

Cretaceous *Laxispira* and a discussion on the monophyly of vermetids and turritellids (Caenogastropoda, Mollusca)

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with 1 text-figure and 3 plates

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The vermetoid mode of life has evolved at least twice in basic caenogastropod relation. The first is represented by the Upper Cretaceous genus *Laxispira* and its potential relatives in the Vermetidae. It is characterized by a regularly coiled protoconch with tuberculate sculpture. *Laxispira* has either lived attached to each other or with a loosely coiled adult shell. With settlement on hard surfaces coiling of the attached shell became irregular and individuals could support each other building reef-like aggregations. Eocene to recent relatives within the Vermetinae show a similar protoconch-morphology, but usually their early ontogeny is more lecithotrophic. After the larval phase they are always attached to hard substrates. Members of the genus *Dendropoma* within the newly introduced subfamily Dendropominae have a similar biology, but they are characterized by an independent cancellate protoconch-sculpture that is documented since the Eocene. The genus *Vermicularia* within the subfamily Vermiculariinae, family Turritellidae, is convergent to *Laxispira* in regard to its mode of life but has a typical spirally keeled turritellid protoconch. In the related family Siliquariidae different strategies of ontogeny have developed. The genera *Tenagodus* and *Pyxipoma* within the subfamily Siliquariinae live embedded in sponges and are characterized by a slit in their shell. The genera *Stephopoma* and *Caporbis*, subfamily Stephopominae nov., lack a slit, live attached to hard substrates and have a planispiral protoconch.

Die vermetoide Lebensweise entstand mindestens zweimal innerhalb der basalen Caenogastropoda. Zum ersten ist die oberkretazische Gattung *Laxispira* durch einen regulär gewundenen Protoconch mit tuberkulater Skulptur gekennzeichnet. Der Teleoconch kann bei einer Lebensweise in Weichsedimenten lose spiralgewunden sein oder bei Besiedlung von Hartsubstraten angeheftet irregulär weiterwachsen und mit anderen Individuen riffartige Strukturen bilden. Eozäne bis rezente Verwandte innerhalb der Vermetinae zeigen eine ähnliche Protoconchmorphologie, sind jedoch durch eine stärker lecithotrophe Frühontogenese gekennzeichnet. Adult leben sie an Hartsubstraten angeheftet. Die Gattung *Dendropoma*, Unterfamilie Dendropominae nov., ist hinsichtlich ihrer Biologie sehr ähnlich, zeigt jedoch eine unabhängige cancellate Protoconchskulptur, die schon seit dem Eozän nachgewiesen ist. Zum zweiten ist die Gattung *Vermicularia* (Turritellidae, Vermiculariinae) durch eine zu *Laxispira* konvergente Lebensweise gekennzeichnet, weist jedoch einen typischen spiral gekielten, turritelliden Protoconch auf. Innerhalb der verwandten Familie Siliquariidae treten verschiedene Ontogenesestrategien auf: Die Gattungen *Tenagodus* und *Pyxipoma*, Unterfamilie Siliquariinae, mit geschlitzter Adultschale leben in Schwämmen, wogegen die schlitzlosen Gattungen *Stephopoma* und *Caporbis*, Unterfamilie Stephopominae nov., angeheftet an Hartsubstraten leben. Sie sind durch eine planspirale Protoconchform gekennzeichnet.

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Introduction

Several genera of caenogastropods attach their shell to the substrate, in this respect resembling tube worms with calcareous shell. Sessile gastropods with vermiform shells were placed all together in the family Vermetidae as MÖRCH (1862) had suggested. Members of the Vermetidae in the classification adopted by THIELE (1931) have an attached, long, uncoiled adult shell, but a normally and regularly coiled embryonic and larval shell. In the case of *Vermicularia* also the juvenile shell is regularly coiled. The irregular shell portion is partly attached to a substrate, or it is surrounded by substrate, as in *Tenagodus* that lives within sponges. Later portions of the tubes of the shell commonly project up and into the water above the surface of attachment as is the case in *Dendropoma* (HUGHES 1978). Some species settle on wave swept rock within the tidal zone like *Petalonchus varians* from the Caribbean Sea while others grow among colonial organisms of the coral reef like *Dendropoma maxima* in the Pacific Ocean. The vermetid shell tube can also run through soft crust-forming organisms as does *Petalonchus erectus* within the colony of the soft coral *Palythoa* in the shallow subtidal in the Caribbean Sea (BANDEL & WEDLER 1987). Species that live on intertidal flats commonly form small reef-like structures with many individuals supporting each other in entangled growth. Single individuals are often attached to rock, hard substrate and larger shell debris lying on soft substrate in competition to tube dwelling polychaetes (BOETTGER 1930). All species of the vermetids feed by filtering particles from the water surrounding them. To do so some are aided by mucous nets produced by the mucus gland on the anterior foot, while others filter with their gill (BOETTGER 1930).

MÖRCH (1862), THIELE (1931) and WENZ (1939) placed the Vermetidae into the superfamily Cerithioidea. Here they have remained in most classifications. MORTON (1951a, b, 1953) demonstrated that two distinct kinds of vermetids are to be differentiated. One of these have large pedal glands and associated pedal tentacles which are used to spin mucus secreted by the pedal gland into a web that traps suspended food particles. These were retained in the Vermetidae (MORTON 1951a, HUGHES 1978). The others, like *Vermicularia*, use only a muco-ciliary branchial filtering mechanism to trap food particles and, thus, closely resemble *Turritella* and are placed within the Turritellidae. ABBOTT (1974) assigned *Vermicularia* to the Vermetidae following suggestions of THIELE (1931) and WENZ (1939). HOUBRICK

(1988) noted that Vermetidae and Turritellidae are quite different from the other groups within the Cerithioidea on anatomical grounds. SCHEUWIMMER (1979) and HEALY (1988) analysed the spermatozoa of members of the Vermetidae and noted that they have euspermatozoa quite of the type observed in the Cerithioidea and paraspermatozoa of an own type with bipolar tailed morphology. MORTON (1951b) demonstrated that *Tenagodus* is also related to the turritellids and not to the vermetids which was confirmed by HUGHES (1985).

Vermetidae and Turritellidae along with the Siliquariidae demonstrate that the vermetoid type of living has developed at least twice in caenogastropods of the cerithiiform relation. In this scenario the different shapes found among the embryonic and larval shell of vermetoids can be fitted. The fossil record indicates that the group appeared rather late in the Mesozoic. The Late Cretaceous *Laxispira* can be considered one of the earliest representatives of the Vermetidae. During the Eocene other types with highly ornamented protoconchs appeared, and with the Oligocene the type of the extant *Stephopoma* is found.

Laxispira from the Upper Cretaceous and its relation

The family Vermetidae, subfamily Vermetinae, is characterized by a regularly coiled, barrel-shaped protoconch with spiral tuberculate sculpture and a loosely coiled to irregularly growing teleoconch.

Laxispira GABB, 1877 with the type species *Laxispira lumbricalis* GABB, 1877 has been placed as subgenus of the genus *Vermicularia* by WENZ (1939) and as an own genus into the Vermetidae by SOHL (1960). Later SOHL (1964) returned it to the proximity of the Turritellidae in placing it with the Vermiculariinae. He followed KEEN's (1961) advice to separate *Vermicularia* and relation from the Vermetidae. This placement was also accepted by DOCKERY (1993).

Laxispira libycus QUAAS, 1902 from the shallow Maastrichtian sea of the Western Desert of Egypt is very similar to *Laxispira lumbricalis* GABB, 1877 from the Upper Campanian and Maastrichtian Gulf of Mexico. *L. lumbricalis* is diagnosed by SOHL (1960) as loosely but regularly coiled shell with round cross section, oval to tear-drop shaped aperture and a sculpture of spiral, slightly beaded lirae. Thus, there are very similar representatives of *Laxispira* found on both shores of the Tethyan Ocean since the Egyptian Western Desert represents the coastal area dominated by carbonate sands and muds on the southern margin of the Tethys (BARTHEL et al. 1981). Similar but more clay rich and less carbonatic deposits of coastal water in Mississippi and Tennessee were deposited on its northern margin (SOHL 1960). The differences of the substrate resulted in some differences in the morphology of *Laxispira*. Post-metamorphosed individuals that lived in soft sediments built a loosely coiled shell that was not attached (Pl. 1 fig. 1). On the coarser shell bottoms of the sea juvenile individuals of *Laxispira* gathered after a more or less extended time and supporting each other formed little reef-like structures (Pl. 1 fig. 2). Their shells in this case ceased to coil openly and grew up straight and parallel supporting each other.

The *Laxispira* relation has been noted on sandy bottoms of the shallow sea in the Upper Cretaceous in several places

around the world. *Laxispira turritelliformis* VOGEL comes from the Campanian Aachener Kreide as well as *L. cochleiformis* (MÜLLER) and *L. piguis* HOLZAPFEL. *L. cochleata* BÖHM has been described from Bavarian Cretaceous. Another record is from the Campanian tropical Tethys-shore of Torallola in the Tremp Basin in northern Spain. These closely resemble *Laxispira* from Egypt and the USA. The teleoconch is openly coiled with round cross section and ornamented by spiral ribs and rows of granules. The same species or very closely related species of *Laxispira*, thus, lived from Campanian to Maastrichtian on both sides of the Tethys ocean in tropical environment (Torallola and Western Desert) as well as in the moderate warm climates (Gulf of Mexico and Aachener Kreide). They lived on a broad shelf area as well as in coastal areas and represent gastropods of the shallow sublittoral sea.

