Order DENTALIIDA

The shell of members of this order tapers posteriorly with the widest diameter always at the aperture. Longitudinal sculpture, such as ribs or striae, is usually present, but may be lacking. The central tooth of the radula is wider than it is high. The marginal teeth are not carinate (Scarabino 1979).

Two pairs of dorso-ventral retractor muscles are present. The foot is a thick-walled, contractile burrowing organ with its longitudinal musculature associated with the pedal body wall (Steiner 1992a). The conical tip of the foot is separated from the proximal parts by a collar of epipodial lobes which are interrupted dorsally (Steiner 1992a).

The anterior mantle margin bears an outer gland region, a ciliary organ and an inner gland region of epithelial gland cells (Steiner 1991). The posterior mantle opening closes to form a horizontal slit. Its dorsal part is a moveable flap, the ventral one forms a bolster of connective tissue (Fig. 10.10). Both portions of the mantle opening are supported by an annular haemolymph sinus. On average, there are 12 to 15 pre-anal ciliary ridges (Steiner 1991). Each captacular stalk contains 10 longitudinal muscles (Steiner 1992b). Paired digestive glands are present. The ultrastructure of the heart, pericardium and the excretory organs of *Rhabdus rectius* has been investigated by Reynolds (1990a, 1990b).

Few ultrastructural studies of dentaliid reproductive organs are available. Reverberi (1970, 1972) analysed oogenesis, and Hou & Maxwell (1991) described spermatogenesis in *Antalis entalis*. *Dentalium conspicuum* (Dinamani 1964b), *A. entalis* and *A. dentalis* (Lacaze-Duthiers 1856–1857; Kowalevsky 1883) are broadcast-spawners, and the yolk-rich eggs become fertilised outside the pallial cavity. This also holds true for *A. vulgaris*, the only species for which the ultrastructure of egg-sperm interaction has been studied (Dufresne-Dube *et al.* 1983). Knowledge of development is poor, especially of organogenesis, and is restricted to the above-mentioned species of *Antalis*. Development includes a modified spiral cleavage and a demersal, lecithotrophic larva of the stenocalymma type (Lacaze-Duthiers 1856–1857; Kowalevsky 1883; Salvini-Plawen 1980).

Six families can be distinguished: Dentaliidae, Fustiariidae, Laevidentaliidae, Gadilinidae, Omniglyptidae and Rhabdidae. All but the last are represented in Australian waters. The distribution of this order is worldwide, and at all depths from the upper sublittoral to the deep sea. The greatest diversity, however, is found in shallow tropical waters. The oldest known scaphopod, from the Ordovician, belongs to the order Dentaliida (Ludbrook 1960).

Family Dentaliidae

Dentaliid shells are usually robust, almost straight to strongly curved and may reach up to 300 mm in length in fossil forms and about 140 mm in extant species. Longitudinal sculpture varies from four prominent ribs to numerous, fine striae that may be restricted to the apical portion of the shell. Accordingly, the cross-section may be polygonal, circular, or rarely, slightly oval (Figs 10.13, 10.14). The number of ribs may be increased by intercalation or division (Simroth 1894; Pilsbry & Sharp 1897–1898). The apex shows great diversity of form. In species of *Dentalium* (Fig. 10.13B) and *Graptacme* (Fig. 10.14N), it is simple or has a shallow notch on the concave side. A deep slit or a series of perforations is typical for the genus *Fissidentalium* (Fig. 10.14F) whereas in the genera *Antalis* (Fig. 10.14J) and *Pictodentalium* (Fig. 10.13J) the posterior opening of the shell is narrowed by a calcareous plug, sometimes with a short pipe attached to it. The family includes the only brightly coloured scaphopods, which may show greenish (for example, *Dentalium elephantinum*), yellow or pink (for example, *Pictodentalium formosum hirasei*) pigmentation.

The central tooth of the radula has an entire, arched surface, which may be smooth or granulated. Similarly, the working area of the lateral teeth can be smooth, granulated or striated (Scarabino 1979). The marginal teeth are curved. In the pavilion, which is a posterior dorsal extension of the mantle, only a few, scattered subepithelial gland cells can be found (Steiner 1991).

