ISSN 0141 - 4593

The Conchological Society of Great Britain and Ireland

(Founded 1876)

Papers for Students No.17.

AN INTRODUCTION TO THE SCAPHOPODA

by

C.P.Palmer

INTRODUCTION.

The Scaphopoda, a small but distinct class of the Mollusca, date back with certainty to the early Devonian, but their origins in the early Palaeozoic still remain an unsolved problem. Slender annulated tubes are, however, known from the Ordovician. These may be either scaphopods or pteropods, the matter is not yet settled.

No agreement exists as to the number of species in the Scaphopoda About 750 are usually acknowledged by most modern workers - 400 fossil and 350 living. The present auther, however, has more than 1,200 described, and named forms, in his card index - 626 fossil and 643 living. Allowing that 20% of these may be synonyms, the truth probably lies somewhere between the two extremes, perhaps in the region of 1,000. The class derives its name from the Greek and roughly means 'shovel-foot', while the vernacular 'tusk-shell' requires no explanation, see figs. 1 and 4.

Scaphopods are fully marine animals, avoiding estuaries and any fresh water. They are the only class of the Mollusca which is exclusively infaunal, using the 'shovel-foot', like the bivalves, as a means of locomotion. The slender ciliated captaculae are used for catching a variety of marine animals, mainly Foraminifera.

Systematically they seem to occupy a position between the Bivalvia and the Gastropoda. The digging foot, absence of eyes, the fused mantle which is open at both ends, and the bilateral symmetry, aligns them with most bivalves. On the other hand, the univalve shell, the presence of a head, albeit rudimentary, with a buccal mass and radula, the predatory habit, and most aspects of the nervous system, relate them to the gastropods.

THE ANIMAL (see fig.2.).

Anatomically, the scaphopods are distinct from most other molluscs in that they are bilaterally symmetrical elongated animals in which mantle fusion occurs along the mid-ventral line leaving both ends open. The anterior opening is for the foot and captaculae, and the posterior is for circulation of water and elimination of faeces. In these arrangements one sees similarities with the infaunal bivalve razor-shells, but the mode of feeding is totally different.

As a result of their infaunal habit, scaphopods have no eyes but statocysts are present in the foot. The probiscis, with two bundles of laterally placed prehensile ciliated filaments called captaculae, lies above the foot, which, together with the captaculae, can be thrust out into the sediment where the foot serves for locomotion, while the captaculae catch infaunal organisms bringing them to the frilled and probably selective lips of the proboscis. The continuous mantle cavity is open at the posterior for the discharge of faeces and the admission of water for respiration which, in the absence of a gill, takes place at the mantle surface. Behind the radula, a stright oesophagus passes food posteriorly into the stomach which receives ducts from a bilobed and much divided liver (see fig.2d.). The liver, having a lung-like appearance, deceived early 19th century workers into believing that it was a respiratory organ. The correct digestive function was demonstrated by Lacaze-Duthiers in the late 19th century. The convoluted intestine continues in an anterior direction and terminates ventrally at the anus opening, posteriorly. The sexes are separate and a single ovary or testis opens into the right kidney.

From singly laid eggs, a floating trochophore larve develops which is succeeded by a veliger stage. After 5-6 days the veliger loses its ciliated velum and settles on the sea floor to begin its benthonic life within the sediment.

The form of the foot divides the class into two orders. In the Dentalioida the foot is short and conical in shape, with an epipodial coller, interrupted dorsally, which expands during locomotion and gives the foot a three-lobed appearance (see fig.1a.). In the Siphonodentaloida the epipodial coller forms a round crenulated pedal disc which is terminal, except in the two genera Pulsellum and Entalina. In these, a distal median filament is present on the pedal disc. This is probably homologous with the conical foot of the dentaloids, since both are anterior to the epipodial collar of the one and the pedal disc of the other (see fig.1b. and c.).

THE SHELL

a). Structure

The scaphopod shell is tubular, tapering, more or less curved, open at both ends and composed of four layers. The outermost layer is a chitinous periostracum while the three inner layers are calcareous and composed entirely of aragonite. The outer calcareous layer is prismatic with the long axes of the prisms normal to the tube axis. The middle layer has a crossed-lamellar structure very similar to that of the Bivalvia. The innermost calcareous layer has a fine crossed-lamellar structure deposited in concentric conical layers (fig. 3a-d.). The chitinous and prismatic layers, being primary deposits, thicken with growth towards the anterior of the shell. The crossed-lamellar and concentric layers strengthen posteriorly, by secondary deposition, and consiquently thicken in that direction. Resorption of the apex with growth results in the inner concentric layer lying discordantly on the other layers at the apex.