Description of the protoconch

SOHL (1960) described the protoconch of *Laxispira lumbricalis* from the Campanian Coffee Sand of Chapelville in Mississippi and Maastrichtian Ripley Formation of Coon Creek in Tennessee as consisting of a little more than two smooth trochoid volutions. DOCKERY (1993) figured the larval shell, and several more shells were studied by us from both localities. According to DOCKERY (1993) the protoconch is trochoid in shape and consists of three convex whorls, the second of which has rows of very fine punctae. The terminus of the protoconch shows the outline of a subsutural sinus. After this terminus the shell becomes widely uncoiled. The early teleoconch consists of broadly uncoiled whorls sculptured with closely spaced spiral lirae that are slightly beaded where crossed by faint growth lines. The inner side of the whorls opposite the axis of coiling is smooth. Growth lines of the juvenile indicate a sinus that follows the whorls's upper surface. The aperture is circular.

Own observations on SCAN photographs indicate that the embryonic shell measures 0.10 to 0.12 mm across, is of dextral coiling mode with about 0.7 whorls with smooth surface. Its transition into the shell formed by the planktonic veliger is indicated by the onset of growth lines and tuberculate sculpture. Simple growth lines are transformed into sinuous course by the formation of a rounded apertural projection of the outer apertural lip. In this way almost 2.5 whorls of larval shell are added to the embryonic shell amounting to a protoconch of about 3.2 whorls (Pl. 1 fig. 4). The protoconch has rounded whorls and measures about 0.5 mm in height and 0.45 mm in width. It is ending with a wide rounded lobe of the outer lip of the aperture accompanied by a deep rounded depression between outer lip and suture and another one on the keeled base. First growth of teleoconch closes these sinuses so that further shell growth continues in more simple straight accretional lines. Uncoiling of the shell becomes obvious with the onset of the teleoconch onto the protoconch and spiral ribbing becomes evident as well (Pl. 1 fig. 3).

The *Vermetus* case

The genera *Vermetus* DAUDIN, 1800 (= *Bivonia* GRAY, 1842) and *Petalocochnus* LEA, 1843 (= *Macrophragma* CARPENTER, 1857) as well as *Serpulorbis* SACCO, 1827 (= *Aletes* CARPENTER, 1857; *Lemintina* RISSO, 1826) belong here. Other genera noted by VAUGHT (1989) are *Eualetes*

KEEN, 1971, *Novastoa* FINLAY, 1927, *Segmentella* THIELE, 1925 (near *Stephopoma* according to LOZOUET 1987) and *Trypsycha* KEEN, 1961.

Similar to the Calyptraeoida (Neomesogastropoda) many vermetids catch their food with the help of a mucus net. But in contrast to the former the later form the mucus net outside of their shell (BOETTGER 1930). The Mediterranean *Vermetus gigas* for example spins 3 to 4 threads secreted by the large pedal gland which opens in the central portion of the foot between the pedal tentacles. These threads drift in the water. After a more or less extended period mucus threads are taken hold off by the lips of the mouth and aided by the radula ingested together with the particles that have become entrapped on their sticky surface. In the transport of sperm the net is also employed like in the genus *Serpulorbis* (SCHEUWIMMER 1979). Spermatozoa suspended in the seawater are entrapped by the mucus net of the female, and sperms are released when the radula opens the capsules holding them together. With the water current entering the pallial cavity sperms enter as well, collect around the genital pore and migrate from there to the receptaculum seminis. Here they remain active and available to serve in the fertilization of eggs once they are ready for it. The foot of some vermetids like *Serpulorbis* discard their operculum and here the tissue of the foot itself serves as seal of the shelly tube when the animal retracts into its shell. Two retractable tentacles manipulate the mucus that is produced by the mucus gland of the foot and spin the net trap (BOETTGER 1930). HUGHES (1978) observed mucus net production and its handling by pedal tentacles in the case of *Serpulorbis* from South Africa.

According to HOUBRICK (1988) the foot is vestigial and has lost the statocysts. Own observations have noted the presence of statocysts in the veligers. A similar case of statocysts being present in the veliger and getting lost during later life occurs in the pelagic drifter *Janthina*. According to HOUBRICK, the edge of the mantle is smooth.

According to MORTON & MILLER (1985) the vermetids of the genus *Serpulorbis* live cemented to hard surfaces or embedded in *Lithothamnium*, with the final half-inch of their tube turned to open upwards. There is no operculum, but the terminal plug of the foot is vividly coloured, yellow on black in *S. aotearoicus* and orange-red in *S. zelandicus*. On disturbance the animal darts back into the deepest reaches of the long tube. The foot contains a large pedal mucous gland from which long threads can be extruded to act as plankton traps supplementing the ciliary food collected by the gill. Two pedal tentacles, held erect in front of the proboscis, help to deploy these strings which are afterwards hauled in by the radula. Embryos are brooded contained within stalked egg-capsules that are attached on the inner shell wall (BANDEL 1976) or in capsules contained within the pallial cavity.

Protoconch morphology

The protoconch of *Vermetus* sp. from Lizard Island (Australia) is about 0.6 mm high and consists of about 1.8 smooth whorls. The first whorl is bulbous and measures 0.54 mm in diameter. *Vermetus* sp. from Banyuls-sur-Mer (Southern France) is very similar in size and shape consisting of about 1.5 whorls. The material is well preserved, and the whorls are sculptured with very fine spiral granulated

lines. HADFIELD et al. (1972: fig. 19D) figured the protoconch of *Vermetus alii* from the Hawaiian Islands as consisting of about two whorls being transparent or brown-tan with darker sutures. The genus *Petalococonchus* is very similar in shape and size of the protoconch. The barrel-shaped protoconch of *Petalococonchus erectus* from Santa Marta (Caribbean coast of Colombia) consists of 1.5 whorls reaching a height of 0.7 mm. The whorls are sculptured with fine spiral granulated lines (Pl. 1 fig. 7). The base is keeled. HADFIELD et al. (1972: fig. 19g) figured the protoconch of *Petalococonchus keenae* from the Hawaiian Islands as consisting of 2.5 to three cylindrical whorls reaching a height of 0.7 mm. Individuals of *Petalococonchus* hatch as free swimming veliger (BANDEL 1975) with well developed vela that could well swim and feed from phytoplankton (own observations, Gulf of Eden) (Pl. 1 fig. 8). In *Petalococonchus floridanus* the protoconch consists of at least three rapidly enlarging smooth whorls of hydroboid outline (WOODRING 1959).

Description of the protoconchs of vermetids from the Oligocene of Peyrère

Two barrel-shaped protoconch-types can be differentiated:

1. The protoconch consists of about two whorls with a height of 0.32 mm. The first whorl measures about 0.16 mm across. The larval whorls are sculptured by fine punctae (Pl. 1 fig. 5). The ultimate whorl is keeled and terminated by a strong sinusigeral notch.
2. The shell of the pediveliger of about 4.5 whorls closely resembles a modern *Vermetus*. The embryonic shell takes one whorl and measures about 0.14–0.15 mm across. It is terminated by the thickened margin of the embryos aperture. The following larval shell is smooth aside from a keel on the base of the whorls and about 0.55 mm high (Pl. 1 fig. 6).

A vermetid present from the Eocene of Gan in Southern France is very similar in shape and sculpture, but the larval shell consists of two more whorls and is 0.5 mm high. The tuberculate sculpture is weaker than in the species from Peyrère (Oligocene of southwestern France).

Dendropoma and the neomesogastropod pattern of its larval shell

Subfamily Dendropominae nov.

Diagnosis: Subfamily of sessil vermetid gastropods with irregular teleoconch and regular protoconch with a cancellate sculpture.

Genus *Dendropoma* MÖRCH, 1861

(= *Siphonium* GRAY, 1850, *Veristoa* IREDALE, 1937, *Spirogylyphus* DAUDIN, 1800)

According to SAFRIEL & HADFIELD (1988) *Dendropoma meroclista* HADFIELD & KAY, 1972 with narrow shell aperture and calcareous domed operculum lives in coralline algae encrusted reef rocks in Hawaii as well as the Red Sea. The 0.4 to 0.5 mm long protoconch is figured by them in Fig. 4 from specimens from Hawaii and Madagascar without a difference present. Its embryonic shell has a simple

groove-ridge pattern, and the larval shell shows inclined growth lines, a larger projection near the base. Several spiral ridges surround base and umbilicus, which is closed. The aperture has a short siphonal notch.

HUGHES (1978) observed the settlement of *Dendropoma* on hard substrates with the early teleoconch growing outward from the protoconch aperture attaching the shell formed in the dorsal lobe of the outer lip of the pediveliger shell. He noted this lobe of the outer lip of the pediveliger shell in *Dendropoma*, *Petalococonchus*, *Serpulorbis* and *Vermetus*.