The greatest diversity of Dentaliidae occurs in tropical and subtropical waters from the upper subtidal to depths of about 1000 m (Scarabino 1979). In higher latitudes and deeper water the number of taxa decreases.

Lamprell & Healy (1997) have identified 59 extant dentaliid species in the Australian fauna. Genera represented are (the number of species per genus is indicated in brackets): *Dentalium sensu stricto* (38, including 16 new); *Dentalium (Pictodentalium)* (one); *Dentalium (Lentigodentalium)* (three, including two new); *Graptacme* (three, including one new); *Fissidentalium* (11, including six new); and *Tesseracme* (three, including one new).

The names *Antalis* and *Paradentalium* have not been used for the Australian fauna by Lamprell & Healy (1997) because of inadequate delineation from *Dentalium sensu stricto*. Similarly, they consider *Pictodentalium* and *Lentigodentalium* to be, at best, subgenera of *Dentalium* and not worthy of full generic status. Within the genus *Dentalium*, Lamprell & Healy have utilised a species-group approach similar to that of Pilsbry & Sharp (1897–1898) and Boissevain (1906), in preference to the establishment of further, probably unjustified, subgeneric taxa.

The genus *Dentalium* is not only the most speciose within the family Dentaliidae, but also clearly the largest genus within the class Scaphopoda. Within the Australian fauna, *Dentalium* species constitute almost two thirds of the represented Dentaliidae and over one third of the Scaphopoda (Lamprell & Healy 1997). In shallow-water species (0–50 m) sandy sediments are preferred, whereas in deeper water (50 m and beyond) sand/mud or fine mud are more typical substrata (Lamprell & Healy 1997). Many species of *Dentalium* recorded from Australia have broad geographic and bathymetric ranges and may be locally common.

The first appearance of the Dentaliidae in the fossil record (genus *Prodentalium*) is from the early Devonian (Pilsbry & Sharp 1897–1898). In Australia 12 fossil dentaliid species have been described in the literature, mostly Tertiary in age (Tate 1887, 1899; Cotton & Ludbrook 1938; Ludbrook 1956), but also one species of *Fissidentalium* from the Carboniferous of New South Wales (Yoo 1988).

Family Fustiariidae

Fustiaria is the sole genus in the Fustiariidae. The gradually tapered shell is thin and slender, and moderate in length and curvature (Fig. 10.15). It is circular in cross-section. Except for faintly visible growth lines, the surface is polished, transparent and lacks sculpture. On the convex side, the apex usually has a long and narrow slit which is continuous with a shallow groove in the internal surface of the shell (Fig. 10.15B). Within a population, however, specimens with and without the slit can be found and are reported repeatedly (for example, Pilsbry & Sharp 1897–1898; Ludbrook 1954). A small notch may also be developed on the concave side, giving the apex a slightly bilobed appearance. These observations demonstrate the problem of defining scaphopod species by their apical features.

The lateral and marginal teeth of the radula resemble those of the genus *Antalis* (Dentaliidae) (Scarabino 1979), but the central tooth is not arched and shows an almost flat surface.

The posterior mantle margin differs from that of other Dentaliida in the absence of the sphincter muscle, the ventral bolster of connective tissue and the ring sinus. Instead, the dorsal flap is enlarged and is the only structure which regulates the width of the posterior mantle opening. Large subepithelial gland cells occur in the pavilion in great abundance and fill the space between the epidermal layers (Steiner 1991).

