - *Notoscrobs*
- *Microdryas*
- *Badepigrus*
- *Afriscrobs* n.gen.
- *Pseudestea*
- *Pisinna*
- *Nodulus*

Key to Subfamilies of Barleeidae

1. Operculum with convex outer surface, composed of one layer and with prominent peg and longitudinal ridge on middle part of inner surface .... BARLEEINAE

—Operculum with flat surface, composed of 2 layers, with or without peg(s); without longitudinal ridge on middle part of inner surface (a ridge may occur along inner [or columellar] edge) .... ANABATHRINAE

Subfamily BARLEEINAE

Synonym: ANSOLIDAE Slavoshevskaya, 1975.

Diagnosis. *Shell:* Small to minute (1-5 mm in length), conical, ovate or elongately ovate to elongately conical, non-umbilicate to narrowly umbilicate, solid, with inner chitinous layer moderately to poorly developed, smooth or with axial or spiral sculpture or both. Aperture with simple peristome, with or without varix, angled posteriorly, angled to convex anteriorly, outer lip prosocline to opisthocline. Protoconch dome-shaped, minutely pitted.

Head-foot: With slender, non-tapering to only slightly tapering cephalic tentacles. Foot usually rather short and broad, with or without posterior mucous gland opening by way of long slit in metapodium. Anterior mucous gland well developed. Metapodial tentacle and posterior (right) pallial tentacle present in one genus.

Anatomy: Penis attached behind right eye, externally and/or internally glandular, large, straight. Prostrate gland enclosed in penis or wholly within right pallial wall, or partly protruding into renal organ; closed or (rarely) open. Female pallial duct (of *Barleeia*) with posterior spermatheca separate from distal oviduct opening and capsule gland with thick ventral wall, or single distal opening and capsule gland with thin ventral wall. Bursa copulatrix present or absent. Oesophageal pouches present in some genera; dorsal folds in mid-oesophagus short.

Operculum: Composed of one layer; oval, yellow or red, outer surface convex, pseudo-concentric, with heavy, internal, longitudinal ridge and prominent peg lying at right angles to longitudinal axis.

Radula: Central teeth with few cusps, lateral margins at 20°–45°, cutting edge triangular; face of tooth with U-shaped ventral projection (absent in one genus) which lies immediately above next tooth (Fig. 17G:*p*)and, below this, ventral margin (Fig. 17G:*m*) projects beneath tooth in front. Lateral teeth with few cusps, cutting edge short relative to total length of tooth. Marginal teeth with several cusps on distal ¼–½ of outer edge of inner marginal teeth and inner and/or outer edge of outer marginal teeth.

Remarks. The members of this small subfamily form a compact group distinguished by their peculiar operculum and pitted protoconch.

Slavoshevskaya (1975) proposed a new genus (*Ansola*) and family for *Assiminea angustata* Pilsbry on the basis of the structure of the reproductive system. From the initial brief account and a later (1976) detailed study, there appear to be very few differences between *A. angustata* and *Barleeia unifasciata*. The main difference appears to be in the presence of a pallial prostrate in *B. unifasciata* whereas in *A. angustata* the prostatic tissue is contained in the penis. As all other aspects of the morphology of *A. angustata* and *B. unifasciata,* including their shell, opercular and radular features, appear to be very similar I regard *Ansola* as a synonym of *Barleeia.*

The species of Barleeinae are centred along the west coast of North and Central America including the Galapagos Islands. A few are found in most other temperate and tropical seas; mainly in shallow water.

General Anatomical Account of the Barleeinae

This description of the anatomy of the Barleeinae is based on five species of *Barleeia: B. acuta* (Carpenter) and *B. haliotiphila* (Carpenter) from Monterey, California, U.S.A., *B. unifasciata* (Montagu) from Bantry Bay, SW Ireland, *B. cf. tincta* (Guppy) from Fort Pierce, Florida, U.S.A., and *B. angustata* (Pilsbry) (the last based on data from Slavoshevskaya, 1975, 1976), *Lirobarleeia galapagensis* (Bartsch), from Academy Bay, Santa Cruz Island, Galapagos Islands, and *Fictonoba carnosa* (Webster) from Takapuna, Auckland, New Zealand.

The pallial cavity. The pallial cavity contains a well-developed, elongately oval osphradium with a central sensory area which contains the osphradial ganglion. The osphradium is surrounded by a border-like ciliated ridge on both sides. The ctenidium is longer than the osphradium (which varies from a little over half the length of the ctenidium to only slightly shorter), and is composed of well-developed, finger-shaped filaments.

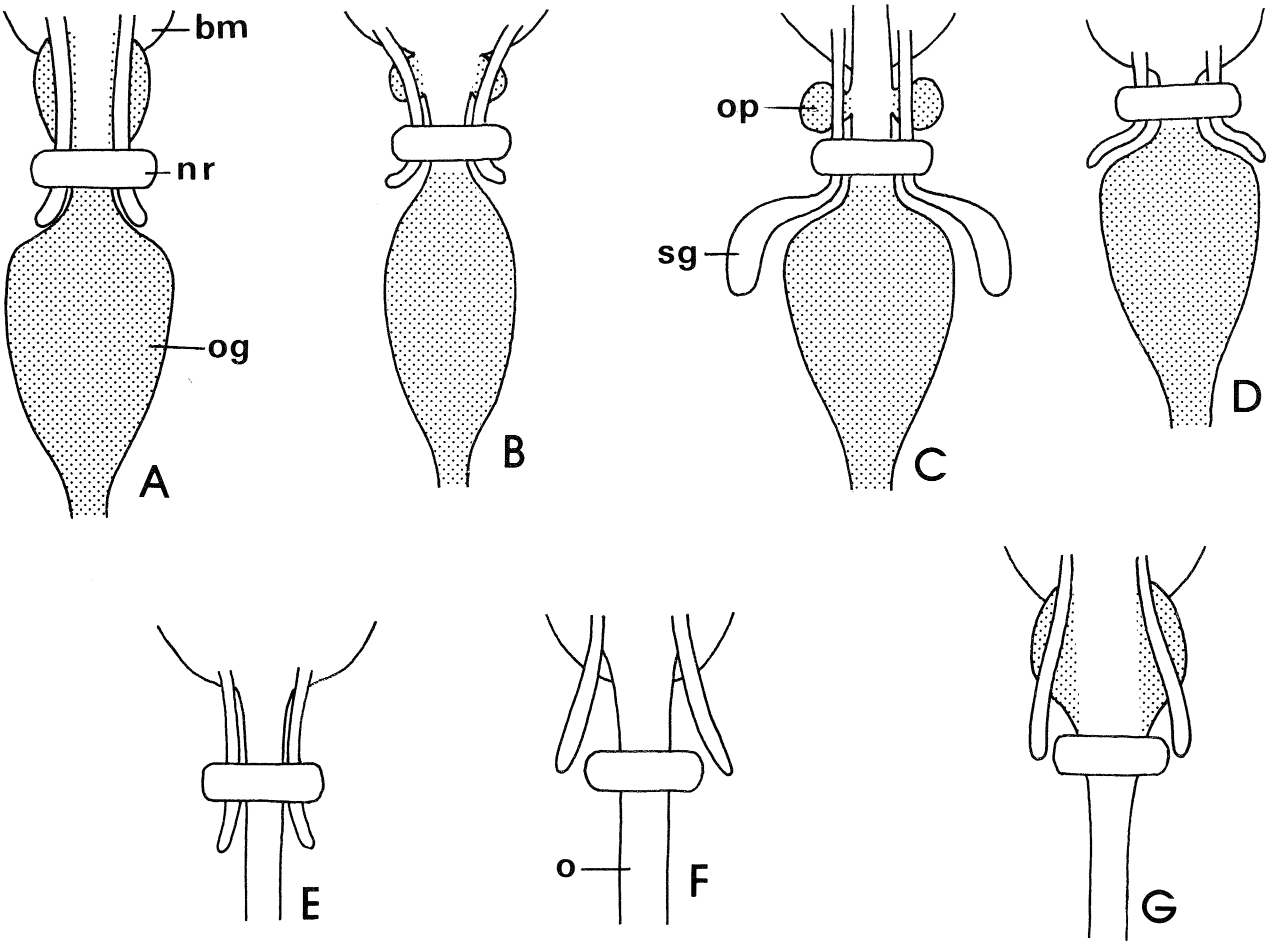

Fig. 2. Diagrammatic representations of the mid-oesophagus of selected rissoacean and littorinacean species to show the relationships of the salivary glands and oesophageal gland to the nerve ring. For further explanation see 'Discussion'. **A,** *Eatoniella* spp. (Eatoniellidae) and *Macquariella kingensis* (May) (Littorinidae). **B,** *Laevilitorina mariae* (T. Woods) (Littorinidae). **C,** *Littorina* spp. (Littorinidae). **D,** *Eatonina rubrilabiata* Ponder & Yoo (Cingulopsidae). **E,** *Skenella castanea* (Laseron) (Cingulopsidae). **F,** Rissoidae and Anabathrinae. **G,** *Barleeia* spp. (Barleeinae).
bm, buccal mass; *nr,* nerve ring; *o,* oesophagus; *og,* oesophageal gland; *op,* oesophageal pouch; *sg,* salivary gland.

A hypobranchial gland is present but is not thickly developed. In *Fictonoba carnosa* the posterior part of the gland is dark brown.

The pedal glands. The foot contains an anterior pedal gland which consists of a core of glandular tissue reaching to the base of the cephalic haemocoel to lie beneath the buccal mass. *Lirobarleeia galapagensis* and species of *Barleeia* also have a posterior pedal gland that opens, in *Barleeia,* into a long midventral slit. No species of *Lirobarleeia* have been observed alive but they probably have a similar slit. *Fictonoba carnosa* lacks the posterior pedal gland but has a similar anterior pedal gland.

The digestive system. There is a well-developed buccal mass with a powerful odontophore. The oral tube does not contain any jaws in *B. angustata* and *B. unifasciata* but a rudimentary jaw is present in *B. haliotiphila.* This is composed of a pair of dark-staining patches of chitin projecting slightly from the oral tube. In *B. acuta* and *B.* cf. *tincta* a pair of small jaws is present consisting of short rodlets. *Fictonoba carnosa* and *Lirobarleeia galapagensis* lack jaws.

The anterior oesophagus opens to the buccal cavity and in the species of *Barleeia* and in *Lirobarleeia galapagensis* is surrounded by a pair of sac-like extensions of the oesophagus. These lie anterior to the nerve ring and are probably homologous with the oesophageal pouches of the Littorinidae. The pouches open laterally to the oesophagus (Fig. 2G) and contain an epithelium similar to that of the oesophageal gland of lower mesogastropods (see 'Discussion' for further comment on the homology of these structures). The anterior oesophagus in *Fictonoba carnosa* is simple, having no trace of similar structures. The dorsal folds in the anterior oesophagus are short in the three genera examined and do not persist behind the nerve ring.

The tubular salivary glands are simple and extend back to the nerve ring and lie dorsal to it. There are two

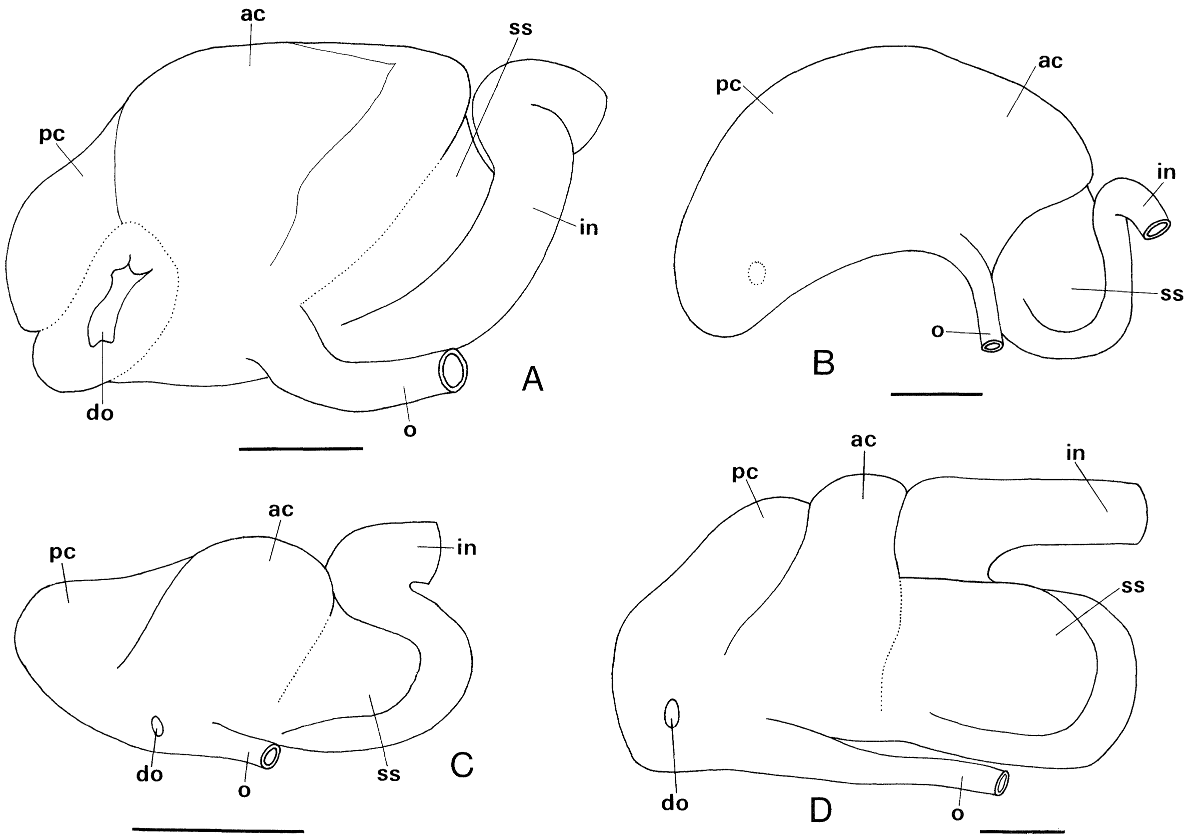

Fig. 3. Stomachs of some species of Barleeidae. **A,** *Barleeia acuta* (Carpenter); Monterey Peninsula, California, USA. **B,** *Fictonoba carnosa* (Webster); Takapuna, Auckland, New Zealand. **C,** *Amphithalamus incidatus* (Frauenfeld); Boat Harbour, Cronulla, NSW. **D,** *Pisinna frauenfeldi* (Frauenfeld). Boat Harbour, Cronulla, NSW. *ac,* anterior chamber; *do,* digestive gland opening; *in,* intestine; *o,* oesophagus; *pc,* posterior chamber; *ss,* style sac. Scale:0.2 mm

types of secretory cell present in all three genera. The simple, narrow posterior oesophagus opens to the spacious stomach (Fig. 3A,B) which is of the usual structure for a microphagous mesogastropod. The stomach has a style sac which contains a crystalline style. The style sac (Fig. 3: *ss*) is short relative to the rest of the stomach in the three genera examined but the stomach is relatively shorter in *Barleeia* (Fig. 3A) than in *Fictonoba* (Fig. 3B) or *Lirobarleeia*. The intestine loops around the style sac towards the outer end of the anterior chamber and then follows a rather straight course along the right pallial wall to a little behind the outer edge of the pallial cavity.

The digestive gland opens to the stomach just behind the oesophageal opening by way of a single opening (Fig. 3: *do*). The excretory cells contain vacuoles with dark brown spherules in *Barleeia* species, although these are less abundant than in many rissoaceans. What appear to be the same vacuoles in *Fictonoba carnosa* are filled with several tiny refringent yellowish granules and lack spherules. The material of *L. galapagensis* was not fixed adequately to determine whether or not spherules were present.

The renal organ. The simple, sac-like renal organ is situated immediately behind the posterior pallial wall, through which it opens by way of a small aperture. There is a thick, glandular pad (nephridial gland) on the outer wall.

The nervous system. This has been studied only for *Barleeia acuta, B. angustata* (by Slavoshevskaya, 1976) and *Fictonoba carnosa.* The cerebral ganglia are separated by a short commissure, the pleural ganglia are fused to the cerebral ganglia and the pedal ganglia are fused to the cerebro-pleurals (in *Barleeia*), but are joined by short connectives in *F. carnosa.* The supraoesophageal connective is about two-thirds the length of the supraoesophageal ganglia in *F. carnosa*, but in the two species of *Barleeia* the ganglia almost abut. The suboesophageal connective is indistinguishable in *Barleeia* spp. and about one-third the length of the suboesophageal ganglion in *F. carnosa.* The pedal ganglia are about the same size as the cerebral ganglia in *Barleeia* spp. (information not available for *F. carnosa*).

Slavoshevskaya (1976) gives some additional details about the nervous system of *Barleeia angustata.*

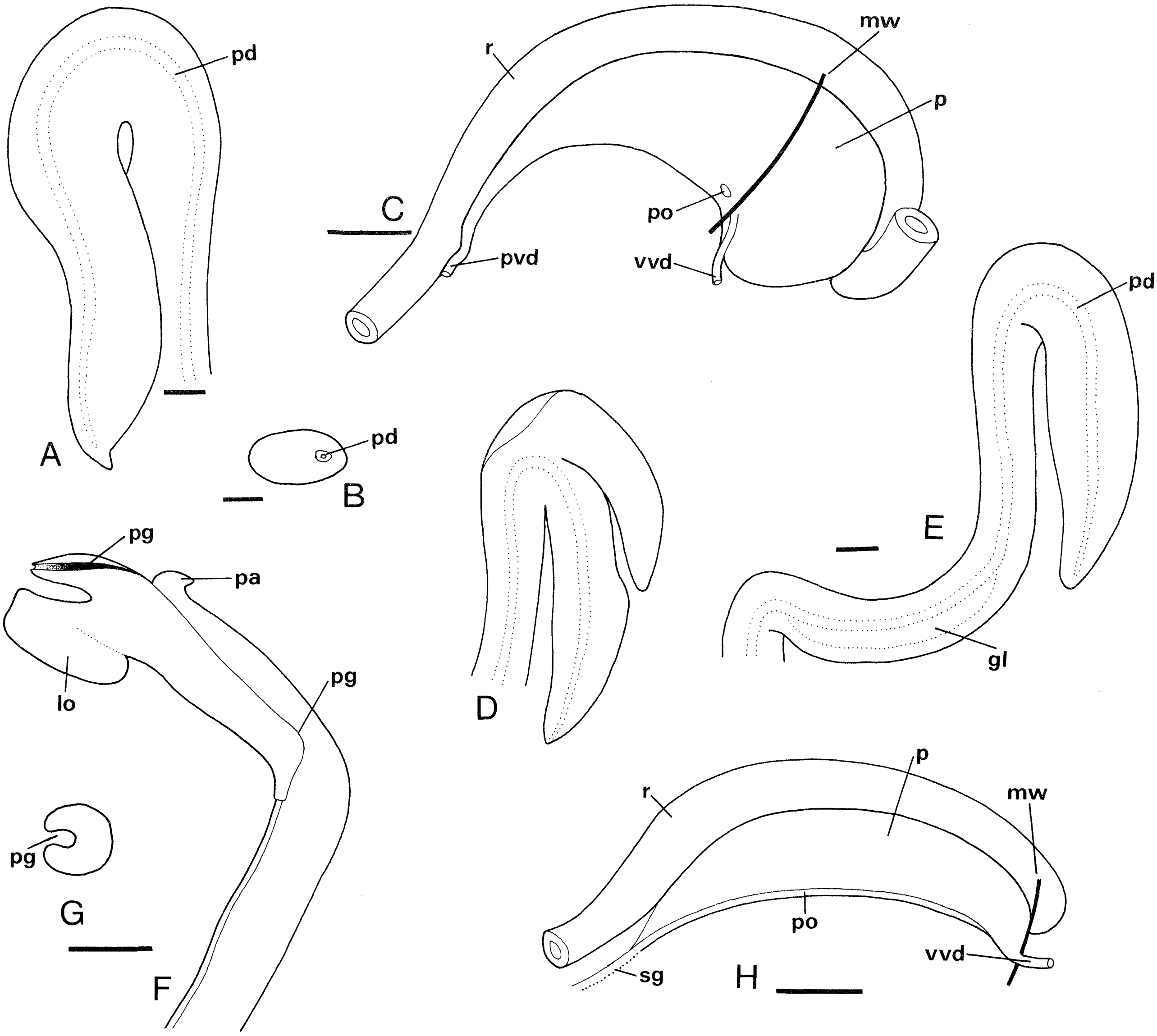

Fig. 4. Male genitalia of Barleeinae. **A–C,** *Barleeia acuta* (Carpenter), Monterey Peninsula, California, USA. **A,** dorsal view of penis at rest (preserved specimen); **B,** transverse section of penis (semi-diagrammatic); **C,** prostate gland and part of the intestine-rectum. **D** & **E,** penis of *Lirobarleeia galapagensis* (Bartsch), Bahia Academy, Isla Santa Cruz, Galapagos Islands. **D,** distal end of specimen with bifurcate penis; **E,** specimen with simple penis. **F–H,** *Fictonoba carnosa* (Webster); Takapuna, Auckland, New Zealand. **F,** penis from preserved specimen; **G,** transverse section of shaft of penis (semi-diagrammatic); **H,** prostate gland and part of the intestine-rectum.
gl, internal glandular area; *lo,* glandular lobe; *mw,* posterior wall of pallial cavity; *p,* prostate gland; *pa,* papilla-like projection; *pd,* penial duct; *pg,* penial groove; *po,* pallial opening to prostate gland; *pvd,* pallial vas deferens; *r,* rectum; *sg,* seminal groove; *vvd,* visceral vas deferens. Scales: 0.1 mm.

The male reproductive system (Fig. 4). Males of all the species listed above were examined histologically except *Lirobarleeia galapagensis,* in which the gross anatomy of the male reproductive system was examined. The testis is rather indistinctly lobed and lies above the digestive gland over all but about the last whorl of the visceral coil. The visceral vas deferens (Fig. 4: *vvd*) is expanded to form a seminal vesicle which either lies loosely undulating behind the stomach (in *L. galapagensis* and *B. acuta*), extends straight over the inside (ventral) wall of the stomach (in *B.* cf. *tincta*), or is coiled over the inside wall of the posterior end of the stomach (in *Fictonoba carnosa*). The seminal vesicle contains typical (eupyrene) and atypical (? apyrene) sperm in *Barleeia* species (as described in detail by Slavoshevskaya, 1976 for *B. angustata*) but only typical sperm in *Fictonoba carnosa.*

The prostate gland (Fig. 4: *p*) lies either entirely in the posterior part of the pallial cavity (as in *B. unifasciata* and *F. carnosa* [Fig. 4H]) or partly embedded in the kidney and partly within the pallial wall (*B. acuta* [Fig. 4C], *B. haliotiphila, B.* cf. *tincta* and *Lirobarleeia galapagensis*), or there is no pallial prostate gland, the pallial vas deferens being a simple, narrow tube (as in *B. angustata*). The prostate gland is open to the pallial cavity by way of a short, narrow, ciliated duct (Fig. 4C: *po*) which arises at the junction of the pallial vas deferens with the prostate gland (at the posterior pallial wall). There appears to be a short slit open to the pallial cavity in the prostate of *Lirobarleeia galapagensis* but this was difficult to ascertain with certainty in the material available. The prostate lumen in both *L. galapagensis* and *Barleeia* spp. is a centrally-placed slit. In *Fictonoba carnosa* (Fig. 4H) the prostate gland is open ventrally in all but the most posterior section. The pallial vas deferens in *F. carnosa* is a ciliated groove (Fig. 4H: *sg*) which emerges from the distal end of the prostate gland. The prostatic tissue contains granules which in *F. carnosa* stain blue and yellowish orange within the same cell but are only blue in *Barleeia* spp. The visceral vas deferens enters the prostate gland immediately behind the posterior pallial wall. The pallial vas deferens leaves immediately in front of this wall in *B. haliotiphila* and at the distal end of the gland in *B. unifasciata* and *Lirobarleeia galapagensis*. The pallial vas deferens lies just beneath the epithelium, is weakly muscular and is ciliated.

The penis in species of *Barleeia* (Fig. 4A,B) is long (longer than the pallial cavity), slender (relative to its length), coated with epithelial gland cells, and usually bent back on itself. In *B. haliotiphila* and *B. acuta,* these cells are modified distally into a clump of glandular columnar cells, the granular contents of which stain purple-red. The penial duct is ciliated, weakly muscular and lined with cuboidal epithelium. In *B. angustata* this epithelium is modified to form prostatic tissue (Slavoshevskaya, 1975, 1976). In *Lirobarleeia galapagensis* (Fig. 4D,E) the penis is also long and rather slender but is expanded distally. Of the three specimens examined one had a discrete flat lobe a little behind the distal end (Fig. 4D), but in the other two specimens the distal end of the penis was simple, flattened and expanded (Fig. 4E). A dense-white, glandular zone (Fig. 4E: *gl*) lies internally alongside the penial duct in the proximal third of the penis in this species and a similar development was evident in sections of *B. acuta.* The penis of *Fictonoba carnosa* (Fig. 4F,G) is similar to that of *Lirobarleeia galapagensis* and *Barleeia* spp. in that it is large relative to the rest of the animal, and is placed behind the right eye. It is, however, more complex in construction and has an open penial groove (*pg*), not a closed duct. The distal portion of the penis has an expanded, flange-like, glandular lobe (*lo*), a narrow distal portion along which the deep penial groove passes and, at the base of this latter part, a smaller, papilla-like projection (*pa*). The glandular lobe contains a mass of purple-red-staining gland cells which lie amongst radial muscle fibres.