HUGHES & LEWIS (1974) observed that the hatching veliger settles after a short time without feeding from the plankton. Own observation on the reefs near Port Sudan indicate, that the freshly hatched veligers settle below rocks and within crevices in the reef area. *Dendropoma* lives in the warm shallow lagoons of the off-shore reefs as well as on the exposed reef crest among rocks and fully integrated into coral and coralline algal growths. Here in 0.5 to 1.0 m deep water they produce the large mucus net which has been described in detail by HUGHES & LEWIS (1974).

Protoconch morphology

The protoconch of *Dendropoma maxima* as it develops within the egg case and is hatching was found in Port Sudan. Egg cases each holding 30–40 embryos are attached to the inner walls of parental tubes taken from the top of coral reefs where the adult shells were hammered off. Usually different capsules found here show a different degree of embryonic development, so that there is a more or less continuous production of hatching pediveliger larvae. The shell consists of one bulbous whorl with a groove and ridge pattern and a half whorl with a regular ornament of axial ribs which are crossed by spiral lirae forming a pattern of ladders (Pl. 2 fig. 4). This ornament of rectangles ends in a low basal spiral keel, and the rounded base up to the narrow umbilicus is smooth. This keel is also observed as spiral line of small tubercles on the first whorl. The aperture is round and about as wide as high, and shell is not mineralized with a continuous layer within.

The protoconch of *Dendropoma* sp. from the Oligocene of Peyrère (Southern France) is very similar (Pl. 2 fig. 2). But here the embryonic whorl measures only about 0.13 mm across while it is 0.37 in *D. maxima*. The pediveliger shell is 0.55 mm high. The base of the ultimate whorl shows three spiral keels. The protoconch of *Dendropoma* sp. from the Eocene of Gan (Southern France) resembles the species from Peyrère in shape and dimensions of the protoconch, but in the former the axial ribs are considerably stronger (Pl. 1 fig. 1).

Discussion

The morphology of the protoconch of *Dendropoma maxima* very closely resembles that of *Provanna* as illustrated and described by WARÉN & PONDER (1991). The tuberculate surface of the first whorl grades into a pattern of axial ribs on the second whorl which is featured by fine spiral lines forming a reticulate sculpture. The shell of the protoconch of *Provanna* is slightly more slender, but otherwise in ornament and dimensions like that of *Dendropoma*. The Provannidae WARÉN & PONDER, 1991 are considered

to be related to the genus *Abyssochrysos* and, thus, the Abyssochrysidae TOMLIN, 1927 which according to a suggestion of HOUBRICK (1979) represent modern members of the Loxonematoidea KOKEN, 1889. WARÉN & PONDER (1991) concluded from this inferred taxonomic relationship that Provannidae represent a very antique group of gastropods of the hydrothermal vents, and they also reject their former doubts about the placement of the Abyssochrysidae within the Loxonematoidea instead of the Cerithioidea (WARÉN & PONDER 1988). A connection to the Loxonematoidea of the Palaeozoic is difficult to keep up. The genus *Loxonema* PHILLIPS, 1841 is based on a Late Silurian type species of which the protoconch is not known. A Devonian species of *Loxonema* from the Eifel in Germany turned out to belong to the Allogastropoda (BANDEL 1993). A possible relative of ancient *Loxonema*, *Polygyrina* KOKEN, 1892, from the Late Triassic of the Alps, represents a caenogastropod with quite different protoconch as found in *Provanna* or any known Cerithioidean species (BANDEL 1993, 1994). Early Devonian relatives of *Loxonema* appear to represent an own group within the Archaeogastropoda (FRYDA & BANDEL 1997).

Another possible relation of *Dendropoma* may be to the family Litiopidae within the Cerithioidea and here especially to the genus *Litiopa*. *Litiopa* is very similar in regard to the shape and dimensions of the protoconch (HOUBRICK 1987: 12, fig. 8). The sculpture of the *Dendropoma* protoconch also resembles that of some members of the genus *Cypraea* (Neomesogastropoda, Pl. 2 fig. 3) (BANDEL 1991, 1993; BANDEL & RIEDEL 1994).

Turritellids

Turritellidae have a tower-shaped shell with many whorls ornamented usually with spiral ridges. The aperture is small and rounded, and the operculum is horny. Representatives of the Turritellidae developed a specific mode of life that is endobenthic sessil within a soft, usually sandy substrate for most of the year. *Turritella* hides in the sediment, pumps water through its pallial cavity and extracts from it food particles. The suspension feeding animal leaves its resting place only when conditions have deteriorated due to sedimentation or once in the year during the short reproduction period (BANDEL 1975, 1976). *Turritella variegata* (LINNÉ, 1758) lives within the muddy soft sediment at water depth greater than 2 m in the Caribbean Sea near Santa Marta/Colombia (BANDEL & WEDLER 1987). The elongate turreted shell is oriented parallel to the sediment surface, but completely hidden below it. Through a pit in the sediment above the operculum sea water is sucked in from which planktonic organisms and suspended particles are extracted for food. If undisturbed *T. variegata* leaves its feeding and resting place only once a year for spawning. Copulating males expell capsules filled with sperma which enter the pallial cavity of the female via the siphon of the mantle. After fertilization the females produce egg capsules which are attached like grapes to a hard substrate. After spawning *T. variegata* disappears again into the bottom substrate to reappear one year later.

As ANKEL (1971) noted, the operculum of the European *Turritella communis* carries bristles that can be applied to keep sediment from entering the pallial cavity when the animal is withdrawn into its shell up to the plane of the aperture. With this position filtering of food is still possible

with a stream coming into the pallial cavity above the head. Here an additional screen of pallial tentacles can keep out unwanted large particles. The water then passes along the ciliated filaments of the gill, and food particles are here trapped by mucus. Particles, thus, collected from the water current are passed on and concentrated in a mucus rod that migrates in a ciliary band on the neck towards the head until it can be picked up by the snout aided with the teeth of the radula. Water leaves the pallial cavity channelled by the foot that forms an open tube directing the current to a stream that moves in a 90° angle to the ingoing water. Thus, ingested water will not mix with egested water. The bristles of the operculum can only be of an aid in keeping out larger particles from the pallial cavity when the animal is half way withdrawn into its shell. When the foot is extended further out it lies outside the zone of water streams. The egestion channel formed by the foot can be directed by the musculature of the foot and can, thus, be employed to blow particles of the sediment out of the way.

The turritellid *Maoricolpus roseus* (QUOY & GAIMARD, 1834) screens with special tentacles on the inner side of the mantle edge and on the siphon the entrance to the pallial cavity (own observation in March 1992). Otherwise it closely resembles *Turritella* and can be regarded to belong to this genus. It lives often quite exposed openly on the rocky and sandy bottom in Otago Harbour/Southern New Zealand. The operculum is concentrically constructed and has no frill and is so small that it has to be pulled far in behind the aperture in order to seal the shell. It is flexible on the margins and closes the shell perfectly when the animal is withdrawn deeply. Water enters the pallial cavity through a hole in the sediment along the mantle covered siphon and is guided out again along a fold formed by the foot. The species occurs from the beach and lower intertidal zone down to greater depth on the shelf and was still dredged off Otago Harbour on the shelf alive from 200 m deep water where it is living within the bryozoan sponge habitat. Variable color patterns occur. For description also see MORTON & MILLER (1968). The turritellid mode of life can be traced back in time to the Lower Cretaceous (SCHRÖDER 1995).

Description of the protoconch

Turritella communis from the Mediterranean Sea was described by RICHTER & THORSON (1975). Own observations on larval shells from the region of Banyuls-sur-Mer (Southern France) indicate that they are about 0.39 mm high and 0.28 mm wide. The embryonic portion measures 0.08 to 0.09 mm in width. The veliger has also been described and sketched by FRETTER & PILKINGTON (1970). The pediveliger-shell of a turritellid from the plankton of the Red Sea consists of 5.5 rounded whorls and reached a height of 0.65 mm (Pl. 2 fig. 5). The initial cap is 0.03 mm wide. It is followed by a bulbous first whorl that takes about 0.1 mm in diameter. The initial cap is smooth. After 0.5 whorls fine spiral lines of tubercles set on which are concentrated on the lower half of the whorls. On the second whorl two keels are present, one median and the other near the basal suture of the whorls.

The protoconch of a turritellid from the Eocene of Gan in Southern France is very similar in regard to the dimensions of the initial whorl and to the sculpture of the larval whorls (Pl. 2 fig. 6). But in contrast to the former the latter

protoconch of 3.5 whorls only reached a height of 0.36 mm. The transition from the protoconch to the teleoconch is marked by thickened rim of the pediveliger shell. The protoconch of the turritellid *Haustator polonicus* SCHRÖDER, 1995 from the Valangin of Tomoschow/Poland is very similar, but in contrast to the former it takes up to six whorls, and the point of hatching is marked by a rim after half a whorl of the embryonic shell. There is no sharp rim between protoconch and teleoconch. SCHRÖDER (1995) interpreted a greater density of growth lines to indicate the point of transition from protoconch to teleoconch.