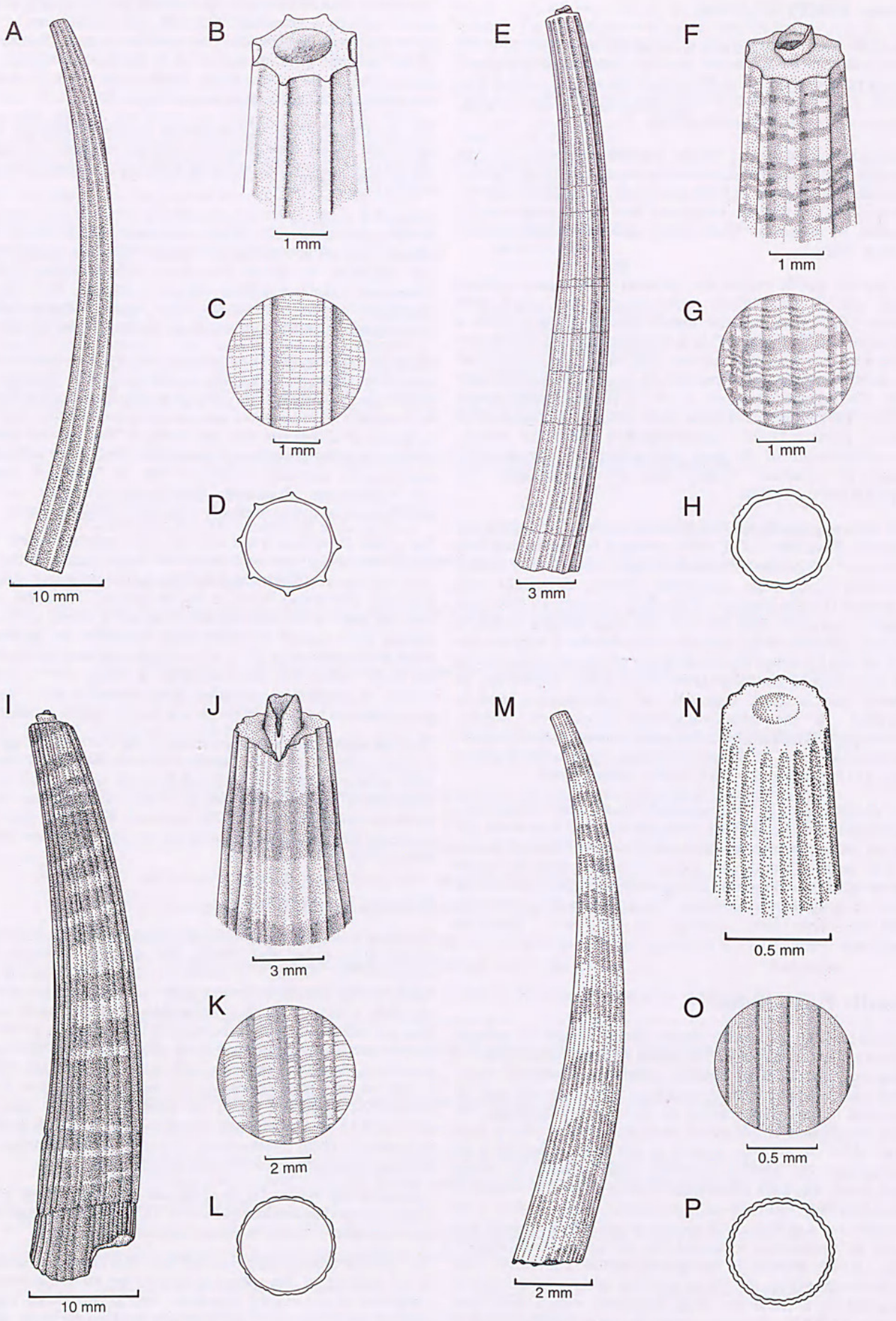

Figure 10.13 Australian Dentaliidae. Shell characters: **A–D**, *Dentalium javanum*; **E–H**, *Paradentalium intercalatum*; **I–L**, *Pictodentalium fomosum* **M–P**, *Lentigodentalium* sp. **A**, **E**, **I**, **M**, profile; **B**, **F**, **J**, **N**, apex; **C**, **G**, **K**, **O**, sculpture; **D**, **H**, **L**, **P**, cross-sectional shape at aperture. [C. Eadie]