The earliest known scaphopods have resorbed apices, that of Prodentalium being slightly notched, while Plagioglypta has a simple apex (see figs. 3. and 4.). Long slits and fissures, accompanying resorption of the apex, are apparently developments of late Cretaceous - early Palaeogene times.

b). Biometrics

In describing and comparing the gross morphological shell characteristics of the dentaliid scaphopods, an increase in precision and some brevity can be achieved if diagnostic characters are given a simple numerical and symbolic expression. A more sophisticated mathematical expression, though impressive, would be too powerful and unwieldy a tool for this simple function.

Thus, if d^1 = aptural diameter, d^2 = apical diameter, 1 = length of median axial line joining d^1 and d^2; then $\frac{d^1 - d^2 \times 100}{1} = E$, expansion rate of the tube (see fig.3.).

Similarly, if ch = length of chord joining d^1 and d^2, h = the greatest distance between the chord and the dorsal surface of the shell; then $\frac{h \times 100}{ch} = a$, the arcuation of the shell (note, this is not the curvature of mathematicians), see fig. 3.

Finally, the notation $\hat{6}$, $\overset{\frown}{12}$, $\bar{24}$, represents use of a ribbing formula which reads "six sharp apical ribs, 12 rounded medial, and 24 obsolescent ribs at the aperture". Apical characters may be symbolised by (O)= simple, (V) = notched, (T) = slit or fissured, (P) = pipe (see fig. 3.).

Thus the principle diagnostic shell features of a dentaliid scaphopod, say _Fissidentalium vernedei_, may be summarised by -

A4·3, E6·3 (T) $\hat{35}$ - $\overset{\frown}{38}$ - $\bar{39}$.

FEEDING

The feeding habits of scaphopods have been well reported by Clark, Dinamani, and Morton (see Palmer 1975) and more recently by Bilyard (1974). All agree that these molluscs have a varied diet, but one consisting mainly of Foraminifera and, occasionally, small infaunal bivalves. These they catch by means of the captaculae (see fig. 1d.) which penetrate the sediment in a broad cone around the foot. Captured prey is brought to the frilled lips of the proboscis, where a certain amount of selection takes place, before passing into the buccal mass to be ground by the radula. About 14 genera of Foraminifera have been reported from the buccal pouches of dentaliid scaphopods and, in addition, Bilyard (1974) found, in the buccal pouches of _Antalis entalis stimpsoni_, eggs, ostracods, bivalve spat, marine mites, copepod eggs, nematodes and small worms. Clarke (1879) found two bivalves _Kellia suborbicularis_ (Montagu) and juvenile _Goodalia triangularis_ (Montagu) in addition to six kinds of Foraminifera in the buccal pouch of Antalis entalis (da Costa). Dinamani (1954) reported "large diatoms, single algal cells and unidentified particles of detritus" in the stomach and intestine of Dentalium conspicuum Melville.

Finally, Palmer (1975) suggested that the fossil foraminifera _Epistomina_, associated with the Upper Jurassic scaphopod _Prodentalium calvertensis_ Palmer, formed the principal part of the diet of the scaphopod.

Evidently scaphopds have a varied diet and may be described as much omnivorous as carnivorous,

HABITAT

Scaphopds live in mud, silt, or sand, with the concave (dorsal) side of the tube uppermost and the posterior tip protruding about 10 mm. above the sediment-water interface. Their depth range is fairly wide, between a few metres just off-shore in _Antalis_, down to more than 6,000 m. in the case of _Fissidentalium candidum_. Most are sublittoral, although a few species can tolerate exposure during spring tides, and occasionally a living specimen may be cast up onto a beach during a violent storm.

Their tolerance of salinity reduction is considerably less than their tolerance of depth, which results in their virtual absence from estuaries and river outflows. Therefore, their presence in sedimentary rocks may be taken, in the absence of cephalopods, brachiopods or echinoderms, as strong evidence of euryhaline conditions of deposition.

