Scaphopods from Middle Liassic erratic boulders of northern Germany; with a review on Liassic Scaphopoda

T. Engeser & F. Riedel

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Three new scaphopod species, one new genus and one new family (*Prodentalium bandeli* sp. nov., *Baltodentalium weitschati* gen. & sp. nov., *Progadilina spaethi* sp. nov., Baltodentaliidae fam. nov.) are described from erratic boulders ('Ahrensburger Geschiebe') of Hoisdorf, northern Germany. The ammonoids indicate a Late Pliensbachian (Domerian, *spinatus*-zone) age. Four preoccupied scaphopod specific names are replaced by new names: *Dentalium richardsoni* Emerson, 1954 non Cossmann, 1907, from the Early Jurassic of England, by '*Dentalium*' *sabrinae* nom. nov.; *Dentalium arctoides* var. *multicostata* Gugenberger, 1934 non Favre, 1869, from the Triassic of Austria, by *Prodentalium angelae* nom. nov.; *Dentalium sublaeve* Hall in Miller, 1877 non Cocconi, 1873, from the Carboniferous of Illinois, U.S.A., by *Prodentalium fredericae* nom. nov.; and *Dentalium robustum* Maurer, 1885 non Brazier, 1877, from the Devonian of Germany by *Laevidentalium patriciae* nom. nov. The protoconch of *Baltodentalium weitschati* gen. & sp. nov. is compared with the protoconch of Recent *Antalis* sp. from the Mediterranean. The shell structure of several species is documented.

Key words: Liassic - review - new species - shell structure - protoconch.

T. Engeser & F. Riedel, Geologisch-Paläontologisches Institut und Museum, University of Hamburg, Bundesstr. 55, D-2000 Hamburg 13, F.R.G.

Introduction

Fossil Scaphopoda are a poorly known mollusk group. The last comprehensive study, a mere listing of species, dates back almost one hundred years (Pilsbry & Sharp, 1897-98). Comparably well known are the Liassic Scaphopoda through the study of Richardson (1906), who described all species under the generic name *Dentalium*. They can, however, no longer be attributed to the genus *Dentalium* Linnaeus, 1758 s. str., which has a stratigraphic range from Miocene to Recent (Palmer, 1988) or from the Late Cretaceous (?) to Recent (according to our own investigations). All Liassic species are therefore briefly reviewed.

The systematics of the Scaphopoda is mainly based on teleoconchs. There are few data about the soft part anatomy. Larval shells are not yet used for systematics. A search in the literature revealed only a few studies which illustrate protoconchs (MacNeil & Dockery, 1984; Ruggieri, 1987). We describe here, for the first time, the protoconch of a Jurassic species, which indicates that the sculpture and ornamentation of the protoconch might be of systematic importance.

MATERIAL, METHODS AND STRATIGRAPHY

The specimens studied were found in erratic boulders from Hoisdorf near Ahrensburg (Schleswig-Holstein, northern Germany). The erratic boulders contain an assemblage of gastropods, bivalves, belemnoids and ammonoids. The latter indicate a Late Pliensbachian (Domerian, *spinatus* Zone) age. The erratic boulder was broken up into small pieces which could then be examined with the SEM, the specimens were coated with gold.

Acknowledgements

Professor K. Bandel (Hamburg) gave information in stimulating discussions on the early ontogeny of scaphopods. Dr P. Ward (Edinburgh, temporarily Hamburg) made this publication readable. Dr W. Weitschat (Hamburg) gave us the erratic boulder material for further study. He also discovered the holotype of *Baltodentalium weitschati*. We are very grateful to these three colleagues.

Review of Liassic Scaphopoda

Richardson (1906) described 16 species from the Liassic under the generic name *Dentalium* Linnaeus, 1758. None of the species, however, can be attributed to *Dentalium* s. str., which is a Miocene to Recent genus (Palmer, 1988). All species are briefly discussed and their generic affinities indicated where possible. It must be noted that the generic assignments were made from figures only. The list of Liassic scaphopods may be incomplete because not all scaphopod studies could be checked. It must also be considered that in most cases the shell structure of these scaphopods is unknown and therefore it cannot be fully excluded that confusion with serpulid tubes has occurred.

Dentalium acutum Richardson, 1906 (non *Dentalium acutum* Hébert, 1849) = *Laevidentalium richardsoni* (Cossmann, 1907)

The holotype of this species originates from the Pliensbachian of western England. The specific name is preoccupied by *Dentalium acutum* Hébert, 1849. It was renamed *Dentalium richardsoni* by Cossmann (1907). This nomenclatorial action was apparently overlooked by Emerson (1954) who proposed the name *Dentalium acutoides* as a replacement name which is therefore a younger, objective synonym of *Dentalium richardsoni* Cossmann, 1907. According to Richardson (1906) the species shows only extremely fine transverse lineae (probably growth lines). The section is circular or only slightly elliptical. The lack of ornamentation and the circular cross section places the species in the genus *Laevidentalium* Cossmann, 1888.

'Dentalium' angulatum Buckman, 1844

The type horizon and the type locality is the Pliensbachian of Gloucestershire, England. The surface shows transverse rugae, the cross section is obtusely quadrangular. The holotype could not be studied by Richardson (1906). The description does not correspond with any known scaphopod genus.

Dentalium elongatum von Münster in Goldfuss, 1841 = *Laevidentalium elongatum* (von Münster in Goldfuss, 1841)

The holotype probably comes from the Pliensbachian of Banz (Franconia, Germany). Apart from fine growth lines there is no ornamentation. The cross section is circular. It can therefore be attributed to *Laevidentalium* Cossmann, 1888. In many papers the publication date of *'Dentalium' elongatum* is wrongly stated as 1844 (for publication dates of Goldfuss, 1841-44, see W. Quenstedt, 1963).

Dentalium etalense Terquem & Piette, 1865 = *Laevidentalium etalense* (Terquem & Piette, 1865)

The holotype of this species derives from the Hettangian of eastern France. The specimens are entirely smooth with a circular cross section and therefore belong to *Laevidentalium* Cossmann, 1888. Nagy (1970) placed it in the subgenus *Dentalium (Antalis)* Adams & Adams, 1854. However, the latter genus is characterised by a striated posterior part of the shell.

Dentalium giganteum Phillips, 1829 = *Laevidentalium giganteum* (Phillips, 1829)

The holotype was found in marls of Pliensbachian age in Yorkshire. It is probably the largest Liassic scaphopod (c. 8 cm). The surface is smooth and the cross section is circular. The species is attributed to *Laevidentalium* Cossmann, 1888.

'Dentalium' hexagonale Richardson, 1906

The holotype comes from the Sinemurian/Pliensbachian boundary beds. The surface of the shell shows closely set, regular, fine, transverse growth lines. The cross section is exteriorly hexagonal; interiorly circular. The features described and figured by Richardson (1906) do not coincide with the diagnosis of any known scaphopod genus.

