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The history and relationship of *Scaliola*, a gastropod that cements particles to its shell

by

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With 3 Plates and 5 Figures

Contents

Abstract

Scaliola attaches grains of sand to its shell. It thus camouflages its shell within its sandy living environment. Living *Scaliola bella* from the Indopacific and fossil *S. jansseni* n. sp. from the Eocene of the Paris Basin are described and compared with relatives from the Maastrichtian of the southeast USA and the Oligocene of the Aquitaine Basin, southern France. The larval shell of *Scaliola* places it in the Cerithioidea near the genus *Bittium* but its own family Scaliolidae. Morphological features of the adult and larval shell show a wide range of variation within the species as is characteristic of some cerithioid species. Their history can be traced back in time to Upper Triassic forms like *Ampezzoscala* n. gen.

Zusammenfassung

Scaliola baut Fremdpartikel in seine Schale mit ein, so wie man das für *Xenophora* weithin kennt. Damit wird das Gehäuse im indopazifischen Lebensbereich der kleinen Schnecke auf sandigen Böden im flachen Meer getarnt. Die heutige *S. bella* zeigt einige Variation sowohl in der Größe der Larvalschale als auch Dimension und Gestalt der Adultschale. Aus dem Eozän des Pariser Beckens wird die neue Art *Scaliola jansseni* beschrieben und in Relation zur rezenten Art wie auch zu weiteren fossilen Arten aus dem

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Oligozän der Aquitaine wie aus dem Maastricht der südöstlichen USA gesetzt. Die Larvalschale von *Scaliola* ähnelt jener der bei Cerithioidea auftretenden Formen, besonders jener von *Bittium*. *Scaliola* präsentiert somit eine eigenständige Gruppe kleinwüchsiger Arten der Scaliolidae innerhalb der Cerithioidea (Caenogastropoda), die sich bis in die Oberkreide zurückverfolgen läßt. Die Cerithioidea mit ähnlichen Gehäusegestalten wie bei der Verwandtschaft von *Scaliola* anzutreffen sind, lassen sich bis in die Obertrias und hier die Gattung *Ampezzoscala* n. gen. belegen.

1. Introduction

Cementation of particles to the shell is rare among gastropods. The best known case of a gastropod that agglutinates particles to its shell is *Xenophora* (Pl. 1, Fig. 1). This large sized caenogastropod has somewhat unclear relation to the Stromboidea and Calyptraeoidea (PONDER 1983). Modern species of *Xenophora* live in tropical seas. The genus can be traced back in time to the Upper Cretaceous (PONDER 1983). Here the Coffee Sand and Coon Creek fauna contains species with all characters of the larval and adult shell of members of the modern seas (SOHL 1960, DOCKERY 1991, own observations). The species of *Xenophora* attach rubble and shells to their conchs until they look like a small heap of debris lying on the bottom of the sea (BANDEL & WEDLER 1987). Particles are selected individually, cleaned with bites of the mouth and held to the shell margin with the aid of the head until they are attached firmly by shell secretions of the tissue of the mantle margin (Pl. 1, Fig. 1).

Similarly conical shells with an overhanging ledge at the basal margin of the last formed whorl were produced by the Devonian carrier shell *Philoxene* (GOLDFUSS, 1844). Members of this genus are thought to belong to the Euomphaloidea (KNIGHT et al. 1960), a group of gastropods of rather uncertain relation (BANDEL 1988). *Philoxene* attached shell debris, preferrably shell remains of brachiopods, to its conch (GOLDFUSS 1844, LINSLEY & YOCHELSON 1973).