CLASSIFICATION

Scaphopods are currently divided into two orders Dentalioida and Siphonodentalioida. Each has two families: Dentaliidae and Laevidentaliidae in the first; Siphonodentaliidae and Cadulidae in the second (Palmer 1974).

a). Dentaliidae, 9 genera

These are the typically ribbed scaphopods which seem to divide naturally into two groups: the symmetrical, paucicostate forms which include Dentalium, Paradentalium, Tesseracme, and Spadentalina, fig.4; and the unsymmetrical multicostate forms which are typified by Fissidentalium and Prodentalium - the oldest group, fig.4.

b). Laevidentaliidae, 10 genera

Dentaloid scaphopods lacking longitudinal sculpture, being either smooth or annulated. These again divide into two groups: smooth forms with or without apical slits, fig. 4; and annulated forms with or without apical slits, fig 4 - the oldest group.

c).Siphonodentaliidae, 5 genera

Scaphopods with vermiform foot lacking apertural constrictions. These divide into two groups: Entalina and Pulsellum with a medial filament on the pedal disc, fig.1c; and Siphonodentalium which lacks the filament but has apical lobes or notches. Calstevenus is a Pulsellum - like Permian fossil.

d). Cadulidae, 6 genera

Scaphopods with vermiform foot and a constricted aperture in the adult. A compact group which does not divide easily. Cadulus has the greatest diameter near the centre. Gadila and the rest have it near the anterior aperture, fig. 4.

RANGE AND EVOLUTION

The earliest undoubted siphonodentaloid is a Gadila (see fig.4.) from the Lower Cretaceous but Emerson records Entalina, with a query, from the Triassic. Calstevenus from the Permian, though similar to Pulsellum, is not a definite siphonodentaloid.

In the Laevidentaliidae the annulated Plagioglypta (see fig.4.) ranges from the Devonian to the present day, and gave rise to the trigonal Progadilina in the Lower Jurassic and the apically slit Fustiaria in the Eocene.

Laevidentalium. smooth and with either simple or notched apex, from the Triassic to the present day (see fig.4.). It gave rise to the apically slit Pseudantalis in the Eocene; the acicular Rhabdus and the trigonal Gadilina in the Miocene; the laterally compressed Bathoxifus in the Holocene; and the two cylindrical, nearly stright, forms with an apical pipe - Episiphon in the Jurassic and Lobantale, with two lateral internal ridges, in the Eocene.

The greatest uncertainty lies in the ranges of genera in the Dentaliidae, due to the indiscriminate use of the name Dentalium in describing fossils. The picture is far from clear but it appears that the unsymmetrical multicostate Prodentalium/Fissidentalium lineage was the central stock from which the symmetrical paucicostate group, typified by Dentalium elephantinum Linne.1758, was derived during the late Cretaceous or early Palaeogene (see fig.4.).

It is unlikely that the partially costate Antalis ranges further back than the late Cretaceous, although this depends upon the interpretation of Antalis, type species Dentalium entalis Linne. 1758. In the strict sense the genus can hardly be applied beyond the Palaeocene.

The problems facing palaeontologists when studying fossil scaphopods include the rarity of complete individuals, and the tendency in dentaloids for the characters of the ribbing to change quite radically with development. These quite normal difficulties, combined with the practice of mature scaphopods to remove by absorbtion the juvenile, and often quite differently ornamented, part of the shell can sometimes prove perplexing when matching the juvenile shells with mature specimens.

REFERENCES

Bilyard, G.R., 1974. The Feeding Habits and Ecology of Dentalium entale stimpsoni Henderson (Mollusca:Scaphopoda). The Veliger 17(2): 126-138, 7 text figs.

Dinamani, P., 1954. Feeding in Dentalium conspicuum Proc. Malac. Soc. Lond. 36 (1):1-5, 1 fig.

Emerson, W.K., 1961, A Classification of the Scaphopod Mollusks. J.Palaeont. 36: 461-482, 5 pls.

Morton, J.F., 1959. The habits and feeding of Dentalium entalis. J. Mar. Biol. Ass. U.K. 38: 225-238, 5 text figs.

Palmer, C.P., 1974. A supraspecific classification of the Scaphopod Mollusca. Veliger 17: 115-123, 4 text figs.