Vermicularia

Hard substrates can also be settled by turritellids. On soft substrates in lagoons and shallow regions of the sea of Bermuda the young individuals of *Vermicularia spirata* move about on mud and through algal thickets up to the seventh or eighth volution of their shell. Individuals of this species not coming into contact with hard substrates form some more volutions of the shell which no longer are in contact with each other forming a more or less regular open spiral coil (Pl. 2 fig. 7). This had already been observed and described by GOULD (1968). He noted that the onset of uncoiling in *Vermicularia spirata* is so variable that under certain conditions the defining character of the genus may not appear at all. More usually individuals leave the soft substrate in this stage of ontogenetic development and crawl up onto a dead coral or some other type of hard substrate. The gastropod remains here from now on and cements the shell to it. One side of the apertural margin it attached solidly to the hard surface of the chosen substrate and reflects its surface during its growth. As own observations in Bermuda indicate the once attached animal reduced the size of the foot which serves from now on as operculum manipulator. It is also employed in channeling water into the pallial cavity and it forms a gutter by which the water leaves that cavity again as is the case in *Turritella*. *Vermicularia pellucida* from Panama feeds in much the same way (HUGHES 1985). He noted feather-like pallial tentacles separating the inhalent from the exhalent aperture, while simpler pallial tentacles around the mantle rim trap larger particles preventing them from entering the pallial cavity.

According to BIELER & HADFIELD (1990) *Vermicularia spirata* (PHILIPPI, 1836) from the Florida Keys lives mainly embedded in the white sponge *Geodia gibberosa*. They observed protandrous hermaphroditism in this species. Small males are free living, become attached and undergo sex reversal. Such a connection between gastropod and sponge was not seen in Bermuda among the individuals studied there in lagoonal waters.

Protoconch morphology of *Vermicularia spirata* from Yucatan (coll. LEHNERT)

The protoconch consists of 2.5 whorls with a height of about 0.7 mm (Pl. 2 fig. 8). The first whorl measures 0.33 mm across. After 1.5 smooth embryonic whorls the onset of a strong median keel may document the beginning of a short larval stage. Another spiral keel is present near the suture or just below it. In this case the second keel may only be seen in pediveliger-shells. The protoconch is terminated by a short sinus.

The ontogeny of *Vermicularia* mediates between those mobile snails of the *Turritella*-relation and attached forms like vermetids and siliquariids.

Stephopoma with a totally different larval strategy

Family Siliquariidae, subfamily Stephopominae nov.

Diagnosis: Subfamily of siliquariid gastropods without slit with ornament of a tuberculate sculpture or ribs on a planispiral protoconch.

Remarks: According to MORTON & MILLER (1968) the family Siliquariidae in New Zealand is typified by the small pinkish white "worm shell" *Stephopoma roseum* (QUOY & GAIMARD, 1832), forming crowded clusters under low tidal stones in the northern part of the Auckland province. They stated that *Stephopoma* differs greatly in detail from *Serpulorbis* and has been found to belong to an independent line derived from the ciliary feeding Turritellidae. The foot bears an operculum crowned with long branched bristles, forming strainers preventing the entry of large particles when the operculum is held partly closed. Food is collected entirely by cilia as in the slipper limpets, and there are no mucous traps or pedal glands.

The bristle rimmed operculum was used by KEEN (1961) as indicator for the placement of *Stephopoma* with the Vermiculariinae. VAUGHT (1989) accepted this, and here *Stephopoma* finds its place in the Turritellidae, subfamily Vermiculariinae. KEEN (1961) considered the Siliquariinae, Turritellopsinae and Turritellinae to represent subfamilies of the Turritellidae, while Vermetidae represent another family.

Protoconch

The early ontogenetic shell is quite different from that of the members of the Vermetidae. As THIELE (1931) stated subgenus *Lilax* FINLEY, 1927 owns a finely granulated nuclear whorl. According to KEEN (1961) the initial whorls are flat, resembling a small *Heliacus*, lighter colored than the adult shell, and studded with radial rows of pustules. A similar shape had been noted by MORTON (1951b) who described the embryonic shell as consisting of 1.5 whorls studded with minute pustules. From the Miocene of Venezuela GIBSON-SMITH & GIBSON-SMITH (1982) described the characteristic protoconch that consists of a planorboid shell of 1.25 whorls. They thought that it represented the oldest known member of this genus and its only fossil representative. But LOZOUET (1987) described *Stephopoma fossilis* from the Upper Oligocene of Peyrère in the Aquitaine (Southern France) and noted that v.KOENEN (1891) had described a member of this genus as *Vermetus calcaratus* from the Oligocene of Lattorf/Northern Germany. LOZOUET (1987) described the protoconch as measuring 1.1 mm in diameter, consisting of 1.5 whorls covered by granules. v.KOENEN described the protoconch of *V. calcaratus* as consisting of 1.5 smooth, bulbous whorls (v.KOENEN 1891: 730, pl. 52 figs. 1–3). Thus, there are no similarities to the genus *Stephopoma*, and v.KOENEN actually described a vermetid species.

In the illustration of GIBSON-SMITH & GIBSON-SMITH (1982: fig. 1) of the protoconch of *Stephopoma pennatum* MÖRCH, 1860 from the Early Miocene of Venezuela it

looks just like that of the Upper Oligocene individuals (material from the Rijksmuseum van Natuurlijke Historie, Leiden from Peyrère).

Description of the protoconch

The protoconch consists of 1.5 whorls which are plan-spirally coiled with only a very slight dextral twist. The shell measures 1.1 mm in diameter in the Oligocene protoconch (Pl. 3 figs. 1, 6) as well as in a modern one from Swain Reef/Australia (Australian Museum, Nr. C 162 429). The initial cup-like onset of the shell measures about 0.1 mm in width (Pl. 3 fig. 6). Here the organic periostracal cover of the mineral shell shows several wrinkled spiral rows which after a half whorl change into rows of large tubercles. These are covered by periostracum and measure up to 0.05 mm in diameter. On the umbilical side the tubercles are present on the whole whorl only increasing in size. The protoconch ends with an upturned rim. There is no differentiation of an embryonic and a larval shell so that the young hatching from the egg capsules either crawl away or may swim off as pediveligers ready to settle after a short stay in the plankton and probably without feeding on planktonic organisms.

There is another Recent Australian species present from Sydney (AM, C 162 419). The protoconch measures up to 1.4 mm across, but the initial cap is only 0.07 mm wide in the visible part (Pl. 3 fig. 4). The tubercles building the sculpture of the larval shell are smaller than in the species described above. They only reach a maximal diameter of 0.02 mm. Another Recent species collected near Satonda/Indonesia is very similar in dimensions of the protoconch, but the tubercles reach a maximal diameter up to 0.04 mm (Pl. 3 figs. 2, 3).

Remarks

The Oligocene shell from France and the Miocene shell from Venezuela closely resemble that of the modern species from the Indopacific and Australia. This indicates that *Stephopoma* has changed very little. From the fossil evidence it appears that modern species have been living since Oligocene time without change in their larval ecology. LOZOUET (1987) indicated that *Segmentella* THIELE, 1925 may belong in the relation of *Stephopoma*.

A related species from Natal/South Africa is *Caporbis africana* BARTSCH, 1915 (Material from Natal Museum in Pietermaritzburg by courtesy of Richard KILBURN & David HERBERT). Its protoconch consists of about 1.5 whorls reaching up to 1.6 mm in diameter (Pl. 3 fig. 5). The onset is about 0.2 mm wide and smooth except of indistinct growth lines. The larval shell bears strong axial ribs. The protoconch is terminated by a thickened rim. It closely resembles that of *Stephopoma*, but differs not only in regard to the ornament, but also that an embryonic and larval shell can be differentiated.

Tenagodus, a slit bearing siliquariid

Siliquariidae ANTON, 1838, subfamily Siliquariinae, often grow with and within sponges. The genus of this group, *Tenagodus* GUETTARD, 1770, according to BIELER (1992), thus, represents commensal animals living within

the shelter of the sponges body. Siliquariid species have separated the food stream from the waste water stream by forming a slit or a row of openings in the shell (Pl. 3 fig. 7). This enables them to push out the waste water to the right side which therefore does not mix with the incoming fresh water. They feed with the gill.