Dentalium liassicum Moore, 1865 = *Prodentalium? liassicum* (Moore, 1865)
The species was found in the Pliensbachian of Somerset, England. It is ornamented with 24 longitudinal ridges at irregular distances to each other. The species has been attributed to *Prodentalium* Young, 1942 (Palmer, 1975) although this genus is characterised by numerous longitudinal striae (50 or more) and transverse undulations which gives the ornamentation a zigzag alignment.

Dentalium limatulum Tate, 1870 = *Baltodentalium limatulum* Tate, 1870
The type horizon and the type locality is in the Sinemurian of Shropshire, England. The species shows a pentagonal cross section and closely set, slightly oblique and acute circular costae on the outer surface. It is attributed to *Baltodentalium* gen. nov. (see below).

Dentalium minimum Buckman, 1844 = *Laevidentalium minimum* (Buckman, 1844)
The species is from the Hettangian of southern England. The surface of the shell is entirely smooth and its cross section is circular. It can therefore be placed in *Laevidentalium* Cossmann, 1888.

'*Dentalium*' *oblongum* Richardson, 1906
The type horizon and type locality of this species is the Pliensbachian of Cheltenham, western England. The cross section is quadrangular interiorly and exteriorly at the anterior end. At the posterior end, the angles are acute with prominent ridges. The surface ornamentation shows numerous fine transverse lineae. This species cannot be attributed to any known scaphopod genus and therefore a new genus should be proposed.

Dentalium parvulum Richardson, 1906 (non *Dentalium parvulum* Philippi, 1887) = *Laevidentalium subparvulum* (Emerson, 1954)
The holotype is from the Pliensbachian of Cheltenham. The surface is smooth except for very fine and closely set transverse growth lines. The cross section is circular. This species has been renamed *Dentalium subparvulum* by Emerson (1954), because of a primary homonymy with *Dentalium parvulum* Philippi, 1887. It can be assigned to *Laevidentalium* Cossmann, 1888.

Dentalium subovatum Richardson, 1906 = *Progadilina subovata* (Richardson, 1906)
'*Dentalium*' *subovatum* can be attributed to *Progadilina* due to the distinctive trigonal cross-section and ornamentation (circular lirae and striae). The holotype comes from the Hettangian of Yorkshire, England.

Dentalium subquadratum Richardson, 1906 (non *Dentalium subquadratum* Meek, 1869) = '*Dentalium*' *sabrinae* nom. nov. (see below)
The holotype is from the Sinemurian of southern England. The shell is small, slightly curved and thin. The cross section is subquadrate exteriorly and interiorly. The posterior portion is more angular than the anterior part. At the posterior portion the dorsal

side is also slightly broader than the other sides which results in a subtrapezoidal cross section. The surface is smooth. The generic assignment is unclear. It probably belongs to a new genus (compare also '*Dentalium*' *oblongum* Richardson, 1906).

Dentalium subtrigonale Richardson, 1906 = *Progadilina subtrigonalis* (Richardson, 1906)

The holotype is from the Pliensbachian of Cheltenham, western England. The cross section is subtrigonal exteriorly and circular to subovate interiorly. The surface ornamentation consists of fine, oblique transverse lineae. Because of its triangular cross section and its ornamentation it can be attributed to the genus *Progadilina* Palmer, 1974.

Dentalium trigonale Moore, 1867 = *Progadilina trigonalis* (Moore, 1867)

This species comes from the Pliensbachian of Somerset, England. The shell is triangular in cross section and displays an ornamentation consisting of circular striae and lirae. It is the type species of the genus *Progadilina* Palmer, 1974 (see discussion there).

'*Dentalium*' *terquemi* Richardson, 1906 - a nomen dubium

The validity of this species, which was never figured, is questioned. The holotype was found in the Hettangian of eastern France by Terquem & Piette (1865). It was very briefly described and determined as *Dentalium giganteum* Phillips, 1829. Richardson (1906) pointed out that it is not identical with that species and named it *Dentalium terquemi*. According to Terquem & Piette (1865) the surface is covered by 'numerous, very fine and closely set striae' (longitudinal or circular?). In absence of a more detailed description and a figure, it is regarded here as a nomen dubium.

Further reports of Liassic scaphopods

Roemer (1836) reported a '*Dentalium cylindricum* Sowerby, 1814' from the Late Liassic of Germany. It is certainly not identical with '*Dentalium*' *cylindricum* of Sowerby, which is a Cretaceous species. From the description it is clear that the species belongs to the genus *Laevidentalium*.

Quenstedt (1856-57) reported a '*Serpula*' *triedra* from the Pliensbachian of southern Germany, the cross section being triangular and the surface smooth (?). He later suspected that the fossil could be a scaphopod. Richardson (1906) questionably regarded it as a synonym of '*Dentalium*' *trigonalis* Moore. If this synonymization is correct, the valid name of this species would be *Progadilina* (or *Gadilina*) *triedra* (Quenstedt, 1857). He also mentioned a *Dentalium angulati* from the Hettangian of southern Germany. Pilsbry & Sharp (1897-98) regarded it a nomen nudum. It therefore never entered the subsequent literature. It is apparently a *Laevidentalium* species (compare remarks in Quenstedt, 1856-57).

A further study that was probably never cited in subsequent scaphopod literature is Quenstedt (1881-84) in which the author proposed several new species (mostly Tertiary species). He figured several indeterminate species from the Liassic.

Dentalium compressum d'Orbigny, 1850 is based on a very short description without a figure. It was therefore subject of speculations and misidentifications (e.g. Terquem, 1855) and was even dismissed by Richardson (1906) as a probable 'tubicolous annelid'. Boule (1908) validated the species by giving a description and a figure. The cross section is elliptical with a slight carina on the concave dorsal side. The surface is completely smooth. It is probably attributable to *Laevidentalium* Cossmann, 1888. Locality and exact age (probably Middle Liassic of northeastern France) were not given.

Brauns (1869) gave descriptions (no figures) of *Dentalium etalense* Terquem & Piette, 1865 and *Dentalium giganteum* Phillips, 1829. From the descriptions it is clear that different species are concerned.

A short description of *Dentalium etalense* Terquem & Piette, 1865 can be found in Stoll (1940) and a more detailed description with figures of *Dentalium trigonale* Moore, 1867 (= (?) *Progadilina subtrigonalis* Richardson, 1906).

In general, the studies of Engel (1890, 1891) have been overlooked. Whereas in 1890 the *Dentalium amalthei* from the Middle Liassic of southern Germany is a nomen nudum, the species is validated in 1891 by a figure and a short description. It can be referred to *Laevidentalium.*

Malling & Grönwall (1909) gave a very short description of a *Dentalium* sp. from the Liassic of Bornholm. The reference of Moberg cited in this paper could not yet be checked.