Palmer, C.P., 1975. A new Jurassic scaphopod from the Oxford Clay of Buckinghamshire. Palaeont. 18(2): 377-383, 1 pl.

Pilsbry, H.A., and Sharp, B., 1897-1898. Scaphopoda. In Tryon, G.W., (ed.) Manual of Conchology 17: xxxii-1-348, 39 pls.

Robson, G.C., 1957. Scaphopoda. Encyclopaedia Brittanica 20: 51, 4 text figs.

Published - 14th May, 1979.

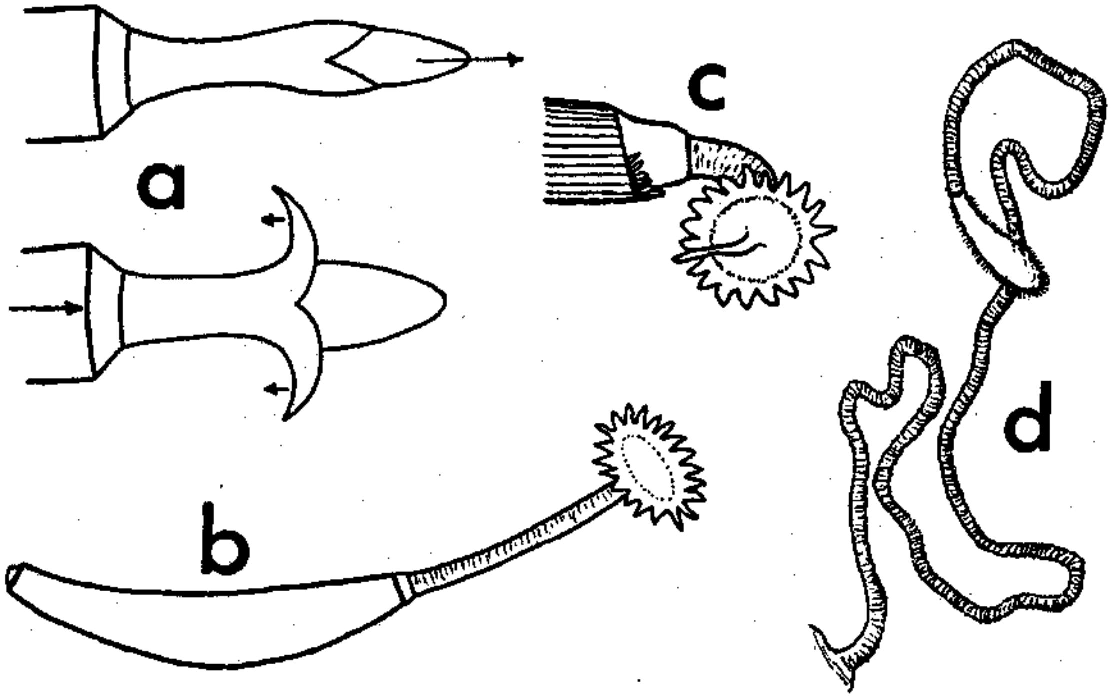


Fig. 1, a. The dentaloid foot showing function of the epipodial collar during burrowing.

The siphonodentaloid foot with pedal disc expanded: c, foot of Entalina with median filament; b, foot of Cadulus.

d. Enlarged view of captacula. (Modified from Trueman and Pilsbry and Sharp).

Fig. 2. Anatomy of *Antalis*: a & b, detailed anatomy of *Antalis entalis* (after Morton); c,d,e, gross anatomy and details of *Antalis vulgaris* (after Lacaze-Duthiers).