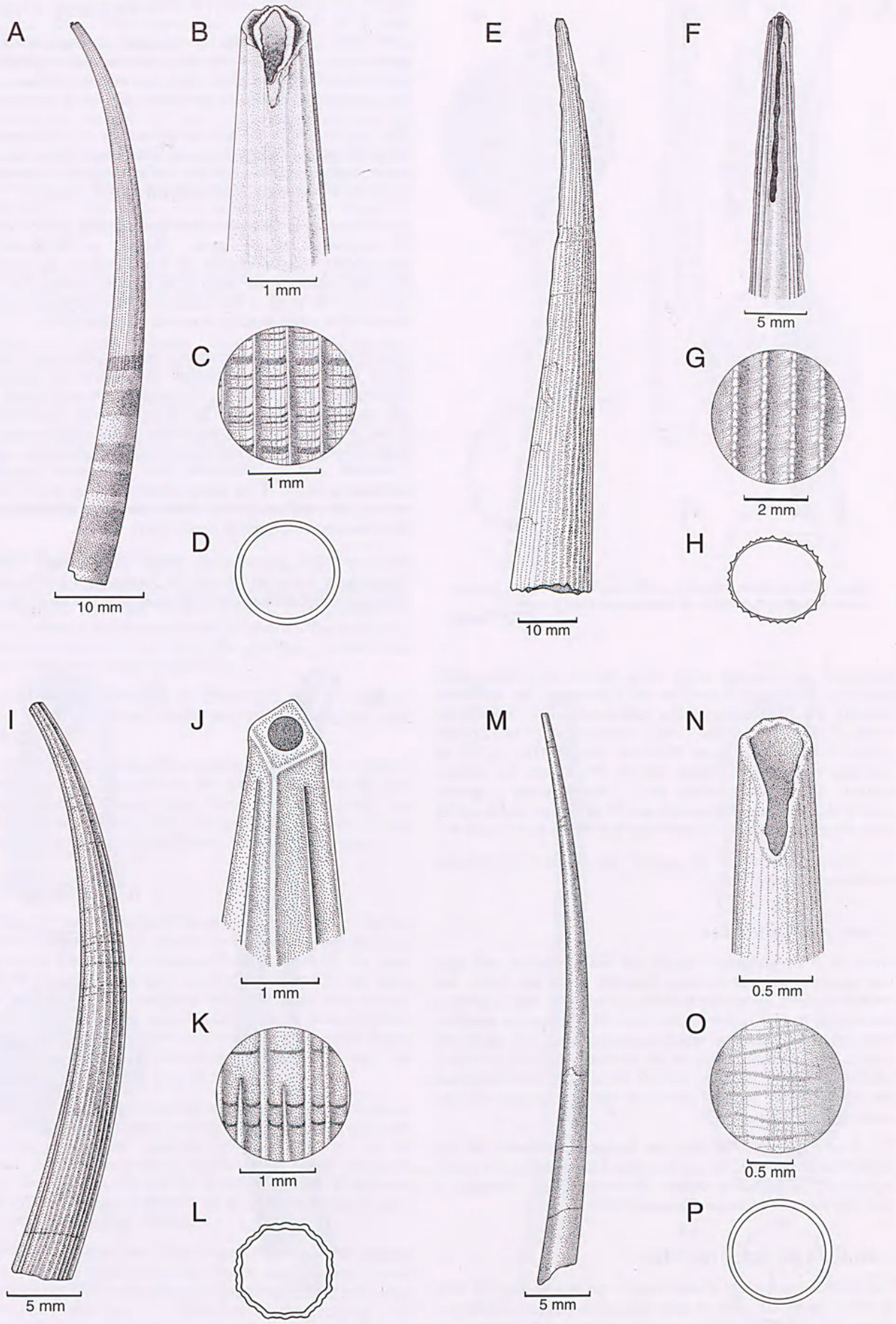

Figure 10.14 Australian Dentaliidae. Shell characters: **A–D**, *Tesseracme quadrapicale*; **E–H**, *Fissidentalium yokoyamai*; **I–L**, *Antalis* sp.; **M–P**, *Graptacme aciculum*. **A**, **E**, **I**, **M**, profile; **B**, **F**, **J**, **N**, apex; **C**, **G**, **K**, **O**, sculpture; **D**, **H**, **L**, **P**, cross-sectional shape at aperture. [C. Eadie]