The female reproductive system (Figs 5, 6). The ovary is compact, and contains large, yolky eggs in all species. The upper oviduct is narrow and thickens slightly before entering the fertilization area. This short, thickened region, the renal oviduct, is lined with cuboidal to short columnar cells and has a narrow lumen in *Barleeia unifasciata, B. acuta, B. haliotiphila* and *Fictonoba carnosa.* The nature of the renal oviduct in *Lirobarleeia* was not determined. In *Barleeia angustata* the renal oviduct is lined with columnar cells with irregular apices and basal nuclei which resorb spermatozoa (Slavoshevskaya, 1976). No indication of this phenomenon was observed in any of the species I have examined. The renal oviduct opens to the 'fertilization chamber' in species of *Barleeia* and in *Lirobarleeia galapagensis*, and to the albumen gland in *Fictonoba carnosa.*

The fertilization chamber (Figs 5G, 6: *fc*) in species of *Barleeia* is a ventral sac just behind the posterior end of the capsule gland. It is lined with ciliated cells and goblet cells and opens by way of a short, ciliated spermathecal duct (Fig. 6: *sd*) to the posterior pallial cavity. The renal oviduct (Fig. 5G: *od*) opens to this chamber in a short, muscular papilla (Fig. 6: *p*). The opening is closed by what is assumed to be a sphincter muscle in all the material sectioned. There is a small, posterior, latero-ventral (left) seminal receptacle (Figs 5G, 6: *sr*) which opens to the fertilization chamber. The fertilization chamber lies below the large albumen gland (Figs 5G, 6: *ag*), which opens to the chamber. This gland is continuous with the capsule gland (Figs 5G, 6: *cg*) and the capsule gland does not open independently to the fertilization chamber. The albumen gland extends anteriorly as a long lobe reaching into the pallial wall to lie above the posterior end of the capsule gland. This anterior lobe (Figs 5G, 6: *ss*) is considerably thinner-walled than the rest of the albumen gland and is lined with pale blue-staining, glandular, short columnar cells with wedge-shaped ciliated cells between. The histology is essentially similar to that of the albumen gland except that the gland cells of that structure are much longer and contain much larger granules which stain dark blue. The lobe contains spermatozoa (Figs 5G, 6: *sz*) which have their heads attached to the epithelium. This structure is referred to as a seminal receptacle in *B. angustata* by Slavoshevskaya (1976), and the structure here referred to as the seminal receptacle was identified as the bursa copulatrix by that author. Although this modified part of the albumen gland was identified in *B. unifasciata*, the rather poor sections available of that species did not show any sperm present.

The capsule gland in species of *Barleeia* is oval in section (Fig. 5H) with a slit-like lumen with glandular epithelium ventral (and dorsal) to the ends of the lumen. The distal opening (Fig. 5G: *ga*) is simple and by way of a narrow, ciliated vestibule.

Lirobarleeia galapagensis has a female reproductive system which is generally similar to that of species of *Barleeia* but differs in several important respects. A seminal receptacle (Fig. 5C: *sr*) is present and opens to

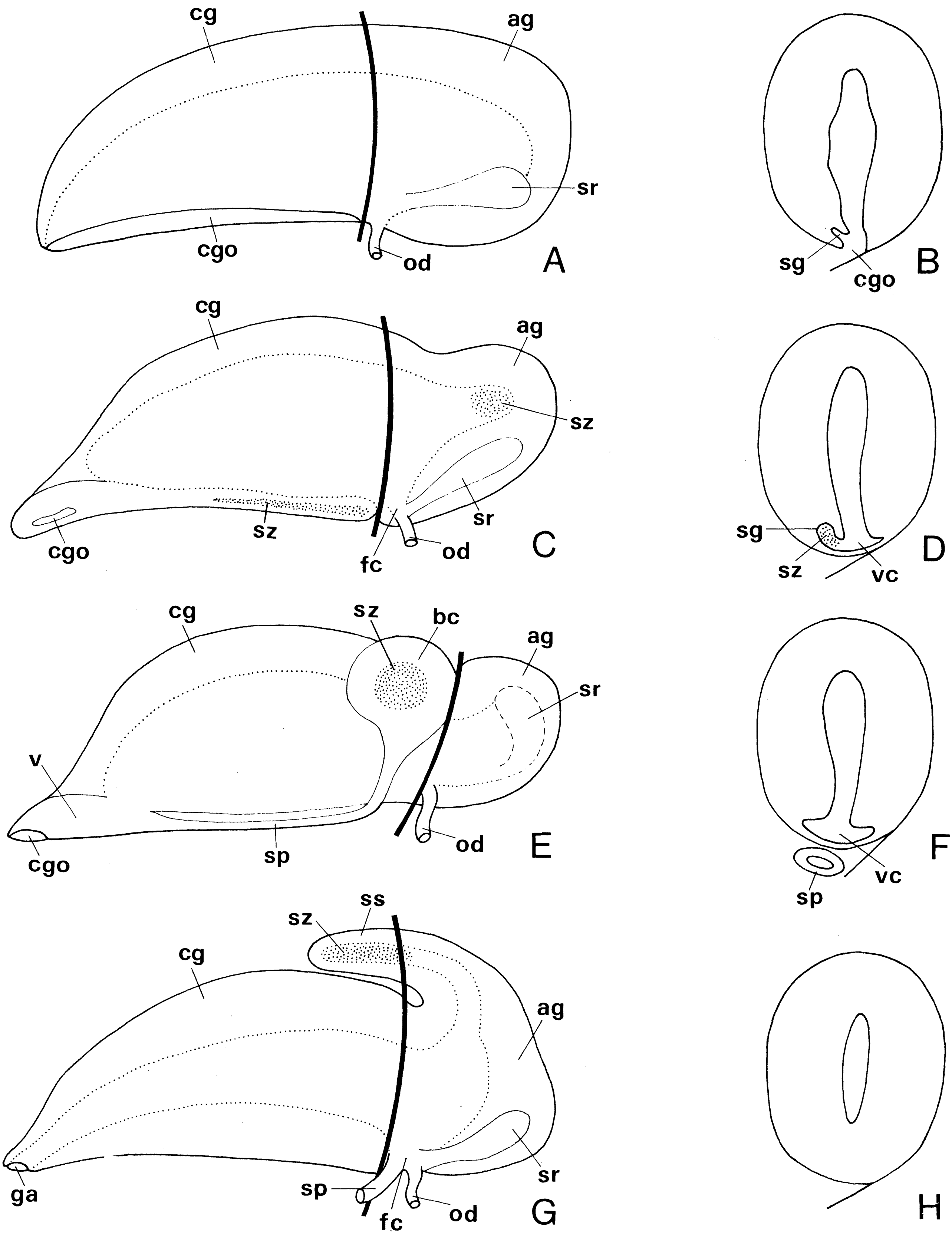

Fig. 5. Semidiagrammatic representations of the female genital systems of some Barleeinae, as seen from the left (inner) side with a section through the middle region of the capsule gland. **A & B**, hypothetical ancestor. **C & D**, *Lirobarleeia galapagensis* (Bartsch). **E & F**, *Fictonoba carnosa* (Webster). **G & H**, *Barleeia* spp.
ag, albumen gland; *bc*, bursa copulatrix; *cg*, capsule gland; *cgo*, common genital opening; *fc*, fertilization chamber; *ga*, oviducal opening; *od*, upper oviduct; *sg*, sperm groove; *sp*, spermathecal tube; *sr*, seminal receptacle; *ss*, sperm storage area; *sz*, spermatozoa; *v*, vestibule; *vc*, ventral channel.

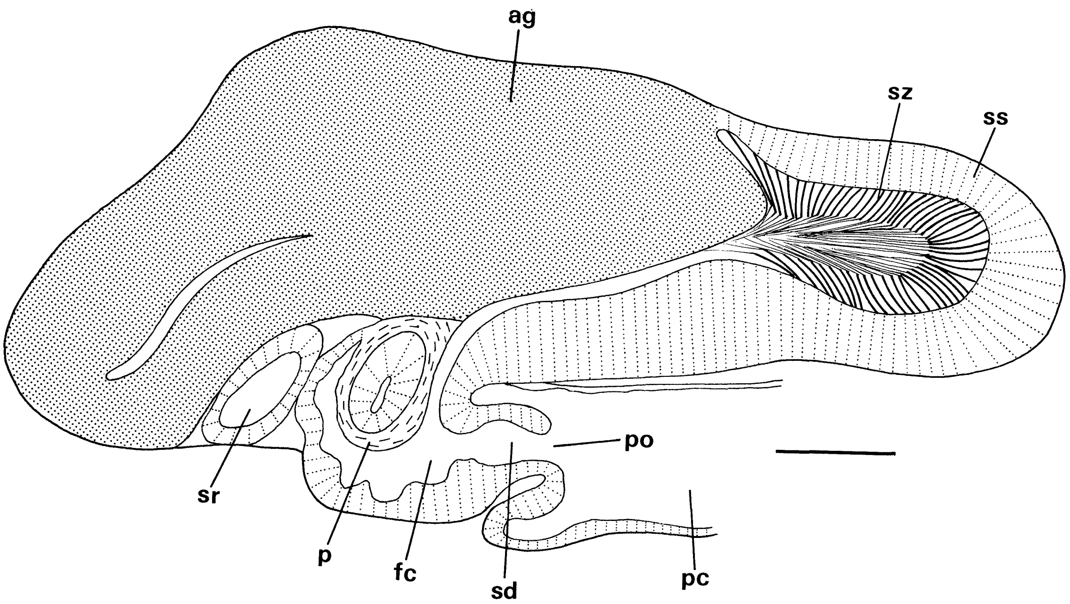

Fig. 6. Longitudinal section of part of the female genital system of *Barleeia haliotiphila* (Carpenter). The figure shows the spermathecal opening to the pallial cavity and the sperm sac derived from the modified albumen gland. *ag*, albumen gland; *fc*, fertilization chamber; *p*, papilla; *pc*, pallial cavity; *po*, pallial spermathecal opening; *sd*, spermathecal duct; *sr*, seminal receptacle; *ss*, sperm sac; *sz*, spermatozoa. Scales: 0.05 mm.

a fertilization chamber along with the renal oviduct (Fig. 5C: *od*), which does not appear to be produced into a muscular papilla. The fertilization chamber (Fig. 5C: *fc*) lies beneath the albumen gland (*ag*) and opens to this gland just behind the capsule gland (*cg*). The albumen gland appears to be folded into at least a U-shaped fold in sections but the details could not be determined in dissection. The albumen gland is partly divided off from the capsule gland although it is continuous with it. There is no dorsal, forwardly-projecting lobe modified for sperm storage but the albumen gland does appear to store small quantities of sperm. The poor fixation of the material, however, did not allow this to be established with certainty. The capsule gland has a thin-walled ventral channel (Fig. 5D: *vc*) which contains a well-developed sperm groove (*sg*) separated from the lumen of the gland by a longitudinal, non-muscular fold on the left side. This groove contains a mass of sperm (Figs 5C,D: *sz*) and appears to terminate blindly at the posterior end of the capsule gland. At this point the rest of the ventral channel (i.e. that part not the sperm groove) opens to a small, thin-walled, ventral sac (= the fertilization chamber) (Fig. 5C: *fc*). Anteriorly the sperm groove closes over just before reaching the vestibule to form a separate duct and then opens within the narrow vestibule/vagina, although the sperm groove and oviduct remain separated by a dorsally-attached, longitudinal flap of tissue right to the terminal opening (*cgo*).

The fertilization chamber in *Fictonoba carnosa* is a thin-walled section of the antero-ventral part of the albumen gland into which the seminal receptacle (Fig. 5E: *sr*) and renal oviduct (*od*) open. The seminal receptacle lies on the right side of the albumen gland, is lined with a pavement epithelium and contains semi-orientated sperm. The renal oviduct opens at a small papilla-like structure, smaller and less muscular than in *Barleeia*. The albumen gland (*ag*) and capsule gland (*cg*) are separate lobes but continuous ventrally. A thin-walled ventral channel (Fig. 5F: *vc*) in the capsule gland does not contain a sperm groove, but instead a separate spermathecal tube (*sp*) lies ventrally to it. This tube opens anteriorly into a large ciliated vestibule (Fig. 5E: *v*) which is apparently not used for sperm storage. The spermathecal tube passes dorsally on the left side of the posterior end of the capsule gland to open to a latero-dorsal bursa copulatrix (Fig. 5E: *bc*). This structure is lined with columnar cells with irregular apices and was empty of sperm in most of the specimens sectioned.

Key to the Genera of the Barleeinae

1. Shell ovate-conic to conic, smooth or with spiral sculpture 2

——Shell elongate-conic to elongate-pupoid, smooth or with spiral and/or axial sculpture 3

2. Shell smooth or with weak spiral striae; protoconch microsculpture of regular, spirally-arranged pits .... *Barleeia*

—— Shell with spiral cords; protoconch microsculpture of spiral ridges and honeycomb-like pits .... *Protobarleeia* n.gen.

3. Teleoconch with microsculpture of minute pits; axial or spiral sculpture, or smooth *Caelatura*

—— Teleoconch without microsculpture of minute pits; axial and/or spiral sculpture, rarely smooth 4

4. Protoconch microsculpture of irregular, shallow pits; penis with open seminal groove .... *Fictonoba*

—— Protoconch microsculpture of irregular, deep pits; penis with closed duct .... *Lirobarleeia* n.gen.

Genus *Barleeia* Clark, 1853

Barleeia Clark, 1853: 292. Type species *Turbo ruber* J. Adams, 1797, *not* von Salis, 1793 (= *T. unifasciatus* Montagu, 1803); by monotypy. Recent, eastern Atlantic and Mediterranean Sea. (Figs 1A,B; 10 A-E).

Barleia, Barleeja err. auct.

Pseudodiala Ponder, 1967: 219. Type-species *Diala acuta* Carpenter, 1864; by original designation. Recent, western North America (Figs 3A, 4A-C; 11 A-D)

Ansola Slavoshevskaya, 1975: 119. Type-species *Assiminea angustata* Pilsbry, 1901; by original designation. Recent, north-western Pacific (Fig. 10F,G).

Diagnosis. *Shell:* Small (1-4 mm), rather solid, conic to ovate-conic, non-umbilicate, smooth or with weak spiral threads, periphery convex to angled. Aperture with simple peristome, angled but not channelled posteriorly, subangled to rounded anteriorly. Outer lip usually prosocline, rarely orthocline or opisthocline, with or without varix, thin, with sharp edge (Figs 10A,F; 11A). Protoconch paucispiral, dome-shaped, with numerous small pits arranged more or less in spiral series; sometimes with narrow, unpitted spiral bands, but no raised spiral ridges (Figs 10B, 11B). Inner chitinous layer moderately well developed.

Head-foot: Pigmented; snout broad, rather short, bilobed. Cephalic tentacles long, not noticeably ciliated, eyes in bulges at their outer bases. Foot rather short and broad, anterior and posterior mucous glands present, posterior gland opens into posterior half of sole by longitudinal slit. No metapodial or pallial tentacles (Fretter & Graham, 1962; fig. 289B; Fretter & Graham, 1978; own observations [*B. unifasciata*, Plymouth, England; *B. calcarea* Kay, Diamond Head, Oahu, Hawaiian Islands; *B.* cf. *tincta,* Fort Lauderdale, Florida; *B. haliotiphila* and *B. acuta,* Monterey, California, U.S.A.]). (Fig. 1A,B.)

Anatomy: Oesophageal pouches present. Penis (Fig. 4A,B) behind right eye, long, tapering to sharp point. Prostate gland pallial + visceral (Fig. 4C) pallial or penial (Slavoshevskaya, 1976, fig.2). Capsule gland with thick ventral wall, spermathecal opening at posterior end of pallial cavity. Albumen gland modified for sperm storage. No bursa copulatrix (Figs 5G, 6). (Based on *B. unifasciata, B.* cf. *tincta, B. haliotiphila, B. acuta* and *B. angustata*; see anatomical account for further details.)

Operculum: Solid, usually red, with strong, internal longitudinal ridge. A long peg emerges from nucleus and extends beyond inner (columellar) edge (Figs 10C,D,G, 11C).

Radula: Central teeth with large, rectangular median cusp, 2-3 small, sharp lateral cusps and a pair of basal denticles; lateral margins narrowly thickened, at about 20°-45°; base with U-shaped projection. Lateral teeth 2 + 1 + 2(-3), median cusp about twice as long as lateral cusps. Marginal teeth with subequal cusps; cusps on outer edge of outer marginal teeth (Figs 10E, 11D).

Egg capsules: Ovoid, with small area of attachment; contain single egg (*B. unifasciata*; Lebour, 1934, Fretter & Graham, 1962, 1978).

Distribution. Western North America (*Barleeia haliotiphila* Carpenter, 1864; *B. subtenuis* Carpenter, 1864; *Jeffreysia alderi* Carpenter, 1856; *Cingula paupercula* C.B. Adams, 1852 = *Barleeia zeteki* Strong & Hertlein, 1939; *Jeffreysia bifasciata* Carpenter, 1856; *Diala acuta* = *Diala marmorea* Carpenter, 1864 = *Barleeia dalli* Bartsch, 1920; *Barleeia oldroydi, B. sanjuanensis, B. bentleyi, B. californica, B. coronadoensis, B. carpenteri, B. orcutti,* all Bartsch, 1920). Caribbean (*Barleeia tincta* Guppy, 1895). South-western Atlantic (*Eatoniella rubrooperculata* Castellanos & Fernandez, 1972). Europe and Mediterranean Sea (*T. unifasciatus* = *ruber* J. Adams, 1797, *not* von Salis, 1793, = *Rissoa fulva* Michaud, 1830 = *Subanea binghamiana* Leach, 1852; *Rissoa seminula* Monterosato, 1877). St. Helena (*Rissoa cala* Smith, 1890, ? = *Rissoa ephamilla* Smith, 1890; *Rissoina congenita* Smith, 1890). East Africa (*Barleeia tropica* Thiele, 1925). South Africa (*Rissoa* (*Cingula*) *caffra* Sowerby, 1897 = *Microsetia kraussi* Turton, 1932). Mauritius (*Barleia* [sic] *?microthyra* Martens, 1880). Japan (*Diala simplex* Smith, 1875; *Barleeia trifasciata* Habe, 1960). South-east Asia (*Cingula annamitica* Dautzenberg & Fischer, 1907). Australia (at least 3 undescribed species). Hawaii (*Barleeia calcarea* Kay, 1979). North Pacific (*A. angustata*). Miocene of Italy (*Barleeia rubra* var. *mioelongata* Sacco, 1895 and var. *miocenica* Sacco, 1895 appear to be the same taxon).

Barleeia simplex Briart & Cornet, 1887, an Eocene species from Europe, has not been examined. It becomes a secondary homonym of *B. simplex* (Smith, 1875) so a replacement name, *B. eocenica* nom. nov., is provided herein for it.

Material examined.

†**T. unifasciatus*: Many lots (BMNH, AMS, etc).
†**R. seminula*: Author's material (BMNH, AMS).
B. tropica: Syntypes (HUM).
J. caffra: Syntypes (BMNH) and a few other specimens (AMS, ANSP).
R. cala: Syntypes (BMNH, ANSP, NHMB, USNM).
R. ephamilla: Syntypes (BMNH), 1 lot (USNM).
B. congenita: Syntypes (BMNH, ANSP).
†**A. angustata*: Holotype (ANSP) and one other lot ex Golikov (AMS).
M. kraussi: Holotype and paratypes (OUM).
D. simplex: Holotype; has operculum visible in shell (BMNH).
†**B. microthyra*: Syntypes (HUM, AMS) and a few other lots (AMS).
B. rubra var. *mioelongata* and var. *miocenica*: Types (TGM).
†**B. calcarea*: A few lots (AMS).
B. tincta: Syntypes (USNM) and a few other lots (USNM, MCZ, ANSP).
†**D. acuta* and several other west American species, including *B. sanjuanensis** (AMS, LACM) and types of all other species listed have been examined.
†*undescribed Australian species (AMS).

Remarks. There is a considerable range of shape, size and colour in this genus, with many species brightly coloured, some banded and others white.

Pseudodiala was erected as a subgenus of *Barleeia* to include the west American species previously included in *Diala* Adams. The type species differs from other species of *Barleeia* in having a strong peripheral angulation and an opisthocline, varicose outer lip. Although it is a distinctive species, a few others show various degrees of angulation of the periphery. There are no significant radular, opercular or anatomical differences between the type species of *Pseudodiala* and *Barleeia*, so that, in the absence of additional supporting evidence, *Pseudodiala* is here regarded as a synonym of *Barleeia*. *Ansola* is discussed in the 'remarks' on the subfamily.

Species of *Barleeia* typically have smooth shells, although the shell of *B. cala* (Smith) is weakly spirally striate.

Protobarleeia n.gen.

Type species: *Amphithalamus* (*Cerostraca?*) *myersi* Ladd, 1966. Late Miocene, Eniwetok Atoll, Pacific Ocean. Also Recent, SW Pacific (Fig. 11E–I).

Diagnosis. *Shell:* Minute (1.5–2 mm in length), solid, ovate-conic, non-umbilicate, with spiral lirae. Teleoconch microsculpture of fine, dense, rather irregular spiral threads. Aperture oval, very weakly subangled anteriorly and posteriorly (Fig. 11E); outer lip orthocline, with a prominent external varix. Protoconch of about 1¾ whorls, sculptured with well-spaced, raised spiral cords, the interspaces with an anastomosing microsculpture giving it an irregularly netted appearance (Fig. 11F).

Head-foot: As in *Barleeia* but unpigmented (Heron Island, Queensland, Australia) (Fig. 1C,D).

Anatomy: Not known.

Operculum: As in *Barleeia*, but yellow (Fig. 11G,H).

Radula: As in *Barleeia*; central teeth $\frac{2+1+2}{1\quad 1}$; lateral edges at 30°. Lateral teeth 2 + 1 + 2 (Fig. 11I).

Distribution. Western Pacific; late Miocene to Recent (*A. myersi* Ladd).

Material examined.

A. myersi: Several lots from Fiji and Queensland, Australia (AMS).

Remarks. This monotypic genus has been created for a peculiar, minute barleeid which differs from the other genera in the subfamily in having spiral sculpture on both protoconch and teleoconch and a yellow operculum. The microsculpture of the protoconch is also quite different from that of *Barleeia* (compare Figs 10B and 11B with 11F).

Ladd (1966) named the type species on the basis of a single specimen from the upper Miocene of Eniwetok. There are in the AMS several lots of this species from localities in Fiji and Australia which agree very closely with Ladd's description and figure.

Lirobarleeia n.gen.

Type species: *Alvania galapagensis* Bartsch, 1911. Recent, Galapagos Islands, eastern Atlantic (Figs 4D,E; 5C,D; 12A–D).

Diagnosis. *Shell*: Small (2–4 mm in length), elongate-conic, solid, non-umbilicate with spiral and axial sculpture, the spiral elements usually predominant, type species clathrate, rarely smooth. Aperture with simple peristome, rounded to weakly angled anteriorly, weakly angled and, in a few species, very weakly channelled, posteriorly. Outer lip weakly opisthocline to orthocline, with varix (Figs 12A,E; 13A; 14A). Protoconch with whole surface very minutely and irregularly pitted, sometimes with weak spiral ridges unrelated to the pitted microsculpture (Fig. 14B, C), or with strong spiral ridges (Figs 12D,F; 13D,E). Inner chitinous layer moderately well developed.

Head-foot: Known only from preserved material of *A. galapagensis*; appears to closely resemble *Barleeia*.

Anatomy: Oesophageal pouches present. Penis (Fig. 4D,E) with broad distal lobe; prostate gland pallial + visceral. Capsule gland with very thin ventral connection between two halves of gland; oviduct opening distal, no separate spermathecal aperture. Albumen gland lacking a modified sperm pouch; no bursa copulatrix (Fig. 5C,D) (*L. galapagensis*) (see anatomical account for further details).

Operculum: As for *Barleeia* (previously described for *L. kelseyi* [Baker, Hanna & Strong, 1930] and *L. lirata* [Carpenter, 1856]) (Figs 12C; 13B,C; 14D,E).

Radula: As for *Barleeia*; central teeth $\frac{2\text{-}3\ +\ 1\ +2\text{-}3}{1 \qquad\quad 1}$, outer lateral cusps very small; lateral angles at 30-40°. Lateral teeth 2-3 + 1 + 2-4. Marginal teeth with several cusps, distal cusps larger than cusps on outer edges, subequal in both teeth (Figs 12B, 13G, 14F).

Distribution. Tropical western North and central America and the Galapagos Islands (*Rissoa albolirata* Carpenter, 1864; *Rissoa kelseyi* Dall & Bartsch, 1902 = *Alaba oldroydi* Dall, 1905 = *Rissoina lapazana* Bartsch, 1915 = *Alvania bartolomensis* Bartsch, 1917 = *Rissoina lowei* Strong, 1938; *Diala electrina* Carpenter, 1864, = *Alvania lucasana* Baker, Hanna & Strong, 1930; *Rissoa lirata* Carpenter, 1856; *Alvania herrerae* Baker, Hanna & Strong, 1930; *Alvania perlata* Mörch, 1860; *Alvania granti* Strong, 1938, ? = *Alvania veleronis* Hertlein & Strong, 1939; *Alvania hoodensis* Bartsch, 1911; *Alvania clarionensis* Bartsch, 1911; *Alvania ingrami* Hertlein & Strong, 1951; ? *Alvania lara* Bartsch, 1911; *Alvania nemo* Bartsch, 1915; *Alvania galapagensis* = *Alvania nigrescens* Bartsch & Rehder, 1939 [the West Indian locality for this last name is erroneous]). Caribbean (*A. chiriquiensis* Olsson & McGinty, 1958). Pleistocene, California (*Rissoina hartmanni* Jordon, 1936). Oligocene, Washington, W. coast N. America (? *Turbella cowlitzensis* Effinger, 1938).