a. Median section of *A. entalis*: An., anus; Br., folds of the mantle wall serving as the respiratory organ; Bu., buccal cavity; Ce., cerebral ganglion; Cil., ciliated fold of the roof of the stomach leading to the intestine; Cil.Div., ciliated folds associated with the caecum and digestive diverticula; Cil.F., ciliated fold of the glandular region of the oesophagus; Cil.Oe., ciliated lining of the oesophagus; Cm., caecum of the stomach; Cut., cuticulated epithelium of the stomach; D.gl., digestive gland tubules spreading round the side of the mantle cavity; Dig., digestive gland in section; Div., digestive diverticulum leading from the stomach; F.Ra., formative cells of the radula at the bottom of the radula sac; Gl.Oe., limits of the glandular region of the oesophagus; Int., intestine; J., jaw; Mar., marginal teeth of left side within the radular caecum; Mo., mouth; Mu., retractor muscles attached posteriorly to the shell; Od.M., muscles of the odontophore; Oe., oesophagus; Oe.P., oesophageal pouch; Oe.2, extent of interrupted section of the oesophagus; Ot., otocyst; Ov., ovary; Pa., pallial cavity; Pe., pedal ganglion; Pr., proboscis; Rd., radula (lateral teeth of left side and median teeth); Sh., vestige of gastric shield; St.Int., anterior part of stomach, tapering forward to intestine.

b. Single row of teeth from the radula.

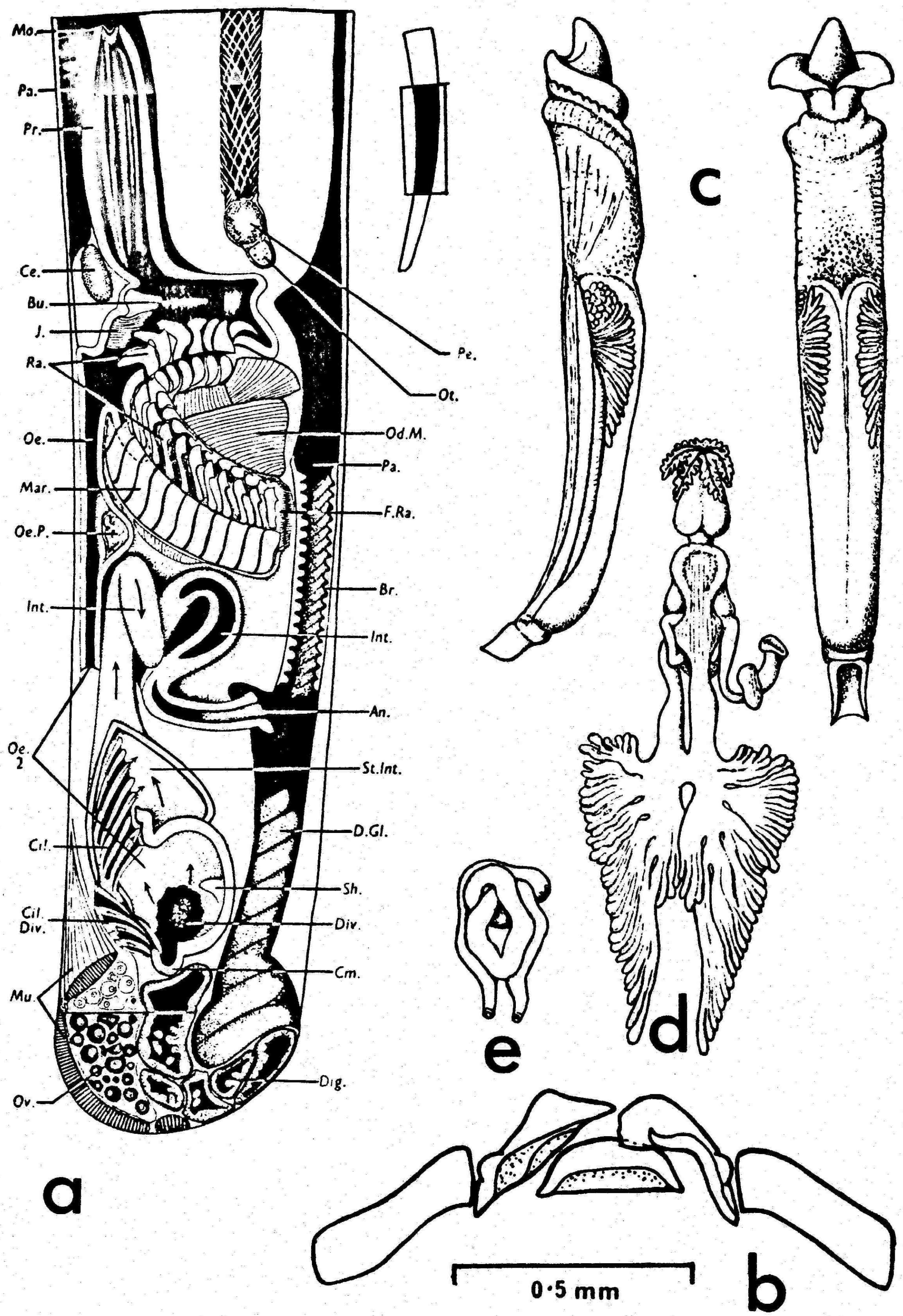
c. Lateral view on the left, ventral view on the right of *A. vulgaris*.

