

Early ontogenetic shells of Recent and fossil Scaphopoda

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The formation of the early ontogenetic shell of Scaphopoda is reviewed. In the few known cases the embryos hatch in the gastrula stage and rapidly develop into a lecithotrophic Trochophora-like larva. Our material indicates that there might be a planktotrophic larva in some species. The clasp-like shell is formed in the larval stage (e.g. *Antalis tarentina* Lamarck, 1818). It later fuses into a tube and mineralises during metamorphosis. Immediately after the metamorphosis the shell increases at the anterior end (early teleoconch) and posterior end (fumarium). During further growth, the fumarium, the larval shell and finally parts of the juvenile shell are gradually resorbed.

We describe several specimens with preserved protoconchs from different stratigraphic units: the Early Jurassic, the Middle Jurassic, the Palaeocene, the Oligocene, the Miocene, the Pliocene, and a Recent example. Some specimens with preserved larval shells illustrated in the literature have not been recognised as such. They are briefly reviewed. At least two different types of protoconchs (and some modifications) can be recognised within the Scaphopoda.

The new data are not yet sufficient to arrange larger systematic units using the different protoconch types. It is evident, however, that in fossil Scaphopoda species with convergent adult shells can only be discovered by a synthesis of larval, juvenile and adult shell characters (shape, size, sculpture).

A new genus and species, *Suevidontus jaegeri* gen. et sp. nov. from the late Middle Jurassic of southern Germany is introduced. The family attribution of the new genus is uncertain.

Contents

Introduction	83
Termini	83
Material and methods	85
General account of the early ontogeny of Scaphopoda	85
Descriptions	86
Comparison with other specimens	96
Discussion	98
Acknowledgements	99
References	99

Introduction

Termini

Teleoconch includes the juvenile and/or the adult shell. **Protoconch** is used as a synonym for the larval shell prior to metamorphosis. As far as known no embryonic

shell is built during the ontogeny of the Scaphopoda. Since there exist no detailed descriptions of the protoconch of scaphopods we introduce several new termini (see also Fig. 1).

The larval shell looks like a clasp before it becomes fused ventrally. The seam of adhesion of the two lateral parts of the protoconch is called suture. The **suture** can be well developed but also very indistinct. The shell of the suture area is often wrinkled.

The lateral parts of the larval shell are mostly 'inflated' and somewhat resemble human cheeks. We therefore called them **genae** (sing. gena) from the Latin word for cheek. The genae are most pronounced when the suture is relatively deepened in regard to the surface.

The posterior opening can be very narrow or of a moderate diameter. It may be surrounded by a low wall or by a pipe. This pipe looks like a chimney and we therefore introduce the Latin word **fumarium** for it. We do not know whether a fumarium is always present during a certain ontogenetic phase. The fumarium is not a part of the protoconch since it is formed after metamorphosis (see below).

The anterior part of one of the larval shell types shows weak to strong circular annulations or undulations. We generally call these structures **annulations** because without destroying the specimens one cannot decide whether the ornamentation is restricted to the outer part of the shell or reaches the inner surface.

The anterior protoconch often shows a **constriction** which is more or less distinct. It does not represent the very end of the larval shell which is marked by the onset of strong growth lines, shell irregularities and/or e.g. the onset of longitudinal ribs.

The surface of the larval shell may be covered by longitudinal **lirae**. Single lirae may bifurcate at the posterior end and can vary in strength as well as distance from each other.

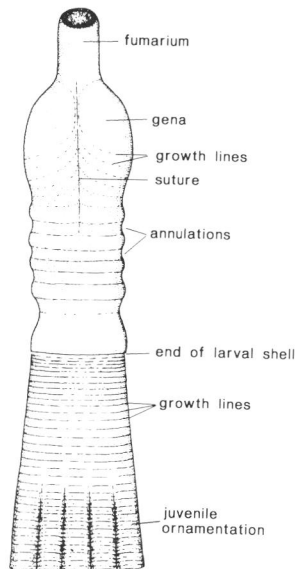


Fig. 1. Schematic drawing of a scaphopod protoconch with parts of the early teleoconch.

Material and methods

The Recent *Antalis tarentina* and another juvenile dentaliid shells (not specifically identified) were collected off the coast of Banyuls-sur-Mer (southern France). The Pliocene scaphopod *Entalinopsis* sp. comes from Le Puget-sur-Argens (southern France), the Middle Miocene samples were borrowed from the Museum of Natural History in Vienna and had been collected at Baden (near Vienna). Samples of the Late Oligocene 'Kasseler Meeressande' (Glimmerode, Germany) contained several juvenile specimens. The Palaeocene material was collected at Matthew's Landing (Alabama, USA). Jurassic specimens come from the Dogger beta (Late Aalenian) of Hambühren (Lower Saxony, Germany), the Dogger zeta (Middle Callovian) of Plettenberg near Stuttgart (southern Germany) and from erratic boulders (Middle Liassic) found at Hoisbüttel (northern Germany).

The fossil material was processed like usual micro samples using H₂O₂. Several samples were again treated with tensides (Rewoquat) to remove remaining clay chips.

The specimens were sorted from the dried residue, mounted on stubs and coated with gold. They were investigated and photographed with the aid of a CamScan scanning electron microscope.

General account of the early ontogeny of Scaphopoda

The early ontogeny of scaphopods is poorly known. Only 7 Recent species out of probably more than 500 have been investigated in this regard (McFadien-Carter, 1979; Lindberg, 1985). In particular the formation and mineralisation of the protoconch are almost unknown. Modern developmental studies mainly concentrate on the early embryogeny (e.g. Verdonk & van den Biggelaar, 1983).

We give a brief general account of the early ontogeny based on Recent *Antalis tarentina* (Lamarck, 1818) and *A. vulgaris* (da Costa, 1778) from the Mediterranean and the Channel (Palmer, 1987). Different stages of shell construction described from fossil specimens (see below) are used as additional data.