Less wellknown is the case of *Scaliola*, a little turriform gastropod that nowadays lives on sandy bottoms in the warm shallow sea of the Indopacific. During Tertiary times (Middle Eocene, Lutet to Upper Oligocen, Chatt) it also occurred in Europe in a similar ecologic situation (COSSMANN & PEYROT 1917, LOZOUET 1986). *Scaliola* cements grains of sand to its shell. Well preserved specimens of *Scaliola* from the Middle Eocene deposits of Saffrè (Paris Basin) could be extracted from samples collected by Arie Janssen (Leiden). Modern individuals of this genus were taken from sediment samples collected from the Red Sea, the Gulf of Eden, the Arabian Gulf and Indonesia (EL-NAKHAL), the Gulf of Aqaba (BANDEL), the Sea near Satonda (Indonesia) and off southern China (EVA VINX, Hamburg) and near Mactan Island (Cebu City) Philippines (GERO HILLMER, Hamburg). Living individuals were collected and studied on Lizard Island in the Australian Barrier Reef (BANDEL, 1991, Lizard Island Research Station). The oldest representatives of the genus *Scaliola* have been collected by N. F. Sohl (U. S. Geological Survey) from the Maastrichtian Ripley Formation of the USA. Studied individuals of recent *Scaliola* are placed in the collection of the Geologisch-Paläontologisches Institut und Museum of the university of Hamburg SGPHM Kat. Nr. 3235–3240 and the fossil individuals are placed in the collection of the National Museum of Natural History in Leiden, Nr. RGM 229.793. The short note: "Geographical distribution of the small gastropod genus *Scaliola*" which appeared in micropaleontology 37, pp. 423–424, 1991 was not authorized by K. Bandel and its form and content are to the responsibility of El-Nakhal alone. Its results disagree to some extent with those presented here.

2. Known data on *Scaliola*

The genus *Scaliola* is based on *S. bella* A. ADAMS 1860 that lives in the Indopacific near Japan. The illustration of the type presented by ADAMS has been reproduced by WENZ (1938, Fig. 2180). A comparison of this illustration with here discussed shells indicates that it could be conspecific to the slender specimen found at the coast of Jemen (Pl. 2, Fig. 4). But in contrast to noted sculpture of the here studied individuals, the diagnosis of A. ADAMS (1860) indicates that the shell is smooth. This information has been accepted by THIELE (1931) and WENZ (1938). COSSMANN (1921) extended this diagnosis to include the fossil *Scaliola*. He characterized them as having a smooth shell beneath a cover of grains.

ADAMS (1860) thought that *Scaliola* represents a member of the Epitonioidea (= Janthinoidea) because of its oval aperture and the uninterupted apertural lip. Due to its small size COSSMANN (1921) preferred to place *Scaliola* into the Rissoidea. The same author (COSSMANN, 1888, p. 317) in his discussion of *Scaliola bouryi* (COSSMANN, 1888) from the Eocene beds at Vaudancourt (Paris Basin) noted a close connection between *Scaliola* and *Mathilda (Tuba)* which is a member of the Allogastropoda HASZPRUNAR, 1985. THIELE (1931, p. 209) expressed the opinion that the genus *Scaliola* contains a few species which are all equipped with elongate, small shell, oval uninterupted aperture and grains of sand agglutinated into the shell. THIELE (1931) and WENZ (1938) include *Scaliola* as a doubtful genus into the Diastomidae (= Finellidae, Alabinidae) of the Cerithioidea without presenting reasons and further evidence for this placement. LOZOUET (1986) figured *Scaliola degrangei* BOURY and *S. cotteaui* (COSSMANN & LAMBERT, 1889) from Upper Oligocene deposits in the Aquitaine basin (SW France). He also placed the genus *Scaliola* among the Cerithioidea.

Scaliola has thus been included into the Epitonioidea, Rissoidea, Cerithioidea, and has been related to *Mathilda* (Allogastropoda). The well preserved early whorls of both fossil and Recent individuals of the genus *Scaliola* provide the opportunity to discuss their systematic relation and history. The anatomy and radula of individuals of recent species are being studied by W. PONDER (Australian Museum, Sydney) and the publication of his data are under way. PONDERS results support the relation of *Scaliola* to the Cerithioidea (personal communication 1991).

3. General features in *Scaliola*

The embryonic shell encompasses the shell that is carried by the veliger hatching from the egg mass (BANDEL 1975). It consists of one whorl, measures about 60 μm at its rounded apex and is 80 to 100 μm wide. Neither growth lines nor sculpture are present until almost one whorl is completed. In its shape and sculpture is closely resembles the embryonic shell of the common *Cerithium vulgatum* (BRUGUIERE) from the Mediterranean Sea and *C. atratum* and *C. litteratum* from the Caribbean Sea (BANDEL 1975, pl. 4).

First growth lines mark the shell of the veliger that is ready to hatch or has just hatched. Here the shell is functional as protective exoskeleton and mantle margin and shell margin are no longer connected to each other (BANDEL 1982). At hatching growth lines are straight reflecting the simple outline of the aperture at this stage of ontogeny of the shell.