Material examined. Types of all Recent species listed except *A. perlata, R. lowei* and *A. lirata,* together with numerous lots in LACM and some in USNM and AMS. Two preserved lots of *A. galapagensis* (CAS). Radulae, opercula and protoconch microsculpture examined for type species, *L. kelseyi* and *L. albolirata.*

R. hartmanni: Holotype (CAS).

T. cowlitzensis: Holotype and paratype (BPC).

Remarks. This genus has been erected to cover a group of species which are convergent with rissoid genera such as *Alvania* Risso (see Fig. 12A,E) and *Onoba* Adams (Fig. 13A) in the development of spiral and axial sculpture. Some species (such as *L. albolirata*) approach *Rissoina* Orbigny in shape (Fig. 14A), although they resemble more closely species of *Fictonoba,* a genus of Barleeinae which includes 3 species from northern New Zealand and the Kermadec Islands. The species of *Fictonoba* differ from those of *Lirobarleeia* (and *Barleeia*) in having a radula with more triangular central teeth and more finely cuspate lateral teeth. In addition, the protoconch sculpture is of a different type of pitting, being much denser and more irregular. There are also anatomical differences between the type species in both genera.

Lirobarleeia differs from *Protobarleeia* in that the species it contains are much larger, and have more elongate shells, different protoconch microsculpture and a red, not yellow, operculum.

Assuming that the anatomy of *L. galapagensis* is typical of the group, *Lirobarleeia* differs from *Barleeia* in having only one female genital opening and in the ventral wall of the capsule gland being thin-walled, not thickly glandular as it is in *Barleeia*. The two genera, in other non-shell characters, are very similar. Their shells, however, differ markedly: the shells of most species of *Lirobarleeia* are strongly sculptured (not smooth) and more elongate-conic, and have thickened apertures with an orthocline to weakly opisthocline (instead of prosocline) outer lip.

Genus *Caelatura* Conrad, 1865

Caelatura Conrad, 1865a: 28 (*not* Fischer, 1883). Type species *Pasithea sulcata* Lea, 1833; here designated. Eocene, Alabama, U.S.A. (Fig. 15F-I).
not *Coelatura* Conrad, 1853 nor Pfeiffer, 1877.

Diagnosis. *Shell:* Small (2-3.5 mm in length), solid, elongate-conic, non-umbilicate, with spiral or axial ribs or smooth. Aperture with simple peristome, oval, subangled but not notched posteriorly, usually with varix behind sharp opisthocline outer lip. Teleoconch with strong, rounded spiral ridges, or with axial ribs, or smooth; microsculpture of irregular, minute pits (Figs 15A,B,F,H,I; 16A,B). Protoconch paucispiral, smooth (?) or with weak spiral lines; microsculpture (known only in Recent species) of very closely-packed, minute, irregular pits (Figs 15C-E,G; 16C).

Head-foot and anatomy: Unknown.

Operculum: As in *Barleeia* (Fig. 16D).

Radula: Central teeth $\frac{3\ +\ 1\ +\ 3}{1 \qquad 1}$, cusps sharp, median cusp narrowly triangular; basal denticles overlap upper edge of tooth in front; lateral margins thickened, at about 45°. Lateral teeth 3 + 1 + 6-7; cusps small, primary cusp narrowly triangular, sharp. Marginal teeth with numerous, small cusps on outer edge of inner marginal teeth and outer marginal teeth (inner edge of outer marginal teeth obscured in mounts) (Fig. 16E,F).

Distribution. Eocene, south-eastern U.S.A. (*P. sulcata*). Western Atlantic (*Rissoa* (*Cingula*) *rustica* Watson, 1886 = *Alaba conoidea* Dall, 1889; *Rissoa* (*Cingula*) *pernambucensis* Watson, 1886; *Rissoa microstoma* Watson, 1886).

Material examined.

†*P. sulcata*: Types and one other lot (ANSP).

R. (*C.*) *rustica*: Syntypes (BMNH).

†**A. conoidea*: Syntypes (many) (USNM).

R. (*C.*) *pernambucensis*: Syntypes (BMNH).

†*R. microstoma*: Syntypes (BMNH), one lot (USNM).

Remarks: Palmer (1937) discussed the complex nomenclatural problems of the interpretation of the type species and its designation in relation to this genus name and *Actaeonema* Conrad, 1865 (see below). She argued that *Actaeonema* was a replacement name for "*Caelatura* Conrad 1865, *nec Caelatura* Martens"—with the type, by subsequent designation by Cossmann

(1893), "*Actaeonema striata* Conrad" which Cossmann considered, incorrectly, to be the same as *Pasithea sulcata* Lea. Palmer's interpretation is not entirely satisfactory because Conrad (1865b) erected *Actaeonema* for *Caelatura* Conrad (1865a) introduced on p. 35 under the Acteonidae. Conrad, in the same article (1865a), had also introduced *Caelatura* under the "Terebridae" on p. 28. The latter introduction has page priority and includes 2 species, *Pasithea sulcata* Lea and *Pasithea striata* Lea. The *Actaeonema* introduced on p. 35 includes only *Pasithea striata.* It is most probable that Conrad, realising his error in introducing the same name twice, proposed a substitute name for the second introduction (p. 35). The inclusion of *P. striata* under both generic names is possibly a *lapsus,* the first name (*Caelatura,* p. 28) possibly being intended for *P. sulcata* alone.

Palmer (1937) has shown that *Pasithea striata* Lea (*not* Conrad, 1865b) is possibly a turritellid protoconch (Palmer, p. 68, pl. 82, fig. 6). It is my contention that *Actaeonema* must have *Pasithea striata* as its type species by monotypy, as this is the only species name mentioned on page 35 under *Caelatura.* Conrad's (1865b, pl. 11, fig. 2) figure of *A. striata* is clearly not *Pasithea striata* Lea, nor is it like *Pasithea sulcata,* having fewer and weaker spiral ridges, more convex whorls, a rounded, not subangled, periphery and a larger and differently-shaped aperture. Palmer (1937, p. 156) suggests that *A. striata* of Conrad is *Tuba cancellata,* a mathildiid. The earlier introduction of *Caelatura* (p. 28) also included *Pasithea striata* but *Pasithea sulcata* is here designated as the type species.

The relationships of the type-species of *Caelatura* are somewhat obscure. It is similar to the rissoid genus *Lironoba* Iredale, 1915 in most shell features although differing in having a simple peristome. The apparently-smooth, paucispiral protoconch was slightly worn in the best specimen available and it was not definitely established whether a microsculpture was present. The teleoconch is unusual in having a microsculpture of minute punctures. The overall shell features suggest a possible relationship with *Lirobarleeia* but these two groups differ in that *Caelatura sulcata* has minute punctures over the teleoconch surface, a more expanded inner lip and stronger spiral lirae. *Protobarleeia* also differs from *Caelatura sulcata* in the characters outlined above and in possessing a spirally-sculptured protoconch.

The Recent species listed above as belonging to this genus are placed here because they possess a similar teleoconch microsculpture (observed in syntypes of *A. conoidea* [= *rustica*] and *R. microstoma*; compare Figures 15H,I with 15B and 16B) and are also similar in their apertural characters and shell outlines. The Recent species are smooth to axially ribbed, a major departure from the strong spiral keels of *C. sulcata.* Given the variation in sculpture in barleeid genera such as *Lirobarleeia* and *Pisinna* and the lack of other characters that could be used to separate them, it seems reasonable to regard those species as congeneric.

The species included herein in *Caelatura* differ from other Barleeinae in their pitted teleoconch surface, shallow irregular protoconch microsculpture and, in the one species where it is known, in radular characters. The radula of *C. rustica* has more numerous, sharper cusps than other Barleeinae and the central teeth lack a U-shaped basal projection on the face of each tooth. This structure appears to have been replaced functionally by the basal cusps overlapping the edge of the tooth in front.

Genus *Fictonoba* Ponder, 1967

Fictonoba Ponder, 1967: 212. Type species *Rissoa carnosa* Webster, 1905; by original designation. Recent, northern New Zealand (Fig. 17).

Diagnosis. *Shell:* Small (2.5–3.5 mm in length), elongate-ovate, solid, non-umbilicate, with axial and sometimes spiral sculpture; axial ribs do not extend over base. Aperture oval, rounded anteriorly, with sharp posterior angulation but lacking distinct channel, peristome simple; outer lip slightly opisthocline to orthocline, rather thin, varix absent (Fig. 17A). Protoconch dome-shaped, paucispiral, with indistinct spiral elements; microsculpture of dense, irregular pits (Fig. 17D,E). Inner chitinous layer rather poorly developed.

Head-foot: Cephalic tentacles long, slender, not tapering, eyes in swellings at their outer bases. Snout long, bilobed, very extensile. Foot long, with anterior pedal gland; no posterior pedal gland. Metapodial tentacle short, triangular. A small posterior pallial tentacle present (Ponder, 1967: pl. 5, figs 2, 3, 7).

Anatomy: Oesophageal pouches absent. Female genitalia with thin-walled ventral channel, no separate spermathecal opening, seminal receptacle on right side of albumen gland and a large bursa copulatrix present. Male with complexly lobed penis (Fig. 4F,G), open prostate gland (Fig. 4H), pallial vas deferens and penial duct (*F. carnosa*) (see anatomical account for further details).

Operculum: Very similar to that of *Barleeia,* red or yellow and red (previously described and figured by Ponder, 1967) (Fig. 17B,C).

Radula: Central teeth $\frac{2+1+2}{1\quad 1}$, lateral margins considerably thickened, at about 45°; cutting edge slightly less than half width of tooth, median cusp narrow, sharp, about twice as long as adjacent cusps; basal denticles prominent; middle part of face thickened to form U-shaped projection. Lateral teeth 2–3 + 1 + 4–6; cusps sharp, primary cusp triangular, much larger than other cusps. Marginal teeth with several small cusps, subequal on both inner and outer marginals, distal cusps larger than others; cusps on outer edge of inner marginal teeth and inner and outer edges of outer marginal teeth (Fig. 17F,G).

Distribution. New Zealand (*F. carnosa; Rissoina rufolactea* Suter, 1908). Kermadec Islands (*Austronoba oliveri* Powell, 1926). Burdwood Bank, near Falkland

Islands, Subantarctic (? *Onoba cymatodes* Melvill & Standen, 1916).

Material examined.

†**R. carnosa*: Several lots (AMS).
†**R. rufolactea*: Paratypes and several other lots (AMS).
R. oliveri: Several lots (AMS).
O. cymatodes: Holotype (RSM).

Remarks: This genus resembles *Barleeia* in its operculum, in having a punctate protoconch microsculpture and chitinous inner shell layer. It differs from *Barleeia* and other Barleeidae in having a metapodial and a posterior pallial tentacle. It also differs from *Barleeia* in the details of the central teeth of the radula, in the pattern of protoconch microsculpture, in lacking a posterior pedal gland and in several anatomical characters. The shell shape and sculpture are similar to that of species of *Lirobarleeia* but the two groups can readily be distinguished on radular characters, *Fictonoba* having smaller cusps on all teeth and a differently constructed central tooth (compare Fig. 17G with Figs 12B, 13G and 14F).

The presence of a metapodial and a pallial tentacle and the lack of a posterior mucous gland are characters that are shared with several genera of Rissoidae (Ponder, 1967). In addition the anatomy of the male and female genital systems is superficially similar to that of *Rissoina* Orbigny. *Fictonoba carnosa* has a partially separated albumen gland but lacks the true upper oviduct gland that is characteristic of the Rissoidae. Its radula, too, is superficially similar to the normal rissoid pattern (although that of *Caelatura* is more similar) and differs at sight from that of *Barleeia*. It has no jaws and in this respect resembles some other Barleeidae, all Rissoidae apparently possessing well-developed jaws. The oesophagus is like that of species of Rissoidae in having short dorsal folds and in lacking oesophageal pouches. *Fictonoba,* like some species of *Rissoina*, appears to feed selectively on Foraminifera (Ponder, 1967), in contrast to the microherbivorous feeding of *Barleeia*. The stomachs of sectioned specimens of *Fictonoba* contained forams, some diatoms and fine detritus.

Fictonoba thus has characters shared by both the Barleeidae and Rissoidae. An analysis of the characters and states, listed in Table 1, that are possessed by *Fictonoba,* shows that it has more characters in common with the Barleeidae than with the Rissoidae (12 character states shared with Rissoidae, 14 with Barleeidae). *Fictonoba* is possibly close to the stem from which the Barleeidae and ancient rissoid genera such as *Rissoina* diverged, although it is also possible that the similarity between *Fictonoba* and *Rissoina* is due to convergence.

Subfamily ANABATHRINAE Coan, 1964

(*nom. correctum* Keen, 1971, for Anabathroninae)

Synonym: AMPHITHALAMIDAE (Ponder MS) Voorwinde, 1966: 41.

Diagnosis. *Shell:* Small or minute, elongately pupoid to broadly ovate, solid, with inner chitinous layer usually well developed, opaque, umbilicate to non-umbilicate. Aperture with simple or duplicated peristome, usually not channelled; outer lip with or without varix, prosocline to opisthocline. Teleoconch smooth or with spiral or axial sculpture, rarely both. Protoconch dome-shaped, paucispiral, usually sculptured with minute pits typically arranged in spiral rows.

Head-foot: Snout short, bilobed; foot short, with anterior pedal gland and with or without posterior pedal gland. Cephalic tentacles short, typically ciliated, usually paddle-shaped.

Anatomy: Male with penis usually attached to mid-line and coiled when at rest. Prostate gland closed, in and/or behind pallial cavity. Bursa copulatrix and seminal receptacle present; bursa on left (inner) side of albumen gland, seminal receptacle posterior and alongside albumen gland. Oviduct with a single distal opening or with an additional, posterior spermathecal opening. Oesophageal pouches and oesophageal gland absent (although rudimentary gland appears to be present in some species); mid-oesophagus with long dorsal folds.

Operculum: Oval, composed of two layers, nucleus eccentric, smooth or with raised ridge near inner (columellar) edge on inner side, or with short peg arising from nucleus (also an accessory peg in one genus); peg rudimentary in some species.

Radula: Variable, ranging from all teeth multicuspate with small cusps and similar to Rissoidae, to rather short teeth with few, large cusps. Central teeth with a pair of basal processes, triangular cutting edge, lateral margins at 45° or less; face with convex ventral margin but no separate U-shaped projection. Lateral teeth with few to several cusps on distal ends and distal ¼–⅓ of outer edge of inner marginal teeth and inner edge of outer marginal teeth.

Remarks. The Anabathrinae can be readily distinguished from the Barleeinae by their flat, 2-layered operculum which usually does not bear a peg. The shells are typically very small and solid. The penis is coiled whereas it is straight in the Barleeinae. *Pisinna* species and *Amphithalamus incidatus* (Frauenfeld) have a spermathecal opening in the posterior part of the pallial cavity so that no important differences appear to occur in the female genitalia. It is very probable, however,that the diaulic condition in *Barleeia,* and *Pisinna* and *Amphithalamus,* has been derived independently. (See 'Discussion'.) The cephalic tentacles are usually prominently ciliated and paddle-shaped, being in marked contrast to the narrow, tapering, indistinctly ciliated tentacles of *Barleeia*. The radula in the Anabathrinae lacks the U-shaped projection seen on the face of the central teeth of all genera of Barleeinae except *Caelatura,* and the outer marginal teeth have cusps on their outer edges in the Barleeinae but not in the Anabathrinae.

Ponder (1968) incorrectly identified an oesophageal gland in this group. The species investigated, however, have rather long dorsal folds in the midoesophagus and there is little trace of an oesophageal gland. The large number of characters listed in the family diagnosis common to the Barleeinae and Anabathrinae suggest that they are closely related and require no more than subfamily distinction (see Table 1 for list of some important characters and character states separating the two subfamilies).

This group is centred in the Southern Hemisphere, particularly in Australasia, whereas the Barleeinae have their centre of diversity in western North and Central America.

General Anatomical Account of the Anabathrinae

The following anatomical information has been obtained from the examination of the species listed: *Anabathron* (*Anabathron*) *contabulatum* (Frauenfeld), Sydney, NSW, *A.* (Scrobs) *hedleyi* (Sute) (from Ponder 1968), *Amphithalamus incidatus* (Frauenfeld), Sydney, NSW, *Pisinna semiplicata* (Powell) (from Ponder, 1968), *P. olivacea* (Frauenfeld) and *P. albizona* (Laseron), Sydney, NSW, *P. zosterophila* (Webster) (from Ponder, 1968), and *Badepigrus pupoides* (Adams), Port Hacking, NSW.

The pallial cavity. All of the species examined have a ctenidium with finger-shaped filaments. The osphradium is elongately oval, and is surrounded by a ciliated ridge. A hypobranchial gland is present and is well developed on the posterior mantle roof.

The pedal glands. The anterior pedal gland is a compact mass which extends to just below the buccal mass. The posterior pedal gland, when present, opens by way of a longitudinal slit to the sole of the metapodium and occupies much of the tissue of the foot.

The alimentary canal. The buccal cavity contains a well-developed odontophore, with a pair of odontophoral cartilages. A pair of very weak jaws is present in *Pisinna albizona* and *P. olivacea* but they have not been confirmed in *P. semiplicata* and *P. zosterophila*. *Anabathron contabulatum* and *Amphithalamus incidatus* also have weak jaws which, like those in the two species of *Pisinna*, are composed of a few chitinous rodlets. *Badepigrus pupoides* and *A.* (*Scrobs*) *hedleyi* apparently lack jaws.

The anterior oesophagus is rather wide and contains a pair of long, straight dorsal folds. There are no oesophageal pouches. The oesophagus passes virtually unchanged through the nerve ring and the conspicuous dorsal folds continue throughout the mid-oesophagus for approximately half the length of the cephalic cavity. There is no oesophageal gland but the tissue on the lateral walls of the anterior oesophagus of *Pisinna albizona* (the largest species sectioned) has irregular apices and resembles the tissue found in the oesophageal pouches of the Barleeinae. In other species the epithelium is more regular and consists mostly of cuboidal cells. The posterior oesophagus is a simple, narrow tube.

The spacious stomach (Fig. 3C,D) has a rather long style sac (Fig. 3: *ss*) (about equal in length to the remainder of the stomach), which contains a crystalline style, and has a single digestive gland opening (*do*). The excretory cells of the digestive gland did not contain brown secretory granules except in *Pisinna olivacea*.

The intestine curves around the style sac and back towards the anterior edge of the anterior gastric chamber and then runs anteriorly. The rectum passes more or less straight along the right mantle wall to open a little behind the mantle edge.

The renal organ. The renal organ differs from that of the Barleeinae in lacking any prominent thickening (nephridial gland) on the outside wall, the epithelium being simple and composed of a single layer of cells throughout. The renal opening is simple and at the posterior end of the pallial cavity.

The nervous system. The nervous systems of the species investigated were not studied except to note the marked concentration of the circumoesophageal ganglia.

The male genital system (Fig. 8). The testis is not distinctly lobulate and lies above the digestive gland, but does not occupy the last ⅓-1 whorl of the visceral coil.

The coiled, expanded seminal vesicle appears to contain only typical (eupyrene) sperm and lies behind and/or across the inner (ventral), posterior end of the stomach. The bean-shaped prostate gland is partly embedded in the kidney wall and partly in the pallial wall in all the species examined. The lumen is a central slit, glandular above and below in species of *Pisinna*, but displaced ventrally in *Anabathron contabulatum*. There is a short ventral slit open to the pallial cavity immediately in front of the posterior pallial wall in *A. contabulatum*. A small posterior pallial opening in *Amphithalamus incidatus* was observed but none was present in *Pisinna albizona* or in the two species of *Pisinna* examined by Ponder (1968). The prostate of *P. olivacea* was badly shattered in the 3 sectioned males and, although a pallial opening was not observed, its absence could not be verified. The pallial vas deferens emerges from the distal end of the prostate gland, or just behind the distal end (as in *A. incidatus*) and the visceral vas deferens enters just behind the posterior pallial wall in all of the species examined. The pallial vas deferens is a narrow, ciliated tube which runs immediately beneath the epithelium on the neck where a few coils or undulations occur before it enters the base of the penis.

The penis is situated at about the midline of the head just behind the eyes and when at rest is coiled (Fig. 8A-C) or U-shaped (Fig. 8D). It is approximately the same length as the pallial cavity when straightened. The penial duct is simple, ciliated, and has a thin, muscular coat. The penial epithelium does not contain conspicuous gland cells except in *P. semiplicata*, which has a zone

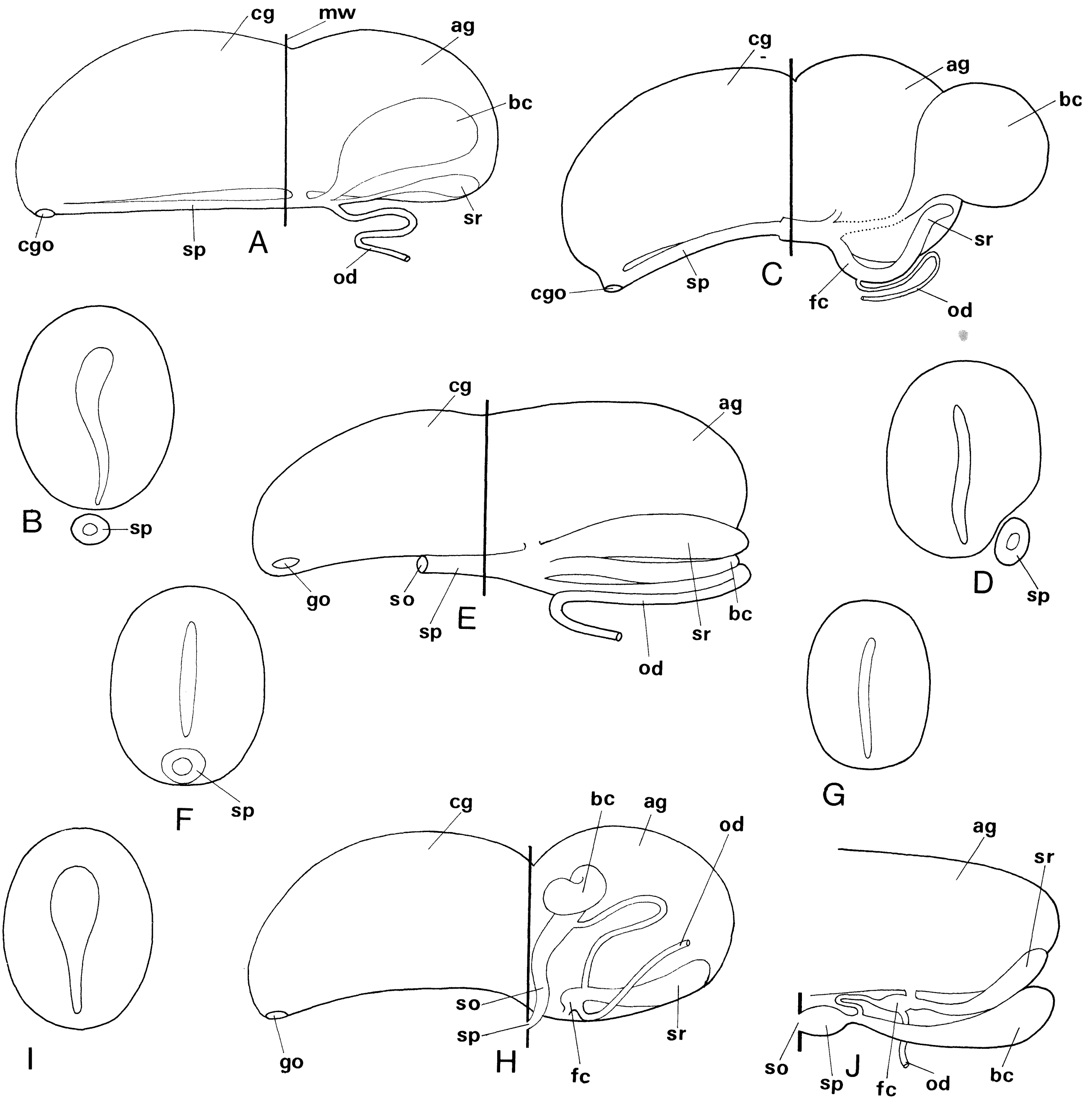

Fig. 7. Semidiagrammatic representations of the female genital systems of some Anabathrinae as seen from the left (inner) side with sections through the middle part of the capsule gland. **A & B**, *Badepigrus pupoides* (Adams). **C & D**, *Anabathron* (*Anabathron*) *contabulatum* (Frauenfeld). **E–G**, *Amphithalamus* (*Amphithalamus*) *incidatus* (Frauenfeld). **F**, section through the posterior end of the capsule gland; **G**, section through the anterior part of the capsule gland. **H & I**, *Pisinna semiplicata* (Powell). **J**, *Pisinna olivacea* (Frauenfeld), showing the posterior part of the oviduct glands and the sperm sacs.
ag, albumen gland; *bc*, bursa copulatrix; *cg*, capsule gland; *cgo*, common genital opening, *fc*, fertilization chamber; *go*, oviducal opening; *mw*, posterior pallial wall; *od*, upper oviduct; *so*, spermathecal opening; *sp*, spermathecal tube; *sr*, seminal receptacle.

of long, glandular epithelial cells. These were incorrectly interpreted as prostatic cells by Ponder (1968, fig. 16). The penial opening is situated at the pointed, distal end of the penis.

