# CLASS SCAPHOPODA

# CHAPTER 10 -

# DEFINITION AND GENERAL DESCRIPTION

Scaphopods are bilaterally symmetrical, burrowing, marine molluscs, commonly called tusk or tooth shells (Fig. 10.1; Pl. 16.5). The external shell is a tapered tube, open at both ends and usually curved. It is smooth or variously sculptured, and ranges in length from 2–50 mm, but may reach 130 mm in the Indo-Pacific *Pictodentalium vernedei*.



Figure 10.1 Dentalium sp. (Dentaliidae) in natural orientation with the captacula extended for feeding. The shell apex does not necessarily protrude from the substratum surface. The foot and captacula are never protruded simultaneously. amm, anterior mantle margin; cpt, captacula; sh, shell. (Modified after Lacaze-Duthiers 1856–1857) [C. Eadie]

A tapered, tubular mantle, fused along the ventral midline and, like the shell, open at both ends, encloses the elongate animal. The foot and feeding organs protrude from the larger, anterior opening of the shell, called the aperture, and the smaller, posterior opening is at the apical end. Through elongation and rotation of the dorso-ventral body axis, the apex is at the posterior end of the shell and the anus lies in the midregion of the body, rather than in a terminal position (Fig. 10.2). In physiological terms and for reasons of convenience, the concave side is referred to as dorsal and the convex side as ventral (Fig. 10.2). Morphologically, only the foot region, between the mouth and the anus, is on the ventral side (Steiner 1992b).

The weakly developed head lacks eyes and is surrounded by clusters of extensible, ciliated filaments, the captacula, which are used to locate and capture food. Osphradia and ctenidia are absent, and respiration takes place via the internal mantle surface. The radula is large, and each row consists of five teeth (Lacaze-Duthiers 1856–1857).

Scaphopods are benthic micro-carnivores inhabiting all types of unconsolidated sediment, at depths from the littoral to the abyssal in euhaline oceans (Shimek 1990). They live completely buried in mud or sand, with only the smaller, posterior end occasionally protruding into the water. The two major systematic groups in the class Scaphopoda are the orders Dentaliida and Gadilida (Palmer 1974; Starobogatov 1974). Worldwide there are 11 families and 500 to 600 living species. Australia has more than 150 named species (Lamprell & Healy 1997), fossil and extant, from eight families.

# HISTORY OF DISCOVERY

Aldrovandi (1642) may have been the first of the pre-Linnaean naturalists to describe a scaphopod. Deshayes (1825) lists him with many others in the synonymy of *Dentalium elephantinum*, though Linnaeus, when he listed four named species in 1758, mentioned only Borani, Lister, Rumphius, Gaultieri and d'Argenville.

In the first scientific monograph on scaphopods, Deshayes (1825) described 42 species, which he distributed between four sections and four sub-sections, all included in his 'Genre Dentale'. Fossil species from the Tertiary deposit of the Paris Basin were also covered, though four of these species were shown subsequently to be serpulid worm tubes. His drawings of the internal anatomy of 'Antalis entalis' (actually Antalis vulgaris) were the first of their kind. Until 1844, when Philippi introduced the genus Cadulus, the only generic name available for scaphopods was Linnaeus' Dentalium. Siphonodentalium and Gadila soon followed.

Lacaze-Duthiers (1856–1857) described the anatomy of *Antalis entalis* in greater detail than Deshayes, accurately elucidating the structure and function of the whole animal. His description of the embryology and larval development, from fertilised ovum to the full-grown larva, were the first, and have hardly been improved on to this day, though valuable contributions were made by Kowalevsky (1883), Fol (1889) and Plate (1892).

Meanwhile, R.B. Watson (1879, 1886) in Britain and W.H. Dall (1881, 1889) in America, were describing scaphopods collected by the *Challenger* and *Blake* expeditions during the 1880s. Pilsbry & Sharp's (1897–1898) magnificent monograph is a bench-mark for taxonomists, and is still the fundamental text for all serious workers on shells and taxonomy of scaphopods. The authors



Figure 10.2 Schematic representation of the body axes in Scaphopoda. The captacula are not shown. an, anus; a-p, antero-posterior axis; ape, aperture, anterior opening of shell; apx, apex; d-v, dorso-ventral axis; ft, foot; mo, mouth; pos, posterior opening of shell. [D. Wahl]



Figure 10.3 Antalis sp. (Dentaliidae) removed from its shell, lateral view. amm, anterior mantle margin; cft, conical tip of foot; dgl, digestive gland; dvm, dorso-ventral retractor muscle; epd, epipodial lobe; exo, excetory organ; gd, gonad; pav, pavilion; vam, vascularised part of the mantle. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

described and figured nearly all the known living scaphopods, listed all known fossils, and removed the serpulid polychaetes and other curved, conical-tubed structures, leaving only scaphopods in the class.

Until 1862 when Bronn proposed the class Scaphopoda within the Prosopocephalia, these molluscs always resided among the gastropods, sometimes near the genus *Diodora* on the grounds of having two openings in the shell. Linnaeus placed them between the perforate limpets and serpulids. Pilsbry & Sharp (1897–1898) recognised that they were certainly not gastropods, though undoubtedly molluscs.

Since the late nineteenth century a great deal of work has been done, outstanding among which are Boissevain's (1906) report on the scaphopods from the *Siboga* expedition, Henderson's (1920) monograph of the eastern American scaphopods and Habe's (1964) thorough account of the scaphopods of Japan. Most

recently, monographs by Scarabino (1995) and Lamprell & Healy (1997) have greatly expanded knowledge of the diversity and distribution of the scaphopods from the tropical Pacific and Indian Oceans, and Australia respectively.