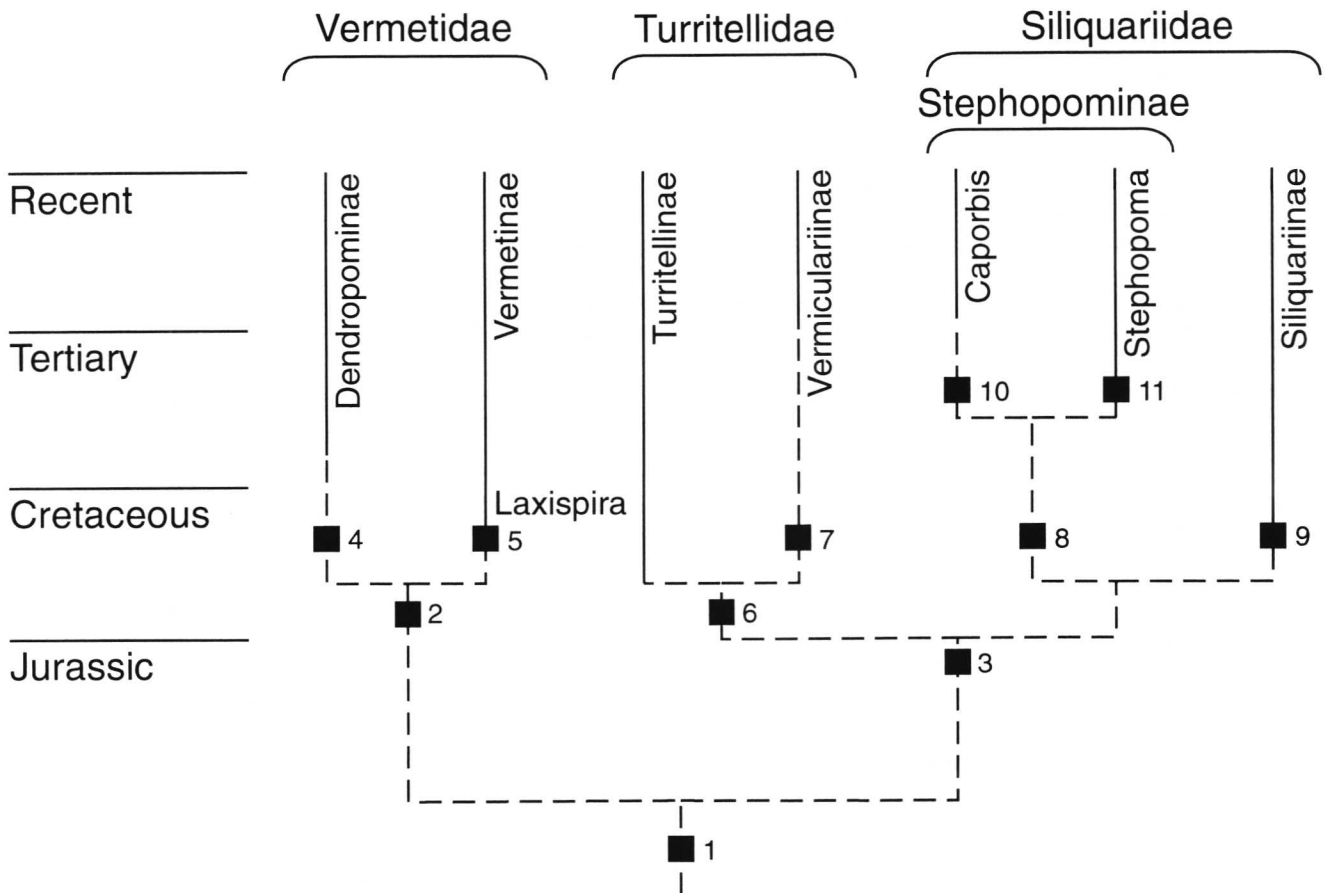
QUAAS (1902: pl. 18 fig. 20) described an openly coiling spiral form with clear slit from the Maastrichtian deposits of the western Desert in Egypt, which still seems to be the oldest record of this group of slit bearing vermetoids. Unfortunately, the original material was destroyed in Munich during the Second World War. v.KOENEN (1891: 745, pl. 51 figs. 6 a, b) described *Siliquaria striolata* and *S. squamulosa* (1891: 746, pl. 51 figs. 5 a-d) from the Lower Oligocene of Lattorf/Northern Germany without preserved protoconchs. The adult shells are spirally ribbed. The selenizone is closed on the early teleoconch whorls. Later a row of elongated holes is present.

Protoconch of modern *Tenagodus*: We studied a protoconch of *Tenagodus* that gives evidence for a lecithotrophic mode of development (Pl. 3 fig. 8). In *Tenagodus* from North Reef in Queensland/Australia (AM C 162 426) the teleoconch succeeds after 1.5 inflated embryonic whorls without an intermission of a shell formed during the planktotrophic larval stage. The embryonic shell measures 0.5 mm across. The whorls are sculptured with fine spiral lines and spiral rows of granules on the bases. GOULD (1966: 5-6, figs. 2, 3) described the planktonic protoconch of *Tenagodus squamatus* from Bermuda as 0.25 mm wide and equally high consisting of two and a quarter whorls. The first two thirds whorl is described as whitish brown and smooth. The following whorls are ornamented with rows of nodes on the upper half of the whorl and with finely granulated spiral striae on the lower.

A related species is the corkscrew shell *Pyxipoma weldii*, figured in MORTON (1951b: 26, pl. 7). It is living embedded in compact yellow sponges, often thrown up on kelp holdfasts after gales. The shell is thin and white, coiled in an elegant open spire and incised by a long slit up to the right side, serving as an exhalant path. The opercula close quickly as the animals dart back into their tubes and are crowned with a scalet sponge, studding the surface of the whole mass like currants on a cake (MORTON & MILLER 1968).

Are there older vermetoids than those of the Upper Cretaceous?

So called Vermetids from the Carboniferous of Ireland seem to represent an independent branch without known Mesozoic relation. WENZ (1939: fig. 1938) mentioned the genus *Provermicularia* from the St. Cassian-Formation/Italy which could not be verified in revision of that fauna and is also not mentioned by ZARDINI (1978-1985). Vermetoid tubes older than the Upper Cretaceous lack preserved protoconchs. So it is difficult to make remarks on their systematic position. Perhaps they represent remains of *Serpulospira* (= *Pseudotubina*) that may be the last surviving but problematic euomphaloid species (ZARDINI 1978: pl. 1 fig. 21, BANDEL 1988).



Text-fig. 1: Proposed phylogenetic model of vermetoid gastropods. – **Characters:**

- | | | |
|-----------------------------------|--|---|
| 1 cerithiimorph protoconch | 5 tuberculate protoconch-sculpture | 9 slit bearing teleoconch |
| 2 feeding by mucous net | 6 turritellid protoconch | 10 axially ribbed protoconch |
| 3 filter-feeding | 7 loosely coiled to irregular teleoconch | 11 protoconch with spiral rows of nodules |
| 4 cancellate protoconch-sculpture | 8 planispiral protoconch | |

Summary

The vermetoid mode of live has evolved at least twice independently in basic caenogastropod relation (text-fig. 1). *Laxispira* within the Vermetoidea from the Upper Cretaceous represents the oldest vermetoid genus with preserved protoconchs. When settling after metamorphosis the animals could either have lived in soft bottoms building a loosely coiled shell without attachment to the substrate, or they could have been attached to hard substrate forming an irregular tube and building reef-like aggregations. Eocene to Recent Vermetinae show similar protoconchs in shape, but the sculpture is weaker in modern species. The embryonic shells of Oligocene to Recent species are more bulbous and reflect a more lecithotrophic mode of early ontogeny. In the modern representatives of this group species are feeding with the aid of a mucous net secreted by a mucus gland of the foot. Their mode of life is always attached to hard substrates.

The genus *Dendropoma*, subfamily Dendropominae, is closely related to the Vermetinae in regard to its biology but shows a rather different cancellate protoconch sculpture that is documented since the Eocene. There is a certain trend to reduce the strength of the ornament from Eocene to Recent. Especially, the axial ribs of modern larval shells are weaker than those seen in Oligocene species. The cancellate pattern of the sculpture closely resembles to that of the families

Provannidae and Litiopidae (Cerithioidea). The protoconchs of Eocene and Oligocene species reflect a less lecithotrophic development with considerably smaller embryonic whorls and a longer planktonic stage than is seen in modern *Dendropoma*. In contrast the protoconchs of modern species have bulbous embryonic shells and the larval shells reflect short-time veliger stages.

Within the family Turritellidae, subfamily Vermiculariinae, the modern genus *Vermicularia* is characterized by a mode of adult life convergent to that of *Laxispira*. It differs in the regularly coiled early teleoconch. Coiling becomes detached and loosely when the animal settles in soft substrates. The shell may grow irregularly when it is attached to hard substrates. In contrast to members of the Vermetoidea members of the turritellids feed only mucociliary, and there is no mucous net. Turritellidae can be traced back to the base of the Cretaceous (SCHRÖDER 1995).

Members of the related family Siliquariidae show different strategies of ontogeny at least since the Eocene. The commensal genus *Tenagodus*, subfamily Siliquariinae, lives within sponges. The teleoconch is characterized by a slit. It is spirally ribbed in Oligocene species and smooth except for growth lines in Recent ones. Early ontogeny may be direct or indirect. The larval shell of planktonic veligers consisting of two and a quarter whorls is ornamented with spiral rows of nodes. In direct development the protoconch

is sculptured with very fine spiral lines and rows of granules on the base of the whorls. The protoconch of the related genus *Pyxipoma* shows a sculpture of fine spiral granulated lirae.

The genus *Stephopoma*, subfamily Stephopominae, lives attached to hard substrates and lacks a slit. The protoconch consists of about 1.5 whorls. Development appears to be direct or almost so. The protoconch morphology of *Stephopoma* has not changed since the Oligocene. The typical sculptural element of the Siliquariidae of fine spiral rows of granules is also present on the first embryonic whorl of the *Stephopoma*-protoconch. *Caporbis* from Natal/South Africa is similar to *Stephopoma* in shape of the protoconch, but

ornament consists of strong axial ribs, and embryonal and larval shell can be well distinguished.