The female genital system (Fig. 7). The ovary is simple, is short compared with the digestive gland, and contains large, yolky eggs. The narrow, thin-walled upper oviduct becomes ciliated as it approaches the oviduct glands but does not noticeably thicken externally. In *A. incidatus, B. pupoides* and *A. contabulatum* the oviduct (Fig. 7: *od*) forms a tight loop ventral to the sperm sacs. The histology of the distal

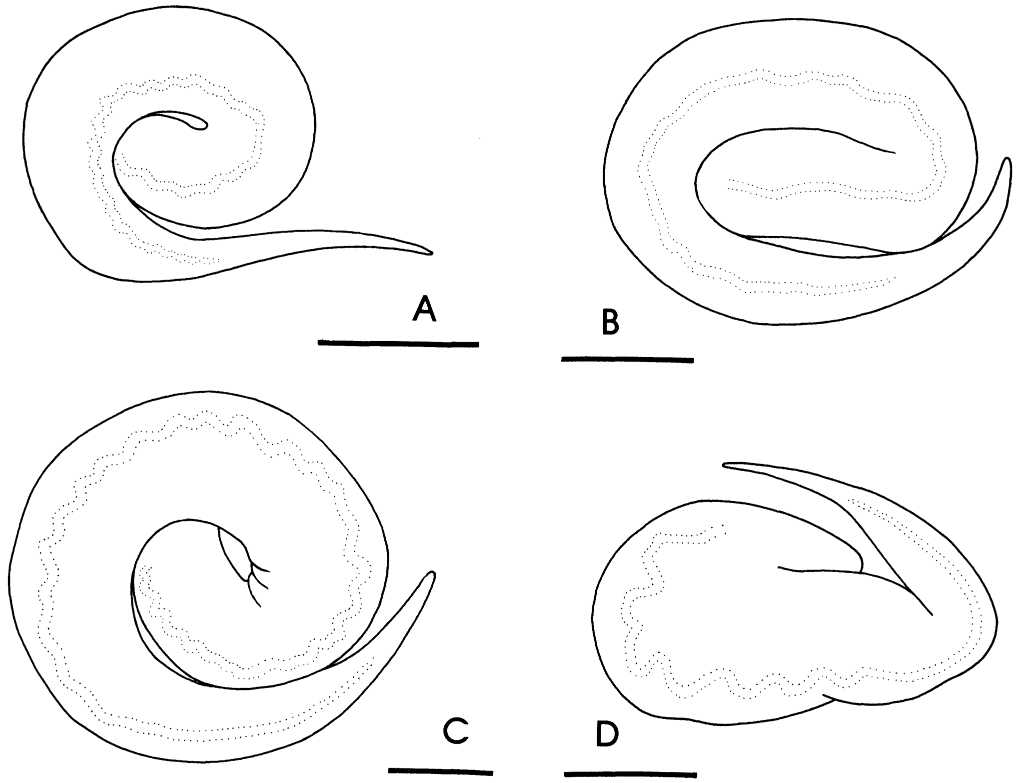

Fig. 8. Penes of the Anabathrinae. **A,** *Anabathron* (*Anabathron*) *contabulatum* (Frauenfeld); Fingal Head, Port Stephens, NSW. **B,** *Amphithalamus* (*Amphithalamus*) *incidatus* (Frauenfeld); Fingal Head, Port Stephens, NSW. **C,** *Pisinna olivacea* (Frauenfeld); Fairlight, Sydney, NSW. **D,** *Badepigrus pupoides* (Adams); Port Hacking, NSW. Scale: 0.1 mm.

arm is different from that of the proximal arm in *A. incidatus*, consisting of an irregular epithelium containing a few blue-staining cuboidal cells and ciliated cells. The proximal arm is lined with a regular cuboidal, ciliated epithelium.

The oviduct opens to a small, ciliated fertilization area (Fig. 7: *fc*) into which the seminal receptacle and the bursa copulatrix, which lie on the left side of the albumen gland, also open. In *Amphithalamus incidatus* (Fig. 7E) this area is muscular and the short ducts of the sperm sacs are contained in a common muscular sheath. In this species the thin-walled seminal receptacle (Fig. 7E: *sr*) is larger than, and lies dorsal to, the muscular bursa copulatrix (Fig. 7: *bc*) and the two sacs are bound together with connective tissue. The seminal receptacle contains orientated sperm lying in its lumen, whereas the bursa copulatrix was not observed to contain sperm in any of the specimens sectioned. The seminal receptacle is lined with pavement epithelium and surrounded by a thin layer of muscle fibres. The bursa has a thickly muscular wall and is lined with ciliated, cuboidal cells thrown into low longitudinal ridges.

In *Anabathron contabulatum* (Fig. 7C) the bursa copulatrix (Fig. 7C: *bc*) is larger than the seminal receptacle (Fig. 7C: *sr*) which lies ventral to it. The seminal receptacle is a long narrow sac with thin walls and opens to the oviduct proximal to the bursal opening. The tubular fertilization area (Fig. 7C: *fc*) is lined with short, orange-staining gland (?) cells. At the point where it receives the bursal duct the oviduct opens to the albumen gland. It then becomes tubular and is lined with relatively large, cuboidal, pale-blue-staining cells and has a very narrow lumen. The large, ovoid bursa copulatrix (Fig. 7C: *bc*) is lined with columnar cells and contains unorientated sperm. Its duct is surrounded by the albumen gland. The arrangement of the sperm sacs and upper oviduct in *Anabathron* (*Scrobs*) *hedleyi* is similar to that of *A. contabulatum* but differs in having the bursal duct free of the albumen gland.

Badepigrus pupoides (Fig. 7A) has fertilization area and sperm sacs similar to *A. contabulatum* and *A.* (*S.*) *hedleyi*, the main difference being that the seminal receptacle (Fig. 7A: *sr*) opens immediately behind the bursal duct (which is not embedded in the albumen gland).

In species of *Pisinna* the fertilization area (Fig. 7H,J: *fc*) is a small sac into which opens the oviduct (Fig. 7H,J: *od*) (which does not loop as it does in the other genera) and the seminal receptacle. The bursa copulatrix (Fig. 7H,J: *bc*) is connected to this area by a rather long, narrow duct. The seminal receptacle (Fig. 7H,J: *sr*) is a long, tubular, thin-walled structure similar to that seen in *A. contabulatum, A.* (*S.*) *hedleyi* and *B. pupoides,* but the bursa copulatrix is rather different. It is located on the left side of the albumen gland (as it is in the other genera), lying opposite the anterior end of the gland in *P. semiplicata* and *P. albizona* but near the posterior end in *P. olivacea.* It is an elongately ovoid, muscular sac and was not observed to contain sperm. It is almost certainly homologous with the bursa copulatrix of the other genera and is similar histologically to the structure regarded as a bursa in *A. incidatus.* The distal ovoid section tapers into a long muscular tube and the narrow duct leading to the fertilization area opens a little more than half-way along its length (i.e. towards the distal end) in *P. semiplicata* and *P. albizona* (Fig. 7H) or very near the proximal end (in *P. olivacea*) (Fig. 7J). The muscular tube then opens (Fig. 7H,J: *so*) to the posterior end of the pallial cavity by way of a short spermatheca (Fig. 7H,J: *sp*) lined with ciliated and mucous cells. The spermatheca is expanded into a vestibule-like structure in *P. olivacea.*

The fertilization area in *A. incidatus* continues anteriorly as a narrow duct (Fig. 7E: *sp*) lined with large, pale-blue-staining cuboidal cells and then, after a short section lined with ciliated and mucous cells, opens to the pallial cavity a little in front of the posterior pallial wall. This opening (Fig. 7E: *go*), in species of *Pisinna* and *A. incidatus*, can be closed with a sphincter muscle. This makes it difficult to discern in sections and I overlooked it in my (1968) account of *P. semiplicata.*

In *Badepigrus pupoides* and *Anabathron contabulatum* a short section of the narrow sperm tube is also lined with pale-blue-staining cells (similar to those seen in the other genera) in the region immediately anterior to the fertilization area. This tube continues anteriorly as a ciliated spermathecal duct (Fig. 7A–D: *sp*) lying beneath the capsule gland and separate from it. In both species it joins with the small vestibule of the capsule gland just behind the common genital aperture (Fig. 7A,C: *cgo*).

The albumen gland (Fig. 7: *ag*) is about the size of the capsule gland (Fig. 7: *cg*) in all the species examined and the two glands are continuous. The capsule gland commences at about the posterior pallial wall, and continues along the right pallial wall to open distally at a small aperture. The capsule gland is oval in section and thin ventrally in *Anabathron contabulatum* (Fig. 7D) and *Badepigrus pupoides* (Fig. 7B). It has a slightly thicker ventral wall in *Pisinna* species (Fig. 7I) and, in *Amphithalamus incidatus*, a thick ventral wall posteriorly (Fig. 7F) which becomes thinner anteriorly (Fig. 7G).

Key to the Genera and Subgenera of the Anabathrinae

1. Shell with cleft between aperture and inner lip closed by callus behind posterior corner of aperture 2

—— Shell with inner lip of aperture fused to parietal wall or separated from it; lacking a callus behind posterior corner of aperture 4

2. Shell minute (less than 1.6 mm in length), usually red, purple, pinkish, pale yellow or white; foot lacking posterior mucous gland .... *Anabathron* (*Scrobs*)

—— Shell minute to small (greater than 1 mm in length), usually brown, yellow or reddish-brown; foot with posterior mucous gland (*Amphithalamus*) 3

3. Shell with prominent axial and/or spiral sculpture ...... *Amphithalamus* (*Notoscrobs*)

—— Shell smooth or with a peripheral groove or cord .... *Amphithalamus* s.s.

4. Shell minute (less than 1.6 mm in length), elongate-pupoid, whorls smooth except for median keel .... *Anabathron* s.s

—— Shell small to minute (more or less than 1.6 mm in length), smooth or with various sculpture (but not elongate-pupoid and smooth with median keel) 5

5. Shell variously sculptured, with circular to subcircular aperture with broad inner lip firmly attached to, and spread over, parietal wall .... *Pisinna*

—— Shell variously sculptured, with narrow inner lip attached to or separated from parietal wall 6

6. Shell pupiform, smooth or spirally sculptured, aperture D-shaped, inner lip attached to parietal wall .... *Microdryas*

—— Shell variously shaped, smooth or variously sculptured; aperture oval to subcircular, inner lip attached to parietal wall or separated from it 7

7. Operculum with 1 or 2 pegs, shell shape and sculpture various 8

—— Operculum simple, shell ovate-conic to conic, smooth .... *Pseudestea*

8. Operculum with 1 very short peg, peristome usually duplicated, shell pupiform to trochiform, smooth or with axial sculpture or spiral keels .... *Afriscrobs* n.gen.

—— Operculum with 2 pegs, peristome duplicated, shell pupiform, with evenly convex whorls and fine spiral threads .... *Nodulus*

Genus *Anabathron* Frauenfeld, 1867

Anabathron Frauenfeld, 1867: 13. Type species *Anabathron contabulata* Frauenfeld, 1867 (= *contabulatum* emend.); by monotypy. Recent, south-eastern Australia (Figs 1E; 7C,D; 8A; 18E–H).

Diagnosis. *Shell:* Shell minute (1–1.5 mm), solid, ovate to elongate-pupoid, non-umbilicate, usually red, pink or yellowish, with or without distinct cleft between inner lip and parietal wall, smooth, with spiral cords, threads or grooves, or with strong spiral keel. Aperture oval, not angled or channelled, with duplicated peristome, outer lip orthocline to slightly prosocline. Protoconch paucispiral, dome-shaped, with spiral rows of minute pits. Inner chitinous layer well developed.

Head-foot: Unpigmented; with paddle-shaped cephalic tentacles bearing long, immobile setae; foot with anterior and posterior pedal glands, or posterior pedal gland absent. Penis simple, coiled, attached to midline of head.

Anatomy: Female genital duct monaulic (Fig. 7C,D); penis simple, coiled, attached to middle of head (Fig. 8A).

Operculum: Oval, of two layers, inner surface with a raised ridge just inside inner (columellar) edge; sometimes a small swelling just inside ridge.

Radula: Central teeth $\frac{(3\text{–})2 + 1 + 2(\text{–}3)}{1 \qquad\qquad 1}$, with long, narrow, sharp cusps; cutting edge slightly more than width of tooth; basal denticles near outer edge of each tooth, well developed; lateral margins narrow, at about 45°, well separated from rest of base; ventral margin of tooth with tongue-like extension. Lateral teeth 2–3 + 1 + 3, with long, sharp cusps. Marginal teeth simple, curved, with rather long, sharp cusps, inner marginal teeth with almost straight cutting edge at right angles to rest of tooth.

Remarks. Ponder (1967) tentatively retained *Anabathron* and *Scrobs* as distinct genera while noting their close relationship. Examination of living material shows that species of *Anabathron* have a very similar external appearance to those of *Scrobs*, differing only in species of *Anabathron* s.s. having a posterior pedal gland. In view of this and the extremely close similarity of the anatomy, radula and operculum, *Scrobs* is here considered to be only subgenerically separable from *Anabathron*.

Subgenus *Anabathron* s.s.

Diagnosis. *Shell:* As for genus but with a single spiral keel on each whorl causing a strong angulation, and a weaker cord on base. Inner lip of aperture only slightly separated from parietal wall (Fig. 18E–H).

Head-foot: As for genus; with posterior pedal gland opening to a longitudinal groove in sole (*A. contabulatum* and *A. lene,* Sydney, New South Wales, Australia) (Fig. 1E).

Operculum: As for genus, inner surface with a small raised area just inside ridge near columellar edge (Fig. 18G).

Radula: As for genus (Fig. 18H).

Distribution. Australia (*A. contabulatum; Anabathron contabulatum lene* Hedley, 1918).

Material examined.

†**A.* (*A.*) *contabulatum*: Types (NHMV) and many other lots (AMS).

†**A. contabulatum lene*: Types (NHMV) and many other lots (AMS).

Remarks. This subgenus contains only the type species and a very similar sympatric species, *A. lene*. They never intergrade, are easily distinguished from each other and are not sexually dimorphic forms of one species. The typical subgenus is distinguished from the next by the strongly keeled shell which has a very narrow groove between the inner lip and the parietal wall, and in having a posterior pedal gland in the foot.

Subgenus *Scrobs* Watson, 1886

Scrobs Watson, 1886: 611. Type species *Rissoa* (*Scrobs*) *scrobiculator* Watson, 1886; by subsequent designation by Cossmann, 1921:36. Recent, south-eastern Australia (Fig. 19A,B).

Nannoscrobs Finlay, 1927: 377. Type species *Amphithalamus hedleyi* Suter, 1908; by original designation. Recent, New Zealand (Fig. 19C–F).

Ultiscrobs Iredale, 1955: 81. Type species *Scrobs pluteus* Laseron, 1950; by original designation. Recent, south-eastern Australia (Fig. 19G).

Diagnosis. *Shell:* As for genus but with distinct channel between inner lip and parietal wall. Whorls rarely angled, sculpture, if present, usually weak, sometimes of spiral lirae or threads (Figs 18A; 19A–D,G).

Head-foot: As for genus; posterior pedal gland absent (Ponder, 1967; *A.* (*S.*) *luteofuscus,* Sydney; New South Wales, Australia. *A.* (*S.*) *hedleyi,* Ponder, 1967, 1968) (Fig. 1F).

Operculum: As for genus but lacking small raised area inside ridge at columellar edge (Ponder, 1967) (Figs 18B, 19E).

Radula: As for genus (Figs 18C,D; 19F).

Distribution. South-eastern and southern Australia (*R.* [*S.*] *scrobiculator*; *S. pluteus*; *Amphithalamus luteofuscus* May, 1919 = *Scrobs delta* Laseron, 1950); New Zealand (*A. hedleyi* and several other species [see Powell, 1979]).

Material examined.

†*R.* (*S.*) *scrobiculator*: Holotype (BMNH) and a few other lots (AMS).
†**A. hedleyi*: Several lots (AMS, NMNZ).
†*S. pluteus*: Syntypes and a few other lots (AMS).
†**A. luteofuscus*: Holotype (TM) and many other lots (AMS).
S. delta: Syntypes (AMS).
Several other New Zealand and temperate Australian species have also been examined.

Remarks. Ponder (1967) placed *Nannoscrobs* in the synonymy of *Scrobs* and *Ultiscrobs* in the synonymy of *Microfossa* (= *Amphithalamus*). Examination of the shell of the type species of *Ultiscrobs* indicates that it is a *Scrobs,* not an *Amphithalamus*. There is, however, a sympatric, undescribed species of *Amphithalamus* which is superficially very similar to *S. pluteus*. Ponder (1968) described the anatomy of *A.* (*S.*) *hedleyi* which is similar to that of *Anabathron contabulatum*. Although the presence of a spermathecal tube ventral to the capsule gland was not recorded, the absence of this structure needs to be confirmed.

Genus *Amphithalamus* Carpenter, 1864

Amphithalamus Carpenter, 1864: 656. Type species *Amphithalamus inclusus* Carpenter, 1864; by monotypy. Recent, California (Fig. 20A–D).
Amphithalmus err. auct.

Diagnosis. *Shell:* Small (1–2 mm in length), solid, ovate-conic to elongate-conic, non-umbilicate with well-developed pit between inner lip and parietal wall. A callus plug at suture terminates posterior end of pit. Teleoconch usually smooth, sometimes with axial and spiral cords (subgenus *Notoscrobs*), or with weak peripheral cord or groove. Aperture oval, not channelled or angled, peristome simple or weakly-duplicated; outer lip orthocline to slightly prosocline. Protoconch paucispiral, dome-shaped; spiral rows of minute pits are the only sculpture. Inner chitinous layer well developed.

Head-foot: Pigmented or unpigmented; cephalic tentacles typical of family; anterior and posterior pedal mucous glands present, sole with posterior mucous slit. Penis simple, coiled, attached to midline behind head.

Anatomy: Female genital tract diaulic (Fig. 7E–G); penis simple, coiled, attached to midline of head behind eyes (Fig. 8B).

Operculum: Oval, thick, distinctly double-layered, often with raised lamella on inner side.

Radula: Central teeth $\frac{(3–)2 + 1 + 2(–3)}{1 \qquad\qquad 1}$, each with broad, blunt median cusp and small, sharp lateral cusps, a pair of small basal denticles near outer edge of each tooth and weakly thickened lateral margins at 20°–45°, ventral margin of tooth with tongue-like extension. Lateral teeth 2 + 1 + 2–4, primary cusp blunt. Marginal teeth simple, curved, with several small cusps, inner marginal teeth with cutting edge at right angles to rest of tooth.

Remarks. This genus is superficially similar to *Anabathron* (*Scrobs*) but differs in its generally larger size, brownish rather than pinkish or purplish coloration, the presence of a mucous slit in the sole, and very different radular features. No other barleeid genus (apart from *Anabathron (Scrobs)*), has the aperture separated from the body whorl by a groove terminated by a callus.

Ponder (1967) tentatively retained *Amphithalamus* and *Notoscrobs* as separate genera but the investigation of the type species and other species of both genera and of *Microfossa* suggest that there is but a single generic unit recognizable.

Subgenus *Amphithalamus* s.s.

Microfossa Laseron, 1950: 267. Type species *Subanaea* [sic; =*Sabanaea*] *incidata* Frauenfeld, 1867; by original designation. Recent, south-eastern Australia (Figs 3C; 7E–G; 8B; 20E–G).
Obescrobs Iredale, 1955:81. Type species *Rissoa jacksoni* Brazier, 1895; by original designation. Recent, south-eastern Australia (Fig. 21A–D).

Diagnosis. *Shell:* As for genus but lacking prominent sculpture, having only a weak spiral thread or groove on the periphery and sometimes a spiral cord on the base (Figs 20A,B,F; 21A,C).

Head-foot: As for genus (Ponder, 1967; also observations on *A.* (*A.*) *inclusus,* Monterey, California, U.S.A., *A.* (*A.*) *vallei,* Missouri Key, Florida, *A.* (*A.*) *incidatus, A.* (*A.*) *pyramis* and *A.* (*A.*) *jacksoni,* Sydney, New South Wales) (Fig. 1G,H).

Operculum and radula: As for genus (Figs 20C–E,G; 21B,D).

Distribution. West America (*A. inclusus* = *Amphithalamus tenuis* Bartsch, 1911 = *Amphithalamus stephensae* Bartsch, 1927 = *Amphithalamus trosti* Strong & Hertlein, 1939). Caribbean Sea (*A. vallei* Aguayo & Jaume, 1947). South Africa (*Sabanaea neglecta* Turton, 1932). Tropical western Pacific (*Scrobs fulcira* Laseron, 1956). Temperate Australia (*S. incidata*; *R. jacksoni* = *Rissoa* (*Scrobs*) *badia* Watson, 1886 *not* Petterd, 1884; *Amphithalamus obesus* H. Adams, 1865 = *Estea erma* Cotton, 1944; *Scrobs pyramis* Laseron, 1950). New Zealand (4 taxa, see Powell, 1979). Miocene of Italy (*Parvisetia ?mioscrobsoides* Sacco, 1895) and Miocene of New Zealand (*Scrobs kaawaensis* Laws, 1936; *Scrobs latoscrobis* Laws, 1948).

Material examined.

†**A. inclusus*: Syntype (USNM) and several other lots (AMS).
A. tenuis: Holotype (USNM).
A. trosti: Holotype (CAS).

†**A. vallei*: A few lots (AMS).
†**S. fulcira*: Holotype and paratypes and many other lots (AMS).
†**A. obesus*: Holotype (BMNH) and many other lots (AMS).
E. erma: Holotype and paratypes (SAM).
†**S. incidata*: Types (NHMV) and many other lots (AMS).
†**R. jacksoni*: Types (of *R. badia* Watson) (BMNH) and many other lots (AMS).
†**S. pyramis*: Syntypes and many other lots (AMS).
S. neglecta: Type (OUM).
R. mioscrobsoides: Holotype (TGM).
S. kaawaensis and *S. latoscrobis*: Paratypes (AUG).

Remarks. The few named American species of *Amphithalamus* probably fall into a single species complex, being very similar and clearly very closely related. They are all very small, with or without a weak peripheral groove or cord, and usually the base is paler than the rest of the shell and bears a weak cord. The subgenus reaches its greatest diversity in temperate Australia and New Zealand where the species are generally larger than their American counterparts, are often uniformly dark brown in colour, and lack any basal cord. Intermediate forms are, however, encountered in the tropical Indo-Pacific and because of this, and because of their very similar opercular and radular features, the Australasian and American groups are here considered to be consubgeneric.

Subgenus *Notoscrobs* Powell, 1927

Notoscrobs Powell, 1927: 547. Type species *Notoscrobs ornatus* Powell, 1927; by original designation. Recent, northern New Zealand (Fig. 21E).

Diagnosis. *Shell:* As for genus but teleoconch with strong spiral cords and, often, axial ribs (Fig. 21E,G).

Head-foot: A few details given by Ponder (1967).

Anatomy: Unknown.

Operculum and radula: As for genus (Fig. 21F,H,I) (also known [Ponder, 1967] for *A.* (*N.*) *erosus*).

Distribution. Northern New Zealand (*N. ornatus, Rissoa erosa* Odhner, 1924) and temperate Australia (*Amphithalamus triangulus* May, 1915; *Amphithalamus liratus* Thiele, 1930). Miocene (*Notoscrobs semiornatus* Laws, 1948) and Pliocene (*Notoscrobs waitemata* Laws, 1950) of New Zealand.

Material examined.
†*N. ornatus*: Holotype (AIM) and a few other specimens (NMNZ).
R. erosa: A few specimens (NMNZ, AMS).
A. triangulus: Holotype (TM) and a few lots (AMS).
†**A. liratus*: Holotype (HUM) and several lots (AMS).
N. semiornatus and *N. waitemata*: Paratypes (AUG).

Remarks. This small group is retained as a separate subgenus on the basis of the heavily sculptured shells of the species it contains, which are in sharp contrast with those of the species in the typical subgenus. No species are known that show intermediate sculptural development.

Genus *Microdryas* Laseron, 1950

Microdryas Laseron, 1950: 277. Type species *Estea iravadioides* Gatliff & Gabriel, 1913, ICZN Opin. 1181. Recent, south-eastern Australia (Fig. 22A,B).

Diagnosis. *Shell:* Small (1–1.5 mm in length), elongate-pupoid, non-umbilicate, of moderate thickness, smooth, spirally striate or with weak spiral cords; aperture ovate, sub-angled posteriorly, not channelled, inner lip nearly straight, obliquely inclined, not separated from parietal wall except by an extremely narrow groove; peristome simple, outer lip orthocline to opisthocline, with or without very weak varix. (Fig. 22A–C). Protoconch dome-shaped, paucispiral, with spiral rows of minute punctures (Fig. 22D).

Head-foot: Cephalic tentacles short, broad, eyes rather small, snout short, bilobed (preserved specimen of *M. striatus* (Powell) from Ponder, 1967).

Anatomy: Not known.

Operculum: Flat, thick, transparent, columellar edge straight, nucleus small; a ridge along inner side of columellar edge (Fig. 22F). (Also known for *M. striatus* Ponder, 1967: 207, pl. 3, fig. 17.)

Radula: Central teeth $\frac{2+1+2}{1\quad 1}$, cusps short, blunt; basal denticles small, laterally placed, ventral margin with tongue-like extension, lateral margins at about 30°. Lateral teeth 2 + 1 + 3, cusps short, blunt. Inner marginal teeth with long, straight cutting edge at right angles to axis of tooth bearing several (about 11) small, sharp cusps. Outer marginal teeth with hook-like distal ends (Fig. 22E).

Distribution. South-eastern Australia (*E. iravadioides*; *Microdryas* sp., Lord Howe I.). South Africa (*Nodulus innotabilis* Turton, 1932 = *Nodulus rietensis* Turton, 1932; *Nodulus rufanensis* Turton, 1932). New Zealand (*Epigrus striatus* Powell, 1927). Japan (?*Hyala pumila* A. Adams, 1870).

Material examined.
†*E. iravadioides*: Holotype (NMV), paratypes (NMV, AMS) and several other lots (AMS).
N. innotabilis: Holotype (OUM).
N. rietensis: Holotype and paratypes (OUM).
N. rufanensis: Holotype and paratypes (OUM).
E. striatus: Holotype (AIM).
H. pumila: Possible type (NMW).
†**M.* n.sp.: Lord Howe Island (AMS).