Ludbrook (1960), Emerson (1962), Palmer (1974), Starobogatov (1974) and Chistikov (1975) provided classifications of the whole class Scaphopoda, and Habe (1977) classified the western Pacific species. Scarabino's (1979) unpublished light microscopy studies on radular morphology provided additional characters for classification. Steiner (1992b) presented the first cladistic analysis of the class using both hard-part and soft-body characters.

Australian scaphopods received some attention for the first time when Brazier (1877) described material from the Chevert expedition to tropical Queensland. Tate (1887, 1899), Tate & May (1900), Hedley (1901, 1903) and Verco (1911) added more fossil and extant species. Cotton & Ludbrook (1938) and Cotton & Godfrey (1940) reviewed the previous descriptions and revised the classification. Subsequently, Colman (1958) reviewed the scaphopods of New South Wales, adding six new species and incorporating useful bathymetric and distributional data. Four fossil scaphopods from the Carboniferous of New South Wales were described by Yoo (1988) who also introduced two new laevidentaliid genera (Scissuradentalium and Pipadentalium). In a comprehensive monograph of the scaphopod fauna of Australia, Lamprell & Healy (1997) recognised 107 extant species from the region, including 46 new species and 28 new records. Their study has clarified the status of several previously named species (some disappearing into synonymy, and leptotypification of others), and has provided photographs and figures of significant type material held in overseas institutions.

# MORPHOLOGY AND PHYSIOLOGY

#### **External Features and the Shell**

The scaphopod shell is composed of two to four aragonitic layers. A periostracum has been described for two dentaliid species, *Pictodentalium vernedei* (Haas 1972) and *Antalis vulgaris* (Alzuria 1985). This outer organic layer is absent in many gadilid species (Steiner unpublished data). The outer prismatic layer consists of elongate crystals usually arranged perpendicular to the long axis. The glossy surface of many gadilids is the result of a special arrangement of these crystals (Shimek & Steiner in press). The cross-lamellate middle layer is sometimes surrounded by a narrow amorphous layer (Shimek & Steiner in press). The inner layer, if present, has a concentric structure.

The shell is thickest at the posterior end and thinnest at the anterior growing edge. During growth, secretion of new shell material by the anterior mantle margin increases the length of the tube and its anterior diameter. Simultaneously, the outer mantle



Figure 10.4 Fissidentalium megathyris (Dentaliidae), with the mantle and superficial muscle layers partly removed, and foot in longitudinal section, showing internal anatomy. apl, anal papilla; apo, anterior pallial orifice; btu, buccal tube; cbg, cerebral ganglia; ctr, ciliated ridges; cpt, captacula; dgl, digestive gland; dpg, diaphragm; dvm, dorso-ventral retractor muscle; epd, epipodial lobes; exo, excretory organ; ft, foot; gas, gastric shield; gd, gonat; gl, glands of anterior mantle margin; int, intestine; lbp, labial appendages; mc, mantle cavity; odt, odontophore; oes, oesophagus; opc, glandular oesophageal pouches; pcd, pericardium; ped, pedal sinus; pga, pedal ganglia with statocysts; pgr, periostracal groove; plg, pleural ganglia; rad, radula; rs, radular sac; sph, sphincter muscle; st, stomach. [G. Steiner]





Figure 10.5 Fissidentalium sp. (Dentaliidae), with the foot extended to reburrow after collection from a depth of 300–400 m in the Great Australian Bight. The conical tip of the foot has penetrated the substratum and the right epipodial lobe is extended. cft, conical tip of foot; epd, epipodial lobe. [K. Gowlett-Holmes]

epithelium adds material to the inner shell surface, increasing shell thickness and decreasing the diameter of the lumen (Lacaze-Duthiers 1856–1857). This is most conspicuous at the posterior end. To prevent complete closure of the posterior opening of the shell, the posterior mantle margin dissolves this surplus shell. A similar decollation is found in the gastropod family Caecidae. Secondary apical shell structures like plugs or pipes are probably secreted by a dorsal extension of the posterior mantle margin, the so-called pavilion (Figs 10.3, 10.10).

## **Musculature and Locomotion**

Pedal morphology differs greatly between the scaphopod orders. The anchoring function of the muscular erectile epipodial lobes in Dentaliida (Figs 10.3, 10.4) is assumed in Gadilida by an inflatable, hydraulic pedal disc which has a crenulated fringe (Steiner 1992a). The common basic pattern of the pedal wall musculature consists of outer circular fibres, two layers of helicoid muscles of opposite handedness, and inner longitudinal muscles. In Dentaliida, in which transverse muscles are also present, the longitudinal muscles are very prominent, allowing only a narrow pedal sinus (Fig. 10.4). In Gadilida, however, the pedal sinus is wide and the longitudinal muscles in the pedal wall are only weakly developed; additionally, there are one to three pairs of central pedal retractor muscles (Steiner 1992a). This arrangement renders the gadilid foot an eversible burrowing organ analogous to the nemertean proboscis.

Scaphopods move through the sediment in a manner similar to bivalves. They extend their burrowing foot, anchor it and drag the shell over it (Fig. 10.5). Trueman (1968) analysed this process in detail in *Antalis inaequicostatum*. Subsequent to some probing movements of its tip, the foot extends by contraction of circular muscles and/or by relocation of haemolymph from other regions into the foot. Then the epipodial lobes are erected, providing anchorage in the sediment. Subsequent contraction of longitudinal muscles pulls the shell forwards over the foot.