Kuhn (1936) gave a description of *Dentalium elongatum* von Münster with some critical remarks on previous determinations, and a *Dentalium* sp. nov. cf. *entaloides* Phillips from the Pliensbachian of Franconia, Germany. According to Kuhn (1936) the second species is small and strongly curved, and has narrow-set annular ridges on the surface. This ornamentation corresponds with the ornamentation of the most posterior part of several *Laevidentalium* species from the Jurassic (see also discussion under *Laevidentalium*). It is unclear whether this feature merits a generic distinction.

More references dealing with Liassic scaphopods can be found in Richardson (1906).

New names for preoccupied scaphopod species

Some 1000 species, subspecies and varieties have been described under the generic name *Dentalium* and which compete for priority. It is therefore no surprise that there exist about a 130 preoccupied names. Although Pilsbry & Sharp (1897-98), Emerson (1954) and Palmer (1974) renamed a lot of preoccupied scaphopod species there are still several unrecognized homonyms. Some of these preoccupied names are replaced herein by new names.

Dentalium subquadratum Richardson, 1906 is preoccupied by *Dentalium subquadratum* Meek, 1860. The replacement name *Dentalium richardsoni* proposed by

Emerson (1954) is again preoccupied by *Dentalium richardsoni* Cossmann, 1907. There exists no younger synonym (see also Emerson, 1954). We propose herein *Dentalium sabrinae* nom. nov. to replace the preoccupied *Dentalium richardsoni* Emerson, 1954. It is named after Sabrina Crafton (Hamburg), collaborator in our mollusk projects.

Dentalium sublaeve Hall in Miller, 1877 from the Carboniferous of Iowa, USA, is a replacement name for *Dentalium obsoletum* Hall, 1858. However, this name is again preoccupied by *Dentalium dentalis* var. *sublaevis* Cocconi, 1873. *Dentalium sublaeve* Hall in Miler, 1877 is regarded as a valid species by Démanet (1943) and Forney & Nitecki (1976). There is no younger synonym available and it is therefore replaced herein by *Prodentalium fredericae* nom. nov., named after Frederike Stichert (Hamburg), collaborator in our mollusk group.

Dentalium ? *arctoides* var. *multicostata* Gugenberger, 1934 from the Middle Triassic of Carinthia, Austria is preoccupied by *Dentalium multicostatum* Favre, 1869. We found no younger synonym in the literature. From the figures and descriptions of Gugenberger (1934) it is obvious that *Dentalium* ? *arctoides* var. *multicostata* Gugenberger, 1934 is different from the other scaphopods described from this locality. The preoccupied name is therefore replaced by *Prodentalium angelae* nom. nov., named after Angela Engelhardt (Hamburg), collaborator in our mollusk projects.

Dentalium robustum Maurer, 1885 from the Middle Devonian of Germany is preoccupied by *Dentalium robustum* Brazier, 1877, a Recent species. It is also not listed in Pilsbry & Sharp (1897-98). There is only one further *Laevidentalium* species in the Middle Devonian, *Laevidentalium antiquum* (Goldfuss, 1841). The holotype of this species (collection Paläontologisches Institut der Universität Bonn) could be investigated. The shell of this species is strongly curved and the growth lines are comparably coarse whereas the teleoconch of '*Dentalium*' *robustum* Maurer is straight and the surface is smooth. A younger synonym is definitely not available. We propose herein *Laevidentalium patriciae* nom. nov. to replace it. It is named after Dr Patricia Ward (Edinburgh/Hamburg), a guest scientist who improved the English of this paper.

Systematic descriptions

The systematics of the Scaphopoda are still in a state of flux. Three new classification systems appeared within 1974-5 (Palmer, 1974; Starobogatov, 1974; Chistikov, 1975). In all three new systems the previous subgenera of *Dentalium* are promoted to full generic rank and several new families have been created. We basically follow here the synthesis of Cunningham Vaught (1989) with a few exceptions. It can already be pointed out that the data gained from the protoconchs indicate many changes in the classification of the Scaphopoda.

For each genus described below we give the full list of attributed fossil species. This allows a much better overview about the content of the genera.

Class Scaphopoda Bronn, 1862
Order Dentaliida Da Costa, 1798

Family Dentaliidae Gray, 1847

Synonym — Prodentaliidae Starobogatov, 1974.

Type genus — *Dentalium* Linnaeus, 1758.

Remarks — Starobogatov (1974) erected a new family for the genus *Prodentalium* Young, 1942 on the basis of the feature of a 'canted aperture'. He thought that the canted aperture indicates a lesser adaptation to burrowing than in Recent Dentaliidae, and a different morphology of the foot. In our opinion this is pure speculation and a poor argument for the creation of a new family. We regard Prodentaliidae Starobogatov, 1974 as a younger synonym of Dentaliidae Gray, 1847.

Genus *Prodentalium* Young, 1942

Type species — *Prodentalium raymondi* Young, 1942.

Diagnosis — The surface is covered by numerous (>20) longitudinal lirae. The cross section is circular or nearly so. The apical end can develop a notch on the ventral side.

Attributed species — *Prodentalium angelae* nom. nov. (pro *Dentalium arctoides* var. *multicostatum* Gugenberger, 1934; non *Dentalium multicostatum* Favre, 1869), Carnian, Carinthia, Austria; *Prodentalium arctoides* (Gugenberger, 1934), Carnian, Carinthia, Austria; *Prodentalium arctum* (Pichler, 1857), Triassic, Alps, Austria; *Prodentalium bandeli* sp. nov., Middle Liassic, northern Germany; *Prodentalium belcheri* Nassichuk & Hodgkinson, 1976, Early Permian, Canada; *Prodentalium calvertense* Palmer, 1974, Middle Jurassic, England; *Prodentalium canna* (White, 1874), Permian, U.S.A.; *Prodentalium dehmi* (Kuhn, 1935), Middle Jurassic, Germany; *Prodentalium dentaloideum* (Phillips, 1836), Carboniferous, England; *Prodentalium fredericae* nom. nov. (pro *Dentalium sublaeve* Hall in Miller, 1877), Carboniferous, Iowa, U.S.A. (non *Dentalium dentalis* var. *sublaevis* Cocconi, 1873); *Prodentalium gallensteini* (Gugenberger, 1934), Carnian, Carinthia, Austria; *Prodentalium herculeum* (de Koninck, 1863), Permian, Pakistan; *Prodentalium herritschi* (Gugenberger, 1934), Carnian, Carinthia, Austria; *Prodentalium ibergense* (Roemer, 1855), Devonian, Harz Mountains, Germany; *Prodentalium klipsteini* (Kittl, 1892), Middle Triassic, Dolomites, Italy; *Prodentalium liassicum* (Moore, 1867), Early Jurassic, England; *Prodentalium mexicanum* Girty, 1909, Permian, New Mexico, U.S.A.; (= ? *Prodentalium canna* (White, 1874) (fide Yancey, 1973); *Prodentalium monolineatum* (Branson, 1930), Permian, U.S.A.; [= *Prodentalium canna* (White, 1874) (fide Yancey, 1973)]; *Prodentalium orahovicense* (Kittl, 1903), Permian, Bosnia; *Prodentalium ornatum* (de Koninck, 1841), Carboniferous, Belgium; *Pro-*

dentalium raymondi Young, 1942, Pennsylvanian, U.S.A.; *Prodentalium semicostatum* (Girty, 1911), Carboniferous, U.S.A.; *Prodentalium subcanaliculatum* (Sandberger & Sandberger, 1856), Devonian, Germany; *Prodentalium turcicum* (Kittl, 1903), Permian, Bosnia.