d. Dorsal view of alimentary tract showing the much divided 'liver' or digestive gland of *A. vulgaris*.

e. Ventral view of gut of *A. vulgaris*.

Fig. 3. Measurable parameters of generalised scaphopod shell shown in median section, together with formulae for arcuation and expansion.
Symbols for expressing character of apex.

a-d. Section of shell showing the four layers: a, chitinous periostracum; b. prismatic layer; c. crossed-lamellar, d, fine crossed-lamellar in concentric conical layers. Layers b,c,d are of aragonite.



Mo.
Pa.
Pr.
Ce.
Bu.
J.
Ra.
Oe.
Mar.
Oe.P.
Int.
Oe.
2
Cil.
Cil.
Div.
Mu.
Ov.
Pe.
Ot.
Od.M.
Pa.
F.Ra.
Br.
Int.
An.
St.Int.
D.Gl.
Sh.
Div.
Cm.
Dig.
a
b
c
d
e
0·5 mm

Fig. 2

$$E\text{, expansion rate of shell} = \frac{d^1 - d^2 \times 100}{l}\ \%$$

$$A\text{, arcuation of shell} = \frac{h \times 100}{ch}\ \%$$

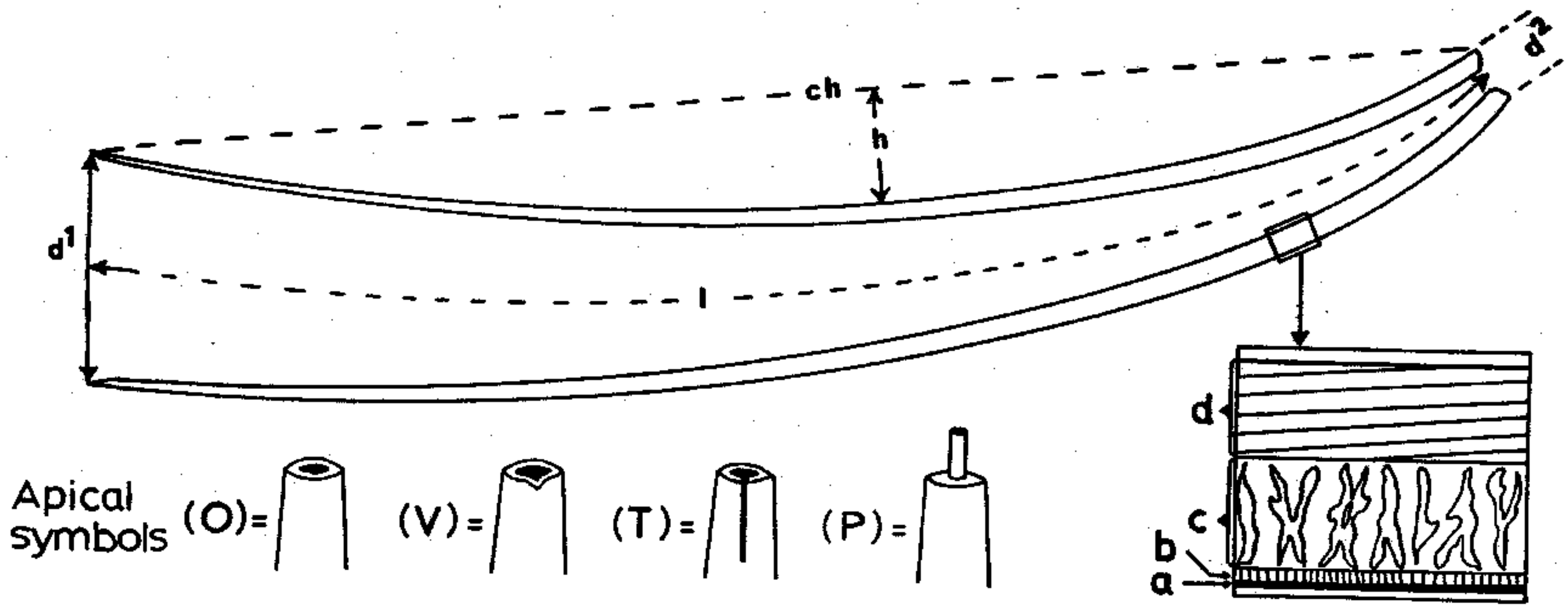


Fig. 3

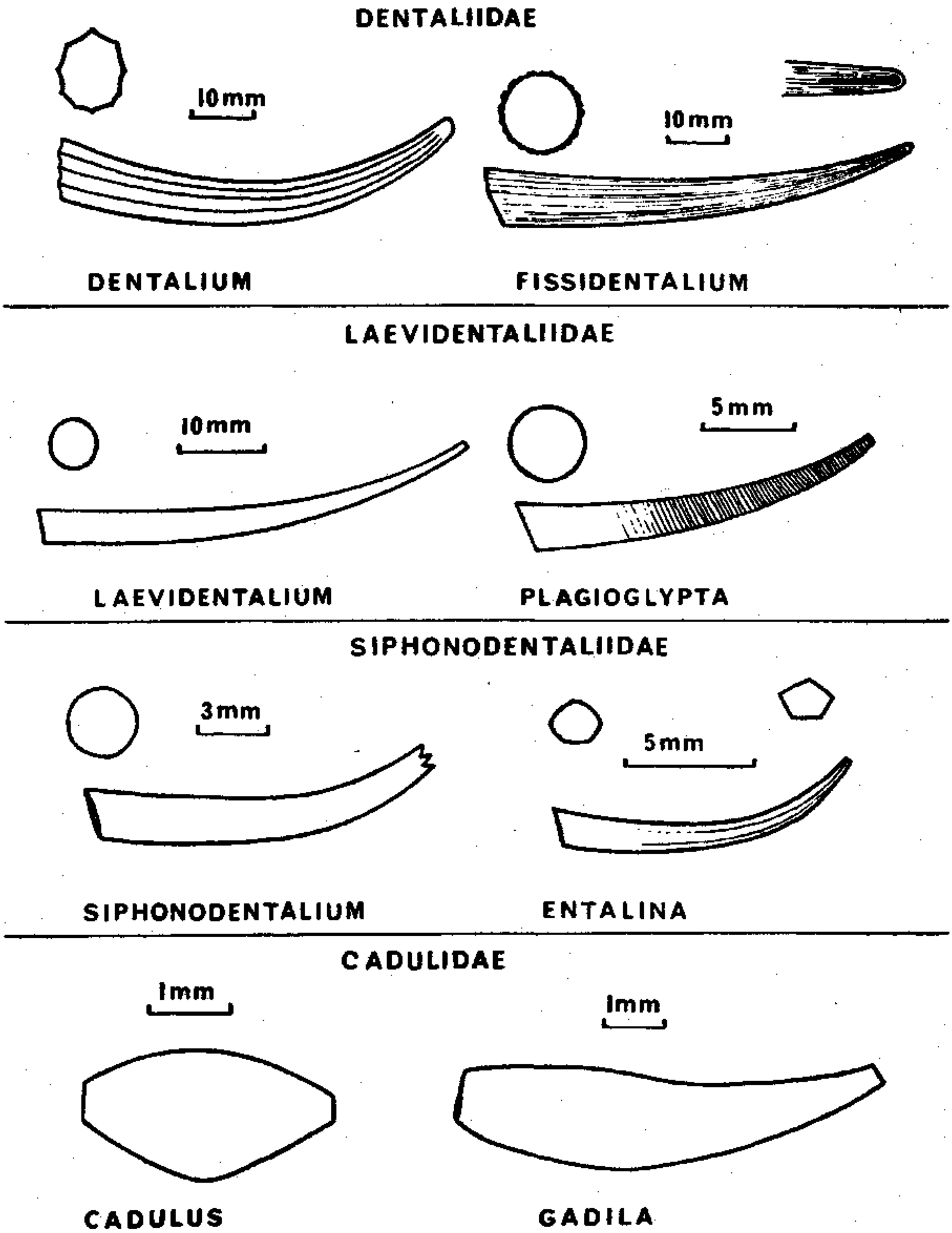


Fig. 4. Diagrammatic sketches to illustrate characters of leading genera in each of the four scaphopod families