The dorso-ventral muscles are the only means by which the animal is fixed to its shell. There is one pair in the Gadilida, and the Dentaliida have two partly fused pairs. These muscles connect the longitudinal pedal muscles with the shell apex. The connection consists of flat muscle sheets in the lateral body walls in Dentaliida and the gadilid suborder Entalimorpha. In the gadilid suborder Gadilimorpha, the central pedal retractors run posteriorly through the pedal and intestinal sinus, where they are continuous with the dorso-ventral muscles (Steiner 1992a).

In addition to forming the pedal musculature, the dorso-ventral muscles give rise to pallial muscles in the anterior part of the mantle. These fibres retract the anterior mantle margin from the shell opening. The only other distinct muscular structures in the scaphopod mantle are the sphincters regulating the width of the anterior (Fig. 10.4) and posterior (Fig. 10.10) mantle openings. In Gadilida, a clasp of vertical muscle fibres draws close the mantle entrance to a vertical slit (Steiner 1991).

# **Feeding and Digestion**

The captacula are the main feeding organs of scaphopods (Fig. 10.1). These thread-like, extensible organs originate from a captacular shield on each side of the buccal tube. Their number ranges, according to the size of the animal, from 30 for *Cadulus subfusiformis* (Steiner unpublished data) to about 300 for *Antalis entalis* (Morton 1959; Sahlmann 1973). Each captaculum consists of a long stalk and a bulbous, ciliated head with a dorsal pit (Fig. 10.6). In Dentaliida, the ciliation extends onto the dorsal side of the stalk for a variable distance before it breaks up into a series of ciliary tufts and finally disappears (Gainey 1972; Shimek 1988). The stalk in Gadilida bears only a few tufts of cilia or lacks ciliation entirely (Shimek & Steiner in press).

Longitudinal muscles only are present in the stalk of each captaculum, 10 in Dentaliida and five to seven in Gadilida (Shimek 1988; Shimek & Steiner in press). Near the head, the muscles split to form a delicate web of fibres that allows the head to change shape and to bend. A cerebral nerve in the centre of the stalk terminates in a small ganglion, the captaculum ganglion, at the base of the captacular head (Fig. 10.6B). The haemolymphatic space in the stalk is extremely narrow. Two types of gland cells occur on the head, one opening into the dorsal pit and producing proteins and cholinesterase, the other secreting base-rich proteins through the lateral epithelium (Sahlmann 1973).

Captacula autotomise frequently and are constantly replaced. Captacular buds arise at the ventral side of the captacular shields. While they are moved dorsally by division of epithelial cells at the shield base, the buds elongate and differentiate the nerve, ciliation and muscles in that order (Plate 1892).

The absence of circular muscles led Morton (1959) to hypothesise that the captacula are extended by hydraulic pressure, analogous to the extension of echinoderm tube feet. The narrow lumen of the stalk, however, does not permit elongation by rising blood pressure. Observations by Davis (1968) that captacula of *Cadulus quadridentatus* move by the beating of cilia on the captacula head have been corroborated by reports on other species (Sahlmann 1973; Poon 1987; Shimek 1988; Steiner 1990). Thus, captacula move over and between sediment particles like interstitial worms, but can also be lifted off the sediment surface. They are retracted by contraction of the longitudinal muscles of the stalk.



Figure 10.6 Dentaliid captacula, lateral view. A, Antalis dentalis, showing the dorsal ciliated pit and stalk ciliation. B, Antalis sp., showing glandular and nervous elements; the connective tissue and muscles are omitted. cgl, captaculum ganglion; cp, ciliated pit; glc, gland cells opening into the ciliated pit; glo, gland cells opening through the lateral epithelium; ner, nerve; stc, stalk ciliation; std, secretory duct. (B, modified after Plate 1892) [G. Steiner]

#### 10. CLASS SCAPHOPODA



Figure 10.7 Cartilage-like radular bolsters of *Antalis* sp. (Dentaliidae): A, dorsal view; B, ventral view. (After Lacaze-Duthiers 1856–1857)

Adhesion to prey is presumably effected by a duo-gland system in the captacular head (Shimek 1988), similar to those found in many invertebrate groups (Hermans 1983). The sucker-like mechanism proposed by Morton (1959) and Bilyard (1974) is unlikely to function in the absence of the necessary musculature (Shimek 1988).

To commence feeding, the foot produces a feeding cavity in the sediment at the anterior shell opening. Exploring the surface of this cavity, the captacula locate and take hold of food items which they withdraw into the mantle cavity. Several captacula may manipulate large prey (Gainey 1972). Dinamani (1964a) and Shimek (1988, 1990) noted transport of sediment particles along the ciliary tracts of captacula in *Dentalium conspicuum* and *Rhabdus rectius*. The foot may also participate in collection of sediment in dentaliids (Dinamani 1964a; Gainey 1972; Poon 1987) and foraminiferans in gadilids (Shimek 1988, 1990). Neither the radula nor the mouth protrudes from the mantle cavity. Food is passed from the captacula to the mouth where final selection seems to be made by the surrounding ciliated and frilled labial appendages.