Remarks — According to Palmer (1974) *Prodentalium* has no notch at the posterior end. However, the type species of *Prodentalium* can develop a notch in the adult stage (Tenery & Rowett, 1979). The diagnosis of *Prodentalium* is changed in accordance with these new results.

Prodentalium bandeli sp. nov.
Pl. 1, figs. 1-3; Fig. 1.

Derivatio nominis — After the palaeontologist Professor Klaus Bandel (Geol.-Paläont. Inst. Museum Universität Hamburg).

Holotype and paratype — GPIMH no. 2516/1 and GPIMH no. 2516/2.

Locus typicus — Erratic boulder, Hoisdorf, Schleswig-Holstein, Germany.

Stratum typicum — 'Ahrensburger Geschiebe', Middle Liassic, Pliensbachian, Domerian, *spinatus* Zone.

Diagnosis — A species of *Prodentalium* with an almost straight shell. The surface is covered with c. 180 longitudinal striae in regular distances. They are interrupted in irregular distances by a few circular annulations, probably growth interruptions. The shell tapers irregularly.

Material — The type material and two additional fragments.

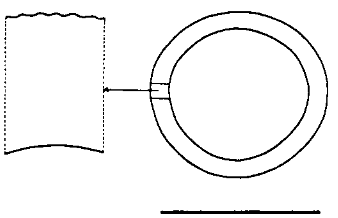

Fig. 1. *Prodentalium bandeli* sp. nov. Cross section and magnified part of it, showing the striated surface. Scale = 2 mm.

Description — The holotype is a fragment of 7 mm length; the paratype is 4 mm long. The outer surface is covered by about 180 fine longitudinal striae at a diameter of 2 mm (Pl. 1, fig. 1). The cross section (Fig. 1) is almost circular interiorly and exteriorly. The shell wall is thick, c. 200 µm at a diameter of 2.1 mm. The shell is characterised by a relatively thick layer (70 µm) of modified cross lamellae (Pl. 1, fig. 2). Towards the interior of the tube the cross lamellae (Pl. 1, fig. 3) (120 µm) are limited through a thin prismatic layer (10 µm). Anterior and posterior ends of the shell are unknown.

Comparison — The new species has the highest number of longitudinal ribs so far recorded from a *Prodentalium* species. Tenery & Rowett (1979) described up to 115 ribs for *Prodentalium raymondi* Young, 1942, the giant-sized type species of *Prodentalium* Young, 1942. *Prodentalium liassicum* Moore, 1867 has fewer (c. 24) and stronger longitudinal striae. A scaphopod from the lowermost Middle Jurassic of Bavaria (Germany) described under open nomenclature is noteworthy. Krumbeck (1925) described a '*Dentalium* sp. Nr. 1' as being covered by very dense and regular longitudinal striae. To our knowledge this species has never formally been described. It might be identical with *Prodentalium dehmi* (Kuhn, 1935) from the lowermost Middle Jurassic of Franconia, Germany.

Family Laevidentaliidae Palmer, 1974

Synonym — Eboreidentidae Chistikov, 1975.

Type genus — *Laevidentalium* Cossmann, 1888.

Remarks — The family includes only the genera *Laevidentalium* Cossmann, 1888, *Eboreidens* Chistikov, 1975, and *Pseudantalis* de Monterosato, 1872. All other genera placed by Palmer (1974) in the Laevidentaliidae are now attributed to other families. The family Eboreidentidae Chistikov, 1975 is probably a younger synonym of the family Laevidentaliidae. Chistikov (1975) was unaware of Palmer's paper. The validity of the family Rhabdidae Chistikov, 1975 seems to be debatable (see also Cunningham Vaught, 1989 who included it in the Laevidentaliidae).

Genus *Laevidentalium* Cossmann, 1888

Type species — *Dentalium incertum* Deshayes, 1825.

Diagnosis — Mostly curved conchs with a circular to oval cross section. The surface is smooth except for fine growth lines. There is no notch at the posterior end.