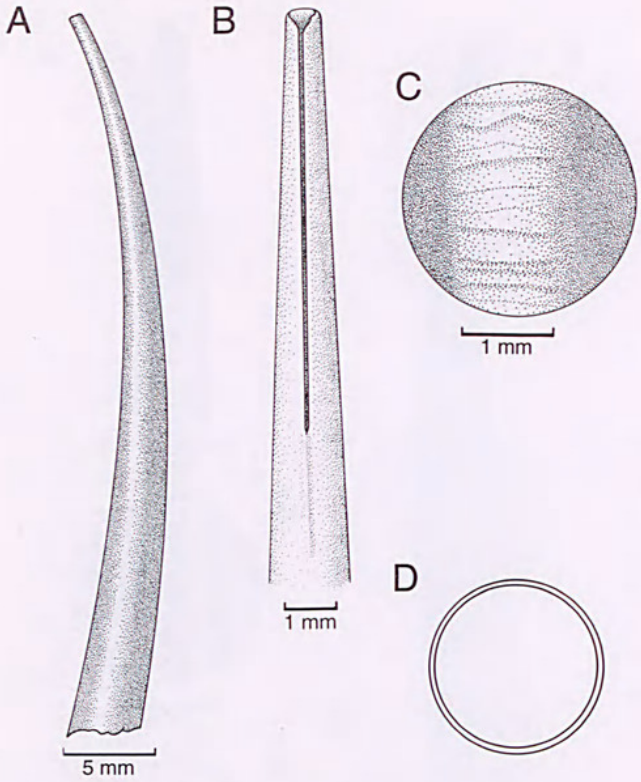

Figure 10.15 Australian Fustiariidae. Shell characters of *Fustiaria caesura*: **A**, profile; **B**, apex; **C**, sculpture; **D**, cross-sectional shape at aperture. [C. Eadie]

Fustiariids are reported from warm waters only. They occur mainly in sublittoral waters of the Caribbean, the equatorial Atlantic, the Mediterranean Sea and the western Indo-Pacific Ocean. Lamprell & Healy (1997) recognise only two species within the Australian fauna, *Fustiaria caesura* (Fig. 10.15), an endemic, occurring at depths of 60–399 m off the eastern, southern and western coasts, and *F. stenoschizum*, a species known also from the Philippines and West Indies, and recorded from Western Australia and Queensland at depths from 2–163 m.

The oldest member of the group was found in Cretaceous sediments (Emerson 1962).

Family Rhabdidae

Shells of this monogeneric family are nearly straight, and taper very gradually towards the apex. The shell is thin and fragile, and semi-transparent, except for whitish, eroded areas. No sculpture is present; the surface is smooth and polished. The apex is simple or extended by a fragile tube, which is continuous with the shell. The surface of the central tooth of the radula is distinctly trilobed, whereas the lateral teeth are massive and strongly sculptured, and the marginals are straight and bear small annulations on the anterior edge (Steiner 1991).

The family is distributed from the north-eastern Pacific and the south-western Atlantic to the Southern Ocean, and is yet to be reported from Australian waters. The oldest genus, *Rhabdus*, is recorded from the Miocene (Emerson 1962).

Family Laevidentaliidae

The shell is moderately curved, and is medium to large in size, reaching up to 100 mm in *Laevidentalium caudani* (Pilsbry & Sharp 1897–1898). It tapers rapidly, so that the diameter of the circular aperture is more than five times that of the posterior opening of the shell (Fig. 10.16). Apart from clearly visible growth lines or longitudinal undulations the shell surface is smooth and polished. However, Lamprell & Healy (1997) found that in *L. lubricatum*, fine longitudinal striae are present posteriorly in the shells of juvenile and uneroded larger specimens, and consequently have emended the diagnosis of the family Laevidentaliidae (and genus *Laevidentalium*) accordingly. The apex can be notched on the convex side, but is usually simple.

The central radular tooth is subrectangular or subpolygonal in shape (Scarabino 1979). The long lateral teeth have flat, almost straight apical portions, with the surface smooth or striated. The marginal teeth are also slender and only slightly curved.

Laevidentalium is the only Recent genus in this family, following the separation of the genus *Rhabdus* to its own family (Rhabdidae). *Laevidentalium* is found mainly in tropical to temperate waters from shallow to bathyal depths. The record depth for this order is for *Laevidentalium leptoskeles* collected from 4760 m depth south of Australia (Watson 1879).

Twelve species of *Laevidentalium* were recorded by Lamprell & Healy (1997) in the Australian fauna, four of which were described as new. One species *L. largicrescens*, previously known only as a fossil from Victoria (Upper Miocene to Pliocene) was shown to be still extant in deep water off the eastern coast (depth range 284–3058m). Some Australian laevidentaliids such as *L. erectum* and *L. lubricatum* not only have considerable bathymetric ranges (from approximately 15 m to over 1300 m or deeper), but occur essentially around the entire coastline, often in large numbers (Lamprell & Healy 1997).