There is little doubt that scaphopods are, and probably have been for long geological periods, predominantly carnivorous (Lacaze-Duthiers 1856–1857; Fischer-Piette & Franc 1968; Palmer 1975; Steiner 1992b). Dentaliida must be considered generalists in their diets (Shimek 1990). Foraminiferans, bivalve spat, ostracods, diatoms, small gastropods, marine mites and invertebrate eggs, as well as sediment particles, have been found in the buccal pouches of certain Dentaliida (Dinamani 1964a; Gainey 1972; Sahlmann 1973; Bilyard 1974; Poon 1987; Shimek 1990). Members of the order Gadilida are more specialised in their diets than the Dentaliida and feed almost exclusively on foraminiferans. Certain foraminiferan species are selectively ingested whereas others are neglected. Deposit-feeding has not been observed in the species investigated (Poon 1987; Shimek 1988, 1990).



Figure 10.8 Radula of Antalis sp. (Dentaliidae), dorsal view. cth, central tooth; lth, lateral tooth; mth, marginal tooth; rmb, radula membrane. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

The mouth is at the tip of the buccal tube or proboscis, which is probably formed by fusion of the postoral tentacles (Steiner 1992b). Laterally, the central lumen communicates with a pair of buccal pouches. Prey are stored here before being masticated by the radula. A single jaw marks the transition to the buccal cavity which contains the radula (Fig. 10.4) and subradular sense organ.

The radular apparatus is enormous relative to body size (Morton 1959). It serves for trituration, but is not used to collect food, as in gastropods. The radula is supported by a large pair of cartilage-like radular bolsters where the buccal muscles attach. The bolsters are somewhat horseshoe-shaped (Fig. 10.7) with the radular sac descending between them (Fig. 10.4). Each row of five teeth consists of a simple, oblong central tooth, flanked on each side by a complex lateral and a plate-like marginal tooth, resting on the radular membrane (Fig. 10.8; Lacaze-Duthiers 1856–1857). The radular sac epithelium secretes the teeth and impregnates them with phosphates and iron salts (Shimek & Steiner in press). Radular function is not well understood. Lamprell & Healy (1997) have presented radular scanning electron micrographs of several Australian species of Dentaliida and Gadilida.

The oesophagus shows the basic pattern typical of chitons and conchiferans (Salvini-Plawen 1988). The anterior part has a tripartite lumen with a central ciliated food groove and large, lateral glandular oesophageal pouches. Posterior to the glands, the oesophagus is a simple tube opening dorso-laterally into the stomach, where the food is rolled into a simple protostyle (Salvini-Plawen 1988; Steiner unpublished data) and exposed to extracellular digestion. The ventral side of the stomach is differentiated into ciliated sorting areas and a gastric shield; a vestigial caecum is present at the posterior end.

In the Dentaliida, the digestive gland is arranged symmetrically on each side of the stomach (Figs 10.3, 10.4), but in the Gadilida it is asymmetrical, extending only along the left side of the body. The tubules extend finger-like between the inner and outer mantle epithelia. In both orders, a pair of posterior diverticula stretch out between the gonad tissues (Salvini-Plawen 1988). Enzymes from the oesophageal pouches and the digestive gland digest food extracellularly in the stomach. Dissolved and particulate matter is processed within amoebocytes and resorptive cells of the digestive gland after phagocytosis (Taib 1981) and pinocytosis (Sahlmann 1973).

Posterior to the stomach, the digestive tract changes direction from posterior to anterior where it forms a convoluted intestine. Three intestinal loops are generally present, but species of *Bathoxiphus* (Entalinidae) have four or five, and *Cadulus aberrans* (Gadilidae) have only two (Steiner 1994). The rectum receives the duct of the rectal gland that probably excretes lipid substances (Sahlmann 1973). The anus opens as an oblique slit on a small papilla on the ventral midline just posterior to the foot (Fig. 10.4).

#### **Respiration and Circulatory System**

Scaphopods lack ctenidia. The delicate inner mantle epithelium is the site of gas exchange. The ventilatory function of ctenidia is performed by cilia on a series of pre-anal ridges (Fig. 10.4), these generate the respiratory current. Dentaliida have a higher number of ridges than Gadilida. In the Gadilida the movement of cilia on the apical valve organ also contributes to water flow. Contrary to Yonge's (1937) opinion, the direction of the current is from the posterior to the anterior mantle opening (Steiner 1991). However, at regular intervals piston-like movements of the foot cause vigorous expulsions of water through the posterior opening of the shell. This behaviour expels faeces and gametes from the mantle cavity (Steiner 1990).

The haemolymph is a transparent fluid containing three types of blood cells: leucoblasts, leucocytes and amoebocytes (Arvy & Gabe 1951). It is circulated by the heart, which is a simple, dorsal invagination of the pericardium, situated ventral to the stomach (Fig. 10.4). Other organs contributing to circulation are the foot and the musculature of the perianal sinus and the abdominal region

#### 10. CLASS SCAPHOPODA



Figure 10.9 The gonad and excretory organs of Antalis sp. (Dentaliidae), ventral view with stomach removed. apl, anal papilla; clu, central lumen; exp, excretory pore; hon, anterior horn of gonad connected to right excretory organ; lal, lateral lobes of gonad; lexo, left excretory organ; rexo, right excretory organ. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

(Steiner 1992a; Shimek & Steiner in press). There are no vessels, but there are several distinct sinuses. These interconnected spaces are named the pedal, perianal, abdominal, intestinal, buccal and cerebral sinuses (Lacaze-Duthiers 1856–1857).