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Plate 1

Vermetidae RAFINESQUE, 1815, subfamily Vermetinae RAFINESQUE, 1815

- Fig. 1: Shell of *Laxispira libycus* OUAAS, 1902 from the Maastrichtian of Western Desert (Egypt). The individual built a loosely coiled shell that was not attached. It measures 3.2 cm in length.
- Fig. 2: Attached individuals of *Laxispira libycus* supporting each others formed little reef-like structures. Max. length: 13.4 cm.
- Fig. 3: Regularly coiled protoconch and loosely coiled early teleoconch of *Laxispira lumbricalis* GABB, 1877 from the Maastrichtian Ripley Formation of Coon Creek (Tennessee). The shell measures 1.7 mm in length.
- Fig. 4: The 0.5 mm high protoconch of *Laxispira lumbricalis* is sculptured with spiral rows of tubercles and terminated by a strong projection of the outer margin of the pediveligers aperture.
- Fig. 5: The 0.32 mm high protoconch of a vermetid from the Oligocene of Peyrère (southern France) is sculptured with spiral rows of granules.
- Fig. 6: Pediveliger-shell of another species from Peyrère is 0.55 mm high and smooth aside from a keel on the base of the larval whorls. It closely resembles a modern *Vermetus*.
- Fig. 7: The 0.7 mm high larval shell of *Petalconchus erectus* from the Caribbean coast of Columbia is sculptured with fine granulated spiral lines.
- Fig. 8: Pediveliger of *Petalconchus* from the plankton of the Gulf of Eden with well developed velum. Length of the shell: 0.6 mm.

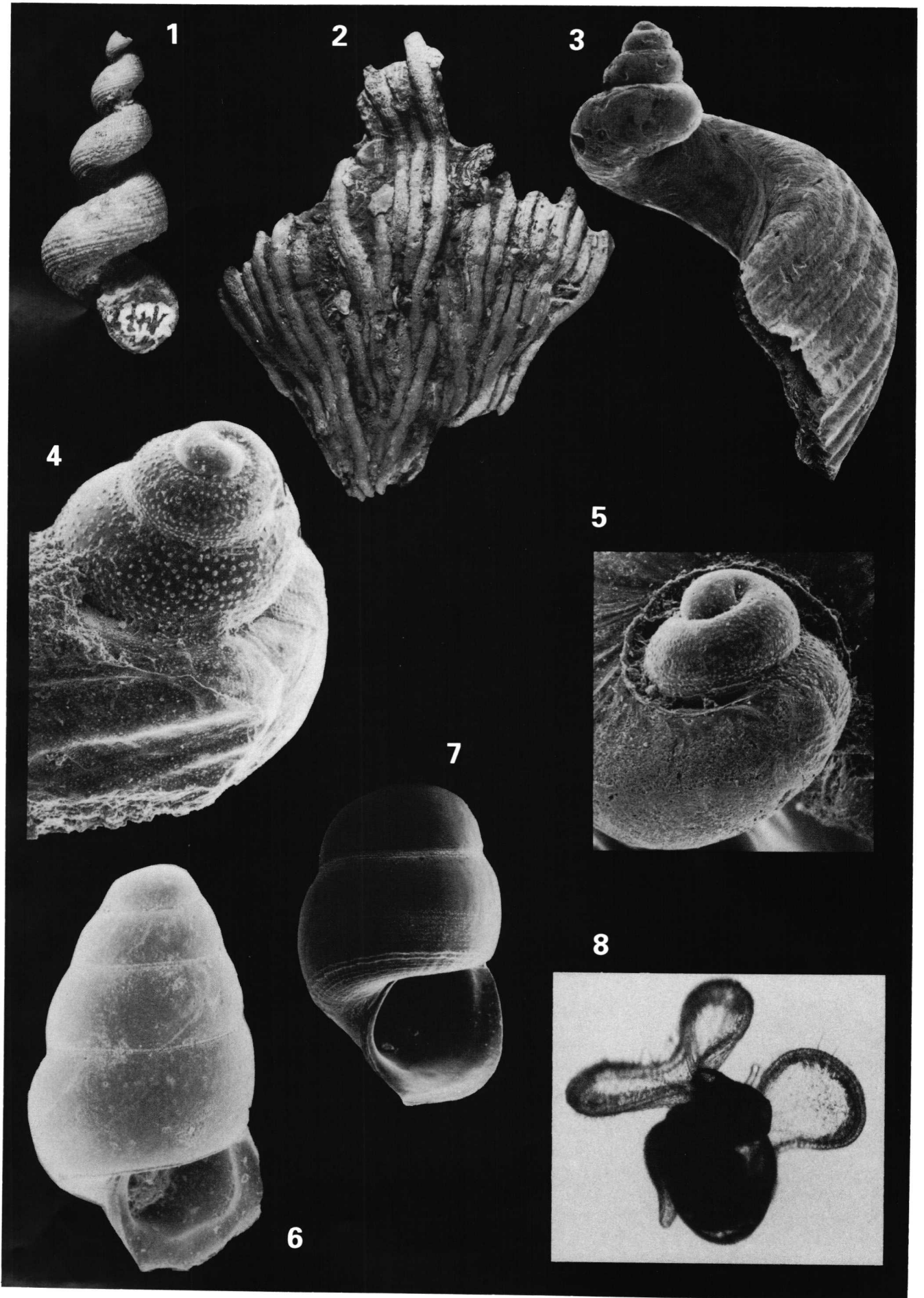


Plate 2

Vermetidae RAFINESQUE, 1815, subfamily Dendropominae nov. and Turritellidae LOVÉN, 1847

- Fig. 1: The juvenile shell of *Dendropoma* from the Eocene of Gan (southern France) is 1.0 mm high. The protoconch is ornamented by strong axial ribs and weak spiral threads.
- Fig. 2: Pediveliger-shell of *Dendropoma* from the Oligocene of Peyrère (southern France) with a sculpture of axial ribs crossed by spiral lirae forming a pattern of ladders is 0.55 mm high.
- Fig. 3: The sculpture of a 0.6 mm high pediveliger-shell of *Cypraea* (Neomesogastropoda) from Peyrère (southern France) closely resembles that of *Dendropoma*.
- Fig. 4: Lecithotrophic protoconch of *Dendropoma maxima* from Port Sudan (Red Sea) with 1.5 inflated whorls that reached a height of 0.5 mm.
- Fig. 5: The pediveliger-shell of a turritellid from the plankton of the Red Sea consists of 5.5 rounded whorls ornamented by two spiral keels. It measures 0.65 mm in height.
- Fig. 6: The protoconch of a turritellid from the Eocene of Gan (southern France) closely resembles that of the modern species but only took 3.5 whorls of 0.36 mm height.
- Fig. 7: Shell of *Vermicularia spirata* from Bermuda. The protoconch and early teleoconch are regularly coiled, later whorls of the teleoconch became loosely coiled. The shell measures 8.45 mm in height.
- Fig. 8: The 0.7 mm high turritellid protoconch of *Vermicularia spirata* from Yucatan (coll. LEHNERT) is terminated by a short sinus.