Attributed species — *Laevidentalium acre* (Sharp & Pilsbry, 1898), Eocene, France; (nom. nov. pro *Dentalium aciculum* Deshayes, 1864, non Gould, 1859); *Laevidentalium alineatum* (Stephenson, 1952), Cenomanian, Texas; *Laevidentalium amalthei* (Engel, 1890), Early Jurassic, Germany; *Laevidentalium angulati* (Quenstedt, 1857), Early Jurassic, Germany; *Laevidentalium antiquum* (Goldfuss, 1841), Devonian, Gerolstein, Germany; *Laevidentalium argoviense* (Loriol, 1881), Middle Jurassic, Switzerland; *Laevidentalium australe* (Pilsbry & Sharp, 1898), Early Miocene, Australia (nom. nov. pro *Entalis annulatum* Tate, 1887 non *Dentalium annulatum* Gmelin, 1788, secondary homonym, however permanently valid, because it was replaced before 1960); *Laevidentalium burdigalinum* (Mayer-Eymar, 1864), Miocene, Italy; *Laevidentalium calafium* Vokes, 1939, Eocene, California, U.S.A.; *Laevidentalium chubutense* Sabattini, 1979, Permian, Argentina; *Laevidentalium danai* (Meyer, 1885), Eocene, Mississippi, U.S.A.; *Laevidentalium demersum* (Pilsbry, 1927), Late Cretaceous, Tennessee, U.S.A.; (nom. nov. pro *Dentalium inornatum* Wade, 1926, non McCoy, 1844); *Laevidentalium ecostatum* (Kirk, 1880), Pliocene to Recent, New Zealand; *Laevidentalium elongatum* (von Münster in Goldfuss, 1841), Early Jurassic, Germany; *Laevidentalium filicauda* (Quenstedt, 1852), Early to Middle Jurassic, southern Germany (= *Laevidentalium elongatum* (von Münster in Goldfuss, 1841 according to Richardson, 1906); *Laevidentalium ganense* Cossmann in O'Gorman, 1923, Eocene, France; *Laevidentalium ? giganteum* (Phillips, 1829), Early Jurassic, England; *Laevidentalium gracile* (Moore, 1867) (non *Dentalium gracile* Hall & Meek, 1854), Early Jurassic, England (= *Laevidentalium elongatum* (von Münster in Goldfuss, 1841 according to Richardson, 1906); *Laevidentalium guineense* Adegoke, 1977, Paleocene, Nigeria; *Laevidentalium hannonicum* (Briart & Cornet, 1887), Tertiary, Belgium; *Laevidentalium haytense* (Gabb, 1873), Miocene, San Domingo; *Laevidentalium illinoisense* (Worthen, 1883), Carboniferous, U.S.A.; *Laevidentalium incertum* (Deshayes, 1825), Eocene, France; *Laevidentalium komiense* Kulikov, 1967, Permian, Russia; *Laevidentalium lacteolum* (Tate, 1899), Early Miocene, Australia; (nom. nov. pro *Dentalium lacteum* Tate, 1887, non Deshayes, 1825); *Laevidentalium largicrescens* (Tate, 1896), Early Pliocene, Australia; *Laevidentalium lighti* Vokes, 1939, Eocene, California, U.S.A.; *Laevidentalium limatum* Stanton 1902, Cretaceous, Patagonia, Argentina; *Laevidentalium morganianum* Wilckens, 1922, Cretaceous, New Zealand; *Laevidentalium multiplicans* (Kittl, 1903), Permian, Bosnia; *Laevidentalium neocomiense* (Péron, 1900), Neocomian, France; *Laevidentalium nigeriense* Adegoke, 1977, Paleocene, Nigeria; *Laevidentalium nitidum* (Deshayes, 1864), Eocene, Paris Basin, France; *Laevidentalium normannianum* (d'Orbigny, 1850), Late Jurassic, France; *Laevidentalium nudum* (Zekeli, 1857), Late Cretaceous, Austria; *Laevidentalium oolithicum* (Piette, 1856), Middle Jurassic, France; *Laevidentalium parkinsonii* (Quenstedt, 1857), Middle Jurassic, Southern Germany (= *Laevidentalium oolithicum* (Piette, 1856); *Laevidentalium patriciae* nom. nov., Middle Devonian, Germany (pro *Dentalium robustum* Maurer, 1885, non *Dentalium robustum* Brazier, 1877)(see above); *Laevidentalium perlongum* (Dall, 1881), Recent to Miocene, Venezuela; *Laevidentalium philippinarum* (Sowerby, 1860), Pliocene to Recent, Philippines; *Laevidentalium pictile* (Tate, 1886), Early Miocene, Australia; *Laevidentalium pseudorhakiense* Eames, 1951, Eocene, Pakistan; *Laevidentalium readi* (Emerson, 1954), Triassic, Southern Alps, Italy; (nom. nov. pro *Dentalium simile* Read in Broili, 1907, non *Dentalium simile* von Münster, 1841, nec Biondi, 1859); *Laevidentalium regium* (Assmann, 1937), Triassic, Silesia, Poland; *Laevidentalium rhakiense* Eames, 1951, Eocene, Pakistan; *Laevidentalium rigauxi* Fischer & Vadet, 1985, Middle Jurassic, France; *Laevidentalium sacheri* (Alth, 1850), Late Cretaceous, Ukraine; *Laevidentalium santarosanum* (Maury, 1911), Miocene, Florida, U.S.A.; *Laevidentalium sorbii* (King, 1850), Permian, England; *Laevidentalium speyeri* (Geinitz, 1852), Permian, Harz Mountains, Germany; *Laevidentalium splendens* (Wollemann, 1903), Early Cretaceous, Northern Germany; *Laevidentalium subcompressum* (Meyer, 1885), Eocene, Mississippi, U.S.A.; *Laevidentalium subfissurum* (Tate, 1887), Early Miocene to Pliocene, Australia; *Laevidentalium subnudum* (Repelin, 1902), Cenomanian, France; *Laevidentalium sulculosum* (von Koenen, 1892), Paleocene, Germany; *Laevidentalium uchauxense* (Cossmann, 1896), Late Cretaceous, France; *Laevidentalium undiferum* (von Koenen, 1885), Paleocene, Denmark; *Laevidentalium venezuelanum* Weisbord, 1964, Miocene, Venezuela; *Laevidentalium venustum* (Meek & Worthen, 1862), Mississippian, U.S.A.; *Laevidentalium waihoraense* (Emerson, 1954), Tertiary, New Zealand; (nom. nov. pro *Dentalium (Laevidentalium) filum* Marwick, 1931, non *Dentalium filum* Sowerby, 1866; *Laevidentalium wymense* Kulikov, 1967, Permian, Russia; *Laevidentalium yamakawai* (Yokoyama, 1927), Tertiary, Japan.

Remarks — Several Jurassic species of *Laevidentalium* are characterised by strong annulations on the most posterior portion of the shell. This feature is only preserved in young specimens or species with a small adult size. It is unclear whether it is characteristic for the entire group of the genus *Laevidentalium* or restricted to these species.

Laevidentalium sp.
Fig. 2.

Material — Several fragments.

Description — The lengths of the fragmentary specimens range from 5 to 10 mm. They are almost straight (see discussion) and circular in cross section interiorly and exteriorly (Fig. 2). The tapering is low. The shell wall measures c. 300 μm at a diameter of 1.2 mm. It consists of two mineralised layers. The inner shell layer is prismatic and c. 10 μm thick. The outer layer shows a cross-lamellar structure and comprises the main part of the shell (c. 270 μm). In the outer part (c. 20 μm) the cross lamellae have more obtuse angles. The outer surface shows oblique growth lines.

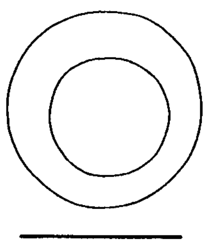

Fig. 2. *Laevidentalium* sp. Cross section. Scale = 1 mm.

Discussion — The fragments do not allow a specific determination. The smooth outer surface and the circular cross section is characteristic for the genus *Laevidentalium* Cossmann, 1888 (see discussion).

Family Gadilinidae Chistikov, 1975

Type genus — *Gadilina* Foresti, 1975.

Remarks — The Gadilinidae Chistikov, 1975 comprises the genera *Gadilina* Foresti, 1895, and *Progadilina* Palmer, 1974, which are characterised by their trigonal cross section with the flat side situated dorsally and the keel ventrally. It is strange that Cunningham Vaught (1989) listed the genera *Episiphon* Pilsbry & Sharp, 1897 and *Anulidentalium* Chistikov, 1975 among the Gadilinidae. The latter genera are characterised by long and slender conchs with a circular cross section. They are placed in the family Episiphonidae Chistikov, 1975.

Genus *Progadilina* Palmer, 1974

Type species — *Dentalium trigonale* Moore, 1867.

Diagnosis (emend.) — Scaphopods with a trigonal outline which can become oval to circular at the aperture. The surface is covered by circular striae and lirae which are orientated more or less oblique to the longitudinal axis of the shell.

Remarks — In our opinion the diagnosis given by Palmer (1974) is on the one hand too broad (it includes quadrate forms), on the other hand too restricted (it includes only forms with 'annular ridges'). We therefore restrict the diagnosis to forms with a trigonal cross section which can change to an oval or circular outline during the ontogeny. It is amended to accommodate forms with a much weaker ornamentation which would not correspond to the definition of 'annular ridges'. There is also a discrepancy between the description of the holotype in Moore (1867) and its redescription in Palmer (1974). In Moore (1867) the holotype is said to have 'numerous very fine annular oblique concentric striae' whereas Palmer (1974) states that the holotype has '6 to 8 annular ridges per millimetre' which is a rather coarse ornamentation. We consider Palmer's redescription more accurate.