#### Excretion

The paired excretory organs lie laterally in the perianal sinus and do not communicate with each other (Figs 10.4, 10.9). Each excretory organ empties into the mantle cavity through a large excretory pore lateral to the anus (Fig. 10.9). There are no consistent reports of a renopericardial connection, and the duct reported by Distaso (1906) between the pericardium and the left excretory organ has not been confirmed. Reynolds (1990a) reported a connection to the right excretory organ in only one of his sections from several specimens of *Rhabdus rectius*. The highly vacuolated excretory epithelium is identical in both excretory organs and is composed of two types of gland cells (Reynolds 1990b).

Lipid substances are excreted by the densely ciliated tubules of the rectal gland (Sahlmann 1973). During the reproductive season gametes are shed via the right excretory pore (Plate 1892; Boissevain 1904).

#### **Nervous System**

The nervous system Scaphopoda is, except for the presence of a buccal system, similar to that of protobranch bivalves (Lacaze-Duthiers 1856–1857) and has been described by Plate (1892) in minute detail. The neurones concentrate mainly in the large cerebral, pleural, visceral and pedal ganglia (Fig. 10.11). Collagenous connective tissue sheaths all ganglia and their connectives and commissures (Gabe & Prenant 1950).

The cerebral ganglia are connected by a short cerebral commissure. Pleural and pedal connectives extend to the respective ganglia. Paired nerves extend into the dorsal part of the anterior mantle region and into the buccal tube. The latter have a common root with the buccal system. Buccal connectives descend to paired subradular ganglia and continue posteriorly to the buccal ganglia between the oesophagus and radular sac. Nerves from the individual captacular ganglia enter the cerebral system via thick captacula nerve trunks. The statocyst nerves run parallel with the pedal connectives.

The large pedal ganglia lie in the pedal sinus with the statocysts closely attached. The cerebropedal and pleuropedal connectives are fused along almost their entire length. In the Gadilida, three pairs of pedal nerves innervate the pedal musculature, and there are six or seven pairs in the Dentaliida (Shimek & Steiner in press).

The elongate pleural ganglia are separated from the cerebral ganglia only by a muscular septum (Fig. 10.4). A single nerve pair extends into the ventral anterior mantle region. The ganglia taper into the visceral connectives that run posteriorly lateral to the bundles of dorso-ventral muscles (Steiner 1992b). The connectives may be cord-like in their posterior part (Steiner 1990).

The visceral ganglia are triangular in shape and communicate by a long commissure. A pair of abdominal nerves extend from their posterior ends. They form small ganglia at the posterior mantle margin from whence nerves enter the pavilion (Fig. 10.10).

Gabe (1949) described acidophilic neurosecretory cells in the cerebral, pleural, and subradular ganglia of *Antalis entalis*.

#### Sense Organs

The totally infaunal mode of life of scaphopods at depths where little or no light penetrates has resulted in a shift of emphasis from a photosensory system to a chemotactile system. Distaso's (1906) report of an osphradium has never been confirmed (Steiner 1991). Thus, the captacula and the epithelia of the mantle margins presumably are the only sources of information on the environment. The selective uptake of food by the captacula (Shimek 1988, 1990), their coordinated movements and presence of a ganglion in each filament indicate the highly developed sensory capability of these feeding organs. However, Sahlmann (1973) found no discrete sensory structures and ascribed perceptive qualities to the entire epithelium of the captacular head.

The statocysts, filled with numerous statoliths, are attached to the posterior side of the pedal ganglia (Fig. 10.4), but their nerves are supplied by the cerebral ganglia.

The subradular organ assumes an unusual position in the buccal cavity. Unlike the situation in other conchiferan molluscs, it rests on the floor of the subradular pouch. The sensory epithelium of the cup-shaped structure is surrounded by mucoid gland cells (Boissevain 1904). It is innervated by the subradular ganglia, and presumably is a 'taste' organ.



Figure 10.10 A, posterior mantle margin of a generalised dentaliid scaphopod, in longitudinal section. B, a cross-section through the pavilion at the position indicated in A. als, annular sinus; cil, ciliated area; dlc, differentiated ledge cells; dvm, dorso-ventral retractor muscle; gd, gonad; lmf, longitudinal muscles; ner, nerve; pav, pavilion; sph, sphincter muscle; smg, supramarginal groove; vbl, ventral bolster of connective tissue. [G. Steiner]



Figure 10.11 The scaphopod nervous system, schematic representation. bg, buccal ganglion; cbg, cerebral ganglion; cpc, fused cerebropedal and pleuropedal connectives; cpt, captacula nerve, indicated by arrowhead; man, mantle nerves; nec, nerve of the oral cone; png, pavilion ganglion; pga, pedal ganglion; plg, pleural ganglion; srg, subradular ganglion; sty, statocyst with nerve; vig, visceral ganglion. [G. Steiner]

The mantle margins are the only tissues that are in constant contact with the environment. Although there are no distinct sense organs, unicellular ciliary receptors are abundant (Reynolds 1988; Steiner 1991). At the anterior mantle margin in the Gadilida, there are collar receptors on papillae on the frontal epithelium. A common feature of the Dentaliida is an annular ciliary organ at the anterior mantle opening; it may function to ventilate the sensory epithelium. This organ is replaced in *Rhabdus rectius* by paired slit-like invaginations of unknown function (Steiner 1991).

# Reproduction

In scaphopods, sexes are separate, and only a single example of hermaphroditism is known, in *Antalis entalis* (d'Anna 1974). The unpaired, elongate gonad lies posterior to the stomach and embraces the posterior diverticula of the digestive gland (Figs 10.3, 10.4). In both sexes, the gonad consists of numerous lobes (Fig. 10.9) which are embedded between the mantle epithelia, like those of the digestive gland. At spawning, the gonad fuses with the right excretory organ, and gametes exit by the right excretory pore into the mantle cavity (Boissevain 1904).