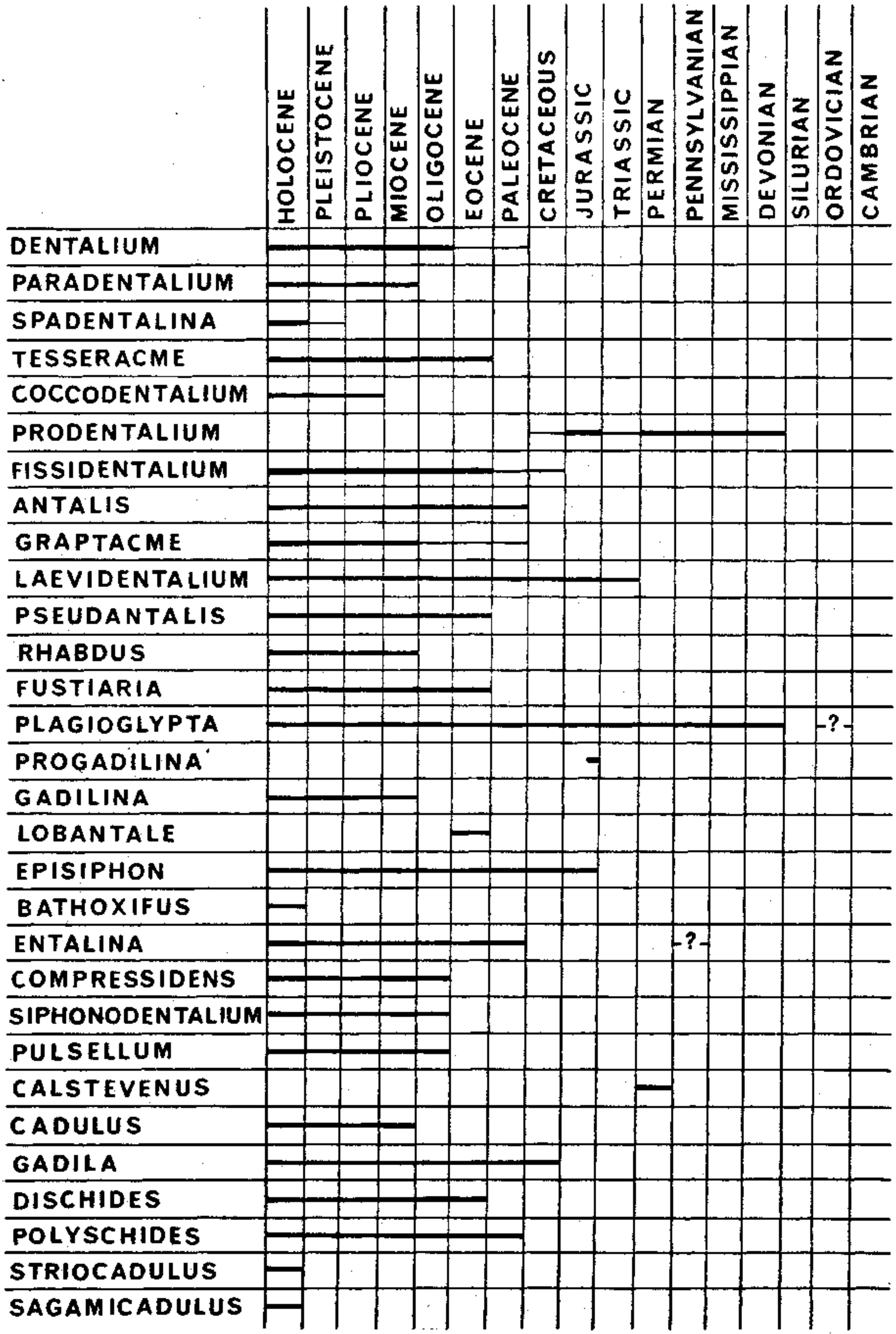


Fig. 5. Table indicating probable ranges of genera through geological time. Thick lines indicate certain ranges, thin lines uncertain.