Female and male scaphopods release mature eggs and sperms through their posterior shell opening into the open sea where fertilization takes place. According to Lindberg (1985) egg sizes in scaphopods vary between 60 µm and 200 µm. Usually the eggs contain a comparably large amount of yolk. In *Antalis vulgaris* (da Costa, 1778) the embryos hatch as gastrulae a few hours after fertilization and rapidly develop into Trochophora-like larvae with lecithotrophic development (Lacaze-Duthiers, 1856-58). The protoconchs of some species indicate that there might be planktotrophic development as well (see Descriptions and Discussion).

Kowalevsky (1883) noted the differentiation of the shell gland of *Antalis* aff. *tarentina* (Lamarck, 1818) during the late gastrula stage. The formation of the first organic shell takes place during the early 'Trochophora' stage (Lacaze-Duthiers, 1856-58). Further construction leads to a clasp-like shell (Bandel, 1982). After 4-5 days in the plankton the larva metamorphoses and becomes benthonic (Lacaze-Duthiers, 1856-58). During metamorphosis the mantle margins and the still organic shell ventrally fuse into a tube. Subsequently, the shell is mineralised. The fumarium (in *Antalis tarentina*) forms immediately after metamorphosis. With further growth the larval

shell and later apical parts of the teleoconch are completely resorbed. This process may begin at a shell length of c. 1 mm.

Descriptions

Antalis tarentina (Lamarck, 1818)

(Pl. 1, figs. 1-2)

Recent, Mediterranean.

The larval shell of this specimen (Pl. 1, fig. 1; compare Bandel, 1982) is 370 μm long and has a diameter of 165 μm . The fumarium has a length of 100 μm and shows distinct growth lines. The posterior opening is oval and orientated obliquely with regard to the long axis of the larval shell. Thus, the ventral part of the fumarium is shorter than the dorsal one. The first 280 μm of the protoconch are almost smooth whereas the remaining 90 μm show growth lines. No constriction is present. The periostracum shows punctation (Pl. 1, fig. 2). The first 100 μm of the early teleoconch have no ornamentation except for growth lines.

The following shell bears c. 15 longitudinal ribs which increase in number, become fainter and finally disappear during the ontogeny. The final (late ontogenetic) teleoconch bears longitudinal ribs on its older apical half and is free of ribs on the younger apertural half. Apical and apertural cross sections are circular.

Entalinopsis sp.

(Pl. 1, figs. 3-4)

Early Pliocene (Zanclian), Le Puget-sur-Argens (France)

This specimen is a juvenile and could therefore not be identified specifically. The six prominent primary ridges and the flat, slightly concave, areas between them are characteristic for the genus *Entalinopsis* Habe, 1957. Several species, subspecies and varieties are known from the Pliocene (group of *Dentalium sexangulum* Schröter, 1784; see Sacco, 1897; Bellini, 1909; Cerulli-Irelli, 1910; Caprotti, 1979).

Plate 1.

Fig. 1. *Antalis tarentina* (Lamarck, 1818), Recent, Mediterranean, juvenile shell shortly after metamorphosis. Scale = 400 μm . Fig. 2. *Antalis tarentina* (Lamarck, 1818), Recent, Mediterranean, same specimen as fig. 1, magnified larval shell, showing periostracum punctation. Scale = 20 μm . Fig. 3. *Entalinopsis* (?) sp., Pliocene of Le Puget-sur-Argens, France, juvenile shell. Scale = 1 mm. Fig. 4. *Entalinopsis* (?) sp., Pliocene of Le Puget-sur-Argens, France, same specimen as fig. 3, protoconch. Scale = 200 μm . Fig. 5. *Entalinopsis* (?) sp., Miocene, Baden near Vienna (Austria), juvenile shell. Scale = 1 mm. Fig. 6. *Entalinopsis* (?) sp., Miocene, Baden near Vienna (Austria), same specimen as Fig. 6, with beginning resorption of the dorsal part of the protoconch. Scale = 200 μm . Fig. 7. *Entalinopsis* (?) sp., Miocene, Baden near Vienna (Austria), same specimen as figs. 5-6, view on the posterior opening. Scale = 100 μm . Fig. 8. *Dentalium* sp., Miocene, Baden near Vienna (Austria), juvenile shell. Scale = 2 mm. Fig. 9. *Dentalium* sp., Miocene, Baden near Vienna (Austria), same specimen as fig. 8, protoconch ventral view. Arrow indicates end of protoconch. Scale = 300 μm .