The testes produce sperm of a primitive type (Franzén 1956). Mature spermatozoa have a simple, apical acrosome and an elongate midpiece with four or five mitochondria surrounding the base of the axoneme (Dufresne-Dube, Picheral & Guerrier 1983). The formation of the acrosome from a single golgi complex is unique among molluscs (Hou & Maxwell 1991).

Oogonia and, during vitellogenesis, oocytes, are surrounded by follicle cells before they detach from the ovary wall (Steiner unpublished data). Vitellogenesis occurs in the postpachytene stage of meiosis (Raven 1966). Two different types of yolk granules are accumulated in the ooplasm of Antalis dentalis (Reverberi 1972), Cadulus subfusiformis and Pulsellum lofotensis (Steiner unpublished data). In living specimens, yolk may appear white, yellow or pink (Reverberi 1972). At the vegetal pole, the ooplasm is devoid of yolk, but mitochondria are abundant (Reverberi 1972). Detachment from the ovary wall is correlated with the appearance of long microvilli, which secrete a thick jelly layer in C. subfusiformis and P. lofotensis (Steiner unpublished data). The eggs of A. dentalis and A. antillarum have symbiotic bacteria of unknown significance attached to the vegetal pole (Timmermans, Geilenkirchen & Verdonk 1970; Geilenkirchen, Timmermans, van Dongen & Arnolds 1971). The jelly layer is the only layer which envelops the egg.

#### Embryology and Development

Spawning in Dentaliida under laboratory conditions has been documented for Antalis entalis (Lacaze-Duthiers 1856–1857) and for a female Dentalium conspicuum (Dinamani 1964b). In each species eggs or sperm were expelled from the mantle cavity through the posterior opening of the shell by repeated retractions of the foot. The gadilids Pulsellum lofotensis and Cadulus subfusiformis shed their eggs through the anterior mantle opening. In members of this order, sperm also leave the mantle cavity anteriorly (Steiner 1993). Fertilisation takes place externally or within the mantle cavity. The interaction of spermatozoa and eggs has been analysed by Dufresne-Dube et al. (1983).

The early studies by Lacaze-Duthiers (1856–1857) and Kowalevsky (1883) remain the only references for larval development. Several generations of scientists elaborated on *Dentalium* as one of the classic cases of polar lobe formation (Verdonk 1968a, 1968b; Geilenkirchen *et al.* 1971; van Dongen & Geilenkirchen 1974a, 1974b, 1974c, 1975; van Dongen 1976a, 1976b, 1976c). Raven (1966), McFadian-Carter (1979) and Moor (1983) provide detailed reviews and references. Apart from the early development of *Antalis*, however, little is known about scaphopod ontogeny.

Cleavage is unequal and follows the general molluscan pattern of spiral cleavage (Raven 1966). The formation of polar lobes occurs during the first three cleavages (Wilson 1904). At gastrulation, the large, yolk-rich macromeres are invaginated to form the archenteron. The blastopore remains open and shifts ventrally, but the anus does not form before metamorphosis (Kowalevsky 1883).

Eventually, cilia appear and the larva starts to swim. The larva is lecithotrophic and short-lived. The preoral region forms the larval locomotory organ, a transient testa (or calymma) comprising three or more rings of large ciliated cells (Fig. 10.12; Lacaze-Duthiers 1856–1857; Kowalevsky 1883). During growth the postoral region elongates, while the calymma is pushed forwards. This larval organisation is intermediate between the pericalymma larvae of Neomeniomorpha (Aplacophora) and trochophores of conchiferans and is referred to as a stenocalymma (Salvini-Plawen 1990).

The postoral region of the larva gives rise to most of the adult organs (Moor 1983). The mantle and larval shell form on the dorsal side. Their margins grow ventrally, and fuse in an anterior direction along the ventral median line (Fig. 10.12), and thus shape the tubular mantle cavity and shell (Lacaze-Duthiers 1856–1857). During elongation of the postoral region, the primordia of the foot with a transitory pedal gland, the stomodeum, and the captacula shields appear (Kowalevsky 1883). Gill rudiments have not been reported. The mesoblast is formed by descendants of the 4d cell, but mesenchymatic tissues are also produced by the ectenchymatic cells of the second quartet (van Dongen 1977).

The larvae metamorphose after 3–5 days (Lacaze-Duthiers 1856–1857) and have never been found in plankton hauls. They are slow swimmers and, in the laboratory, often rest at the bottom of their dish (G. Steiner personal observation). At metamorphosis the preoral region with the locomotory prototroch is abandoned (Lacaze-Duthiers 1856–1857; Kowalevsky 1883).

Unlike the larval shells of planktotrophic bivalves and gastropods, those of scaphopods are dissolved or broken away during growth. Only rarely are complete series of shells from juvenile to adult growth stages available for study. Henderson (1920) found such a growth series and published a figure of the larval shell of *Dentalium laqueatum* still attached to the apex of the juvenile shell. It resembled a swollen bulb with two annular constrictions at the posterior opening and about twelve annulations in the anterior part, which give way to the longitudinal ribbing of the adult form. Illustrations or descriptions of larval shells other than *Antalis* are found in Henderson (1920), Cotton & Godfrey (1940), Scarabino (1979), Burch & Burch (1989) and Steiner (1995). Engeser, Riedel & Bandel (1993) discovered similar structures in fossil scaphopods.