Remarks. Laseron (1950) designated *Cingula australiae* Frauenfeld as the type species of *Microdryas* but he misidentified Frauenfeld's species: his specimens so named are *M. iravadioides*. The shells of species in this genus differ from others in the subfamily in their tall spire, somewhat D-shaped aperture with an almost straight inner lip, and smooth or spirally sculptured surface.

Genus *Badepigrus* Iredale, 1955

Badepigrus Iredale, 1955: 81. Type species *Rissoa badia* Petterd, 1884; by original designation. Recent, south-eastern Australia (Fig. 23A,B).

Laseronula Whitley, 1959: 60, new name for *Saltatricula* Laseron, 1956: 445, *not* Burmeister, 1861, new name for *Saltatrix* Laseron, 1950: 277, *not* Klug, 1833. Type species *Epigrus protractus* Hedley, 1904; by original designation. Recent, eastern Australia (Fig. 23C,D).

Saltratricula err. auct.

Diagnosis. *Shell:* Minute (1-1.5 mm in length), solid, elongate to pupoid, sometimes last whorl disjunct; orange-brown in colour. Teleoconch smooth except for axial growth lines, one species with 2 strong, spiral keels. Whorls usually weakly to moderately convex, sometimes sharply-angled. Aperture with simple, oval peristome, edge blunt, outer lip opisthocline, without varix; inner lip widely to slightly separated from parietal wall (Fig. 23A,C,E). Protoconch dome-shaped, of about 1½ whorls, sculptured with minute pits arranged in spiral series, each series consisting of a narrow band of irregularly arranged pits (Fig. 23B,D,F). Inner chitinous layer poorly developed.

Head-foot: Pigmented; cephalic tentacles short, parallel-sided, with rounded ends, ciliated but without immobile 'setae'. No accessory tentacles. Snout long, broad, not distinctly bilobed. Sole without posterior mucous gland; anterior pedal gland present. (*B. pupoides*, Port Hacking, New South Wales, Australia) (Fig. 1I).

Anatomy: Female genital tract monaulic (Fig. 7A,B); penis simple, U-shaped when at rest, with narrow, pointed distal portion and large, broad proximal portion (Fig. 8D).

Operculum: Oval, double-layered, inner face with weak ridge on inner (columellar) edge (*B. pupoides*) (Fig. 23G).

Radula: Central teeth $\frac{(1)+1+(1)}{1 \qquad 1}$ small, elongate, each with 2 prominent basal processes close together at base of tooth, cutting edge very narrow, with small, blunt median cusp and a pair of rudimentary lateral cusps; lateral margins thin, at about 15°. Lateral teeth 1 + 1 + 1, with massive, blunt primary cusp and 2 heavy basal supports. Inner marginal teeth short, with 4–5 large cusps on distal end and a large basal process. Outer marginal teeth smaller than inner marginal teeth, lacking large cusps but cusp pattern on inner edge (if any present) obscured in mounts (Fig. 23H,I).

Distribution. South-eastern and eastern Australia (*R. badia* = *Rissoa* (*Amphithalamus*) *verconis* Tate, 1899 = *Rissoa verconis* var. *apicilata* Gatliff & Gabriel, 1913 = *Saltatricula improrsa* Laseron, 1956; *Amphithalamus pupoides* H. Adams, 1865 = *Amphithalmus* [sic] *pellyae* Nevill, 1881 = *Rissoa pulchella* Petterd, 1884, = *Rissoa* (*Amphithalamus*) *petterdi* Brazier, 1895; *Epigrus protractus* Hedley, 1904 = *Saltatricula stringera* Laseron, 1956 = *Saltatricula ballerina* Laseron, 1956; *Anabathron contortum* Hedley, 1907; *Epigrus semicinctus* May, 1915).

Material examined.

†*R. badia*: Holotype (TM) and several other lots (AMS).

R. verconis var. *apicilata*: Syntypes (NMV).

S. improrsa: Holotype and paratypes (AMS).

†*E. protractus*: Holotype and paratype and several other lots (AMS).

S. ballerina and *S. stringera*: Types (AMS).

†**Amphithalamus pupoides*: Holotype (BMNH) and many other lots (AMS).

R. pulchella (= *R. petterdi*): Holotype (TM).

A. contortum: Syntypes and a few other lots (AMS).

E. semicinctus: Holotype (TM) and a few other lots (AMS).

Remarks. Unfortunately only the shell is known for the type species of this genus but *B. pupoides* appears to be closely related and the animal of the type species should be similar in most respects. The radula is quite distinct from that of *Amphithalamus, Anabathron* and *Nodulus.* The external features of the animal differ from *Amphithalamus* and *Anabathron* in the cephalic tentacles being narrower. *Badepigrus* is most closely allied to *Afriscrobs* n.gen. and is contrasted under that genus. The synonymy follows Ponder (1967).

Afriscrobs n. gen.

Type species: *Amphithalamus africanus* Bartsch, 1915. Recent, South Africa (Fig. 24A-C).

Diagnosis. *Shell:* Minute (0.8 mm-1.5 mm in length), pupoid to trochiform, non-umbilicate to umbilicate, smooth, with spiral keels, or axially ribbed. Aperture ovate to subcircular, with simple or weakly duplicated non-channelled peristome; inner lip slightly separated from, or fused to, parietal wall; outer lip orthocline to prosocline, with sharp edge, not varicose (Fig. 24A,D,G). Protoconch paucispiral, dome-shaped, sculptured with exceedingly minute puncta not arranged in spiral rows (Fig. 24E).

Head-foot and anatomy: Not known.

Operculum: Oval, with 2 layers, inner side with a short, blunt, peg-like process emerging from nucleus and a raised rim along inner (columellar) edge (Fig. 24B,F).

Radula: Central tooth $\frac{2\text{–}1+1+1\text{–}2}{1 \qquad 1}$, with a pair of prominent basal denticles emerging from lower face; lateral margins thin at 15°–35°; cutting edge with large, triangular median cusp (blunt, broad, short in *A. saldadinensis*), and small, lateral cusps; ventral margin produced into long U-shaped extension. Lateral teeth 2–4 + 1 + 1–2, cusps sharp in most species. Inner marginal teeth with cutting edge at right angles to axis of tooth, 1-3 + 1 + 1-3, cusp, sharp; outer marginal teeth with a few sharp cusps (Fig. 24C,H).

Distribution. South Africa (*A. africanus* = *Amphithalamus multistriatus* Turton, 1932 = *A. denseplicatus* Turton, 1932, ? = *Turritella eucosmia* Turton, 1932; *Amphithalamus muiri* Barnard, 1963; *Rissoa adjacens* Smith, 1910, ? = *Nodulus dilectus* Turton, 1932; *Solariella quantilla* Turton, 1932; ?*Alvania minutissima* Turton, 1932; *Amphithalamus turtoni* Bartsch, 1915); Red Sea (?*Nodulus saldadinensis* Hornung & Mermod, 1928). ?Miocene, Italy (?*Nodulus tauromiocenicus* Sacco, 1895).

Material examined.

†**A. africanus*: Turton coll. (OUM) and a few other lots (AMS).
A. multistriatus: Holotype (OUM).
A. densiplicatus: Syntypes (OUM).
†**T. eucosmia*: One lot (AMS).
R. adjacens: Syntypes (BMNH).
N. dilectus: Holotype (OUM).
†**S. quantilla*: A few lots (AMS).
A. minutissima: Holotype (OUM) and a few other lots (AMS).
A. turtoni: Holotype (USNM), one other lot (OUM).
N. tauromiocenicus: Type (TGM).
†*one undescribed South African species (AMS).

Remarks. This genus is proposed for a small group of South African species having diverse shells but appearing to agree closely in radular and opercular characters. The radula shows some similarity with that of *Badepigrus*, particularly in the position of the basal denticles and in the thin lateral margins. It differs from the one species (*B. petterdi*) in that genus for which the radula is known in having a much squarer central tooth and more cusps on the lateral and inner marginal teeth. There are also more cusps on the inner side of the primary cusp of the lateral teeth than on the outer side, a feature not encountered in other genera. The operculum of *B. petterdi* lacks a peg and the aperture of all the species of *Badepigrus* has a simple, not a duplicated, peristome. *Anabathron, Amphithalamus, Nodulus, Microdryas* and *Pseudestea* all differ markedly in their radular and opercular characters.

Nodulus saldadinensis from the Red Sea is tentatively placed in this genus although the shell more closely resembled *Badepigrus* in its shape and simple peristome. The operculum has a very reduced peg but the radula more closely resembles that of species of *Amphithalamus*. The lateral teeth have the formula 2 + 1 + 2, this being intermediate between *Amphithalamus*, which typically has more cusps outside the primary cusp, and *Afriscrobs*, which has the reverse condition.

Genus *Pseudestea* Ponder, 1967

Pseudestea Ponder, 1967: 208. Type species *Scrobs pyramidatus* Hedley, 1903; by original designation. Recent, south-eastern Australia (Fig. 25A-E).

Diagnosis. *Shell:* Minute (1.2-1.5 mm in length), conic to ovate-conic, imperforate, smooth. Aperture oval, peristome simple, lacking channels; inner lip separated from parietal wall by simple, narrow groove; outer lip slightly opisthocline, with blunt edge, lacking varix (Fig. 25A). Protoconch large, dome-shaped, of about 1½ whorls, terminated by distinct varix; sculptured with spiral rows of minute punctures (Fig. 25B). Inner chitinous layer well developed.

Head-foot: Known only from restored dried animal. Pigmented; cephalic tentacles short, blunt, eyes at their outer bases, of medium size. Snout short, broad, bilobed. Sole with posterior mucous groove. (From Ponder, 1967.)

Anatomy: Penis of about 1 coil, attached to midline of head, distal ⅓ swollen and with about 11 chitinous spines, the proximal ones largest (from Ponder, 1967).

Operculum: Oval, simple, of two layers, with low ridge just inside columellar edge and small, low knob-like thickening at nucleus on inner surface (Fig. 25C).

Radula: Central tooth $\frac{3+1+3}{1\quad 1}$, median cusp narrow, sharp, lateral cusps small, sharp; basal denticles prominent, extend beyond ventral margin; ventral margin U-shaped, lateral margins weakly thickened, at about 15°. Lateral teeth 4 + 1 + 6-7, primary cusp large, sharp, lateral cusps small, sharp. Marginal teeth with numerous small sharp cusps, cutting edges curved (Fig. 25D,E).

Distribution. Southern and south-eastern Australia (*S. pyramidatus*) and northern New Zealand (*Scrobs crassiconus* Powell, 1933).

Material examined.

†**S. pyramidatus*: Holotype and paratypes and many other lots (AMS).
S. crassiconus: Holotype (AIM) and 3 other lots (AMS).

Remarks. This genus is characterized by a conic to ovate-conic shell with the aperture separated from the parietal wall by a simple groove. It resembles some species of *Amphithalamus* in size but differs in the simple groove between the inner lip and the parietal wall and the spinose penis. The radular features also differ, the sharp primary cusps of the central and lateral teeth being in contrast with the broad, blunt cusps seen in *Amphithalamus* species. The lateral teeth are closer to those seen in species of Rissoidae than to other genera in the Anabathrinae.

Pseudestea contains a few species (mostly undescribed) found on the Continental Shelf and upper Continental Slope of southern and south-eastern Australia. *Scrobs crassiconus* Powell from northern New Zealand is (somewhat tentatively) referred here because of its similar shell.

Genus *Pisinna* Monterosato, 1878

Pisinna Monterosato, 1878:86. Type species *Rissoa punctulum* Philippi, 1836, by subsequent designation by Cossmann, 1921: 33. Recent, Mediterranean Sea (Figs 25F,G; 26F,G).

Hagenmulleria Bourguignat, 1881: 9. Type species *Hagenmulleria pechaudi* Bourguignat, 1881; here designated (= *Pisinna punctulum* (Philippi) *fide* Monterosato, 1894:114). Recent, Mediterranean Sea.

Estea Iredale, 1915: 451. Type species *Rissoa zosterophila* Webster, 1905; by original designation. Recent, New Zealand (Fig. 27A-D).

Nodulestea Iredale, 1955: 81. Type species *Estea castella* Laseron, 1950; by original designation. Recent, south-eastern Australia (Fig. 27G-I).

Feldestea Iredale, 1955: 81. Type species *Rissoa salebrosa* Frauenfeld, 1867; by original designation. Recent, south-eastern Australia (Fig. 27E,F).

? Microestea Ponder, 1965c: 156. Type species *Estea angustata* Powell, 1927; by original designation. Recent, northern New Zealand (Fig. 22G,H).

Diagnosis. *Shell:* Small to moderate size (1.2-3.8 mm in length), pupiform to elongate-ovate or ovate-conic, non-umbilicate. Aperture subcircular, with simple peristome; inner lip usually broad, attached to parietal wall; outer lip prosocline to opisthocline, with or without varix. Sculpture of axial or spiral ribs or both, or surface smooth (Figs 22G; 26F; 27C,E,G). Protoconch dome-shaped, of about 1½-2 whorls, surface minutely pitted, pits usually in close spiral rows (Figs 22H; 25G; 27A,F,H). Inner chitinous layer well developed.

Head-foot: Unpigmented or pigmented; cephalic tentacles paddle-shaped, snout bilobed; anterior mucous gland and propodium present; sole with long posterior mucous slit (Ponder, 1965c, 1968; Ponder & Yoo, 1976).

Anatomy: Female genital tract diaulic, spermathecal aperture at posterior end of pallial cavity (Fig. 7H,I,J). Penis simple, coiled, attached to midline of head (Fig. 8C).

Operculum: Simple, of 2 layers, oval, usually with low ridge just inside inner (columellar) edge. A weak projection just below nucleus in one species (*P. tropica* (Laseron), Ponder & Yoo, 1976, fig. 13e,f). Other species figured by Ponder (1965c) and Ponder & Yoo (1976) (Figs 26G, 27B).

Radula: Central teeth $\frac{3\text{-}1+1\text{-}3}{1\qquad 1}$, each with broad and blunt to narrow and sharp median cusp, basal denticles short; ventral edge more or less extended as a tongue-like structure in middle portion; lateral edges thickened, at 30°-40°. Lateral teeth 2-3 + 1 + 2-5, with cutting edge slightly longer than, or equal to, that of central teeth; primary cusp blunt to moderately sharp. Marginal teeth both simple, with several small, sharp cusps, those on inner marginal teeth slightly larger than those on outer marginal teeth; cutting edge of inner marginal teeth straight and at right angles to axis of tooth (Ponder & Yoo, 1976, figure the radula of several species) (Figs 25F; 27D,I).

Distribution. Mediterranean Sea, South Africa, Australia, New Zealand, tropical Western Pacific (see Ponder & Yoo, 1976).

Material examined.

†**P. punctulum*: Specimens ex Monterosato so named, ex Philippi (BMNH). Many other lots (AMS and other museums).

†**R. zosterophila*: Paratypes and several other lots (AMS).

†**E. castella*: Types and many other lots (AMS).

†**E. salebrosa*: Types (NHMV) and many other lots (AMS).

**E. angustata*: Types (AIM) and a few other lots (NMNZ).

Many other species have also been examined.

Remarks. The species in this genus have been reviewed by Ponder (1965c) and Ponder & Yoo (1976). The radula, like the teleoconch sculpture, shows considerable diversity (Ponder & Yoo, 1976).

Pisinna appears to have had a southern origin (Ponder & Yoo, 1976) with the centre of speciation in New Zealand and temperate Australia. One of the species (*Barleia* [sic] *microthyra* Martens) included in *Pisinna* by Ponder & Yoo (1976) is a *Barleeia*.

Genus *Nodulus* Monterosato, 1878

Nodulus Monterosato, 1878:86. Type species *Rissoa contorta* Jeffreys, 1856; by subsequent designation by Bucquoy, Dautzenberg & Dollfus, 1884: 311. Recent, Mediterranean Sea (Fig. 26A-E).

Diagnosis. *Shell:* Minute (up to about 1.3 mm in length), solid, pupiform, non-umbilicate, with fine spiral sculpture, whorls convex, aperture broadly oval, with simple peristome, inner lip slightly separated from parietal wall; outer lip orthocline to weakly prosocline, non-varicose, with blunt edge (Fig. 25A). Protoconch of about 1½ whorls, dome-shaped, sculptured with rather irregular pits, the surface between sometimes raised into weak, irregular wrinkles (Fig. 26B). Inner chitinous layer poorly developed.

Head-foot: Tentacles rather short, of even thickness, without obvious cilia or 'setae', held rather far to the sides of the head, showing little movement; eyes large. Foot short and slender, anterior corners forming right angles; posterior end simple, lanceolate. Snout bilobed, especially ventrally. No pallial or metapodial tentacles. Yellowish to brownish-greyish, very lightly coloured, with yellow spots behind eyes (Corsica; A Warén, *in. lit.*).

Operculum: Oval, flat, composed of two layers, paucispiral; inner surface with ridge along inner (columellar) edge and with two processes. One process rising from nucleus, subspiral, rather prominent, its distal portion vertical; other process small and vertical. Both connected by short, low, narrow ridge. Outer surface smooth except for radial growth lines (Fig. 26C,D).

Radula: Central teeth $\frac{3+1+3}{1\qquad 1}$, cusps sharp, primary cusp not conspicuously longer than adjacent cusps; each tooth with very small pair of processes high on outer edges of face; lateral thickenings rather weak, at about 30°; base with short, tongue-like process. Lateral teeth 2 + 1 + 2, with cutting edge narrower than that of central teeth, cusps sharp. Inner marginal teeth with longer cutting edge than lateral teeth, with about 9 sharp cusps. Outer marginal teeth with smaller, sharp cusps (Fig. 26E).

Distribution. Mediterranean Sea (*R. contorta*).

Material examined.

†**R. contorta:* Probable syntypes (BMNH) and many other lots (several museums).

Remarks. This genus differs from others in the subfamily in the relatively large central teeth of the radula and in possessing two opercular pegs. In addition, the protoconch microsculpture, the lanceolate foot and the parallel-sided non-ciliated cephalic tentacles are also atypical. The presence of an opercular peg has resulted in this genus usually being classified with *Barleeia* by earlier authors. The general form of the operculum is, however, quite unlike that of *Barleeia* and is similar to that of some Anabathrinae, particularly in its possessing two discrete layers. The number of unique characters that *Nodulus* possesses suggests, however, that it has little close relationship with the other genera in the subfamily.

Discussion

Anatomy and Relationships: Convergence or Divergence?

Anatomically, as well as in shell characters, barleeids resemble rissoids and have long been included in the same family. Some of these resemblances are basic rissoacean characters (e.g. presence of a style sac containing a crystalline style, lack of an oesophageal gland, and the salivary glands or their ducts not passing through the circumoesophageal nerve ring). Other features shared with the Rissoidae, such as the closed pallial genital ducts and some shell characters, may either be due to convergence or be an indication of phyletic relationship. Some additional characters, which may be primitive, are shared with several rissoacean families and include the presence of metapodial and pallial tentacles (in *Fictonoba* and in many Rissoidae, Vitrinellidae, *Hydrobia* [Hydrobiidae] and some Iravadiidae), an opercular peg (also in *Rissoina* [Rissoidae], Cingulopsidae and Rastodentidae as well as the littorinacean Eatoniellidae), and the presence of an inner chitinous shell layer (also found in the Cingulopsidae and Eatoniellidae). The oesophageal pouches are almost certainly primitive, and are found in the Littorinidae (Fretter & Graham, 1962) and the Eatoniellidae (Ponder, 1968). Oesophageal pouches are possibly not present in the Cingulopsidae (although reported by Fretter & Patil, 1958), but in that family an oesophageal gland lies behind the nerve ring in some species (unpublished observations and Fig. 2D). The punctate or pitted protoconch microsculpture, so characteristic of the Barleeidae, is found in a few species of *Rissoina* but is otherwise rare in the Rissoidae (occurring in only four other genera). A shallow pitted protoconch microsculpture is typical of the Hydrobiidae but most other rissoacean families lack such sculpture.

An inner chitinous shell layer, a pegged operculum and a minute, conical, simple shell are found in the littorinacean Eatoniellidae (Ponder, 1965a; Ponder & Yoo, 1978) and the rissoacean Cingulopsidae (Ponder & Yoo, 1980) and Rastodentidae (Ponder, 1966), as well as the Barleeidae. The barleeids differ from the above families in being phallate. These families may form a closely related group which evolved separately from the rest of the Rissoacea from an eatoniellid-like ancestor. Further work is required to establish whether or not this is the case. A major problem with such a scenario is the similarity between *Fictonoba* and the rissoids, especially *Rissoina*. Given the number of characters in common, it is possible that *Rissoina* and *Fictonoba* are related and that the Rissoidae (i.e. a *Rissoina*-like ancestor) evolved from a *Fictonoba*-like barleeid. This question was also addressed in the discussion on *Fictonoba* where it was suggested that the resemblances between *Fictonoba* and the Rissoidae may also be due to convergence.

The evolutionary relationships of most of the families mentioned in the Discussion are summarized in Fig. 9.

The Radula

The central teeth of the radula of species of Barleeinae have, with the exception of *Caelatura*, a U-shaped projection on their lower face which abuts against the upper edge of the tooth in front, probably preventing it from sliding forwards when pressure is applied during scraping. The ventral margin extends beneath the tooth in front where it fits into a shallow socket behind the upper part of the tooth. This arrangement would prevent the base of the tooth from tipping forwards and, perhaps, tearing loose from the basement membrane during scraping.

In *Caelatura* the U-shaped projection is absent but the basal denticles overlap the teeth in front and probably serve the same purpose. The basal denticles in the other genera do not appear to be in a position to function in this way and their role is obscure. Species of the Anabathrinae have no U-shaped basal projection and the basal denticles do not overlap the tooth in front. Whereas it seems probable that these different radular structures are related to different feeding strategies, the gut contents of all the species examined anatomically were similar, consisting of diatoms, algal cells and some detrital material. Differences may occur in the amount of force exerted by the radula while scraping the substratum enabling subtly different types of grazing to occur.

The Oesophageal Pouches

The oesophageal pouches of *Barleeia* resemble an oesophageal gland and appear to be an anterior extension of that gland. Similar structures are found in *Lacuna* sp. (Fretter *in lit.*) *Littorina* spp. (Fig. 2C) (Fretter & Graham, 1962), and *Laevilitorina mariae* (T. Woods) (my own observations) (Fig. 2B). In these species the anterior oesophagus narrows considerably through the nerve ring with a consequent disappearance

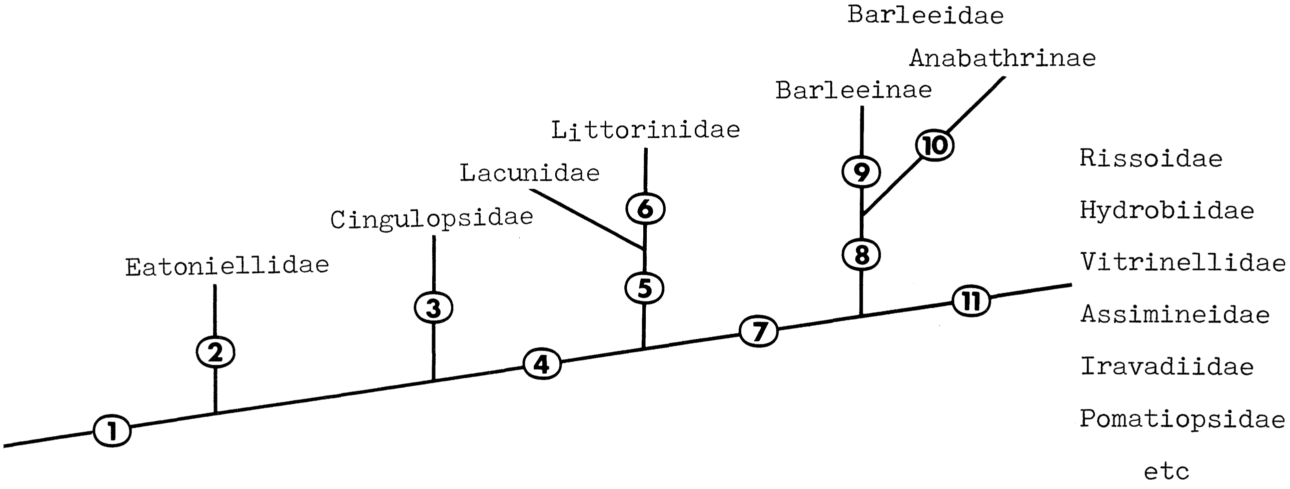

Fig. 9. Diagrammatic representation of the possible relationships of some of the littorinacean and rissoacean families. Numbers in the diagrams represent the presence of the following characters and states.

1. Inner chitinous shell layer; opercular peg; salivary glands/ducts pass through the nerve ring; oesophageal gland and pouches present; style sac but no crystalline style; male and female pallial genital ducts open; aphallate, with posterior sac for sperm storage (seminal receptacle); larval development pelagic; tentacles on opercular lobe present; posterior pedal gland present with long, slit-like opening reaching to posterior end of foot.
2. Direct development; development of pallial sperm-receiving structure in some; posterior pallial tentacle in one genus.
3. Closure of pallial genital duct and development of visceral bursa copulatrix; oesophageal gland lost in some species; style sac lost; loss of accessory tentacles.
4. Penis developed.
5. Loss of inner chitinous shell layer; loss of opercular peg; partial or complete closure of pallial genital ducts; tendency to coiling of oviduct glands; development of anterior bursa copulatrix; loss of slit-like posterior pedal gland opening.
6. Loss of tentacles on opercular lobe.
7. Development of crystalline style; salivary glands/ducts do not pass through nerve ring; development of secondary sperm storage (usually a bursa copulatrix derived from sperm groove); development of metapodial and pallial tentacles; loss of opercular lobe tentacles.
8. Loss of oesophageal gland; complete closure of male and female pallial genital ducts; direct development.
9. Loss of metapodial and pallial tentacles in all but one genus.
10. Partial or complete loss of opercular peg; loss of oesophageal pouches, operculum two-layered, loss of metapodial and pallial tentacles.
11. Loss of inner chitinous shell layer, oesophageal gland and oesophageal pouches; posterior pedal gland lost or, in some, present with small opening in middle of metapodial sole.

of the glandular epithelium of the oesophageal gland and the oesophageal gland proper lies behind the nerve ring. In the most primitive state, as seen in some species of *Eatoniella* (Eatoniellidae) and *Macquariella kingensis* (May) (Littorinidae), the glandular epithelium of the oesophageal gland passes through the nerve ring and is continuous with that of the oesophageal pouches (Fig. 2A). The oesophageal pouches seen in *Barleeia* (Fig. 2G) are histologically and morphologically so similar to those of the Littorinidae that they are almost certainly homologous. It appears that the oesophageal pouches in the Littorinacea and the Barleeidae are an anterior remnant of the oesophageal gland.