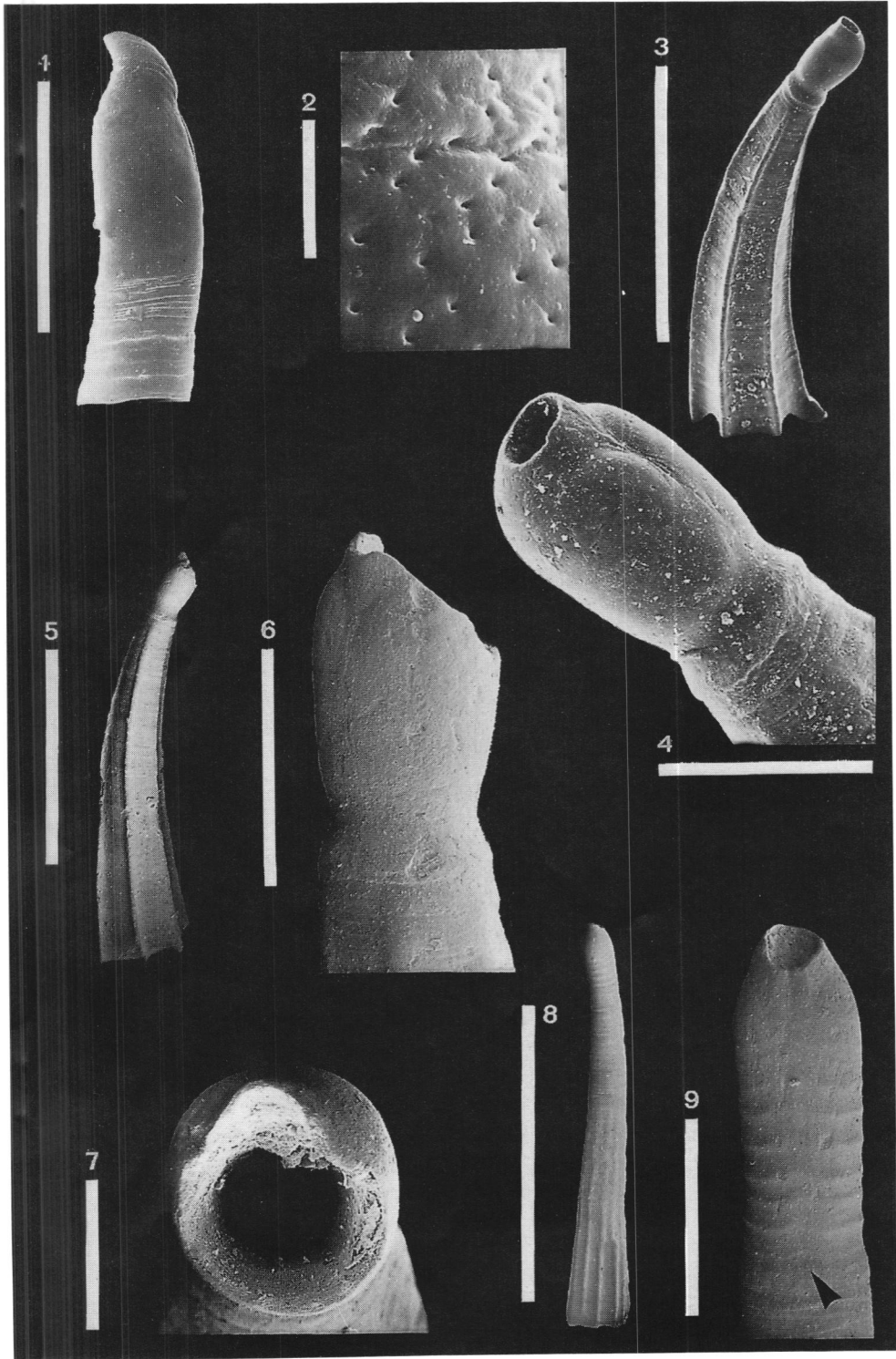


Plate 1

The specimen (Pl. 1, fig. 3) is 1.6 mm long and has a maximum diameter of 420 μm . The larval shell (Pl. 1, fig. 4) measures 290 μm in length, and 170 μm in diameter; 240 μm from its posterior end it is constricted to a diameter of 125 μm . Its surface is almost smooth, except for the suture area where a few wrinkles are present. The genae are strongly inflated and the fumarium is short.

The first 50 μm of the teleoconch are only covered by distinct growth lines before six prominent ridges appear.

Remarks — In his 'Supraspecific Classification of the Scaphopod Mollusca' Palmer (1974) outlines a hexagonal cross section for the genus *Paradentalium* Cotton & Godfrey, 1933. Cotton & Godfrey (1933) designated *Dentalium intercalatum* Gould, 1859 as type species. Cotton & Ludbrook (1938) pointed out that *Dentalium intercalatum* Gould, 1859 sensu Cotton & Godfrey, 1933 is identical with *Dentalium bednalli* Pilsbry & Sharp, 1897 and has nothing to do with Gould's species. Consequently, Palmer (1974) listed *Dentalium bednalli* Pilsbry & Sharp, 1897 as the type species. This case of a misidentified type species should be referred to the 'Commission' to ask for a ruling (Art. 70 ICZN). The cross section of '*Dentalium*' *bednalli* Pilsbry & Sharp, 1897 is, however, heptagonal and not hexagonal (see Pilsbry & Sharp, 1897-98).

Emerson (1962) synonymised *Entalinopsis* Habe, 1957 with *Entalina* Monterosato, 1872. The type species of *Entalina* is *Dentalium tetragonum* Brocchi, 1814 a scaphopod with a tetragonal anterior cross section and a pentagonal posterior cross section (see e.g. Rossi Ronchetti, 1956; Emerson, 1962). The type species of *Entalinopsis* is *Dentalium nivosum* Kuroda & Kikuchi, 1933 (= *Dentalium intercostatum* Boissevain, 1906) which shows, however, a hexagonal cross section anteriorly and posteriorly. We provisionally recognise *Entalinopsis* Habe, 1957 (Habe, 1954, 1977) as a valid genus.

Entalinopsis (?) sp.

(Pl. 1, figs. 5-7)

Middle Miocene (Badenian), Baden (Austria).

The specimen is 1.8 mm long (Pl. 1, fig. 5) and has a maximum diameter of 430 μm . The protoconch (Pl. 1, fig. 6) is 280 μm long with a maximum diameter of 170 μm . At a distance of 235 μm from the posterior end a strong constriction reduces the diameter to 130 μm . The larval shell bears no ornamentation. The suture is weakly developed, the genae are only slightly inflated. The fumarium is dorsally already partly resorbed (Pl. 1, fig. 7) leaving a rest of c. 25 μm in length. The six primary ribs start immediately after the beginning of the teleoconch.

There are probably two species of the genus *Entalinopsis* Habe, 1957 to be found in the Middle Miocene of Baden (cf. Hörnes, 1856). Since we have no intermediate sizes of shells to correlate juvenile and adult forms, a specific identification was not possible.

Dentalium sp. or *Fissidentalium* sp.

(Pl. 1, fig. 8-9)

Middle Miocene (Badenian), Baden (Austria).