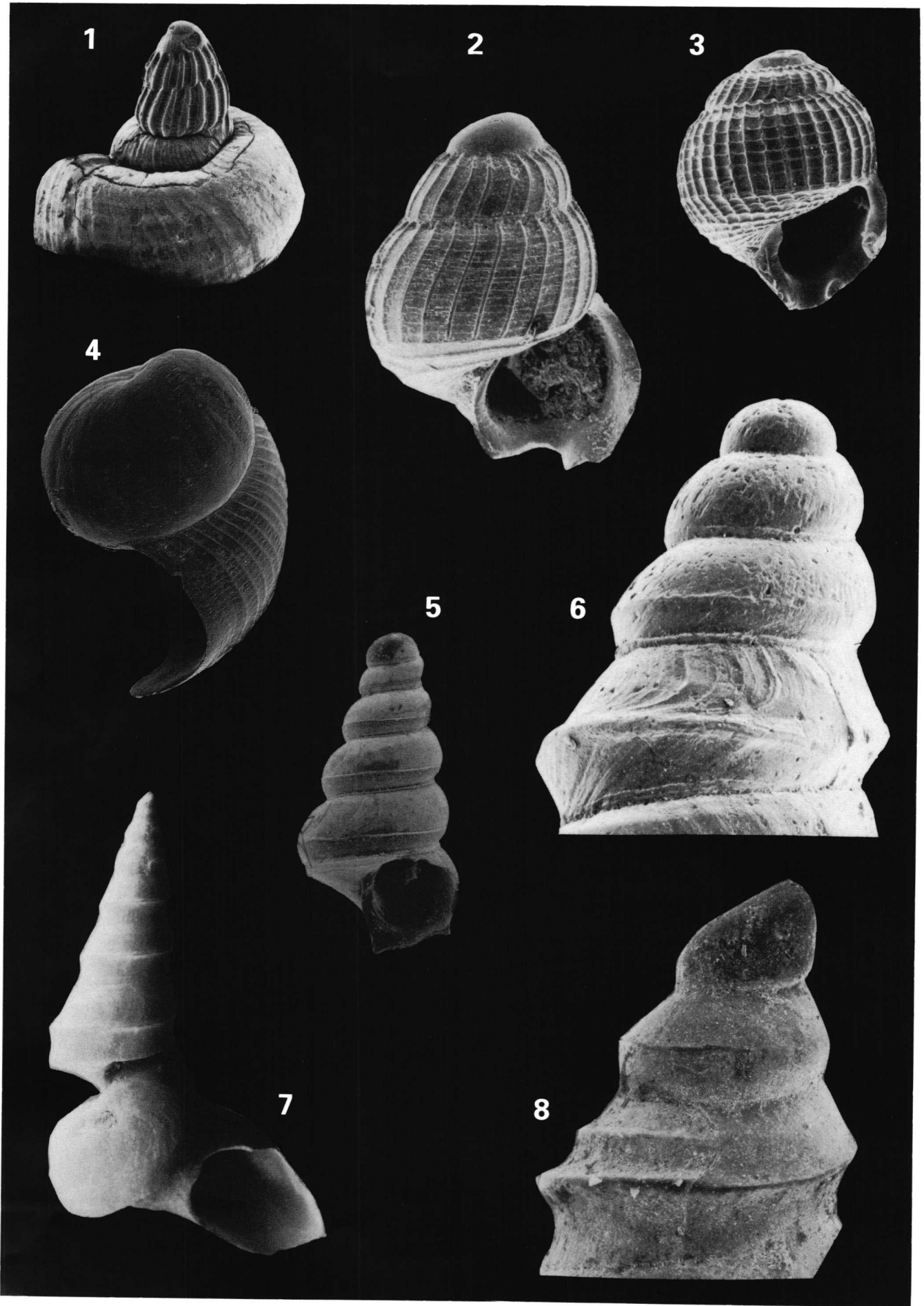
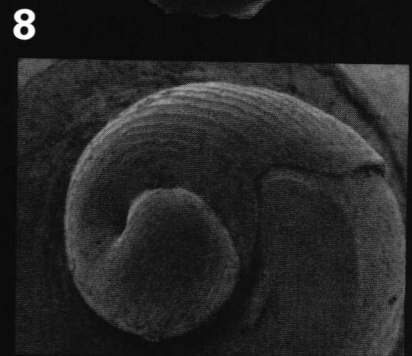
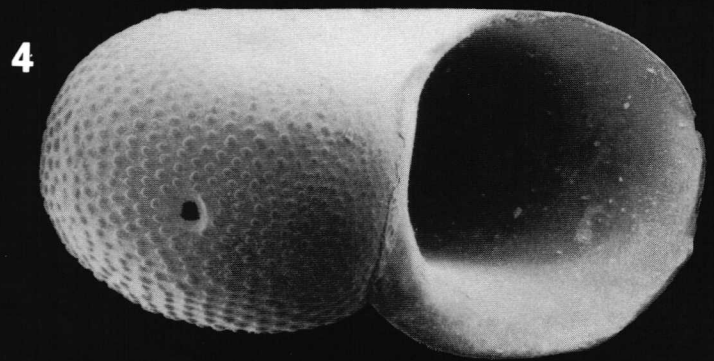
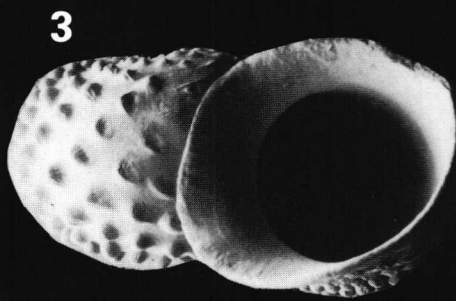
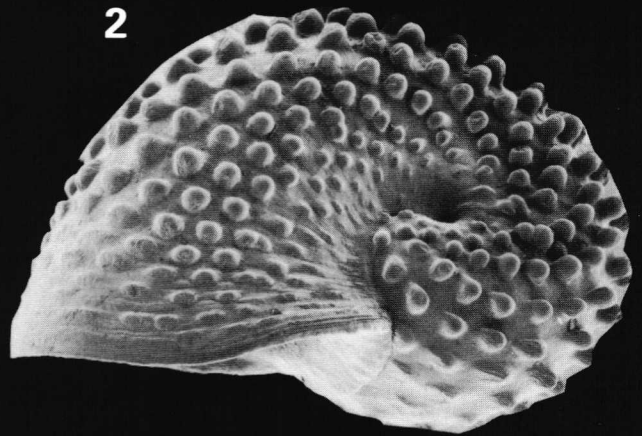
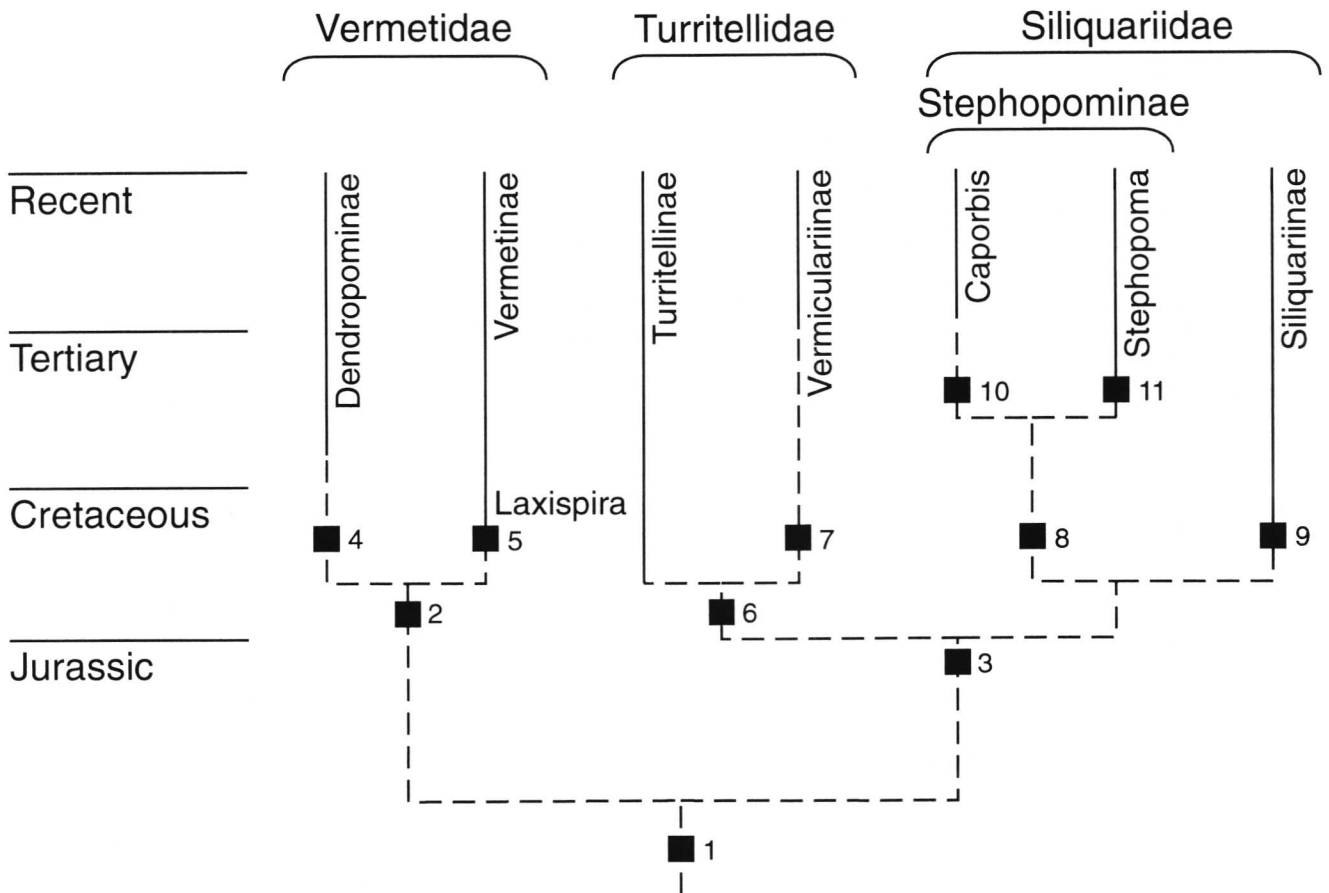


Plate 3

Siliquariidae ANTON, 1838

- Fig. 1: Apical view of an early ontogenetic shell of *Stephopoma fossilis* from the Oligocene of Peyrère (southern France). The protoconch with a slight dextral twist measures 1.1 mm across.
- Fig. 2: Umbilical view of a recent *Stephopoma* sp. from Satonda (Indonesia). The shell measures 1.4 mm in diameter and closely resembles the fossil species.
- Fig. 3: Apertural view of the same specimen as in fig. 2. The shell measures 1.25 mm in length.
- Fig. 4: Apertural view of a protoconch of a recent *Stephopoma* sp. from Swain Reef (Australia) (AM 162 419) with small tubercles only reaching a diameter of 0.02 mm. The shell measures 1.3 mm in length.
- Fig. 5: The protoconch of *Caporbis africana* BARTSCH, 1915 from Natal (South Africa) bears strong axial ribs. The shell measures 1.6 mm in diameter.
- Fig. 6: Detail of the nuclear whorl of the specimen in fig. 1 with a sculpture of fine spiral threads that change into rows of large tubercles after half a whorl. The cup-like nonspiral measures 0.1 mm in width.
- Fig. 7: The 2.4 mm high shell of *Tenagodus* from Queensland (Australia) is characterized by a slit separating the food stream from the waste water stream.
- Fig. 8: Early ontogenetic shell of *Tenagodus* from Queensland (Australia) (AM C 162 426). The teleoconch succeeds after 1.5 inflated embryonic whorls measuring 0.5 mm across without an intermission of a shell formed during a planktotrophic larval stage.