Differences — The only difference with the Recent and Tertiary genus *Gadilina* Foresti, 1895 is the annulated surface of *Progadilina* Palmer, 1974. In *Gadilina* the surface is smooth and shows only growth lines.

Attributed species — *Progadilina spaethi* sp. nov., Pliensbachian, Germany; *P. subovata* (Richardson, 1906), Early Jurassic, England; *P. subtrigonalis* (Richardson, 1906), Early Jurassic, England; *P. trigonalis* (Moore, 1867), Early Jurassic, England.

Progadilina spaethi sp. nov.
Pl. 1, fig. 4; Figs. 3-4.

Derivatio nominis — After Professor Chr. Spaeth (Geol.-Paläont. Inst. Museum Univ. Hamburg).

Holotype and paratype — GPIMH no.2516/3 and GPIMH no. 2516/4.

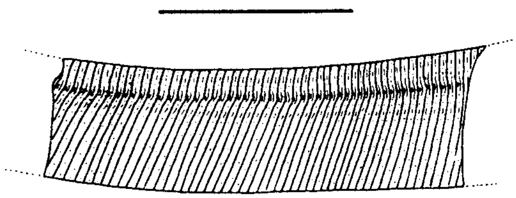

Fig. 3. *Progadilina spaethi* sp. nov. Holotype. Scale = 3 mm.

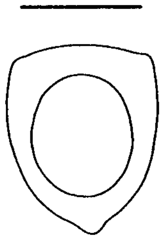

Fig. 4. *Progadilina spaethi* sp. nov. Cross section. Scale = 2 mm.

Locus typicus — Erratic boulder, Hoisdorf, Schleswig-Holstein, Germany.

Stratum typicum — 'Ahrensburger Geschiebe', Middle Liassic, Pliensbachian, Domerian, *spinatus* Zone.

Diagnosis — A curved species of *Progadilina* with fine but distinct oblique lirae and striae. There are c. 12-17 lirae per mm at a diameter of approx. 2 mm.

Description — The holotype is a fragment of 6 mm length (Fig. 3), the paratype measures 4 mm. The outer surface is characterised by 15-20 lirae and striae per mm length (Pl. 1, fig. 4). One ventral keel and two dorsal/lateral keels, which are more distinct at the posterior shell, are present. The lateral sides of the posterior part are as convex as those of the anterior part (Fig. 4) while the dorsal side is flat in the first case and convex in the second case. The posterior part's diameter is 1.74 mm, compared to 2.18 mm of the anterior shell. The cross section interiorly is egg-shaped. The shell wall is c. 200 µm thick but can reach 400 µm where the keels are more pronounced. The shell-structure is mainly characterised by cross lamellae or modified cross lamellae. The tube is interiorly coated with a 15 µm thin prismatic layer.

Differences — The cross section of *Progadilina subtrigonalis* (Richardson, 1906) differs from *P. spaethi* sp. nov. when compared at the same diameter. In *P. spaethi* sp. nov. the conch shows three convexly curved sides (Fig. 4) whereas *P. subtrigonalis* has two convexly curved sides and one concavely curved side (Fig. 5). The ornamentation of *P. trigonalis* consists of finer oblique lirae and striae. *P. subovata* Richardson shows a more oval cross section with rounded edges. In *P. spaethi* sp. nov. the edges are angular.

Progadilina subtrigonalis (Richardson, 1906)
Pl. 2, figs. 1-2; Fig.5.

1906 *Dentalium subtrigonale* sp. nov. — Richardson, p. 589, pl. 45, figs. 2a-d.
(?) 1940 *Dentalium trigonale* Moore. — Stoll, p. 98, pl.1, fig. 14-16.

Material — Several fragments.

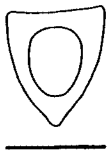

Fig. 5. *Progadilina subtrigonalis* (Richardson) Cross section of the posterior part of the shell. Scale = 1 mm.

Description — The fragments range from 4 to 14 mm in length. The cross section is triangular with subangular keels. The dorsal side is shorter than the lateral sides. The interior cross section is oval. Measured at a diameter of 1.1 mm the shell's maximal thickness is 350 µm (at the keel), minimal thickness is 140 µm. The main structure of the shell is cross lamellar or modified cross lamellar (Pl. 2, fig. 1). The inner shell layer is prismatic and 40 µm thick. At the posterior part of the shell all three sides are concavely curved. At a diameter of c. 1.1 mm the lateral sides are convexly curved whereas the dorsal side still is very slightly concavely curved or flat (Fig. 5). At 1.2 mm all three sides are convexly arched. The triangle is orientated with the dorsal side flat and the ventral side keeled. At a diameter of 1.1 mm the specimens show 20 circular ribs per millimetre (Pl. 2, fig. 2). At a diameter of 2 mm it has 14 ribs per millimetre.

Discussion — From the description we find that the so-called '*Dentalium trigonale* Richardson' described and figured by Stoll (1940) is more similar to *Progadilina subtrigonalis* (Richardson).

Family Baltodentaliidae fam. nov.

Type genus — *Baltodentalium* gen. nov.

Diagnosis — Scaphopods with a pentagonal cross section of the conch. The keel of the pentagon is ventral, the dorsal side is rounded. The protoconch is striated. The surface of the teleoconch bears more or less developed circular striae and lirae.

Differences — See the genus description below.

Attributed genera — Only *Baltodentalium* gen. nov.

Baltodentalium gen. nov.

Type species — *Baltodentalium weitschati* gen. & sp. nov.

Derivatio nominis — After the Baltic Sea.

Diagnosis — The cross section is pentagonal and compressed. The surface shows slightly oblique circular ridges, and the shell is relatively thin.

Differences — *Baltodentalium* gen. nov. is distinguished from all other scaphopod genera except *Entalina* de Monterosato, 1872 by its pentagonal cross section. However, *Entalina* de Monterosato, 1872 differs by its depressed shell and the pentagon is orientated the other way round; i.e. the dorsal side is keeled and the ventral side flat or slightly convexly curved. There are several more species with a pentagonal cross section which are still attributed to *Dentalium*. However, the restricted diagnosis of *Dentalium* excludes such species and they should be transferred to new genera.

Attributed species — *Baltodentalium limatulum* (Tate, 1870), Early Jurassic, England; *Baltodentalium limatuloides* (Kuhn, 1935), Middle Jurassic, Germany; *Baltodentalium weitschati* gen. & sp. nov., Early Jurassic, northern Germany.

Baltodentalium weitschati gen. & sp. nov.
Pl. 2, figs. 3-4; Figs. 6-7.

Derivatio nominis — After Dr Wolfgang Weitschat, curator of the collection of the Geol.-Paläont. Inst. Museum Univ. Hamburg, who found the fossil.