The specimen (Pl. 1, fig. 8) reaches a total length of 3.3 mm, and the maximum diameter is 400 μm . The larval shell (Pl. 1, fig. 9) is 500 μm long with a maximum di-

iameter of 200 μm . The cross section is circular. The suture of the protoconch is clearly visible and extends throughout the entire length. The first 200 μm of the larval shell (measured from the posterior end) are smooth whereas the anterior part of the larval shell shows c. eight distinct circular annulations which are only interrupted by the suture. The diameter of the tube decreases slightly towards the anterior part of the protoconch before it increases again on the early teleoconch. A short wall around the posterior opening may indicate a fumarium which has already been resorbed. The early teleoconch (c. 600 μm) is covered by densely spaced growth lines. The remaining part shows ten strong longitudinal ribs.

The material is not sufficient to give a specific identification.

Antalis cf. *pseudofissura* Janssen, 1978
(Pl. 2, figs. 1-3)

Late Oligocene (Chattian), Glimmerode (Germany).

A juvenile specimen (Pl. 2, fig. 1) measures c. 1.2 mm in length and 280 μm in diameter. The cross section of the shell is circular. The protoconch (Pl. 2, fig. 2) is 430 μm long and has a maximum diameter of 180 μm . A fumarium adds c. 50 μm to the total length and measures 80 μm in diameter. Its ventral side is partly resorbed.

The diameter of the larval shell remains almost constant throughout its entire length. The first 200 μm are almost smooth except for very weak growth increments which demonstrate the stages of construction of the larval shell (Pl. 2, fig. 3, arrow). There are six circular annulations which increase in strength towards the anterior end of the protoconch.

The early teleoconch shows (besides growth lines) a very weak longitudinal striation. A similar striation can also be found on larger shells which are still circular in cross section. An apical ventral slit is constructed after the protoconch is resorbed (cf. Janssen, 1978).

Gadila turgida (Meyer, 1886)
(Pl. 2, fig. 4-5)

Palaeocene of Matthew's Landing (Alabama, USA).

Two of the available specimens are preserved with complete protoconchs and one with a rest of it. Several juvenile and adult shells could also be examined. A detailed

Table 1. Measurements (in μm) of *Gadila turgida* (Meyer, 1886) from the Palaeocene of Matthew's Landing.

	Juvenile		Protoconch		
	total length	maximum diameter	total length	maximum diameter	posterior opening
specimen 1	950	280	200	130	60
specimen 2	650	180	200	140	60
specimen 3	1220	280	?	?	(85)

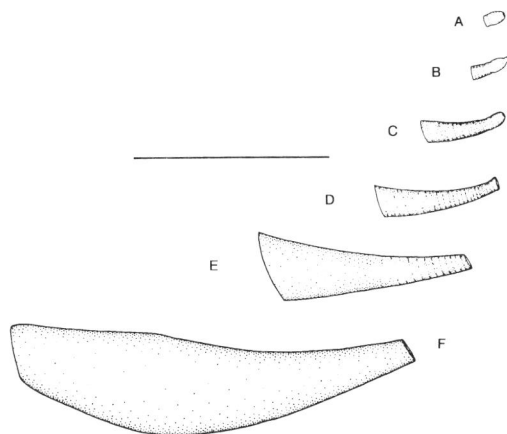


Fig. 2. Different growth stages of *Gadila turgida* (Meyer, 1886), Palaeocene, Matthews Landing (Alabama), with successive stages of resorption of the protoconch and the early teleoconch. Stage B, hypothetical. Scale = 2 mm.

comparison of all specimens allowed the reconstruction of the different ontogenetic stages of this species (Fig. 2).

The measurements of the protoconchs are compiled in Table 1. They have a marked constriction which reduces the diameter by c. 20 μm . The suture and the genae are poorly developed. Specimen 2 (Pl. 2, fig. 5) shows the sculpture of the periostracum (Pl. 2, fig. 4). A fumarium could not be observed. The early teleoconch is covered by growth lines which are slightly oblique to the long axis. The adult shell is smooth and glossy. The species has been listed by Palmer & Brann (1965) as *Gadila turgida* (Meyer, 1886).

Plate 2.

Fig. 1. *Antalis* cf. *pseudofissura* Janssen, 1978, Oligocene, Glimmerode (Germany), juvenile shell. Scale = 500 μm . Fig. 2. *Antalis* cf. *pseudofissura* Janssen, 1978, Oligocene, Glimmerode (Germany), same specimen as fig. 1, ventral side of protoconch. Scale = 300 μm . Fig. 3. *Antalis* cf. *pseudofissura* Janssen, 1978, Oligocene, Glimmerode (Germany), same specimen as figs. 1-2, suture and growth increments on genae (arrow). Scale = 100 μm . Fig. 4. *Gadila turgida* (Meyer, 1886), Palaeocene, Matthew's Landing (Alabama), juvenile shell, specimen 2. Scale = 300 μm . Fig. 5. *Gadila turgida* (Meyer, 1886), Palaeocene, Matthew's Landing (Alabama), sculpture of the periostracum, specimen 2. Scale = 20 μm . Fig. 6. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), protoconch of specimen 1, lateral view. Scale = 100 μm . Fig. 7. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), protoconch of specimen 1, ventral view. Scale = 200 μm . Fig. 8. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), apical opening showing shell resorption, specimen 7. Scale = 50 μm .