Both the oesophageal gland and the oesophageal pouches are lost in *Fictonoba,* as well as in the Anabathrinae, although this subfamily has well-developed dorsal folds in the oesophagus. The Cingulopsidae have apparently lost the oesophageal pouches but some have an oesophageal gland (Fig. 2D), although this is lost in at least one species—*Skenella* (= *Eatoniopsis*) *castanea* (Laseron) (Fig. 2E).

The salivary glands pass through the nerve ring in the majority of mesogastropods and this state is observed in the littorinacean families Eatoniellidae (Fig. 2A) and Littorinidae (Fig. 2A–C) and in the rissoacean family Cingulopsidae (Fig. 2D,E). The other rissoacean families have the salivary glands placed above the nerve ring (Fig. 2F,G), this presumably being a derived state.

Ponder (1973) considered the oesophageal pouches of *Littorina* to be homologous with the buccal pouches seen in some Archaeogastropoda. If the oesophageal pouches are derived from the oesophageal gland they are clearly not homologous.

The Female Genital System

The female genitalia of the Barleeidae can be derived from an ancestral state having an open, pallial capsule gland with a sperm groove along the ventral edge of the left (inner) side (Fig. 5A,B). This gland would have been continuous with the albumen gland, which lies behind the posterior pallial wall, displacing the kidney. A posterior seminal receptacle on the left side of the albumen gland probably opened adjacent to the short, renal oviduct, into the ventral wall of the anterior end of the albumen gland.

Of all the species examined *Lirobarleeia galapagensis* (Fig. 5C,D) is the most similar to this basic type. The capsule gland is closed and the sperm groove is contained within the ventral channel formed from the fusion of the two ventral edges of the walls of the capsule gland. This sperm groove has been nipped off to form a spermathecal tube in *Fictonoba carnosa* (Fig. 5E,F), *Anabathron contabulatum* (Fig. 7C,D) and *Badepigrus pupoides* (Fig. 7A,B), but it maintains communication with the anteriorly placed vestibule in all these species. In *Barleeia* spp. (Fig. 5G,H), *Pisinna* spp. (Fig. 7H–J) and *Amphithalamus incidatus* (Fig. 7E–G) the spermatheca has severed its connection with the anterior oviduct and opens in the posterior part of the pallial cavity. In *Pisinna* and *Barleeia* this opening is at the posterior end of the pallial cavity but in *A. incidatus* it is placed more anteriorly. It is highly probable, given their dissimilarity in many other characters, that the diaulic condition in *Pisinna* and *Barleeia* was independently derived. Similar short spermathecal ducts with an independent opening are found in the Pomatiopsidae (Davis, 1979, 1980), the Stenothyridae (Kosuge, 1969), the Cingulopsidae (Fretter & Patil, 1958) and the Hydrococcidae (in which the bursa opens directly to the exterior) (Ponder, 1982).

An alternative derivation of the posterior spermathecal opening in *Barleeia* is that the ventral walls of the capsule gland may have sealed in the middle section, leaving a posterior and an anterior opening. This explanation is, in my view, much less likely than the loss of the pallial part of the spermathecal tube. The ventral fusion of the walls of the capsule gland in those species with a separate spermathecal opening is more complete than in *Lirobarleeia* and *Fictonoba*, and has resulted in a central lumen in *Barleeia*.

The sperm groove in *Lirobarleeia* appears to be enlarged posteriorly to store sperm (Fig. 5C,D: *sz*) and is thus analogous to that of *Iravadia* (*Pseudomerelina*) *mahimensis* (Melvill) (Ponder, 1984). In the Iravadiidae this sperm groove appears to have moved dorsally to provide a greater storage area in some species. A parallel situation appears to have occurred in the Barleeidae. *Fictonoba* (Barleeinae) has a bursal sac placed dorsally between the capsule and albumen glands and similar sacs occur in all species of Anabathrinae studied. Species of *Barleeia* do not have a bursa copulatrix but have developed a sperm storage area in a lobe of the albumen gland.

The seminal receptacle was in the same position in all the species studied and shows little modification.

The fertilization area is unmodified in *Fictonoba*, where it is simply the ventral anterior portion of the albumen gland. The histology of this area is markedly modified in *Lirobarleeia* and *Barleeia* but it is widely open to the albumen gland. In the Anabathrinae it is a separate structure, presumably budded off from the albumen gland. It is tubular in some and a simple cavity in others. The area anterior to the fertilization chamber is a narrow tube lined with large, cuboidal, pale-blue-staining cells in all species of Anabathrinae except those in *Pisinna*. Those species have lost the tube because of their posterior spermathecal opening.

The renal section of the oviduct is short and simple in *Pisinna* and in the Barleeinae but has developed into a U-shaped loop in the other species of the Anabathrinae investigated. In these the U-shaped tube lies ventrally along the albumen gland and is narrow throughout. It is analogous to the coiled oviduct of the Hydrobiidae and the upper oviduct of the Rissoidae but is almost certainly independently derived.

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Table 1. Character states of some important characters in the Rissoidae and Barleeidae (+, present; -, absent; (+), rarely present; (-), rarely absent. Characters have been selected that show differences between the groups under consideration. Characters or states present only in the atypical barleeid genus *Fictonoba* are in parentheses and marked with an asterisk in the Barleeinae column.

	Rissoidae	**Barleeidae**	
		Barleeinae	**Anabathrinae**
Shell			
With inner chitinous layer	-	+	+
With punctate protoconch	- (+)	+	+
Operculum			
With peg on inner surface	- (+)	+	- (+)
With prominent longitudinal ridge on middle of inner surface	-	+	-
Composed of two layers	-	-	+
Radula			
Cusps on outer edge of outer marginal teeth	- (+)	+	-
Head-foot			
Metapodial tentacle(s) present	+ -	- (+)*	-
Pallial tentacle(s) present	+ -	- (+)*	-
Cephalic tentacles long and slender	+	+	-
Posterior pedal gland opening (when present) extends to posterior end of foot	-	+	+
Anatomy			
Jaws present	+	+ -	+ -
Buccal pouches present	-	+ (-)*	-
Dorsal folds in mid-oesophagus long	-	-	+
Spermathecal duct opens to posterior end of pallial cavity	-	+ -	- (+)
Oviduct with two separate glands	+	-	-
Lower oviduct gland (capsule gland) with ventral sperm gutter	+(-)	- (+)	-
Bursa copulatrix (when present) on left side of albumen gland	-	+	+
Seminal receptacle on left side of albumen gland	-	+(-)*	+

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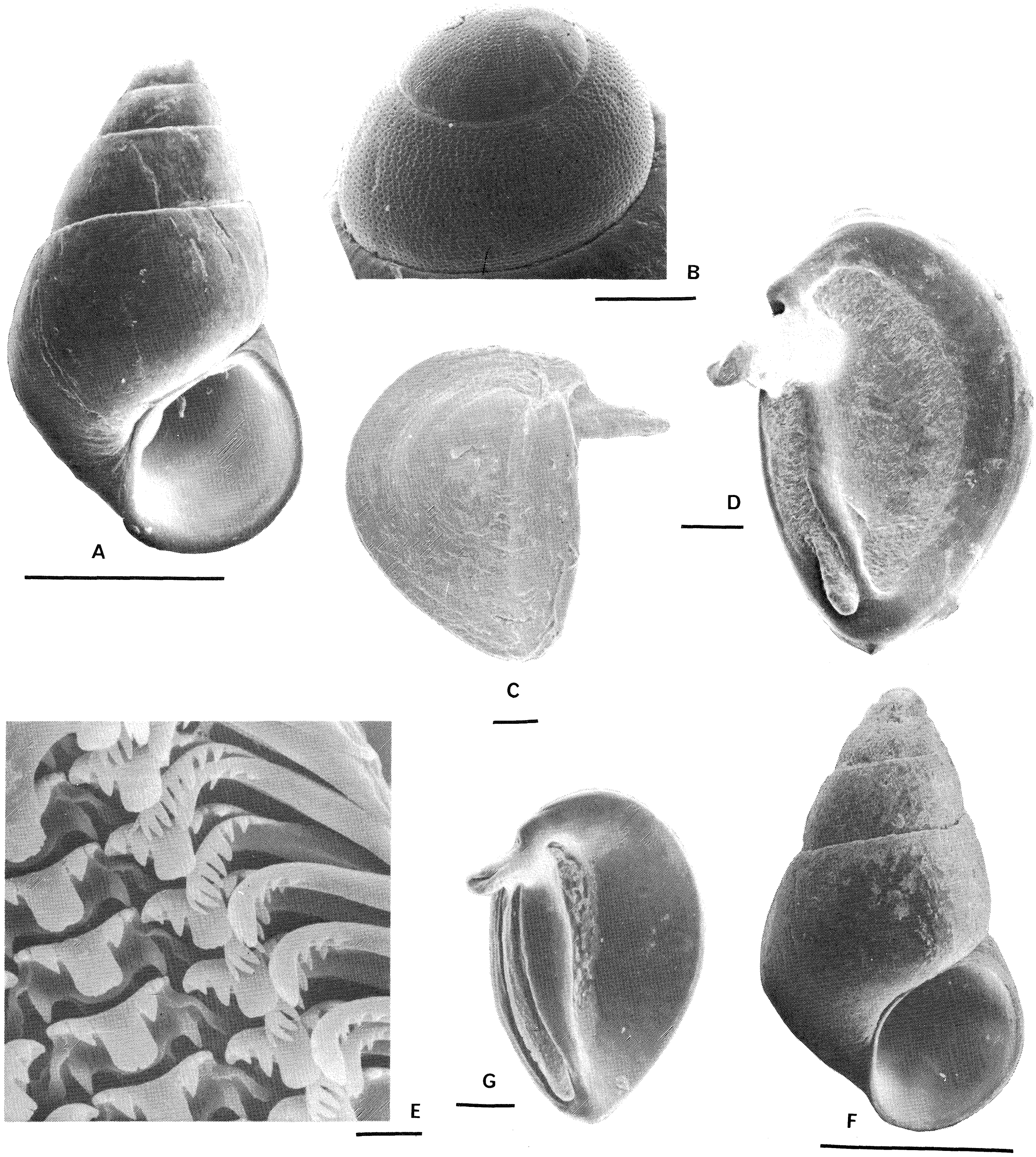
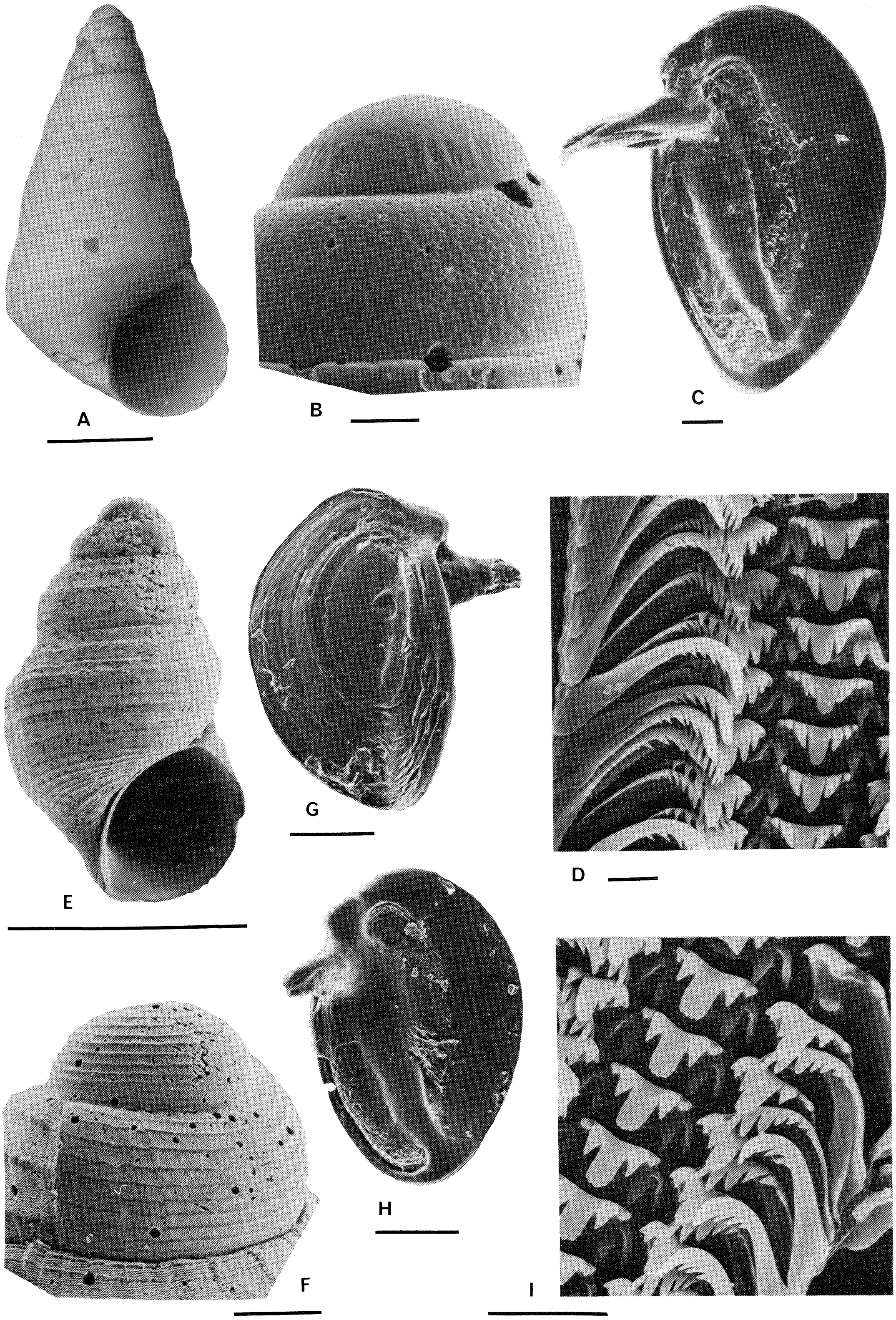


Fig. 10. **A–E,** *Barleeia unifasciata* (Montagu), type species of *Barleeia* Clark: **A**, shell; **B**, protoconch; **C** & **D**, operculum (**C**, outer side, **D**, inner side); **E**, radula. (A–D, Wembury, England, AMS C. 137204; E, Devon, England, NMV F26633). **F** & **G**, *Barleeia angustata* (Pilsbry), type species of *Ansola* Slavoshevskaya; Posyet Bay, USSR, AMS C.139454.
Scales: shells—1 mm; protoconch and opercula—0.1 mm; radula—0.01 mm.



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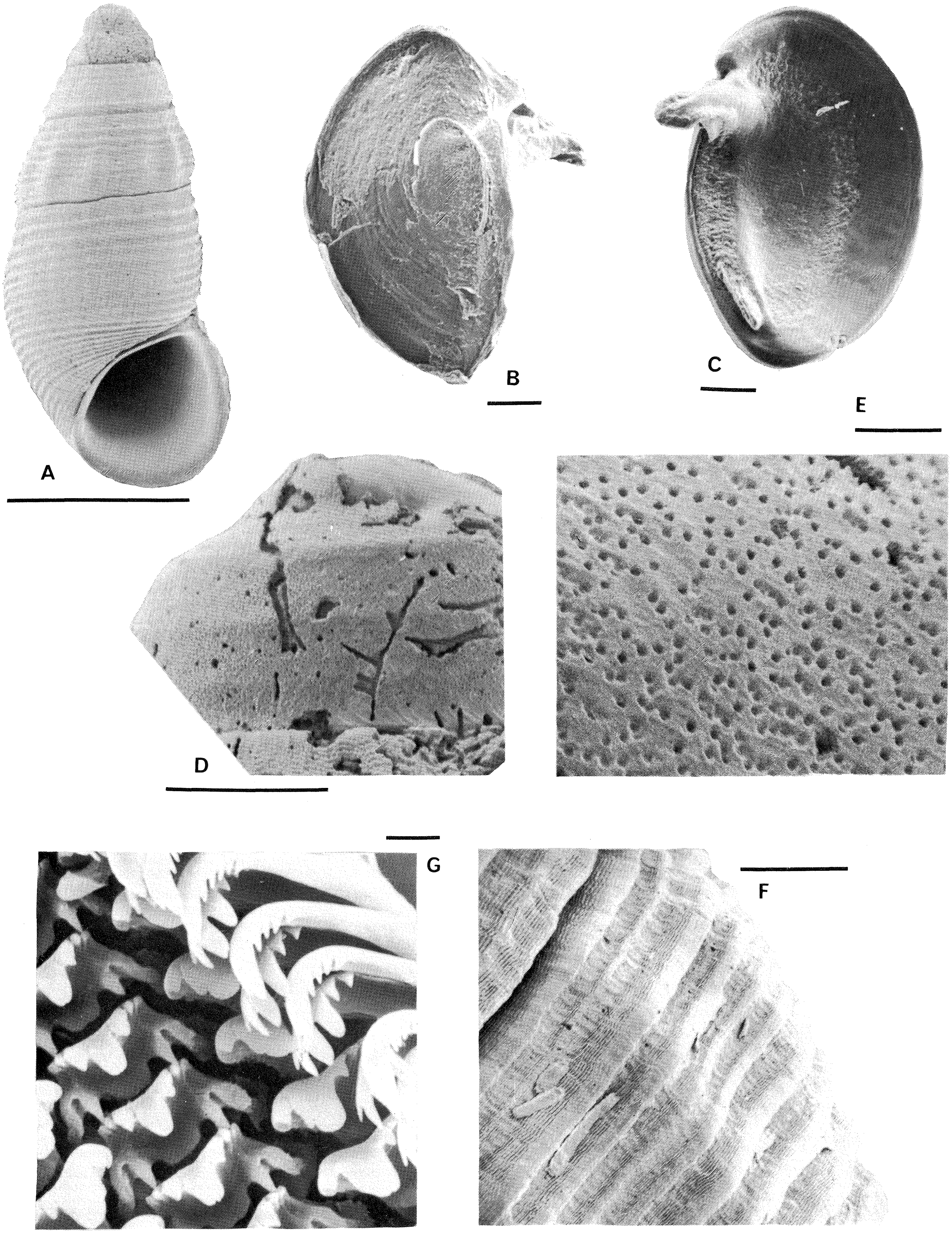

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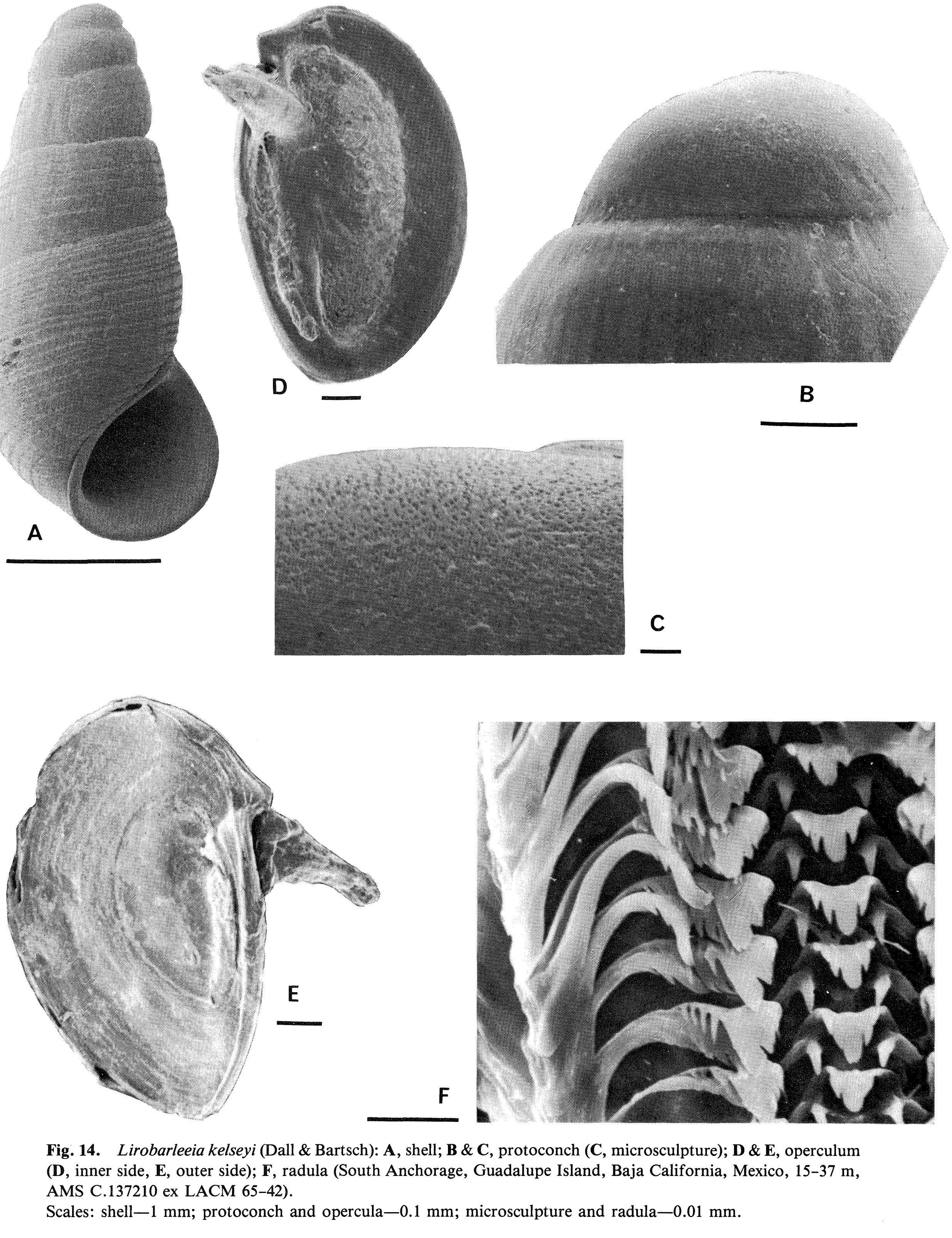
Scales; shell—1 mm; protoconch, opercula, and microsculpture figure F—0.1 mm; microsculpture figure E and radula—0.01 mm.



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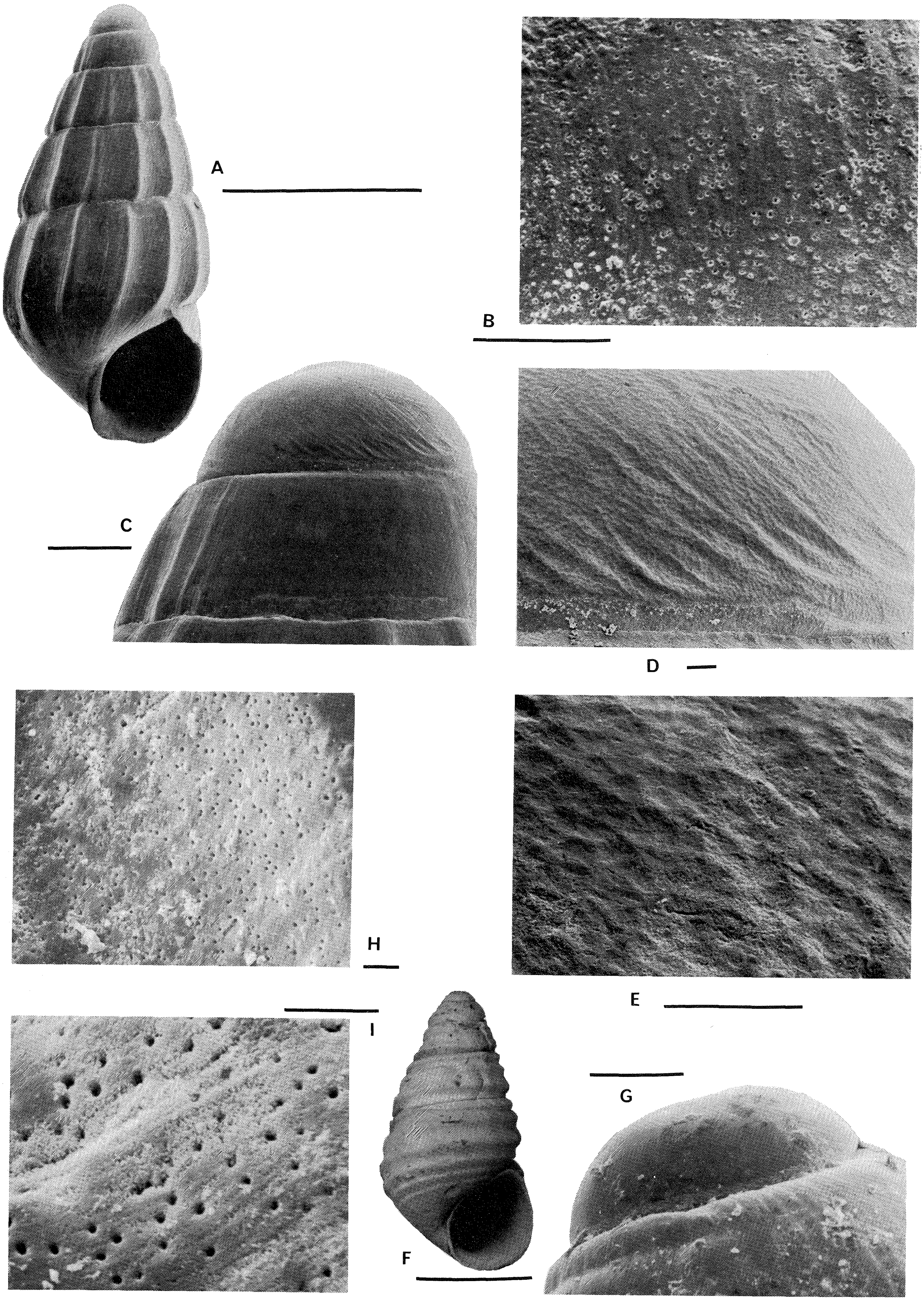
Scales: shell—1 mm; protoconch and opercula—0.1 mm; microsculpture and radula—0.01 mm.