Text-fig. 1: Proposed phylogenetic model of vermetoid gastropods. – **Characters:**

- | | | |
|-----------------------------------|--|---|
| 1 cerithiimorph protoconch | 5 tuberculate protoconch-sculpture | 9 slit bearing teleoconch |
| 2 feeding by mucous net | 6 turritellid protoconch | 10 axially ribbed protoconch |
| 3 filter-feeding | 7 loosely coiled to irregular teleoconch | 11 protoconch with spiral rows of nodules |
| 4 cancellate protoconch-sculpture | 8 planispiral protoconch | |

Summary

The vermetoid mode of live has evolved at least twice independently in basic caenogastropod relation (text-fig. 1). *Laxispira* within the Vermetoidea from the Upper Cretaceous represents the oldest vermetoid genus with preserved protoconchs. When settling after metamorphosis the animals could either have lived in soft bottoms building a loosely coiled shell without attachment to the substrate, or they could have been attached to hard substrate forming an irregular tube and building reef-like aggregations. Eocene to Recent Vermetinae show similar protoconchs in shape, but the sculpture is weaker in modern species. The embryonic shells of Oligocene to Recent species are more bulbous and reflect a more lecithotrophic mode of early ontogeny. In the modern representatives of this group species are feeding with the aid of a mucous net secreted by a mucus gland of the foot. Their mode of life is always attached to hard substrates.

The genus *Dendropoma*, subfamily Dendropominae, is closely related to the Vermetinae in regard to its biology but shows a rather different cancellate protoconch sculpture that is documented since the Eocene. There is a certain trend to reduce the strength of the ornament from Eocene to Recent. Especially, the axial ribs of modern larval shells are weaker than those seen in Oligocene species. The cancellate pattern of the sculpture closely resembles to that of the families

Provannidae and Litiopidae (Cerithioidea). The protoconchs of Eocene and Oligocene species reflect a less lecithotrophic development with considerably smaller embryonic whorls and a longer planktonic stage than is seen in modern *Dendropoma*. In contrast the protoconchs of modern species have bulbous embryonic shells and the larval shells reflect short-time veliger stages.

Within the family Turritellidae, subfamily Vermiculariinae, the modern genus *Vermicularia* is characterized by a mode of adult life convergent to that of *Laxispira*. It differs in the regularly coiled early teleoconch. Coiling becomes detached and loosely when the animal settles in soft substrates. The shell may grow irregularly when it is attached to hard substrates. In contrast to members of the Vermetoidea members of the turritellids feed only mucociliary, and there is no mucous net. Turritellidae can be traced back to the base of the Cretaceous (SCHRÖDER 1995).

Members of the related family Siliquariidae show different strategies of ontogeny at least since the Eocene. The commensal genus *Tenagodus*, subfamily Siliquariinae, lives within sponges. The teleoconch is characterized by a slit. It is spirally ribbed in Oligocene species and smooth except for growth lines in Recent ones. Early ontogeny may be direct or indirect. The larval shell of planktonic veligers consisting of two and a quarter whorls is ornamented with spiral rows of nodes. In direct development the protoconch

looks just like that of the Upper Oligocene individuals (material from the Rijksmuseum van Natuurlijke Historie, Leiden from Peyrère).

Description of the protoconch

The protoconch consists of 1.5 whorls which are planispirally coiled with only a very slight dextral twist. The shell measures 1.1 mm in diameter in the Oligocene protoconch (Pl. 3 figs. 1, 6) as well as in a modern one from Swain Reef/Australia (Australian Museum, Nr. C 162 429). The initial cup-like onset of the shell measures about 0,1 mm in width (Pl. 3 fig. 6). Here the organic periostracal cover of the mineral shell shows several wrinkled spiral rows which after a half whorl change into rows of large tubercles. These are covered by periostracum and measure up to 0.05 mm in diameter. On the umbilical side the tubercles are present on the whole whorl only increasing in size. The protoconch ends with an upturned rim. There is no differentiation of an embryonic and a larval shell so that the young hatching from the egg capsules either crawl away or may swim off as pediveligers ready to settle after a short stay in the plankton and probably without feeding on planktonic organisms.

There is another Recent Australian species present from Sydney (AM, C 162 419). The protoconch measures up to 1.4 mm across, but the initial cap is only 0.07 mm wide in the visible part (Pl. 3 fig. 4). The tubercles building the sculpture of the larval shell are smaller than in the species described above. They only reach a maximal diameter of 0.02 mm. Another Recent species collected near Satonda/Indonesia is very similar in dimensions of the protoconch, but the tubercles reach a maximal diameter up to 0.04 mm (Pl. 3 figs. 2, 3).

Remarks

The Oligocene shell from France and the Miocene shell from Venezuela closely resemble that of the modern species from the Indopacific and Australia. This indicates that *Stephopoma* has changed very little. From the fossil evidence it appears that modern species have been living since Oligocene time without change in their larval ecology. LOZOUET (1987) indicated that *Segmentella* THIELE, 1925 may belong in the relation of *Stephopoma*.

A related species from Natal/South Africa is *Caporbis africana* BARTSCH, 1915 (Material from Natal Museum in Pietermaritzburg by courtesy of Richard KILBURN & David HERBERT). Its protoconch consists of about 1.5 whorls reaching up to 1.6 mm in diameter (Pl. 3 fig. 5). The onset is about 0.2 mm wide and smooth except of indistinct growth lines. The larval shell bears strong axial ribs. The protoconch is terminated by a thickened rim. It closely resembles that of *Stephopoma*, but differs not only in regard to the ornament, but also that an embryonic and larval shell can be differentiated.

Tenagodus, a slit bearing siliquariid

Siliquariidae ANTON, 1838, subfamily Siliquariinae, often grow with and within sponges. The genus of this group, *Tenagodus* GUETTARD, 1770, according to BIELER (1992), thus, represents commensal animals living within

the shelter of the sponges body. Siliquariid species have separated the food stream from the waste water stream by forming a slit or a row of openings in the shell (Pl. 3 fig. 7). This enables them to push out the waste water to the right side which therefore does not mix with the incoming fresh water. They feed with the gill.

QUAAS (1902: pl. 18 fig.20) described an openly coiling spiral form with clear slit from the Maastrichtian deposits of the western Desert in Egypt, which still seems to be the oldest record of this group of slit bearing vermetoids. Unfortunately, the original material was destroyed in Munich during the Second World War. v.KOENEN (1891: 745, pl. 51 figs. 6 a, b) described *Siliquaria striolata* and *S. squamulosa* (1891: 746, pl. 51 figs. 5 a-d) from the Lower Oligocene of Lattorf/Northern Germany without preserved protoconchs. The adult shells are spirally ribbed. The selenizone is closed on the early teleoconch whorls. Later a row of elongated holes is present.

Protoconch of modern *Tenagodus*: We studied a protoconch of *Tenagodus* that gives evidence for a lecithotrophic mode of development (Pl. 3 fig. 8). In *Tenagodus* from North Reef in Queensland/Australia (AM C 162 426) the teleoconch succeeds after 1.5 inflated embryonic whorls without an intermission of a shell formed during the planktotrophic larval stage. The embryonic shell measures 0.5 mm across. The whorls are sculptured with fine spiral lines and spiral rows of granules on the bases. GOULD (1966: 5-6, figs. 2, 3) described the planktonic protoconch of *Tenagodus squamatus* from Bermuda as 0.25 mm wide and equally high consisting of two and a quarter whorls. The first two thirds whorl is described as whitish brown and smooth. The following whorls are ornamented with rows of nodes on the upper half of the whorl and with finely granulated spiral striae on the lower.

A related species is the corkscrew shell *Pyxipoma weldii*, figured in MORTON (1951b: 26, pl. 7). It is living embedded in compact yellow sponges, often thrown up on kelp holdfasts after gales. The shell is thin and white, coiled in an elegant open spire and incised by a long slit up to the right side, serving as an exhalant path. The opercula close quickly as the animals dart back into their tubes and are crowned with a scalet sponge, studding the surface of the whole mass like currants on a cake (MORTON & MILLER 1968).

Are there older vermetoids than those of the Upper Cretaceous?

So called Vermetids from the Carboniferous of Ireland seem to represent an independent branch without known Mesozoic relation. WENZ (1939: fig. 1938) mentioned the genus *Provermicularia* from the St. Cassian-Formation/Italy which could not be verified in revision of that fauna and is also not mentioned by ZARDINI (1978-1985). Vermetoid tubes older than the Upper Cretaceous lack preserved protoconchs. So it is difficult to make remarks on their systematic position. Perhaps they represent remains of *Serpulospira* (= *Pseudotubina*) that may be the last surviving but problematic euomphaloid species (ZARDINI 1978: pl. 1 fig. 21, BANDEL 1988).