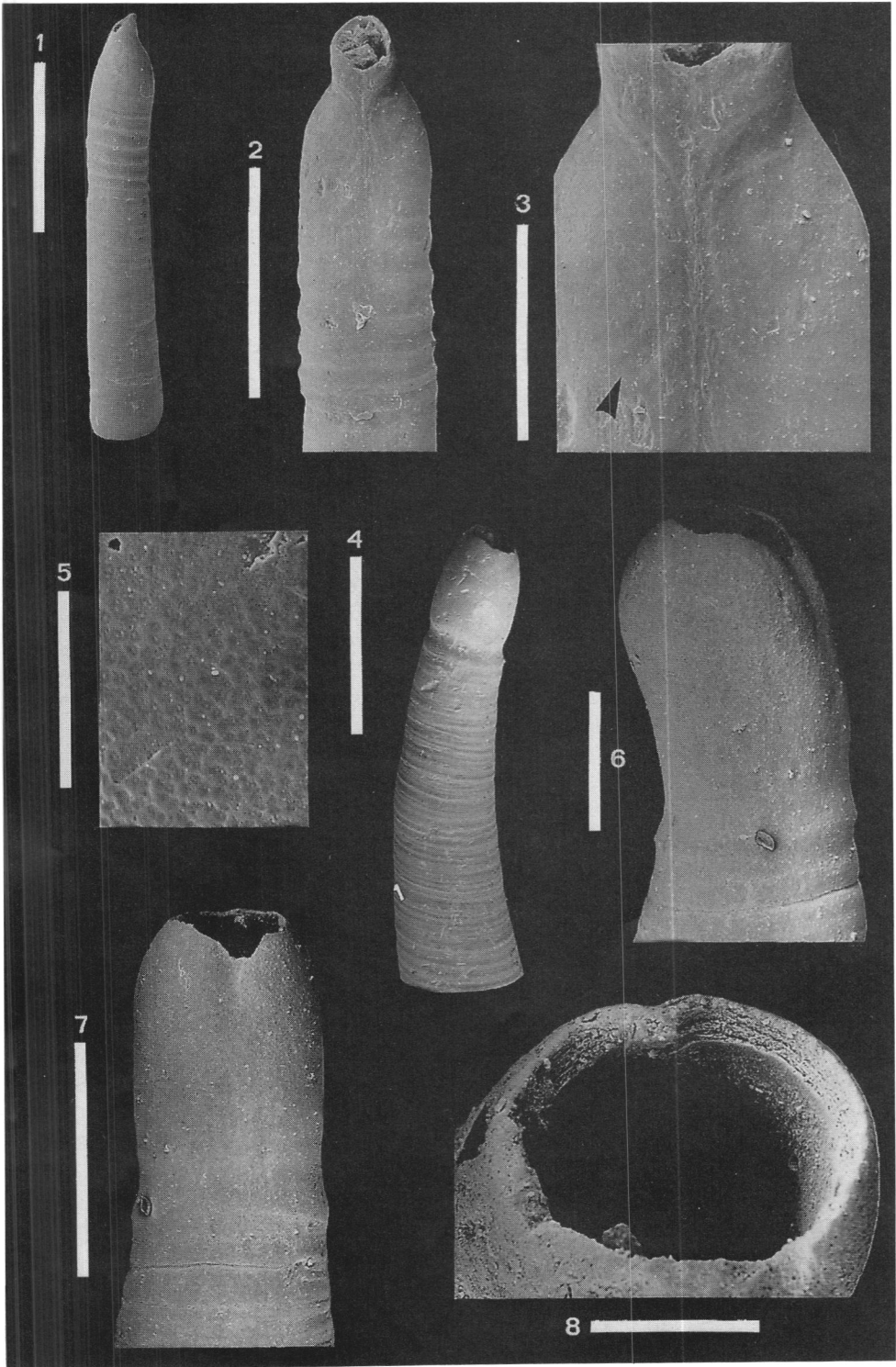


Plate 2

Table 2. Measurements (in μm) of '*Laevidentalium*' sp. from the Dogger beta (Late Aalenian) of Hambühren

	Juvenile		Protoconch		
	total length	maximum diameter	total length	maximum diameter	posterior opening
specimen 1	1000	250	270	150	75
specimen 2	1250	320	270	150	65
specimen 3	930	260	250	140	75
specimen 4	1170	350	300	140	75
specimen 5	1050	310	260	140	75
specimen 6	1250	320	270	135	65
specimen 7	950	280	220	120	90

'Laevidentalium' sp.
(Pl. 2, figs. 6-8; Pl. 3, figs. 1-3)

Dogger beta (Late Aalenian), Hambühren (Germany).

We have seven juvenile specimens with protoconchs at our disposal. The measurements are given in Table 2. The surface of the protoconch (Pl. 2, figs. 6-7) is generally smooth but in the region of the suture the shell is slightly wrinkled. The suture is clearly visible, the genae are moderately inflated. There is no fumarium at the posterior end of the protoconch but resorption can be recognised (Pl. 2, fig. 8) and some specimens display a very low wall around the circular posterior opening (Pl. 3, figs. 1-2). Length axes of protoconch and teleoconch form a slight angle with each other. The early teleoconch is covered by close-set annulations only (Pl. 3, fig. 3).

Plate 3.

Fig. 1. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), ventral view showing the suture, arrow points to possible rest of the fumarium, specimen 2. Scale = 200 μm . Fig. 2. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), apical opening, specimen 2. Scale = 200 μm . Fig. 3. '*Laevidentalium*' sp., Dogger beta (Late Aalenian), Hambühren (Germany), juvenile shell, specimen 1. Scale = 500 μm . Fig. 4. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), holotype, lateral views, fragmentary teleoconch. Scale = 3 mm. Fig. 5. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), Paratype 1, juvenile shell. Scale = 400 μm . Fig. 6. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), Paratype 2, juvenile shell. Scale = 500 μm . Fig. 7. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), Paratype 3, incomplete teleoconch. Scale = 3 mm. Fig. 8. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), Paratype 4, incomplete teleoconch. Scale = 3 mm. Fig. 9. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), Paratype 5, incomplete teleoconch. Scale = 3 mm. Fig. 10. *Suevidontus jaegeri* gen. et sp. nov., Dogger zeta (Middle Callovian), Plettenberg near Dotternhausen (southern Germany), protoconch with juvenile shell, arrow points to longitudinal lirae, specimen 3. Scale = 200 μm .