In the first whorl of the larval shell growth line become sinuate. Strong subsutural and umbilical lobes develop along with a wide projection of the outer lip. The modification of the outer lip of the larval shell enables the veliger to hold the bases of the velum in stable position during swimming and feeding (Pl. 2, Figs. 1, 2).

Only growth lines sculpture the larval shell. A thickened apertural rim marks the end of its growth and the phase of development of a pediveliger (Pl. 1, Fig. 6, 7, Pl. 2, Figs. 1, 2, 3, 7, 8). With an about 0.3 mm high shell the veliger is ready to metamorphose from pelagic to benthic life. The upper edge of the apertural projection of the outer lip may become angular and ridge-like (Pl. 2, Figs. 1, 2).

The shell of the benthic *Scaliola* is sculptured by spiral lines or ridges crossed by simple growth lines. The aperture of juveniles has a straight columellar lip and a blunt anterior end (Pl. 1, Fig. 2). During further growth the angular aperture of the juvenile changes into the rounded and later also thickened aperture of the older or adult individual (Pl. 1, Figs. 4, 5, Pl. 2, Fig. 4). From the first whorl of the teleoconch onward grains of sand become integrated into the periostracum of the shell. The size and composition of the integrated sand grains depend on the type of sediment on which the individual of *Scaliola* is living. After death and decomposition of the organic periostracum grains may fall off, leaving a pit in the shell surface. Worn shells thus present a much more slender outline than those with sand still attached to them.

In the lagoon at Lizard Island living individuals were found mainly on sandy bottoms, rarely on rubble covered sea floor in 2–4 m of depth among algae and sand. The paucispiral operculum carried on the back of a narrow foot can seal the aperture well. The proboscis is broad and extends further out in the search for small plant- food particles than do the short tentacles. These carry eyes at their outer base and have a club-like bulging end. The foot is densely ciliated and moves the snail rapidly foreward, the shell being pulled behind in short rapid contractions of the shell muscle. The proboscis is long and used for burrowing as well as feeding. It probes through the sand and algal growths and thus opens the way for the whole animal to move through. The body coloration is opaque with yellowish pigment inside and dark pigment on the outer side. In contrast to most other cerithioids studied at Lizard Island Research Station the edge of the mantel is smooth and shows no tentacles or wart-like processes.

4. Description of species

Scaliola bella A. ADAMS 1860; Textfig. 1, 2, 3

Diagnosis: Larval shell smooth, with 3–4 rounded whorls, adult shell with 4 to 5 additional whorls, densely covered by grains of sand. Where periostracum is free of sand grains fine spiral lines are developed (more than 12 are seen on a flank). Aperture subangular in first three whorls of teleoconch. When no sand grains are attached the base is flattened with angular edge of the margin. When sand is attached to the base, it is rounded. Adult shell with 7 to 8.5 whorls are 3 to 5 mm long. Width of last whorl between on fourth to on third of length of shell. The third to fifth whorl may detach from tight coiling and also the base of each whorl is covered by grains (Pl. 1, Fig. 3). Following whorls rest on grains of sand. The aperture of adults is detached from the spiral and rounded.

Occurrence: *Scaliola bella* is found over wide ranges in the Indopacific. We studied individuals from the Arabian Gulf, the Gulf of Aqaba, the Red Sea (Pl. 2, Fig. 4), the southern Sea of China (Pl. 1, Fig. 5), the sea around the

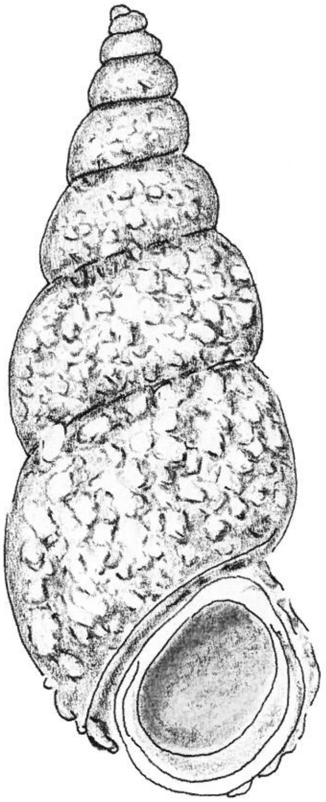

Fig. 1: Sketch of *Scaliola bella* from the shallow sea near Jemen with last whorl tight to the spire.