Holotype — GPIMH no. 2516/5.

Locus typicus — Erratic boulder, Hoisdorf, Schleswig-Holstein, Germany.

Stratum typicum — 'Ahrensburger Geschiebe', Middle Liassic, Pliensbachian, Domerian, *spinatus* Zone.

Diagnosis — As for the genus.

Description — The total preserved length reaches 3 mm (Fig. 6). The shell is already curved at this stage. The dorsal side is convex and the ventral side is developed as a keel. Midway the lateral sides have weak longitudinal ridges. This results in a pentag-

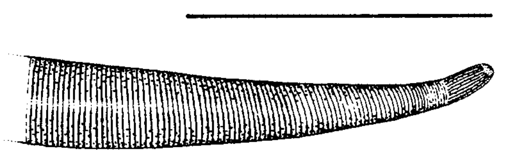

Fig. 6. *Baltodentalium weitschati* gen. & sp. nov. Holotype with striated protoconch. Scale = 2 mm.

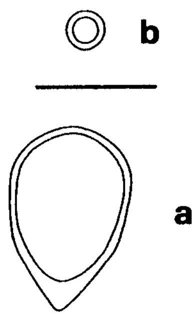

Fig. 7. *Baltodentalium weitschati* gen. & sp. nov. Scale = 400 µm. a: Cross section of the maximal diameter of the holotype. b: Cross section of the protoconch of the holotype.

onal exterior cross section. The maximal diameter is 600 μm in the dorsoventral extension. The lateral extension is 400 μm which gives a compressed section. The shell is comparably thin, the lateral sides 20 μm, the ventral side with its keel-like enforcement c. 70 μm. The cross section at the largest known diameter (Fig. 7a) interiorly is roughly pentagonal. The adult shell is covered by bluntly circular slightly oblique ridges. Approximately 30 ridges are equivalent to a millimetre. Towards the protoconch the shell gradually becomes circular. The general form of the protoconch is bullet-shaped (Pl. 2, fig. 3) with a length of 250 μm and diameter of c. 130 μm. Its cross section is circular (Fig. 7b).

The length was determined by a strong annulation between larval and juvenile shell. The protoconch is covered by c. 20 longitudinal striae in regular distances which partly bifurcate at the posterior part. At the ventral side three striae are more distant from each other. The size of the posterior opening (Pl. 2, fig. 4) could not be precisely determined but is comparably small (c. 30 μm). The very posterior part, around the opening, is free of striae. The thickness of the protoconch's shell is c. 20 μm.

Differences — In *Baltodentalium limatuloides* (Kuhn, 1936) two sides are concavely and three sides are convexly curved, whereas in *B. weitschati* gen. & sp. nov. all sides are convexly curved. In *B. limatulum* (Tate, 1870) the shell is much thicker than in *B. weitschati* gen. & sp. nov. and as in *B. limatuloides* (Kuhn).

Discussion — In comparison with other specimens with preserved protoconch the holotype is probably complete. At larger sizes the protoconch would be resorbed. The early ontogeny of scaphopods, in particular the formation and mineralisation of the larval shell is relatively unknown (Lacaze-Duthiers, 1856-57; Kowalevsky, 1883; McFadien-Carter, 1979). It is therefore difficult to interpret the initial shell of *Baltodentalium weitschati* sp. nov. in regard to the development. We refrain here from further discussion, giving only a brief comparison with the larval shell of a Recent *Antalis* sp. The length of the protoconch of *B. weitschati* measures c. 250 μm, the diameter c. 130 μm. The larval shell of *Antalis* sp. has approximately similar dimensions. It is 330 μm in length with a maximum diameter of 170 μm (Bandel, 1982). *B. weitschati* lacks the apical protrusion that can be seen at the juvenile shell of *Antalis*. The ventral side is not visible and the seam of adhesion cannot be observed. It is well pronounced on the protoconch of *Antalis* sp. The surface of the protoconch of *Antalis* sp. is smooth or nearly so at the other parts. The larval shell of *B. weitschati* bears longitudinal striae which partly bifurcate at the posterior part before they end. A more detailed comparison of the protoconchs of several species of scaphopods from different stratigraphic ages is in preparation.

Discussion

Many descriptions of fossil scaphopods are not sufficient for a proper identification. Most species must be redescribed. For example, it is insufficient to give numbers of ribs of a species for a certain section of the shell without giving the diameter at which it was measured. In many cases the number of ribs per millimetre decreases towards the anterior part of the shell. Discussing the curvature of a scaphopod shell's fragment raises the same problem. When comparing complete shells, it becomes obvious that in most cases different parts can be curved differently. For all fragmental comparisons the dates of the diameter are substantial.

The structure of the scaphopod shell was previously described by Couvreur (1929) based on three Recent species. Fantinet (1959) studied several Pliocene species from Tunisia. Haas (1972) studied the shell of Recent *Fissidentalium vernedei* Sowerby, 1860, *Dentalium rectum* Gmelin, 1788 from the Pliocene of Sicily and '*Dentalium*' sp. from the Devonian of Germany. As early as 1855 McCoy mentioned that 'the intimate structure (of *Plagioglypta ingens* (de Koninck) from the Carboniferous of England) proved perfectly analogous to that of the living small Dentalia.' He used the microstructure to assure himself that this gigantic species was a scaphopod. No figure was given.

The shell of the scaphopods is normally composed of an organic periostracum and a thick layer of a basically cross-lamellar structure and a prismatic inner layer. The parts of the shell with the same angle of cross lamellae can be different in diameter in different species. In some species we observed a thin prismatic layer underneath the periostracum. The inner prismatic layer is of variable thickness. Within a species its thickness is dependent on the growth stage. Consequently, the thickness of inner prismatic layer can only be used as a shell character when comparing the same growth stages. The thickness of the whole shell differs between many species and can be used as a criterium.

The description of the protoconch of *Baltodentalium weitschati* raises a number of questions. Are dimensions of larval shell and teleoconch proportional, i. e., does a small protoconch indicate a small adult shell? Are the striae on the protoconch of *B. weitschati* built during the shell formation, or secondarily by the juvenile animal? A publication presenting and discussing facts of different larval shells of Scaphopoda is in preparation.

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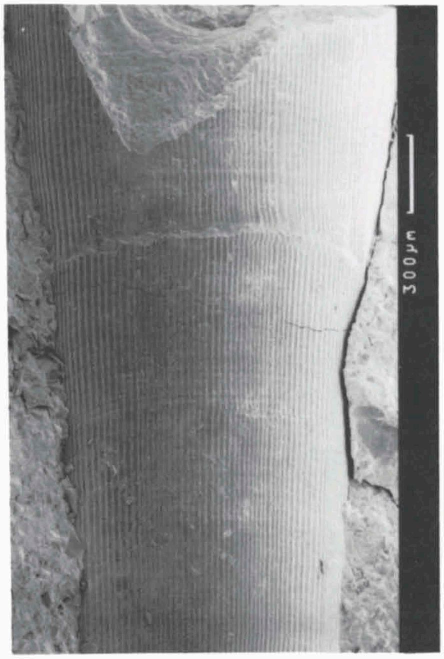
Plate 1

Fig. 1. *Prodentalium bandeli* sp. nov. Paratype, showing the striated surface.