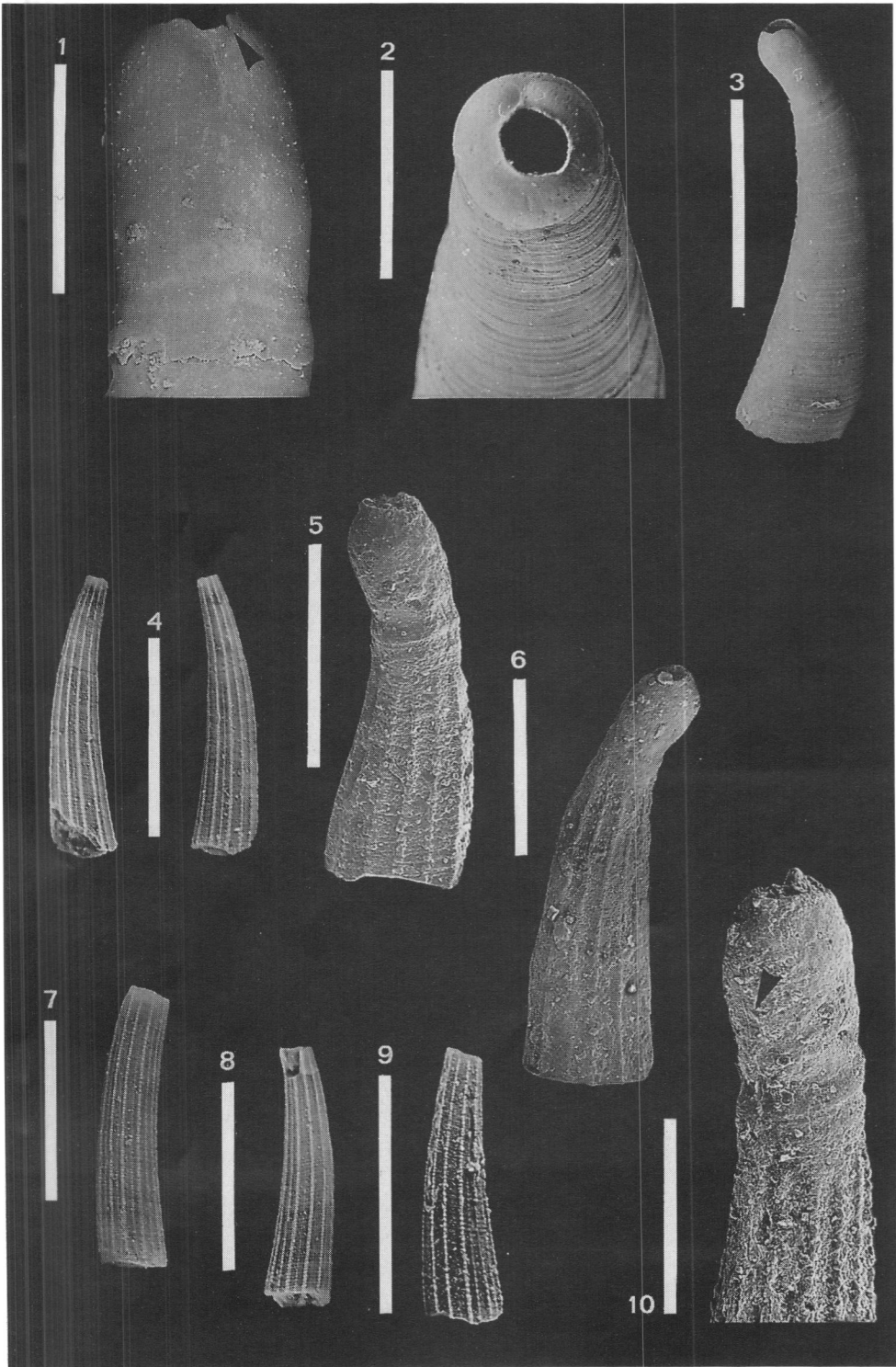


Plate 3

Remarks — We did not find a description of this species in the literature. Quenstedt (1856-57, 1881-84) mentioned the occurrence of scaphopods in the Dogger beta of southern Germany. He gave only a brief description and very small figures. According to his short descriptions the adult shells are smooth. The specimens were left in open nomenclature by Quenstedt (1856-57, 1881-84).

Whether or not our specimens really belong to *Laevidentalium* Cossmann, 1888 is unclear. The type species of *Laevidentalium* is an Eocene fossil whose early ontogenetic development is completely unknown. Its teleoconch is smooth and the cross section is circular. These simple characters may have been developed several times independently from ribbed or annulated species and *Laevidentalium* may therefore be a polyphyletic taxon.

The larval shell of specimen 7 is significantly smaller and the posterior opening much wider. The general form of this protoconch is the same as in the other specimens. It may represent a different species of the same genus. Alternatively it could be interpreted as a specimen of the same species which developed from an egg with a lower yolk content.

Suevidontus gen. nov.

Type species — *Suevidontus jaegeri* gen. et sp. nov.

Diagnosis — A small moderately curved scaphopod with c. 12 longitudinal sharp ridges in juvenile specimens. The number of ridges may increase due to the intercalation of weaker secondary ridges during the ontogeny. No slit or notch at the posterior end is known. The increase in shell diameter is moderate. The protoconch is comparatively small (less than 300 µm), bears c. 20 longitudinal lirae and has a marked constriction at the anterior end.

Differences — *Prodentalium* Young, 1942 has a much higher number of much weaker ridges (more than 20). *Fissidentalium* Fischer, 1885 is characterised by numerous and comparatively strong ribs, and a fissure at the apical end of the conch. *Paleodentalium* Gentile, 1974 is distinguished by c. 15 primary, acute ribs which gradually diminish towards the anterior end of the shell. *Dentalium* Linnaeus, 1758 is characterised by 9-11 primary, strong ribs and a polygonal cross section. The larval shells of *Prodentalium*, *Fissidentalium* and *Paleodentalium* are unknown.

Remarks — The familiar attribution is left open for the moment. The general form and the ornamentation suggests a representative of the family Dentaliidae Gray, 1847. However, the protoconch is different (compare *Antalis*, Pl. 1, fig. 1). Shape and sculpture of the teleoconchs must then have been developed convergently (see also discussion below). A very similar protoconch is found in *Baltodentalium weitschati* Engeser & Riedel, 1992, but the teleoconch of that species is very different.