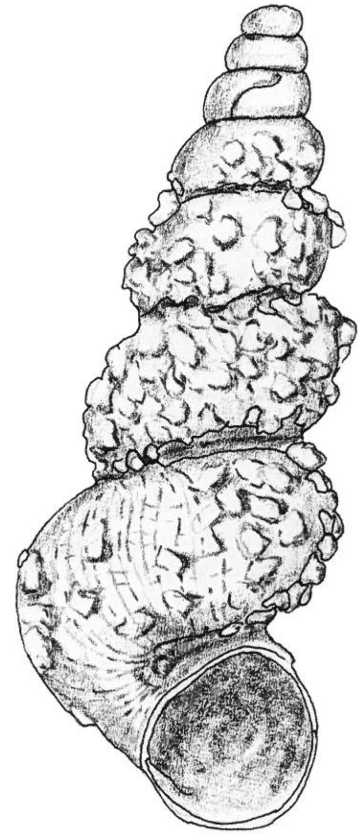

Fig. 2: Sketch of *Scaliola bella* from the Indonesian sea near the island Satonda with last whorl detached from the spire.

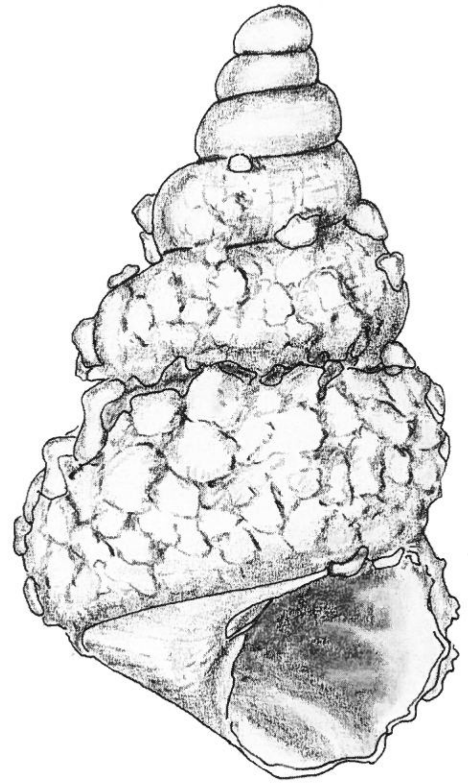

Fig. 3: Sketch of juvenile shell of *Scaliola* bella from Satonda island.

Philippine Islands and from near Satonda in the Indonesian islands (Pl. 1, Fig. 4). Individuals of this species live from shallow littoral water (backreef in Gulf of Aqaba) to water of several meters in depth. In the lagoon of Lizzard Island individuals were mainly found on sandy bottoms in 2–4 m of depth. Shells are commonly carried into deeper water by currents and slumping of shallow water debris as is the case in the sample from the northern slope of the Hilutangan Channel near Mactan Island on Cebu where shells are quite common and have been washed in from the area of fringing reefe just to the North and from shallow water. Size and width vary considerably, not only that of the adult shell but also that of the larval shell.

KAY (1979) noted the species *Scaliola bella* with a 4 mm long and 2 mm wide shell and a larval shell of 3,5 whorls, *Scaliola glareosa* A. ADAMS, 1862 with a 3 mm long and 1 mm wide shell and a larval shell of 3 whorls and *Scaliola gracilis* A. ADAMS, 1862 with an adult shell like *S. bella* and a larval shell like *S. glareosa* but with the last whorl slightly detached from the shell to live near Hawaii. With the studied material all forms appeared to merge and these three species seem to represent variations of the one species *S. bella* but according to studies carried out by W. PONDER (pers. communication) several species exist. If so there should be more than one species of *Scaliola* living in more or less the same type of environment in the lagoon of Lizard Island, where these differences were also observed from individuals collected alive.

Scaliola jansseni n. sp.; Textfig. 4

Diagnosis: The larval shell consists of 4 to 4.3 whorls and shows a strong apertural thickening in the subsutural lobe of the outgrown shell of the pediveliger. The hook-like projection of the outer lip extends over a distance of 0.2 to 0.3 whorls. Whorls of the teleoconch bear 7 to 8 spiral ridges on their evenly rounded flank (Pl. 2, Fig. 3, 5). The basal-most of these sculptural ridges forms an angle with the flattened smooth base. The aperture is subangular in the juvenile shell and detaches from the spiral at the adult shell, here becoming rounded and thickened (Pl. 2, Fig. 5). Sand grains may cover most part of the teleoconch or may be loosely integrated into the shell surface. In the later case the ornament of spiral ridges is well visible, in the former case it is more hidden. Turriform shell with 9 whorls are of adult size and vary between 3 and 4 mm.