Fig. 2. *Prodentalium bandeli* sp. nov. Modified cross lamellae.

Fig. 3. *Prodentalium bandeli* sp. nov. Cross lamellae of a more interior part of the shell than in Fig. 2.

Fig. 4. *Progadilina spaethi* sp. nov. Surface of the shell.



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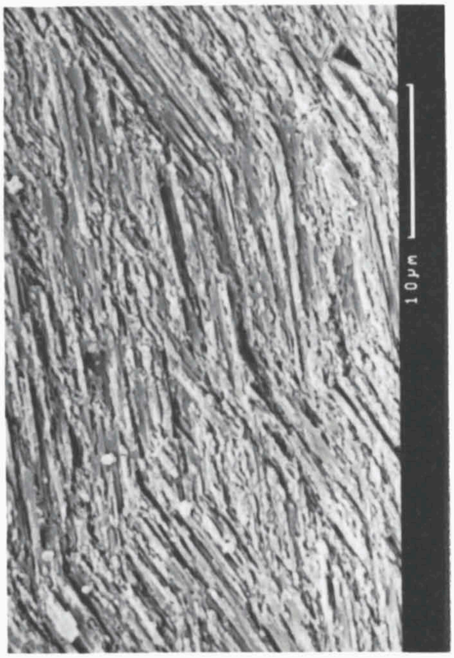

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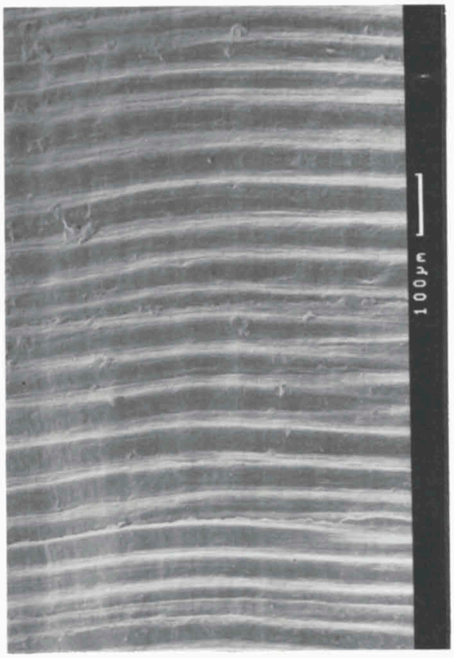

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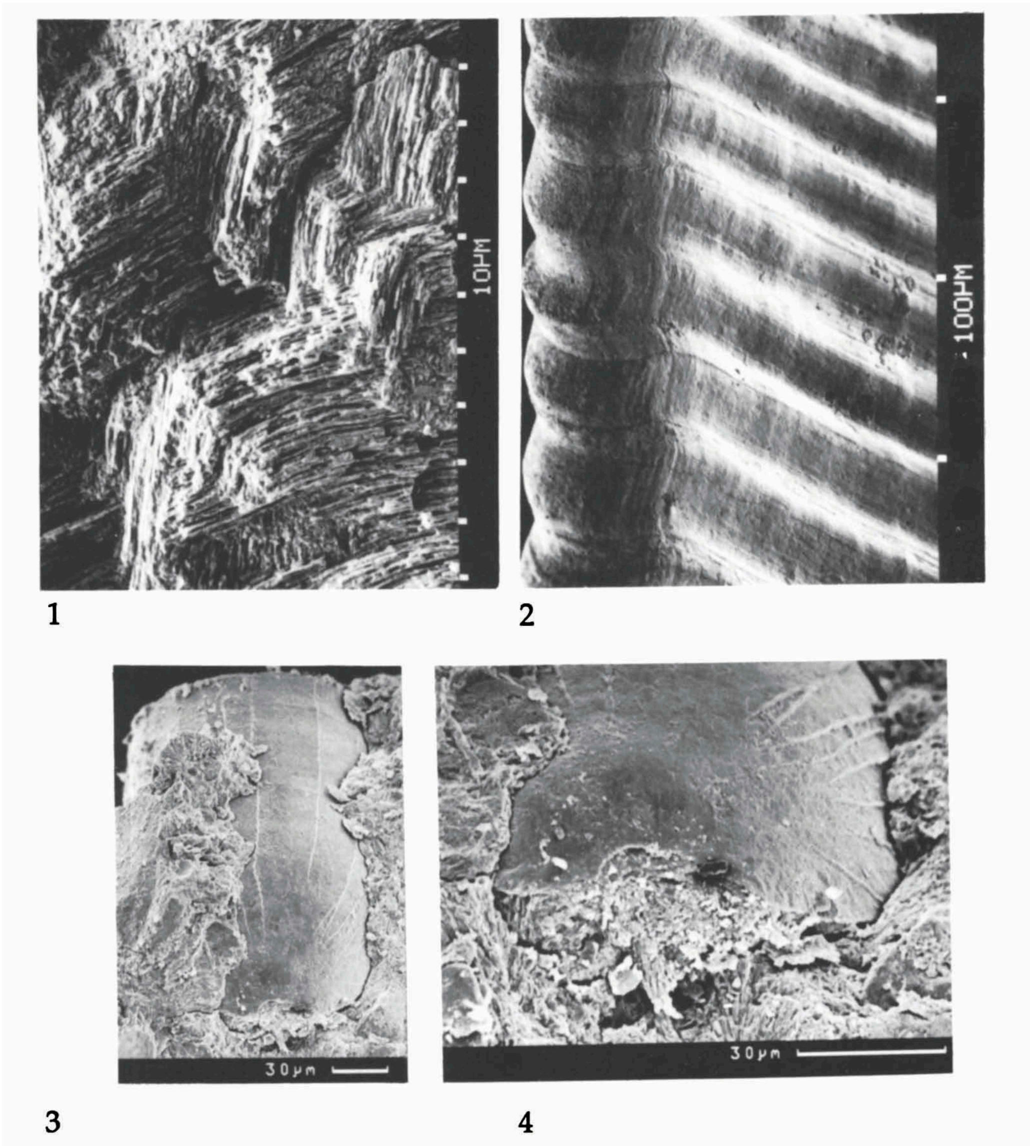

Plate 2

Fig. 1. *Progadilina subtrigonalis* (Richardson). Cross lamellae.
Fig. 2. *Progadilina subtrigonalis* (Richardson). Surface of the shell showing the ribs and the ventral keel.
Fig. 3. *Baltodentalium weitschati* gen. & sp. nov. Protoconch in ventral view.
Fig. 4. *Baltodentalium weitschati* gen. & sp. nov. Posterior part of the protoconch showing the apical opening.