Suevidontus jaegeri gen. et sp. nov.

(Pl. 3, figs. 4-10)

Derivatio nominis — Named in honour of the palaeontologist Dr Manfred Jäger (Dotternhausen) who found the horizon with scaphopods and provided us with a sample.

Holotype — GPIMH no. 2834, Pl. 3, fig. 4

Paratypes — GPIMH no. 2835-2839, Pl. 3, figs. 5-8.

Type locality — Temporary outcrop, Plettenberg near Dotternhausen, c. 40 km south of Stuttgart (southern Germany).

Type level — 'Ornaton-Ton' (*coronatum* or *jason* Zone), Dogger zeta, Middle Callovian, Late Middle Jurassic.

Diagnosis — A small (up to 1 cm long) species with 12 primary longitudinal ridges. The number of ridges may increase to a maximum of 24 during ontogeny by intercalation of weaker secondary ridges. The increase in diameter is moderate (maximum c. 1.2-1.3 mm). The protoconch measures c. 280 μm in length.

Description — The measurements are compiled in Table 3. The specimens are strongly recrystallised and most have become flattened laterally, making an estimation of diameter and cross section difficult. We therefore give largest and smallest diameters.

The protoconch bears c. 20 longitudinal lirae (Pl. 3, fig. 10, arrow). A constriction near the apertural end of the larval shell is well pronounced. A posterior opening is visible but the preservation of the material does not allow to observe more details (e.g. about a fumarium).

The teleoconch almost immediately starts with 12 longitudinal ridges. The number of ridges in larger specimens (which we assume to be adult shells) increases up to 24 by intercalation of 12 weaker secondary ridges. The adult length has been extrapolated from fragments and their diameter.

Differences — See under the genus.

Baltodentalium weitschati Engeser & Riedel, 1992

(Fig. 3)

Middle Liassic erratic boulders, Hoisbüttel (Germany).

The general shape of the protoconch is bullet-like (Fig. 3). It has a length of 250 μm , the diameter reaches c. 130 μm . The larval shell is covered by c. 20 longitudinal lirae, arranged in more or less regular distances. The posteriormost part around the opening is free of lirae. At the ventral side (where the suture has to be assumed) three lirae are more distant from each other. Some of the lirae bifurcate at their posterior part. It was not possible to determine exactly the width of the posterior opening but it is relatively small (maximum 30 μm). There are no traces of a wall or pipe

Table 3. Measurements (in μm) of *Suevidontus jaegeri* gen. et sp. nov. from the Dogger zeta (Middle Callovian) of Plettenberg

	Juvenile total length	maximum diameter	Protoconch total length	maximum diameter
paratype 1	680	230/145	280	150/95
paratype 2	1150	350/185	280	170/115
specimen 3	1000	320/165	280	190/95

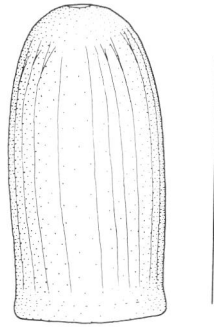


Fig. 3. *Baltodentalium weitschati* Engeser & Riedel, 1992, Pliensbachian, erratic boulders, northern Germany, protoconch. Scale = 200 μm .

around it. The shell of the protoconch is c. 20 μm thick. The teleoconch has an approximately pentagonal cross section.

Remarks — This species has already been described in more detail in a previous paper by Engeser & Riedel (1992).

Comparison with other specimens

In the literature we found only eight species where the more or less complete larval shell has been figured. These are in the studies of Sars (1864), Kowalevsky (1883), Henderson (1920), Bandel (1982), MacNeil & Dockery (1984), and Ruggieri (1987). We briefly review these specimens.

Sars (1864) gave a rough draft of a juvenile *Siphonodentalium pentagonum* Sars, 1864 [= *Entalina tetragona* (Brocchi, 1814)]. The protoconch is not annulated and more or less bulbous. The dimensions are not quite clear because he gives controversial magnifications for the two figures.

Kowalevsky (1883) intended to complete the developmental studies of Lacaze-Duthiers (1856-1857) but examined a different (Mediterranean) species. The larval shell is 360 μm long with a maximum diameter of c. 160 μm . Size and shape of the protoconch are very similar to *Antalis tarentina* (Lamarck, 1818) (see descriptions).

The specimen of the Recent *Dentalium laqueatum* Verrill, 1885 described by Henderson (1920) measures 1.4 mm in length and has a diameter of 200 μm at the anterior end. The protoconch is not clearly demarcated. It measures c. 440 μm in length. The posterior part has a diameter of 150 μm and a length of 220 μm . The following part of the protoconch gradually decreases in diameter (to 110 μm). The anterior part of the bulbous and the slender part are covered by c. 20 strong annulations which terminate with the beginning of the juvenile shell. The fumarium has a length of 65 μm and a width of 75 μm at the base. According to Henderson (1920) the early teleoconch has a circular apical cross section which becomes polygonal in later ontogeny. The specimen has 10 or 11 primary ribs. The number of primary ribs and the cross section correspond to the diagnosis of the genus *Dentalium* Linnaeus, 1758 given by Palmer (1974). However, the early ontogeny of the type species of *Dentalium*, *D. elephantinum* Linnaeus from

the Philippines is unknown and the generic attribution remains doubtful.

MacNeil & Dockery (1984) figured SEM photographs of two juvenile specimens with preserved larval shells from the Oligocene of Mississippi. They are shortly described but no measurements are given. The following measurements were extracted from the figures. The specimen of '*Dentalium*' *zephyrinum* Casey, 1903 has a length of 1.5 mm and a maximum diameter of 240 μm . The protoconch measures 400 μm with a maximum diameter of 160 μm . The first 160 μm are smooth followed by nine circular annulations which account for the remaining 240 μm . A fumarium adds 60 μm to the total length and has a diameter of 80 μm . C. 100 μm of the early juvenile shell show distinct growth lines only. On the remaining part of the juvenile shell they are crossed by c. 16 longitudinal ridges which steadily increase in strength towards the aperture. The generic attribution of this species is unclear. The type species of *Dentalium*, *D. elephantinum* Linnaeus, 1758 is a Recent East Asian species (Pilsbry & Sharp 1897-98). The adult shell is characterised by a polygonal cross section and by 9 to 11 strong longitudinal ribs. The interval between the ribs are broader than the ribs themselves. The larval shell and the early teleoconch are unknown. Unfortunately MacNeil & Dockery (1984) did not mention the cross section of '*Dentalium*' *zephyrinum* Casey, 1903. It is therefore impossible to attribute '*D.*' *zephyrinum* to a certain genus.