Occurrence: Common in sediment samples from Saffré, Paris Basin, Middle-Eocene.

Holotypus: National Museum of Natural History in Leiden Nr. RGM 229.793.

Stratum typicum: Middle Eocene

Locus typicus: Saffré, Paris Basin

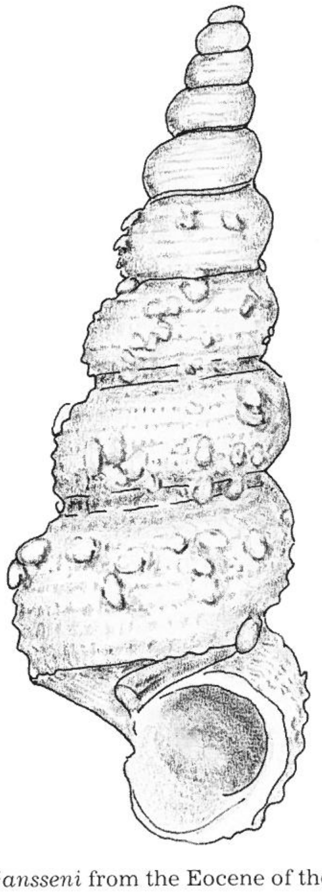

Fig. 4: Sketch of *Scaliola jansseni* from the Eocene of the Paris Basin.

Discussion: COSSMANN (1888, p. 317, pl. 11, Fig. 24–25) described and figured *Scaliola bouryi* from the Eocene beds of the Paris Basin at Vaudancourt, with 9 whorls, rounded shoulders and almost round aperture. In contrast to *S. jansseni* it is described as having a smooth shell no spiral ridges and basal edge.

According to Cossmann the individuals of *Scaliola bouryi* of his study had no grains attached to them and were worn. The diagnosis of *Scaliola bouryi* COSSMANN, 1888 can not be applied to characterize *S. jansseni*. It may well be that several species of *Scaliola* have been living in the warm Sea that covered much of France during Eocene times.

5. Comparison of fossil and recent *Scaliola*

Some larvae of *Scaliola bella* from Indonesian waters and all those of *S. jansseni* metamorphosed when the shell had almost four or more than four whorls. But recent *S. bella* is able to end its larval life even with only 3 whorls completed. Aside from number of whorls the larval shells of both species are much alike and characterized by a large hook-like projection of the apertural lip. The Upper Oligocene species *Scaliola cotteaui* and *S. degrangei* had four larval whorls of the same shape as present in *S. bella* and *S. jansseni* (LOZOUET, 1986, fig. 63) (Pl. 2, Fig. 6).

S. jansseni twists off its aperture only in the adult while *S. bella* is more variable in this respect. Here individuals may detach their whorls from the tight spiral coil during juvenile growth while others remain tightly coiled to the end. In size both species are rather variable and the type of grains agglutinated to the shell may add to this variability. The species from the Eocene, *S. jansseni* has a flattened base throughout its growth, while the Recent *S. bella* owns such a base only in the juvenile teleoconch or not at all. When the shape of the aperture is considered only the adult *S. jansseni* transforms the subangular aperture into almost round shape. In the case of *S. bella* this transformation occurs during the growth of the teleoconch or in the earlier whorls of the benthic juvenile. The spiral sculpture present below agglutinated grains is coarser and well visible in the Eocene species while it is rather delicate and less obvious in the modern species.

When *Scaliola cotteaui* and *S. degrangei* from the Upper Oligocene are compared with the modern *S. bella* differences between both species disappear. It is also quite impossible to distinguish both species from modern *S. bella*. It thus seems that since Oligocene time species very close to *S. bella* lived in warm seas and had much more extended occurrence than now. It remains unknown whether *S. bouryi* may not represent an even older representative of the modern species *S. bella*.