Rhytiodentalium kentuckyensis (Pojeta & Runnegar 1979) and *Plagioglypta iowaensis* (Bretsky & Bermingham 1970), the oldest known scaphopods from the Ordovician, may belong to this group.

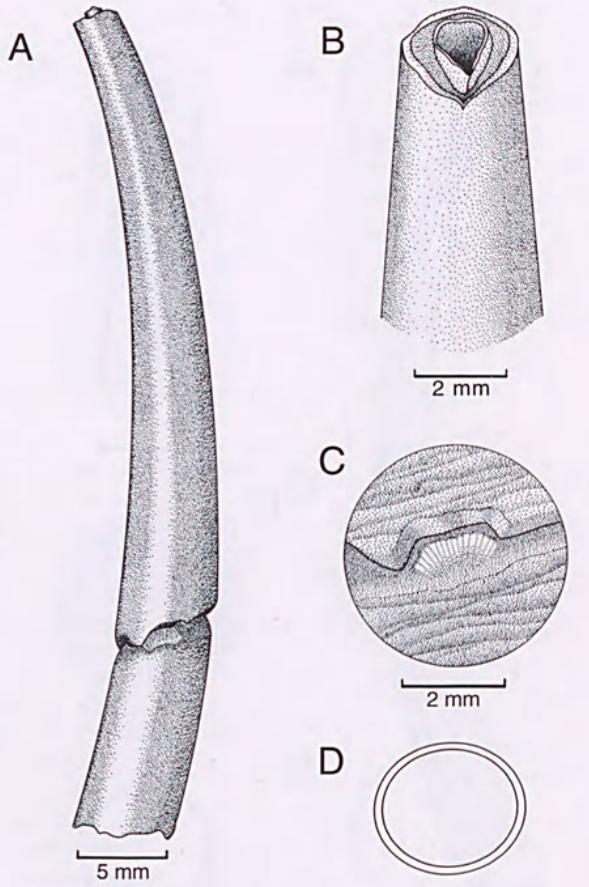

Figure 10.16 Australian Laevidentaliidae. Shell characters of *Laevidentalium crocinum*: **A**, profile; **B**, apex; **C**, sculpture, on each side of a healed fracture; **D**, cross-sectional shape at aperture. [C. Eadie]

Family Gadilinidae

The shell is small to moderate in size, sometimes fragile, and varies considerably in curvature. Its cross-section is subcircular or nearly triangular. The sculpture consists of apical annulations, three longitudinal ribs, or is lacking (Fig. 10.17). Frequently, the apex is truncate, plugged, and a tube usually arises near the ventral rim of the plug (Fig. 10.17B, F). In juveniles, and sometimes in adult specimens, the apex is simple and not notched.

The central radular tooth has a somewhat triangular shape with a tricuspid surface. The bases of the lateral teeth are slender in relation to their crowns and the marginal teeth are curved (Scarabino 1979).

Scarabino (1979) united *Episiphon*, *Gadilina*, *Anulidentalium* and the fossil genus *Lobantale* in this family. Extant species occur worldwide in all depths.

According to Lamprell & Healy (1997) *Episiphon* is the only gadilinid genus known from Australian waters. They recorded four species, *E. virgula* (Fig. 10.17A–D), *E. bordaensis* (both largely southern in distribution) and two new species (both largely northern in distribution; see Fig. 10.17E–H). All four show a wide bathymetric range, but are commonest at depths of over 100 m, chiefly in sand and mud sediments (see Lamprell & Healy 1997).

The fossil record dates back to the Jurassic (Emerson 1962).

Family Omniglyptidae

The shell in this monogeneric family is small to medium-sized with a moderate curvature (Chistikov 1975). The sculpture of dense annulations is confined to the apical portion. The aperture is circular in cross-section (Fig. 10.18). The apex has a simple rim or features a small notch on the convex side.

The radula is characterised by a central tooth with an irregular surface, tricuspidate lateral teeth, and curved marginal teeth (Scarabino 1979).