The second specimen described by MacNeil & Dockery (1984) belongs to the species '*Dentalium*' *polygonuum* Casey, 1903. The larval shell is 400 μm long and has a diameter of 150 μm . The smooth part of the protoconch measures 140 μm . The remaining part shows eight distinct annulations. A fumarium is not present. The first 200 μm of the teleoconch are smooth except for growth lines. The seven primary ribs set on after this interval and the cross section becomes heptagonal. On the later teleoconch the intervals between the seven primary ribs show two to four finer threads. The adult shell becomes smooth again at the anterior end. According to the figures and description given by MacNeil & Dockery (1984) '*Dentalium*' *polygonuum* fits in the diagnosis of the genus *Paradentalium* Cotton & Godfrey, 1933 which has a heptagonal cross section. This generic name was erroneously used by Palmer (1974) for scaphopods with a hexagonal anterior cross section.

Ruggieri (1987) described 3 specimens with preserved protoconchs of '*Dentalium* *rectum* Gmelin' from Lower Pleistocene (Emilian) deposits of Sicily (Italy). One protoconch measures 800 μm in length and has a maximum diameter of 250 μm . The posterior part (c. 270 μm) is smooth, the anterior part (530 μm) bears c. 10 strong annulations. A fumarium is 100 μm long. The second protoconch measures 730 μm with a maximum diameter of 230 μm . The anterior part shows three to four strong annulations. This larval shell has a posterior smooth part with a length of 400 μm and an annulated part of 330 μm . A fumarium is already resorbed but still 90 μm long.

We doubt Ruggieri's identification of these specimens with '*Dentalium*' *rectum* for several reasons. The specimens illustrated by the author belong to at least two different species (see above measurements). Moreover, '*D.*' *rectum* Gmelin, 1788 represents a species living in the Indian Ocean (Pilsbry & Sharp, 1897-98). It seems unlikely that this species lived in the Mediterranean during the Early Pleistocene and became extinct in the Late Pleistocene or Holocene. Ruggieri (1987) did not figure a teleoconch which could be compared with '*Dentalium*' *rectum*. Moreover, this species does not belong to *Dentalium* s.str. because it has a circular cross section and more ribs.

Discussion

The classification of the Scaphopoda has been revised several times during the last hundred years (Simroth, 1894; Pilsbry & Sharp, 1897; Hoffmann, 1930; Emerson, 1962; Habe, 1964; Palmer, 1974; Starobogatov, 1974; Scarabino, 1979; Steiner, 1992). The larger systematic units (orders) are usually based on different morphologies and functions of the feet. The radula and mantle anatomy (e.g. Steiner, 1991, 1992) together with shell characters (e.g. Palmer, 1974) are used to organise the family level. In most cases teleoconch characters define a genus or a species. A certain species is thus usually determined by its (adult) shell and anatomical data are added to give a better definition of this species.

The data presented in this paper show that shells of early ontogenetic stages can be used to discover convergence of the teleoconch. At least two protoconch types are developed: a short one (200-290 μm) which is more or less bulbous and becomes constricted shortly before metamorphosis is finished, as documented for *Baltodentalium*, *Entalinopsis*, *Gadila*, *Siphonodentalium*, and *Suevidontus* gen. nov., and a long one (360-800 μm) with its anterior part more or less annulated, as found in *Antalis*, *Dentalium*, *Paradentalium*, and another Recent dentaliid scaphopod from the Mediterranean which is not described in the text (Fig. 4).

The two types of protoconchs indicate differences in developmental patterns. A 'long' (annulated) larval shell does not necessarily mean that planktotrophy occurs but the larvae probably have a much longer free-swimming phase (also indicated by the developmental studies of Lacaze-Duthiers, 1856-58) compared to the species bearing 'short' (constricted) protoconchs.

The importance of fossil scaphopod protoconch characters can be demonstrated for *Suevidontus* gen. nov. This genus has a teleoconch which fits in the diagnosis of the Dentaliidae given by Palmer (1974). The larval shell, however, indicates that *Suevidontus* belongs to a different taxon.

Aside from the larval and the adult shell the juvenile conch is also of some importance. It can bear ornamentations which may not be found on the later adult shell and these 'early' parts of the teleoconch are usually resorbed during ontogeny like the protoconch; i.e. a smooth adult shell may have had a smooth or a sculptured early juvenile shell.

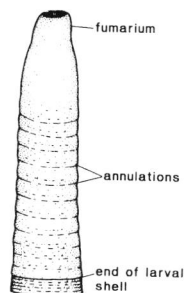


Fig. 4. Recent dentaliid scaphopod shell, presumably shortly after metamorphosis, dredge sample off Banyuls-sur-Mer (southern France). No scale.

Another useful character to separate taxa seems to be the different ontogenetic level at which a scaphopod starts to resorb its posterior shell and to which extent. The Miocene *Dentalium* sp. from Baden still bears a complete protoconch at a shell length of 3.3 mm while the Palaeocene *Gadila turgida* begins to resorb the larval shell at a total length of c. 1.1 mm.

One consequence of our data is that most scaphopod genotypes have to be restudied with regard to the morphology of the early ontogenetic shells before they can be utilised in palaeontology. Moreover, it should be tried to find the protoconchs of fossil genotypes at the type localities. We propose that in future holotype and paratypes should include shells of different ontogenetic stages.

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