The comparison with the oldest known representative of the genus *Scaliola* from the Maastrichtian of the USA (Ripley Formation) was carried out on SCAN-photographs kindly made available by NORMAN SOHL from the US Geological Survey in Washington. A scetch is presented (Textfig. 5) and shows the keeled larval shell with about 4,5 whorls succeeded by two whorls of the slender teleoconch with carbonate sand grains and shells of foraminifers agglutinated to the shell. A shallow spiral pattern of low ribs similar to those of *Scaliola jansseni* is present. The main difference to relatives living many millions of years later in the Eocene, Oligocene and recent Indo-Pacific is seen in the keel found on the median flank of the larval shell.

Fig. 5: Sketch of *Scaliola* sp. from the Maastrichtian of the southwestern USA redrawn from a photo provided by courtesy of NORMAN F. SOHL.

6. Scaliola in its position among Cerithioidea

Until the data on the anatomy and the morphology of the radula are published by PONDER the best clues to the relationship of this genus to other genera are provided by the larval shell.

The size of the veliger hatching from the egg capsule and the morphology of its shell resembles that of modern Cerithioidea with a planktotrophic larva (BANDEL 1975).

Modern cerithioid larvae have a rather stable position in the water column with the larger of the two unequal wings of the velum held above the shell and the other in front of the shell (Pl. 3, Fig. 8). The velar wing held above the shell is the larger one and propells the larva upwards while the smaller wing extends in front of the shell and may be held inclined directing swimming motion into a certain direction away from a vertically upward spiral motion.

Veliger shells with similar shape, well rounded whorls, and large larval hook on the outer lip of the aperture can commonly be found among Ceritho-idea. Here many species have larval shells sculptured by axial und spiral ribs or lines of nodules. The larval shell of species of the genera *Finella* (Pl. 3, Fig. 3), *Bittium*, and *Diastoma* may be quite similar to those of *Scaliola* (HOUBRICK pers. communication, own data from Red Sea, Caribbean Sea and Mediterra-nean Sea). Here the shell is basically smooth and a median spiral ridge may be present or absent. The original larval shell may have carried one spiral keel in central position of the flank as is found in the oldest representative of *Scaliola* from the Maastrichtian of the southeastern USA (Textfig. 5). A Lower Cretace-ous member of the genus *Bittium* from Poland had a similar larval shell with one spiral keel ending in the upper side of the apertural projection of the pediveliger shell (SCHRÖDER 1992).

Finella dubia (ORBIGNY 1842) from the Caribbean Sea resembles *Scaliola* in regard to the morphology of the aperture in the teleococh. Like *Scaliola*, the subangular aperture of young *Finella* becomes more rounded and thickened in the adult. Species of all three genera of *Bittium*, *Diastoma* and *Finella* usually have a wide range of sizes among individuals of one or different populations. Like in *Scaliola jansseni* and juvenile *S. bella* the base is usually flattened and spiral ornaments are common. In contrast to *Scaliola* sand grains are never agglutinated to the periostracum and the sculpture consists of axial ribs as well as spiral ones. According to HOUBRICK (1988) a smooth margin of the mantle is a characteristic feature only of the Litiopidae among the Cerithioidea. All other groups have papillae on the mantle edge. *Scaliola* thus differs from all these other groups in this respect. It can certainly not be included in the Litiopidae which have a much more ornamented larval shell and tentacles projecting from the foot in addition to a life preferably on algae especially when they are adrift in the open sea (HOUBRICK 1988, BANDEL & WEDLER 1987).

7. History of the Cerithioidea

The special feature of the larval shell can be noted from the fossil record and thus Cerithioidea can be traced from the Upper Cretaceous of the Gosau beds of the northern Alps (BANDEL in press) into Lower Cretaceous of Poland and Northwest German Jurassic strata (SCHRÖDER, 1992) and into the Upper Triassic of the Dolomites of the southern Alps. Here *Turritella ornata* MÜNSTER, 1841 has a larval shell with all features seen in modern Cerithioidea (Pl. 3, Figs. 5, 7). This species is a member of a group of gastropods of the St. Cassian Formation representing the earliest known Cerithioidea up to date (BANDEL, in prep.).

Genus *Ampezzoscala* n. gen.; Pl. 3, Figs. 5, 7 of *Ampezzoscala ornata* (MÜNSTER).