Figure 10.12 Larval stages of *Antalis* sp. (Dentaliidae): A, at appearance of larval shell; B, at commencement of ventral shell fusion. apt, apical tuft; clr, locomotive ciliary rings; ft, foot anlage; sh, larval shell; pos, posterior opening of shell. (After Lacaze-Duthiers 1856–1857) [C. Eadie]

The larval shells are always bulbous at the tip with a distinct fusion scar along the ventral midline. The younger parts are conical, showing one (in Gadilida) or several (in Dentaliida) transverse annulations (Scarabino 1979). There is a sharp transition in surface texture between the larval/juvenile and the adult shell (G. Steiner personal observation).

# NATURAL HISTORY

#### Ecology

Scaphopods are benthic marine infaunal micro-carnivores inhabiting all types of sediment from soft mud and silts to coarse muddy shell gravels. They are found in euhaline waters in all latitudes and in depths from the littoral fringe to the abyssal. Though they are not normally littoral, an exceptionally low tide may uncover sediments which contain living scaphopods. On the other hand *Siphonodentalium galatheae* is recorded from 7000 m depth. Many species, including several Australian species, are found over a wide depth range. For example, *Cadulus vincentianus* is recorded from 3–2780 m (Lamprell & Healy 1997) and *Laevidentalium erectum* is recorded from 11–2569 m.

Feeding ecology of a few species has been investigated. Bilyard (1974), Poon (1987) and Shimek (1990) found that most scaphopods are highly selective predators on certain foraminiferan species, bivalve spat and other small metazoa. *Rhabdus rectius*, however, is reported to be more of a generalist, also ingesting detritus (Shimek 1990).

Scaphopoda are preyed upon by demersal fish, naticid gastropods, decapod crustaceans and certain asteroids (Fankboner 1969; Shimek 1989; Kropp 1992). Empty shells are frequently inhabited by hermit crabs or sipunculids.

Reproduction, as far as known, is strictly seasonal in coastal waters of the northern Atlantic and eastern Pacific (Steiner 1993; R.L. Shimek personal communication), but seasonality has been reported also in the deep-sea species, *Cadulus californicus* (Rokop 1977).

# **Economic Significance**

No records are available of scaphopods being eaten by humans, the majority being, perhaps, too small. They undoubtedly form part of the diet of bottom-feeding fish, since scaphopod shells have been recovered from the stomachs of these fish (Shimek 1989).

Indians from the north-west of America once used shells of *Antalis pretiosum* for decoration as well as a form of currency. Scaphopod shells, when available, have always figured in shell art – necklaces, pictures and shell-covered boxes – forming part of the economy of coastal resorts (Clark 1963).

### FOSSIL RECORD AND PHYLOGENY

The earliest unequivocal scaphopod is *Rhytiodentalium kentuckyensis*, a presumably smooth dentaliid from the Middle Ordovician of Kentucky, United States of America. In the Devonian there are smooth, but obscure, forms which continue into the succeeding Carboniferous period when the first longitudinally ribbed scaphopod makes it appearance. This is *Prodentalium*, a multi-costate form, some specimens of which attain a length of up to 305 mm.

The Palaeozoic–Mesozoic transition witnessed the appearance of scaphopods with concentric annulations now grouped in the genus *Plagioglypta*. This genus has a doubtful record in the Ordovician (Emerson 1962), but appears more frequently, although intermittently, in Mesozoic to Recent faunas (see Scarabino 1995). It is not certain, however, whether the concentric annulations are uniquely derived or are of polyphyletic origin. Throughout the Mesozoic and Cainozoic, two distinct types of scaphopods co-existed. These were smooth laevidentaliids, apparently present continuously from Middle Ordovician times to the present day, and longitudinally ribbed multi-costate forms grouped in *Prodentalium*. These parallel successions are accompanied by sporadic appearances of annulated forms in the Middle Triassic, Lower Jurassic, Lower Cretaceous and early Cainozoic.

It is easy to argue on the evidence of occurrence, that smooth and ribbed multi-costate dentaliids were represented continuously from the Palaeozoic to the present day, but not so easy to make the same case for annulated forms.

In the Cainozoic, during the Miocene period, the first symmetrical, pauci-costate forms (with fewer than about 10 ribs) appear, culminating in the numerous forms of *Dentalium sexangulum* in the Pliocene period. *Dentalium elephantinum*, the scaphopod type species, has no fossil history before the Pleistocene.

The history of the Scaphopoda appears to be quite complex. The earliest member of the Gadilidae is the Lower Cretaceous Gadila gaultina. This is a true Gadila which is succeeded by Polyschides in the Eocene of the Paris Basin. The barrel-shaped Cadulus does not occur before the Miocene period. A smooth, thin scaphopod from the Permian of Nevada, United States of America, named Calstevenus by Yancey (1973), was placed by him in the family Siphonodentaliidae, based on the strong curvature of the shell and rapid expansion rate. If this is correct, then the very long time gap between Calstevenus in the Permian and Gadila gaultina in the Lower Cretaceous, requires some explanation. A simpler explanation is that Calstevenus was a novel Permian offshoot of the Laevidentaliidae. However, the matter will not be easily settled.

The Dentaliida is an ancient and conservative lineage, showing little anatomical variation. The derived Gadilida are more diverse in their anatomy, which makes it easier to deduce family relationships (Steiner 1992b).