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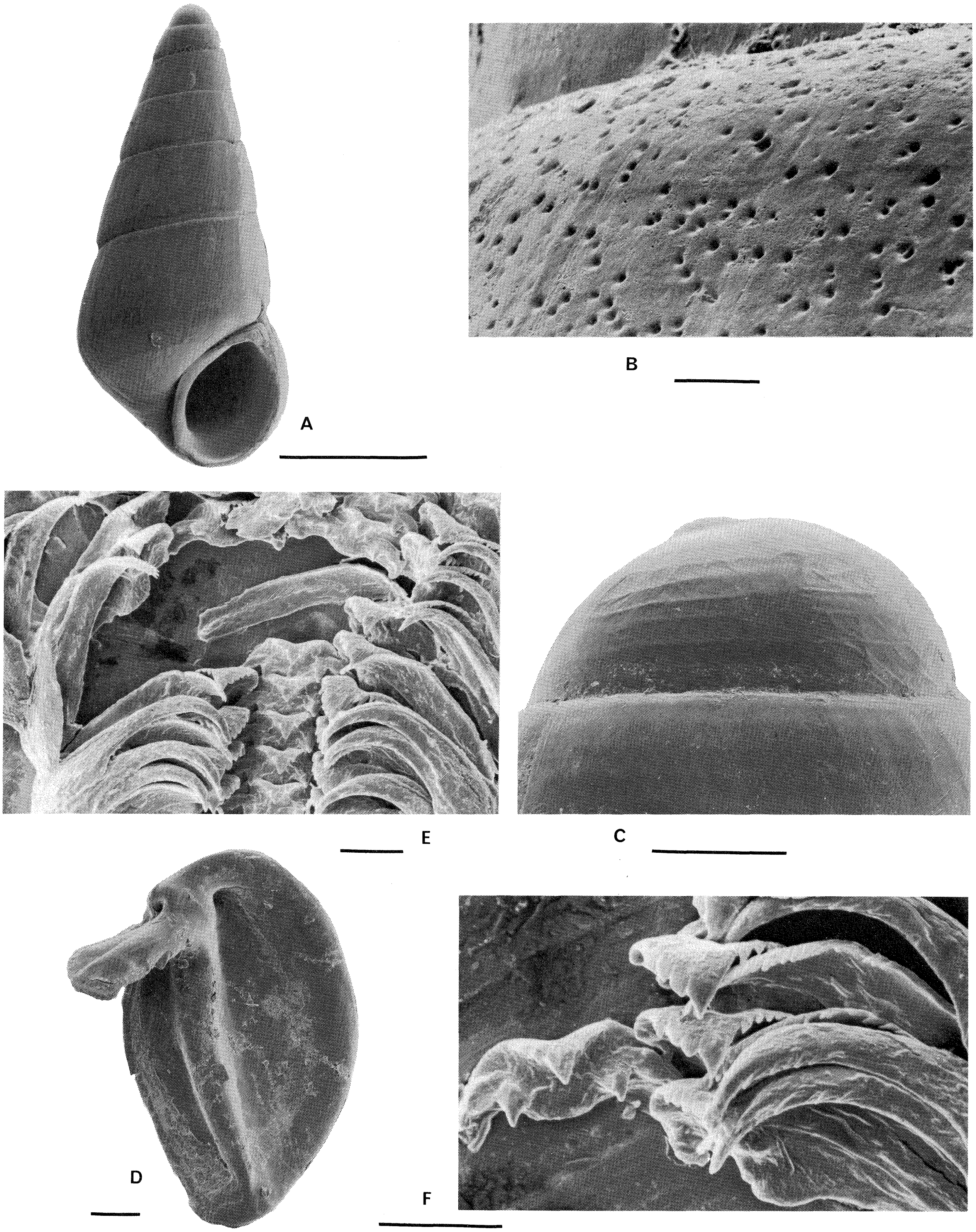
Scales: shells—1 mm; protoconchs, and microsculpture figure H—0.1 mm; microsculpture figures B,D,E,I—0.01 mm.



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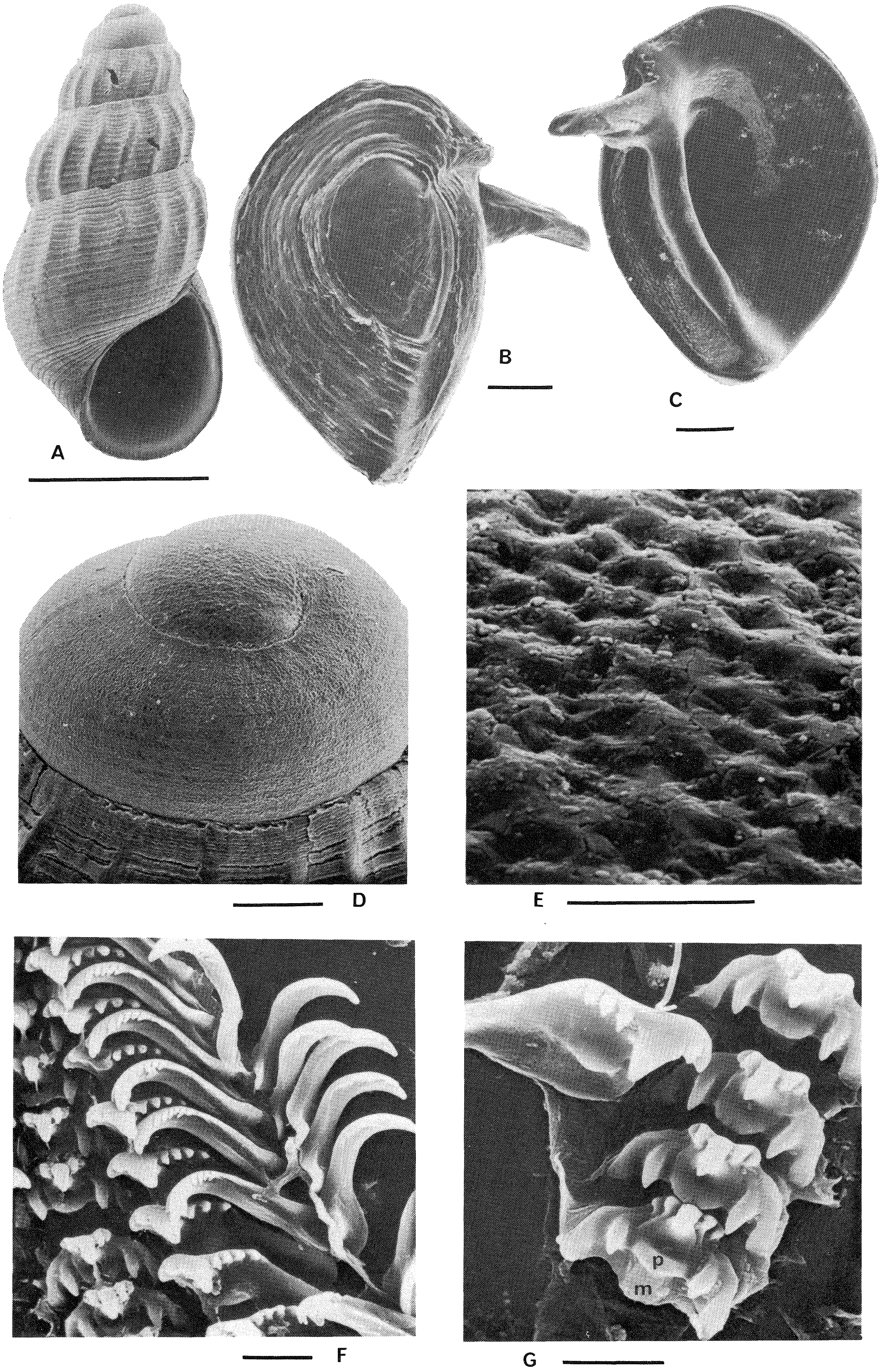
Scales: shell—1 mm; protoconch and operculum—0.1 mm; microsculpture and radulae—0.01 mm.



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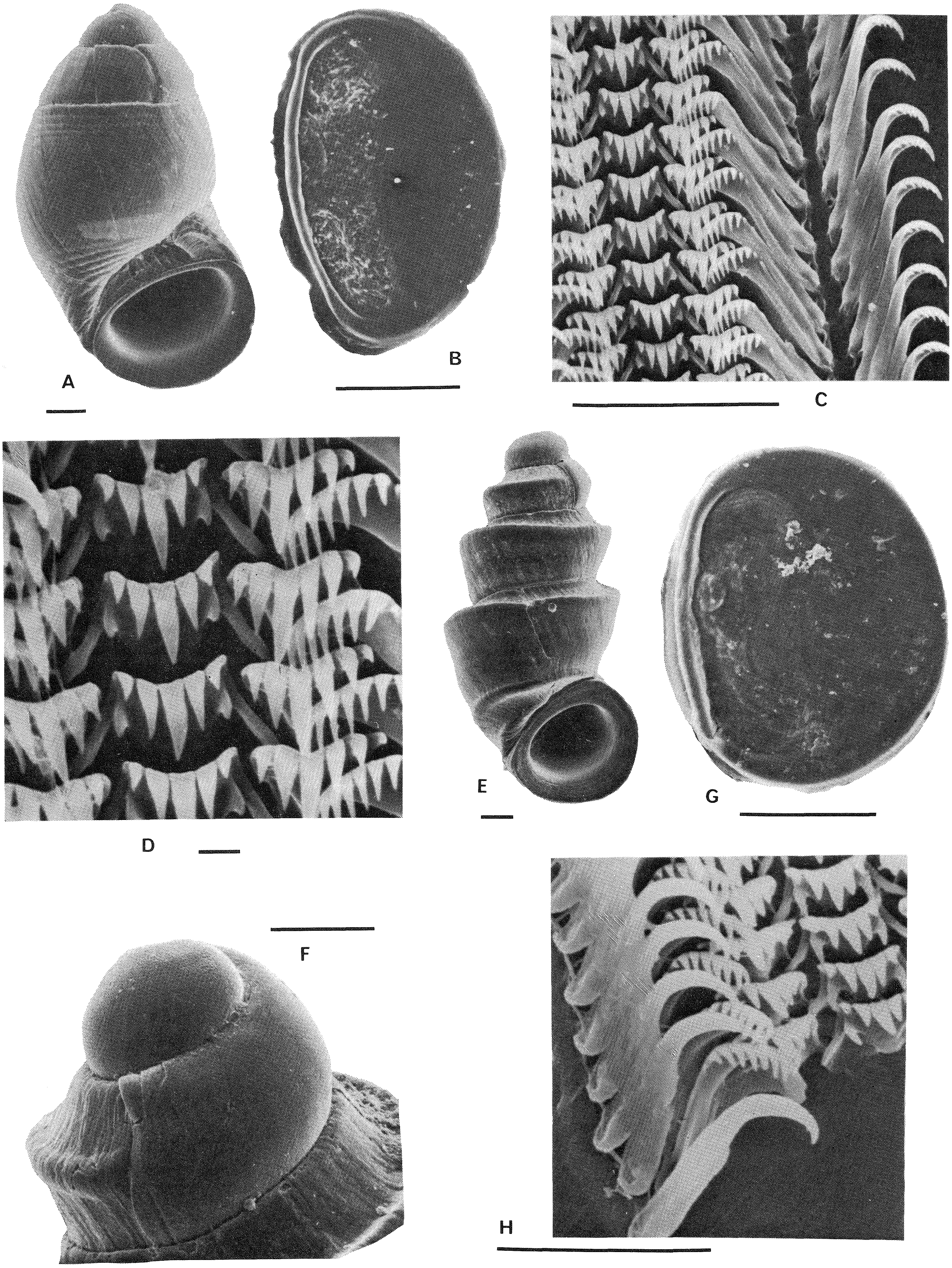
Scales: shell—1 mm; protoconch and opercula—0.1 mm; microsculpture and radulae—0.01 mm.



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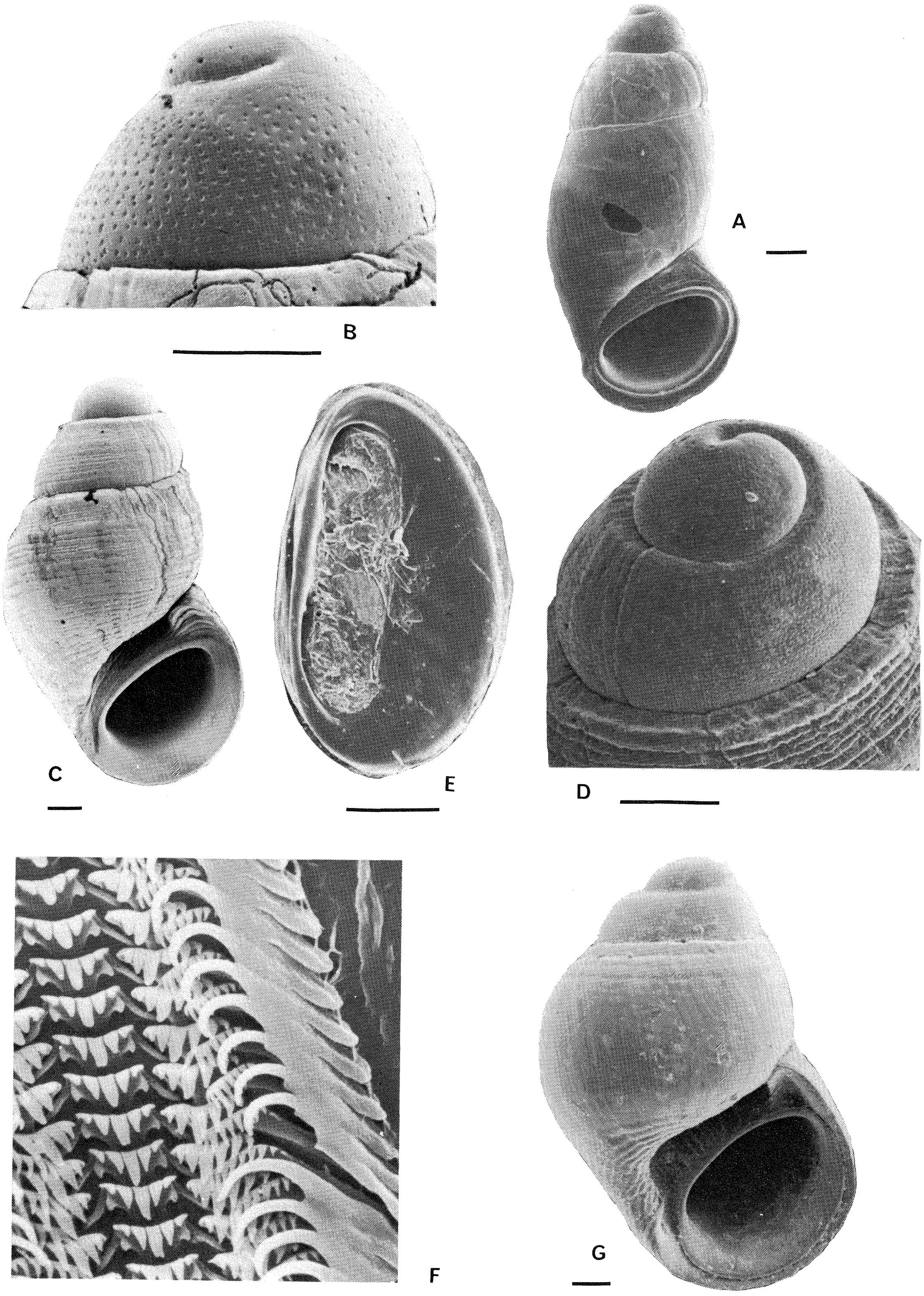
Scales: shells, protoconch and opercula—0.1 mm; radulae figures C and H—0.01 mm; radula figure D—0.001 mm.



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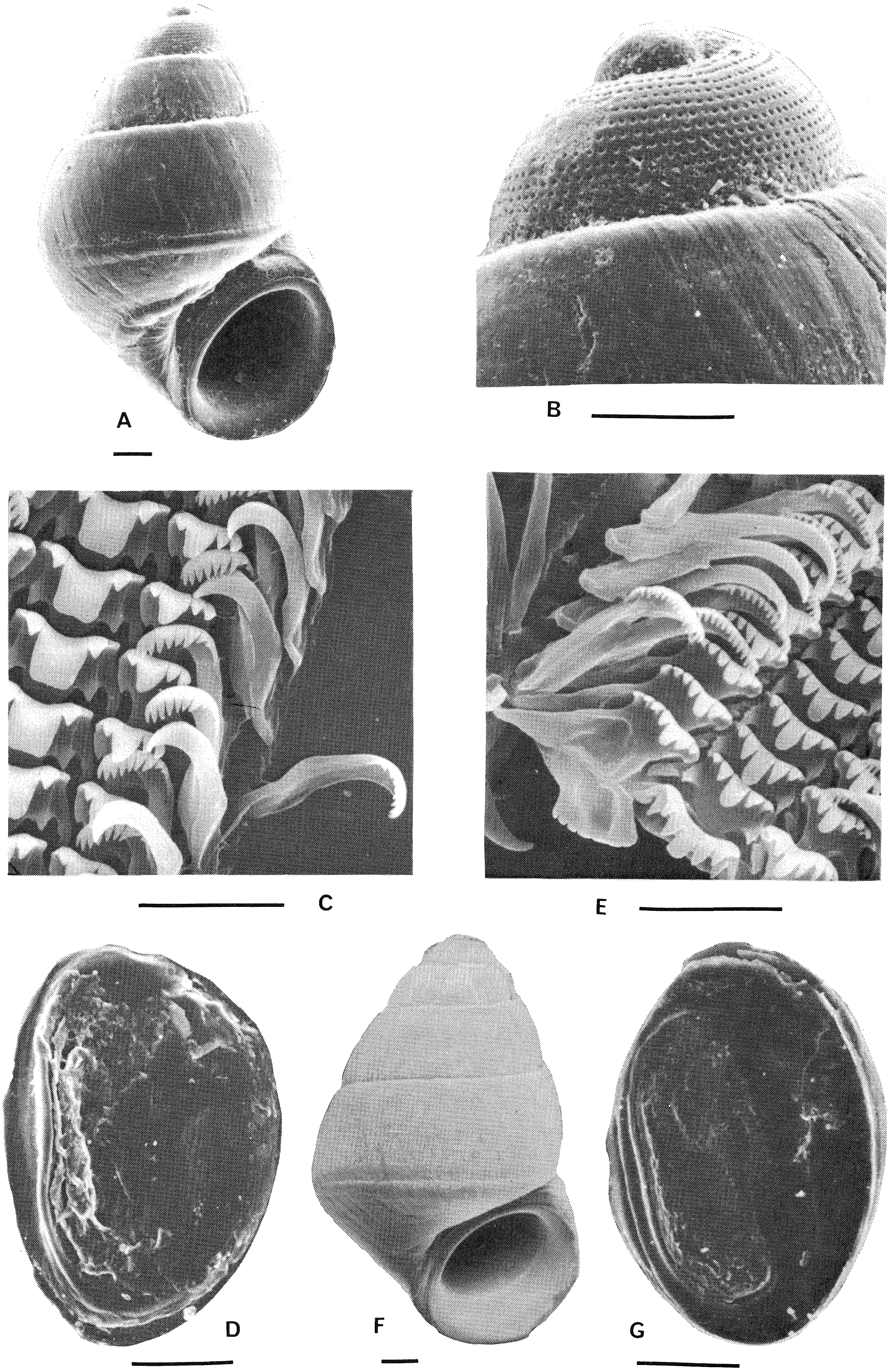
Scales: shells, protoconchs, and operculum—0.1 mm; radula—0.01 mm.



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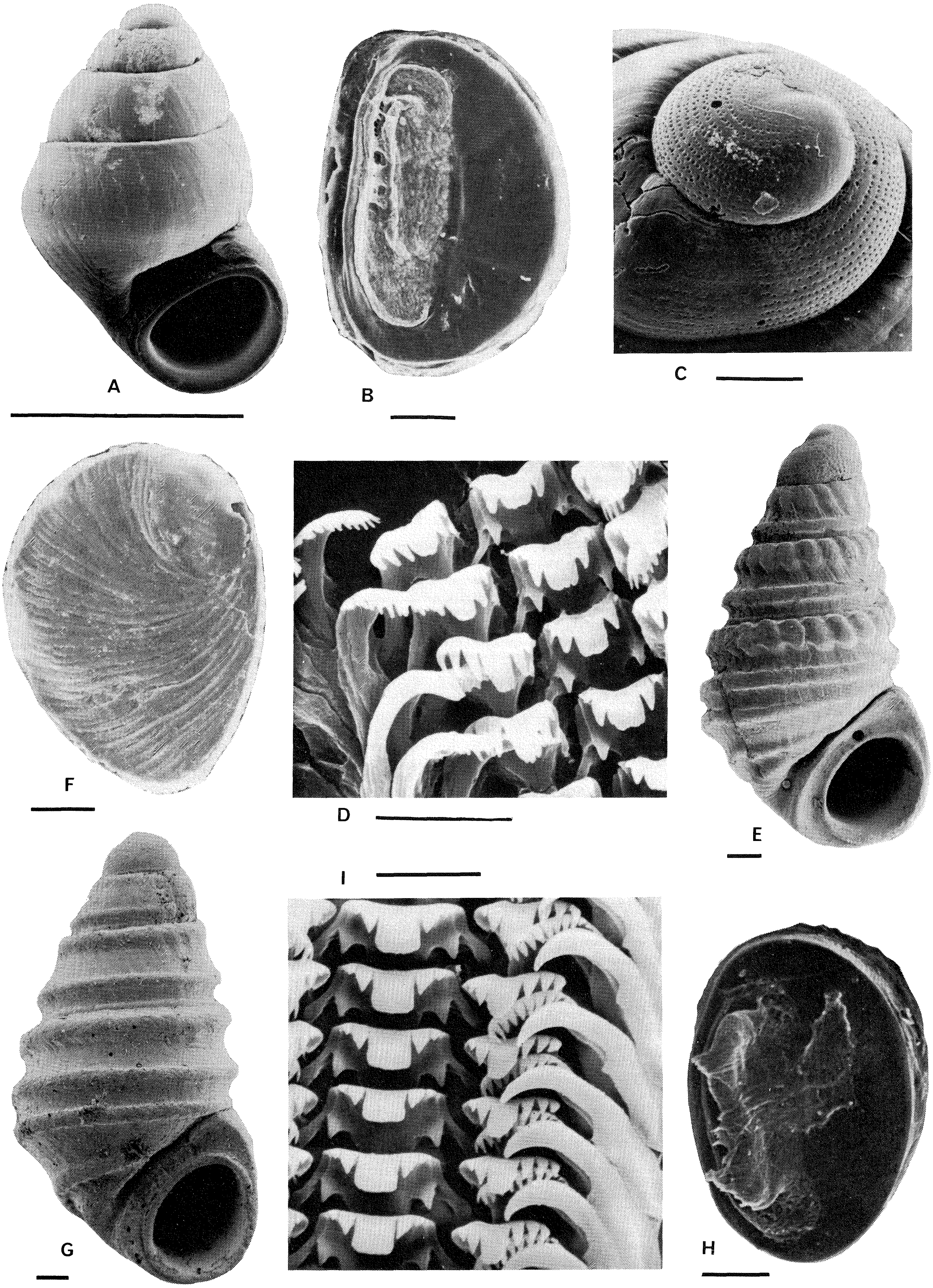
Scales: shells, protoconch and opercula—0.1 mm; radulae—0.01 mm.