Diagnosis: Slender moderate to high spired shells with convex whorls bearing axial ribs crossed by few spiral ribs and minute spiral threads. The aperture in juvenile shells angular, later round with thickened margin. The shell is aragonitic with crossed lamellar structure. The larval shell consists of several whorls and owns an apertural projection of the outer lip. Its sculpture consists of spirally arranged ribs and rows of tubercules. In the transition to the teleoconch the apertural projection ends and increments of growth follow a more simple contour. The type of the genus is *Ampezzoscala ornata* (MÜNSTER 1841) from the St. Cassian Formation.

Ampezzoscala has a similar teleoconch as is found among modern members of the genus *Cerithium* connected to an apertural morphology as is found in *Bittium*. The larval shell is transitional in shape to Cretaceous *Bittium* on one side with moderate spiral ribs and Jurassic *Procerithium* on the other side with strong spiral ribs (SCHRÖDER, 1992). It also resembles those of modern *Argyropeza* as described by HOUBRICK (1979). In contrast to the similaritis found regarding the larval shell, modern *Argyropeza* has a siphonate aperture while that of *Ampezzoscala* is subcircular with broad, shallow anterior canal.

Discussion: The diagnosis is based on the species *Ampezzoscala ornata* (MÜNSTER 1841) from the Upper Triassic St. Cassian Formation of the localities Alpe di Specie and Misurina (ZARDINI 1978) which was also described as *Turbo elegans* by MÜNSTER (1841), transferred to the genus *Scalaria* by KITTL (1892), raised to a new genus *Eucycloscala* by COSSMANN (1895) with the type *Eucyclo-*

scala binodosa (MÜNSTER 1841). A reexamination of *E. binodosa* demonstrated, that it is a member of the Archaeogastropoda with characteristic embryonic shell and nacreous inner shell layer (BANDEL, in press). Along with *Ampezzoscala ornata* the species *E. biserta*, *E. pusilla* and *E. elegans* have to be transferred from the genus *Eucycloscala* to the new genus *Ampezzoscala*. All occur in the Upper Triassic St. Cassian Formation of the area of Cortina d'Ampezzo and St. Kassian in the Dolomites.

8. Conclusions

As is the case with quite a number of taxa, *Scaliola* from the Eocene and Oligocene of Europe have living relatives in the modern Indopacific Ocean. The European Neogene species of *Scaliola* differ only little from their modern relatives. In the Atlantic Ocean and the Caribbean Sea no members of the genus *Scaliola* have survived, even though the genus has its oldest representative in the Gulf of Mexico Bay of the Cretaceous Tethys. Ontogeny, formation of a larval shell, transformation of morphology of the juvenile teleoconch into that of the adult are similar in modern and fossil species.

THIELE's (1931, p. 209) suggestion that *Scaliola* is related to the Finellidae (= Diastomatidae) of the Cerithioidea is supported by characters of the shell, especially those of the early ontogenetic stages. Features of the radula allow to differentiate *Finella* from *Bittium* and *Diastoma* (BANDEL, 1984). According to PONDER (written communication) the radula of *Finella* differs from that of *Scaliola*. The adult shell of *Finella (Alabina)* with its almost round aperture is similar to that of *Scaliola*. The adult shell of *Bittium* from the Lower Cretaceous is similar to that of modern *Bittium*, while the larval shell resembles that of *Finella (Alabina)* (SCHRÖDER 1991, Pl. 3, Fig. 3) and *Scaliola* from the Upper Cretaceous.

Scaliola is related to members of the families Cerithiidae and Diastomatidae in HOUBRICK's (1988) recent, most modern phylogenetic sheme of the Cerithioidea but it belongs to neither of these families. A relationship with the Epitoniidae as suggested by ADAMS (1860) can be excluded. Larval shells of Epitoniidae and related Ctenoglossa have a quite different sculpture dominated by regular axial elements and usually are more slender (BANDEL 1991). It is now possible to trace the evolution of the Ctenoglossa into the Triassic time and even beyond that into the Paleozoic periods (BANDEL, 1991). Their independant status in regard to the Cerithioidea can be documented to have existed in the Triassic St. Cassian Formation and it probably goes beyond that but fossile evidence is still missing. Convergence of the adult shell of Cerithioidea and Ctenoglossa is common in the modern fauna and it certainly also occurs in fossil faunas. Species can commonly be placed in either one systematic group only when the larval shells are preserved, as is the case in the Upper Triassic St. Cassian Formation.