The occurrence of the single, Recent genus, *Omniglypta*, is limited to depths less than 1800 m in the western Indo-Pacific and the south-western Atlantic Ocean. Two Australian species are known (Lamprell & Healy 1997): *O. anulosum* (Fig. 10.18) and *O. cerina*, both previously classified as species of *Dentalium*.

Order GADILIDA

In members of the Gadilida, the largest diameter of the shell is around the mid-point, at the aperture, or immediately behind it. In this order, the Entalinidae (suborder Entalimorpha) are the only family with thick, longitudinally ribbed shells. Generally, the other families have thin shells with glossy surfaces. Apical, longitudinal striae are known in a few genera, for example, *Striopulsellum* (Scarabino 1979). On the inner shell surface, a pre-apical callus marks the site of insertion of the retractor muscles. The height of the central tooth of the radula exceeds its width.

The single pair of dorso-ventral retractor muscles extend almost directly into the foot. There, the major part of the longitudinal musculature is detached from the pedal body wall and is continuous with large portions of the dorso-ventral retractor muscles. The foot is a thin-walled, retractile and eversible organ (Steiner 1992a). The tip is formed by a crenulate terminal disc, with or without a terminal filament.

The outer gland region and ciliary organ of the anterior mantle margin as found in the Dentaliida are not present. The inner gland region comprises both epithelial and subepithelial gland cells. The posterior mantle opening can be narrowed to a vertical slit by a dorso-ventral muscle clasp, where an annular ciliary organ for generating an inhalant water current is present. The ledges of the pavilion are covered by a ciliated epithelium. Usually there are four to eight pre-anal ciliated ridges (Steiner 1991).

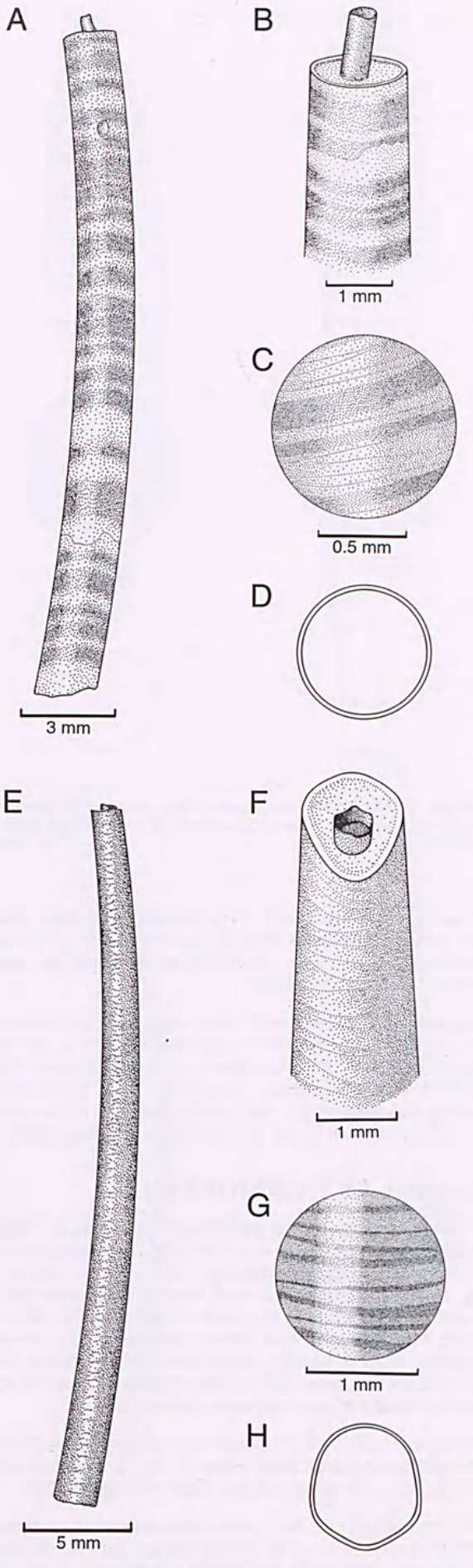

Figure 10.17 Australian Gadilinidae. Shell characters: **A–D**, *Episiphon virgula*; **E–H**, *Episiphon* sp. **A**, **E**, profile; **B**, **F**, apex; **C**, **G**, sculpture; **D**, **H**, cross-sectional shape at aperture. [C. Eadie]