Allowing that we know nothing of the geological history of the Aplacophora, the Scaphopoda is the youngest class of the Mollusca known. By the Middle Ordovician, all other classes of Mollusca had earlier representatives. The rather poor Palaeozoic fossil record Scaphopoda suggests that the ancestral stock of all scaphopods was the smooth Laevidentaliidae, first appearing in the Middle Ordovician, giving rise to ribbed *Prodentalium* in the Carboniferous, annulated *Plagioglypta* in the Permian–Triassic, and the Gadilidae, beginning with *Gadila*, in the Lower Cretaceous. The distribution of shell sculpture in Recent scaphopods, however, renders a longitudinally striated form equally probable as a common ancestor (Steiner 1992b).

A widely accepted theory places scaphopods, bivalves and the fossil rostroconchs in the clade Loboconcha (Salvini-Plawen 1990) or Diasoma (Pojeta & Runnegar 1976), based on the comparable development of mantle and shell and on similarities in the burrowing foot and the nervous system (Steiner 1992b).

#### 10. CLASS SCAPHOPODA

# CLASSIFICATION

Scaphopoda are classified into two orders, Dentaliida and Gadilida (Palmer 1974; Starobogatov 1974), the latter being subdivided into the suborders Entalimorpha and Gadilimorpha (Steiner 1992b). Compilations and many original descriptions of Australian species are given by Cotton & Ludbrook (1938), Cotton & Godfrey (1940), Colman (1958), Powell (1960), Zeidler & McPhail (1978) and Lamprell & Healy (1997). Scarabino (1995) described 42 new species from the tropical waters of the Indian and Pacific Oceans; some of them from Australian waters.

Family groupings are based mainly on shell and radular characters as very little is known of the variations in soft-part anatomy. Only a few mantle characters are available for classification (Steiner 1991). The shell apices may show slits, notches, plugs or pipes which are still used for classification. Because of the continuous modification of the tip of the shell by the mantle tissue (Shimek 1989; Steiner 1991; Reynolds 1992), these features are neither constant nor reliable enough to be used as diagnostic characters. They may, however, be of help for the identification of the animal and are, therefore, included in the family descriptions, and in the key to the families in one instance. For identification of genera consult Palmer (1974). The family Omniglytidae has been recorded recently from Australia (Lamprell & Healy 1997).

Table 10.1 Classification of the Scaphopoda. Families marked with an asterisk are not represented in Australia.

Class SCAPHOPODA	
Order DENTALIIDA Family Dentaliidae Family Fustiariidae Family Rhabdidae Family Laevidentaliidae Family Gadilinidae Family Omniglyptidae	
Order GADILIDA	
Suborder ENTALIMORPHA Family Entalinidae	
Suborder GADILIMORPHA Family Pulsellidae Family Wemersoniellidae Family Gadilidae	

# Key to the families and subfamilies of the class Scaphopoda

1 (a)	Maximum diameter of shell at the aperture
(b)	Maximum diameter of shell not at the aperture
2 (a)	Central tooth wider than high; epipodial lobes of foot interrupted dorsally; two pairs of dorso-ventral muscles; digestive gland paired
(b)	Central tooth higher than wide; foot eversible with terminal disc; one pair of dorso-ventral muscles; left digestive gland only
3 (a)	Shell surface with longitudinal striae or at least four ribs, at least in the apical region Dentaliidae
(b)	Shell surface smooth or with three ribs
4 (a)	Shell surface with three ribs
(b)	Shell surface smooth
5 (a)	Superior border of central tooth smooth; marginal teeth recurved; apex often with a deep, straight, ventral slit
(b)	Superior border of central tooth not smooth; marginal teeth not recurved; apical slit irregular or absent 6
6 (a)	Shell surface always smooth, sometimes eroded; marginal teeth almost straight
(b)	Shell surface smooth or with apical transverse annulations; marginal teeth curved
7 (a)	Shell weakly tapered, slender, aperture less than five times as wide as posterior opening of the shell; central tooth tricuspidate; anterior mantle margin with two dorso-lateral slits
(b)	Shell strongly tapered, aperture at least five times as wide as posterior opening of the shell; central tooth rectangular to polygonal
8 (a)	Shell with apical annulations or smooth, triangular to circular in cross-section; central tooth tricuspidate Gadilinidae (part)
(b)	Shell always with apical annulation, always circular in cross-section; central tooth with irregular denticles . Omniglyptidae
9 (a)	Shell surface with four to 13 more or less prominent ribs, often eroded; apical cross-section polygonal or laterally compressed; central tooth with smooth superior edge; lateral teeth bear five to nine denticles; marginal teeth not keeled
(b)	Shell surface smooth, sometimes with fine striae; apical cross-section circular; central tooth with at least one cusp; lateral teeth tricuspidate; marginal teeth keeled
10 (a)	Shell circular in cross-section throughout Pulsellidae
(b)	Shell dorso-ventrally depressed in cross-section, at least at the aperture 11
11 (a)	Shell strongly curved
(b)	Shell weakly curved to straight



Palmer, Charles P and Steiner, Gerhard. 1998. "Class Scaphopoda: Introduction." *Mollusca: The Southern Synthesis [Fauna of Australia. Vol. 5]* 5, 431–438.

View This Item Online: <u>https://www.biodiversitylibrary.org/item/291106</u> Permalink: <u>https://www.biodiversitylibrary.org/partpdf/334179</u>

Holding Institution Australian Biological Resources Study

**Sponsored by** Atlas of Living Australia

**Copyright & Reuse** Copyright Status: In copyright. Digitized with the permission of the rights holder. Rights Holder: Australian Biological Resources Study License: <u>http://creativecommons.org/licenses/by-nc-sa/4.0/</u> Rights: <u>http://biodiversitylibrary.org/permissions</u>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.