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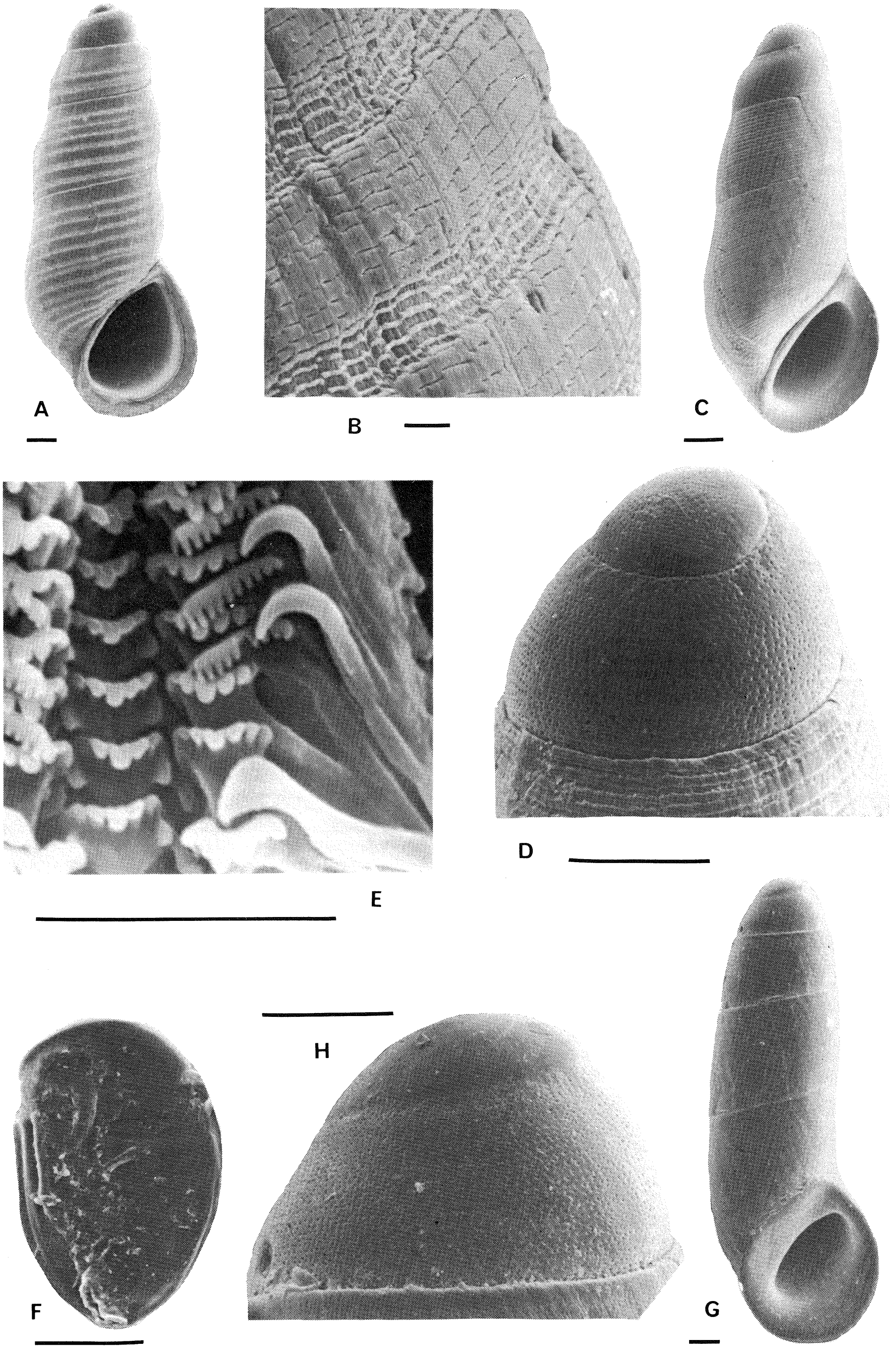

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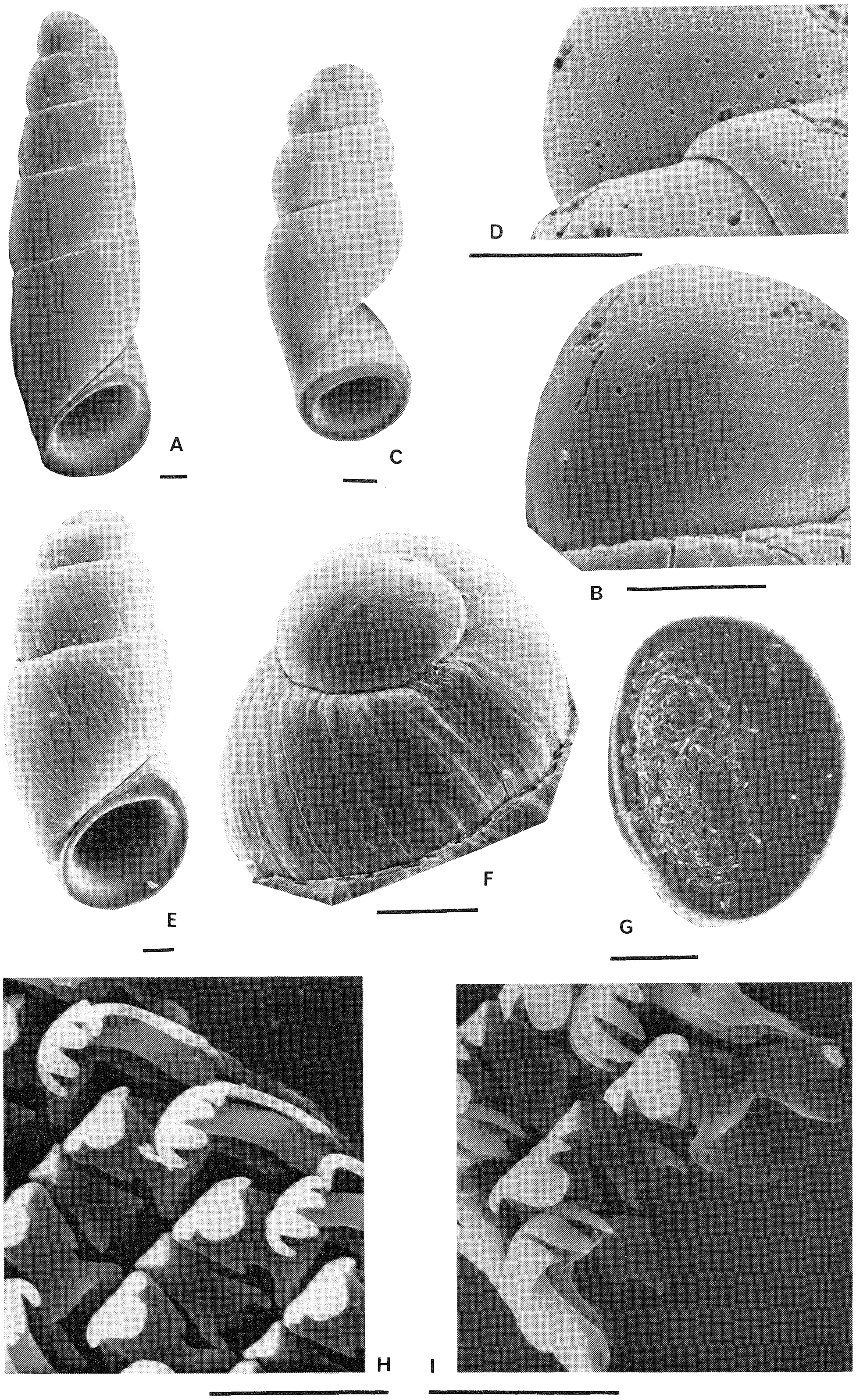
Scales: shells, protoconch and operculum—0.1 mm; microsculpture and radula—0.01 mm.



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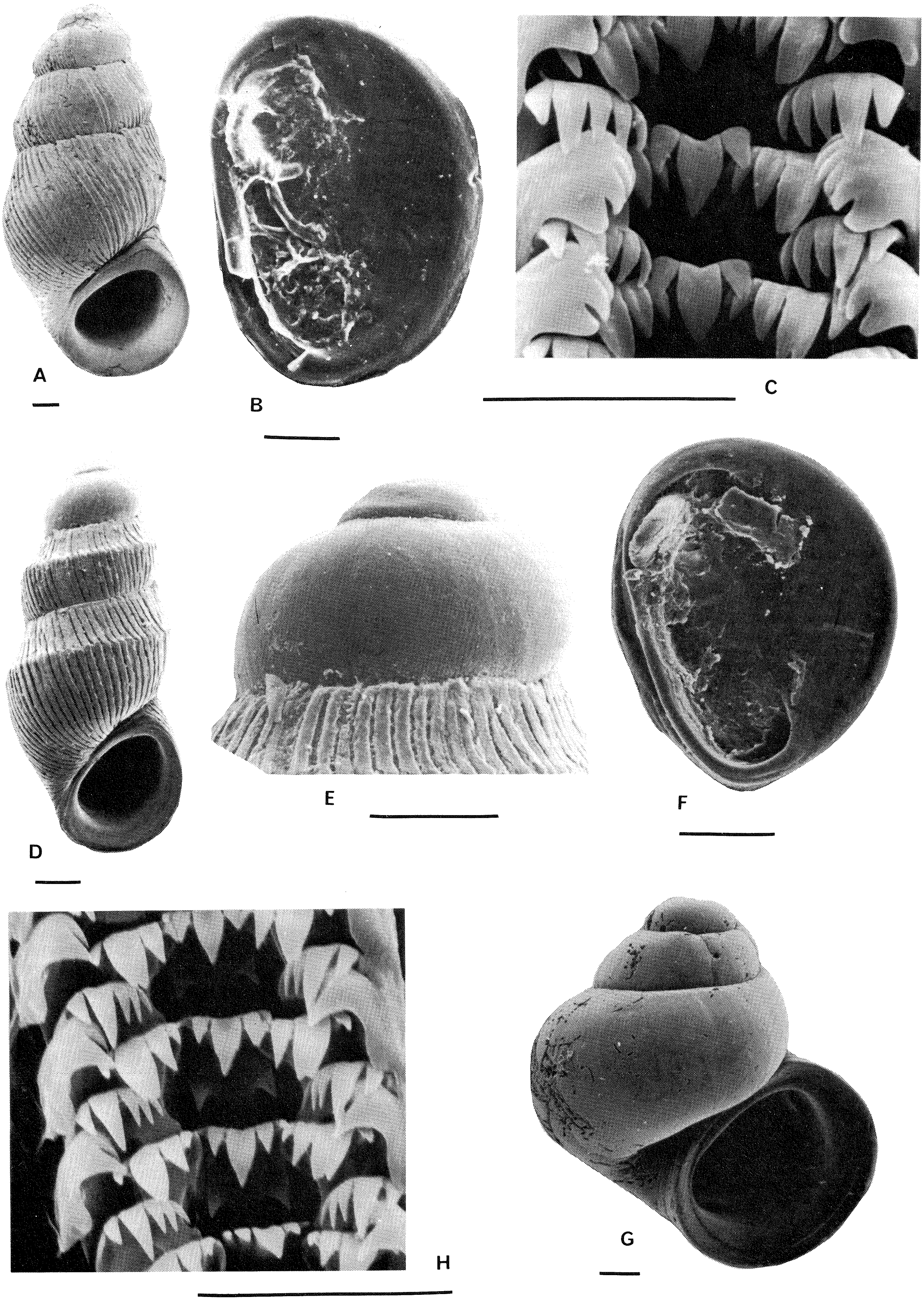
Scales: shells, protoconchs and operculum—0.1 mm; radulae—0.01 mm.



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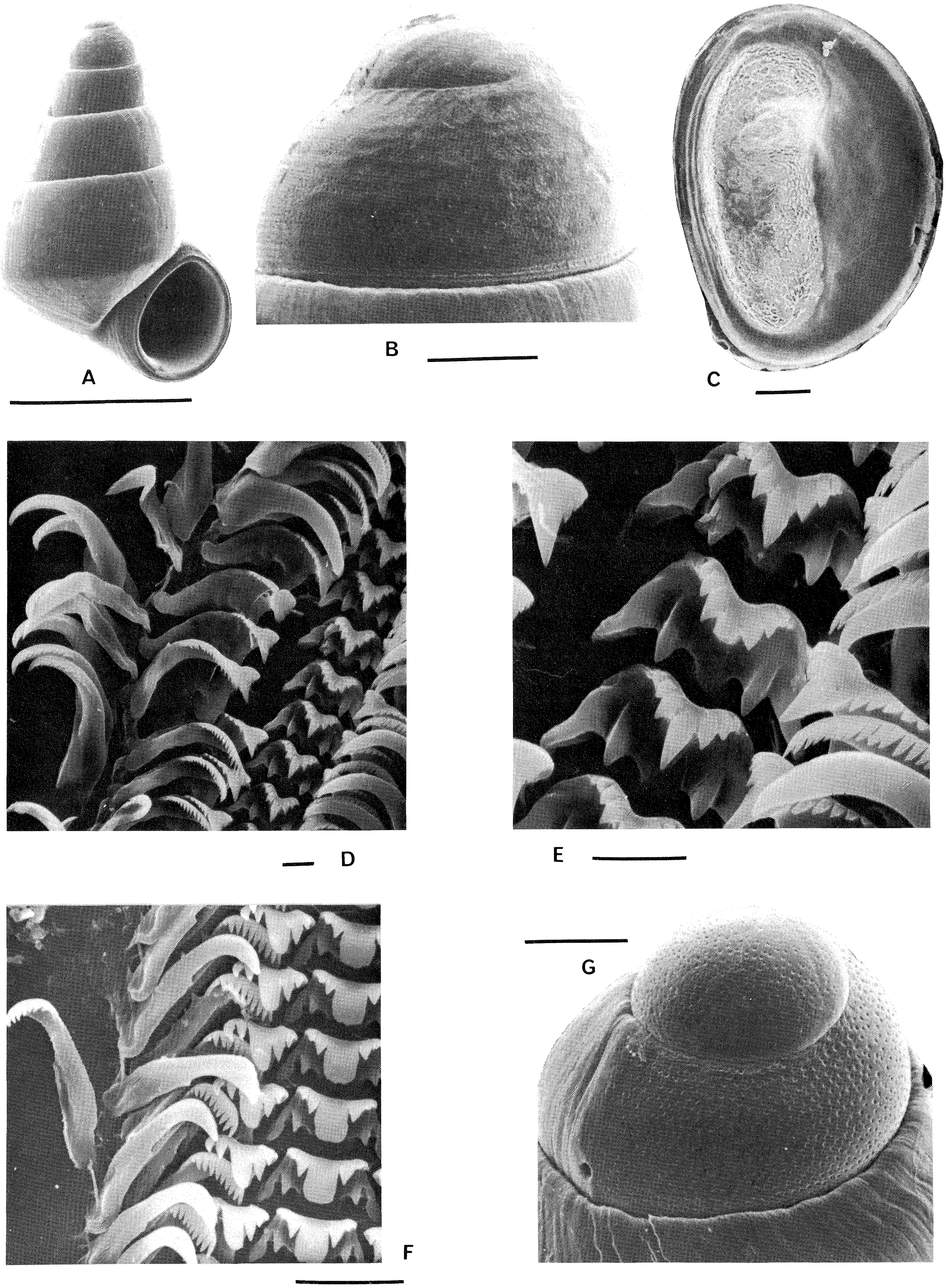

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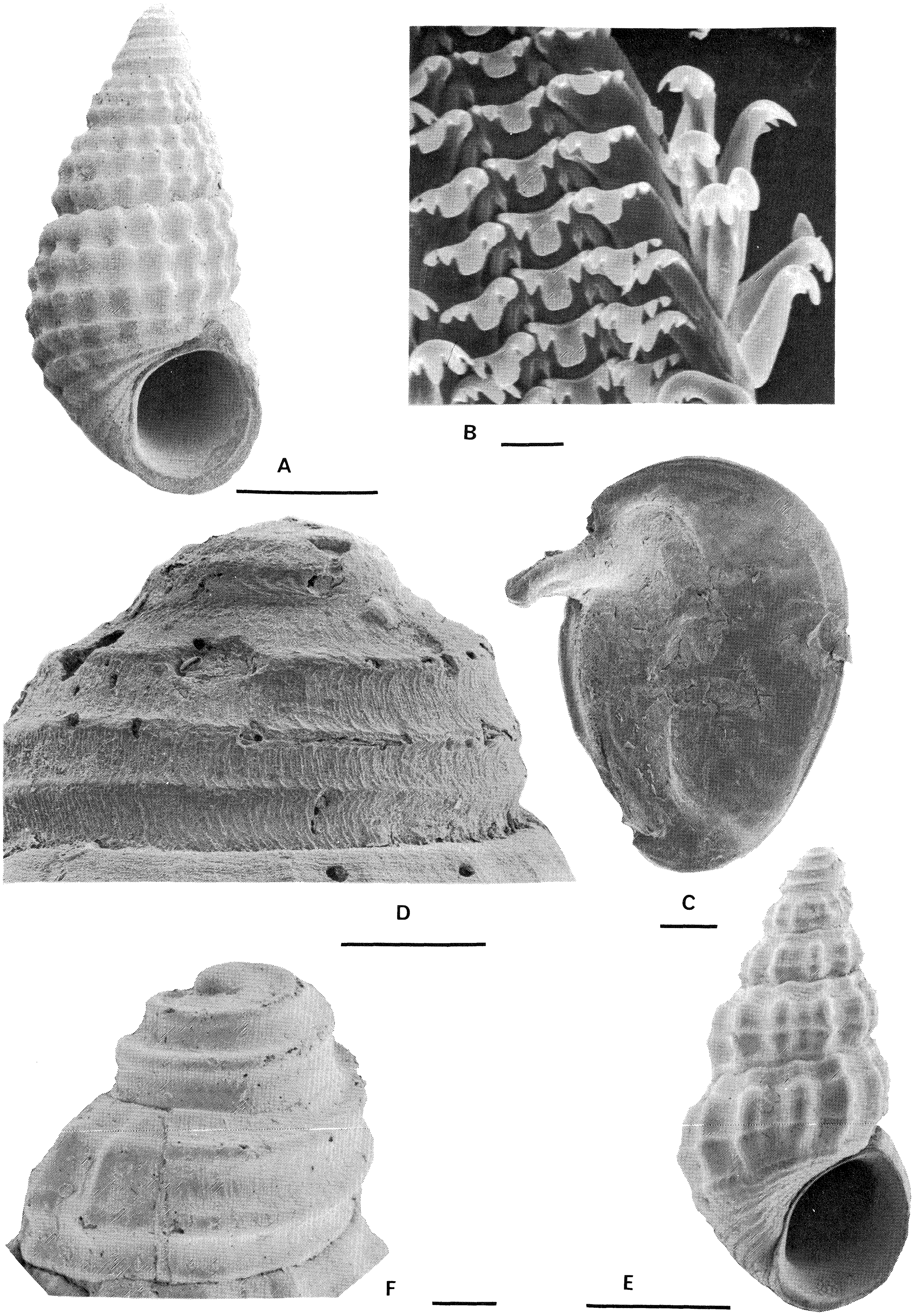
Scales; shell—1 mm; protoconchs and operculum—0.1 mm; radulae—0.01 mm.



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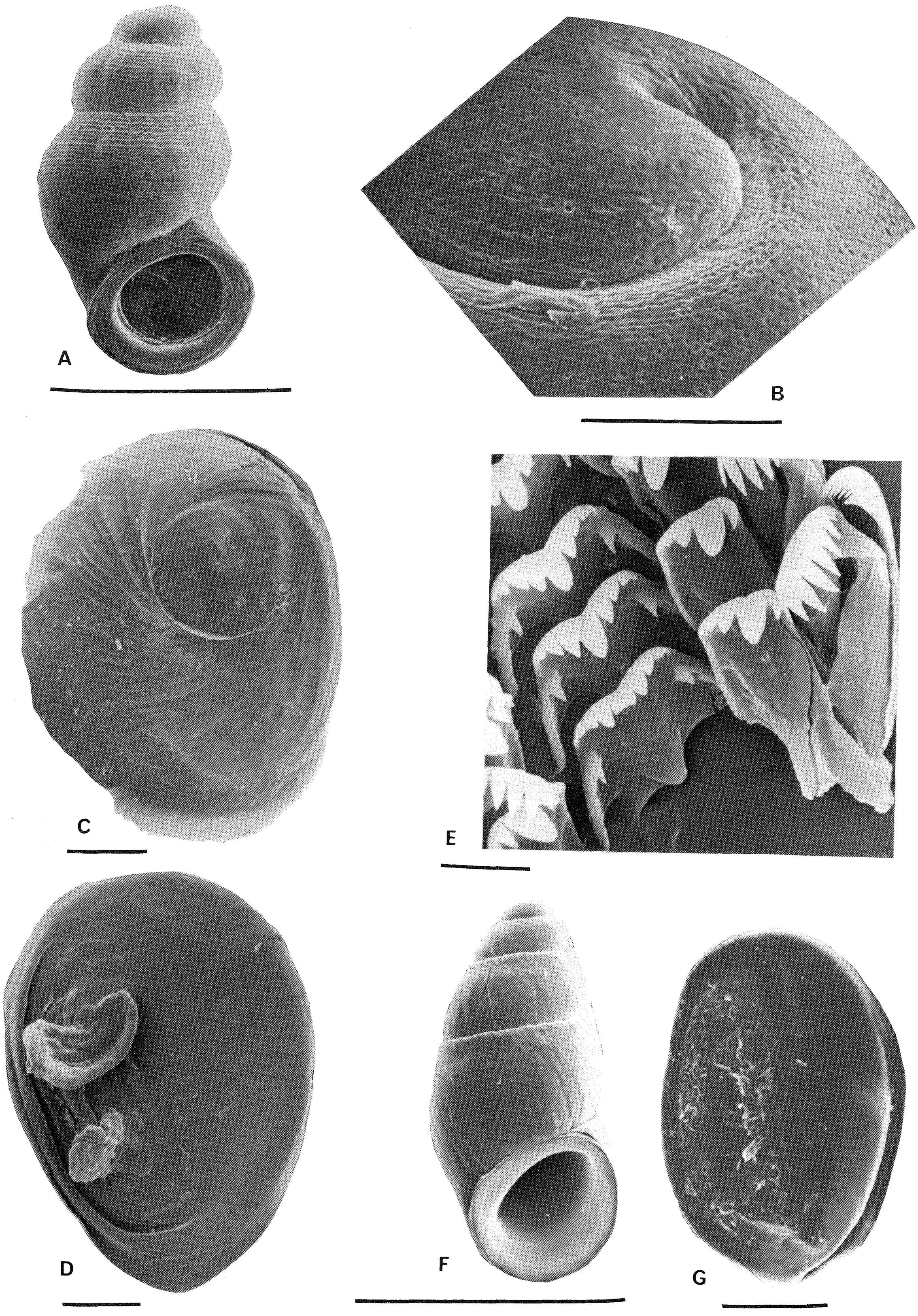
Scales: shells—1 mm; protoconchs and operculum—0.1 mm; radula—0.01 mm.



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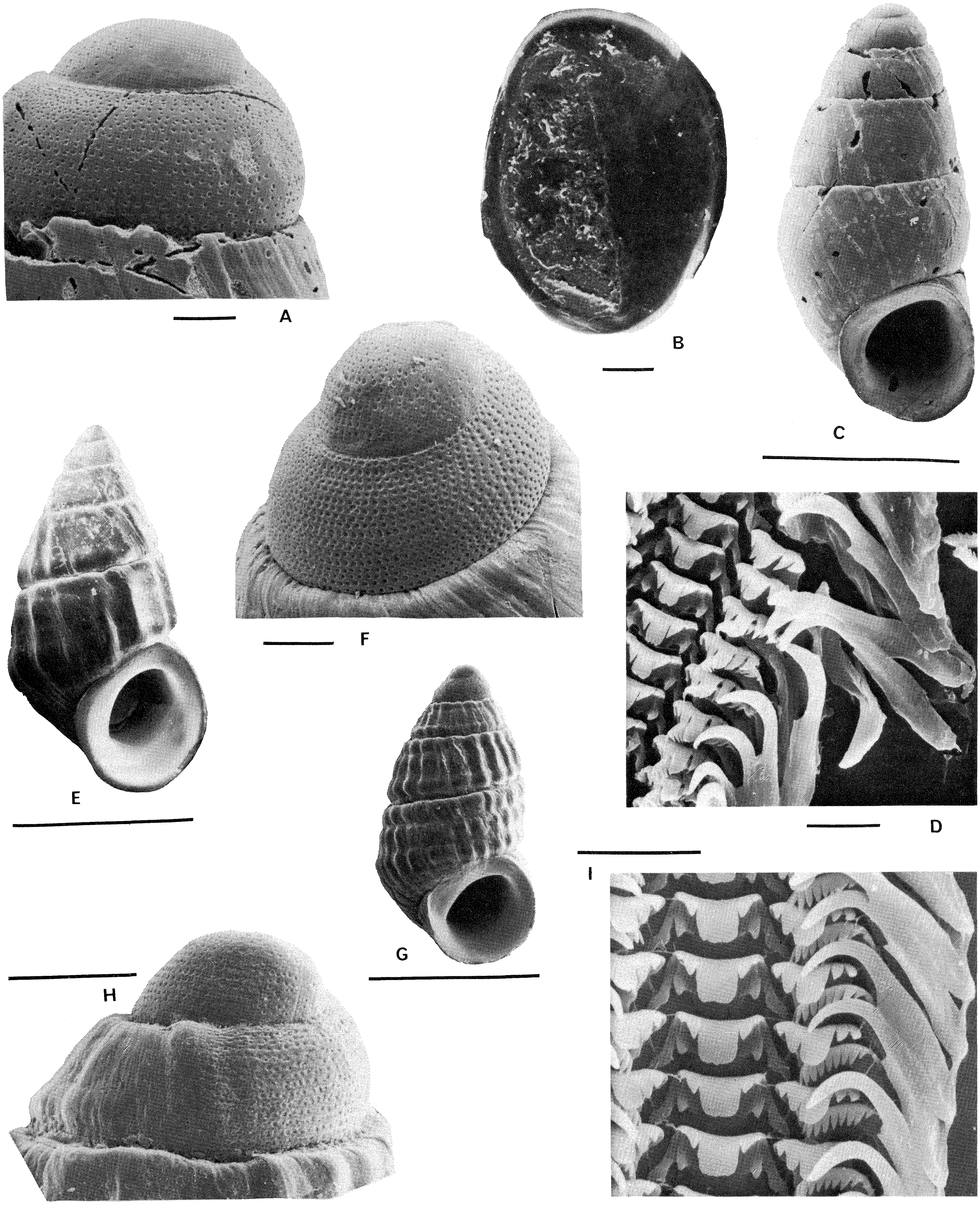
Scales: shells—1 mm; protoconch and opercula—0.1 mm; radula—0.01 mm.



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Scales; shells—1 mm; protoconchs and operculum—0.1 mm; radulae—0.01 mm.

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