A large projection of the outer lip is characteristic for *Scaliola* (Pl. 2; Figs. 1, 2) and to those members of the Cerithioidea that have a planktotrophic larva (HOUBRICK 1980, 1986, 1987). This feature can be noted from modern to Triassic time (RICHTER & THORSON 1975, ROBERTSON 1971, BANDEL 1988, 1991) (Pl. 3, Figs. 5, 7). A systematic connection with the genus *Mathilda* is quite impossible because larvae of members of that genus have a sinstral shell that twists into the right coil before metamorphosis is completed. This feature is characteristic of all marine members of the Architectonicoidea and Mathildoidea as well as most Allogastropoda of HASZPRUNAR's (1985) classification and allows their recognition since Paleozoic times (BANDEL, 1988, 1991, YOO 1988). Rissoid larvae commonly produce a sculptured larval shell which usually is shorter than that of the Cerithioidea and does not carry a large projection of the outer lip (BANDEL 1975, RICHTER & THORSON 1975, PONDER 1985).

The larval shell of modern members of the Cerithioidea including *Scaliola* present characteristic features both in dimension and in morphology and sculpture that can be traced in time back to the Triassic genus *Ampezzoscala*. The Jurassic *Procerithium* has a larval shell with two prominent spiral keels (SCHRÖDER, 1992) similar to that of *Bittium spina* (HOERNES, 1855) from the Middle Miocene of Western Germany (Pl. 3, Figs. 4, 9) and also found among some Indo-Pacific small cerithioids that need to be revised (own data).

A comparison of the larval shell of modern Mediterranean *Bittium reticulatum* with simple sculptural pattern consisting of tubercules and Miocene *Bittium spina* with two spiral ribs demonstrates that characters of the larval shell and the adult shell are not in agreement and the systematic position of the fossil species may have to be corrected. *Bittium spina* closely resembles modern species of the deep water cerithioid *Argyropeza* as revised by HOUBRICK (1980). Modern *Bittium reticulatum* larvae carry a shell that looks almost identically to that of Upper Triassic *Ampezzoscala*. Miocene *Bittium spina* larvae had a shell very much like that of Mesozoic *Procerithium* indicating that the familiy Procerithiidae supposedly existing from the Triassic to the earliest Tertiary (WENZ, 1938) may fall into bits and pieces of which several will be members of units of the Cerithioidea as they are recognized from the modern fauna (HOUBRICK, 1980). Thus convergence of the adult shell present within distinct groups of the Cerithioidea may be detected with the aid of differences seen in the larval shell.

Scaliola from the Upper Cretaceous had larval shells very similar to the older *Bittium* from the Lower Cretaceous of Poland (SCHRÖDER, 1991) and to the modern *Diastoma varia* (Pl. 3, Fig. 2). This may be an indication for a closer relation within this group of small sized Cerithioidea. As long as so little is known about the taxonomic value of sculpture of the larval shell within the Cerithioidea this problem can not be resolved. Taxonomic placement of small sized Cerithioidea is not sufficiently resolved at the moment. The Scaliolidae represent an own familiy within the Cerithioidea that is characterized by grains added to the shell, smooth mantle edge, simple slender foot carrying a paucispiral operculum, club-like tentacles on the sides of the broad snout that serves as burrowing divice and hooked turreted larval shell with or without one median spiral rib.

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Plates 1-3

Plate 1:

Fig. 1: Juvenile shell of *Xenophora* with smooth larval shell succeeded by the first whorls of the teleoconch with fragments of shell and foraminifera agglutiated to them. ×15.

Fig. 2: Juvenile *Scaliola bella* from near Satonda in the Indonesian Indo-Pacific with subangular aperture and coarse grains of sand agglutinated to the teleoconch. ×55.

Fig. 3: Variety of *Scaliola bella* from Indonesia with the last whorls detached and round aperture with unbroken rim. ×40.

Fig. 4: Variety of *Scaliola bella* from Indonesia with the last whorls in contact to former whorls and inner lip overlying the former whorl and not free. ×45.

Fig. 5: *Scaliola bella* from the Southern Chinese Sea. ×33.

Fig. 6: The larval shell of the variety of *Scaliola bella* from Indonesia consists of 3 whorls and is about 0,2 mm high.

Fig. 7: The larval shell of the variiety of *Scaliola bella* from the Southern Chinese Sea is about 0,22 mm wide and consists of 3,3 whorls.

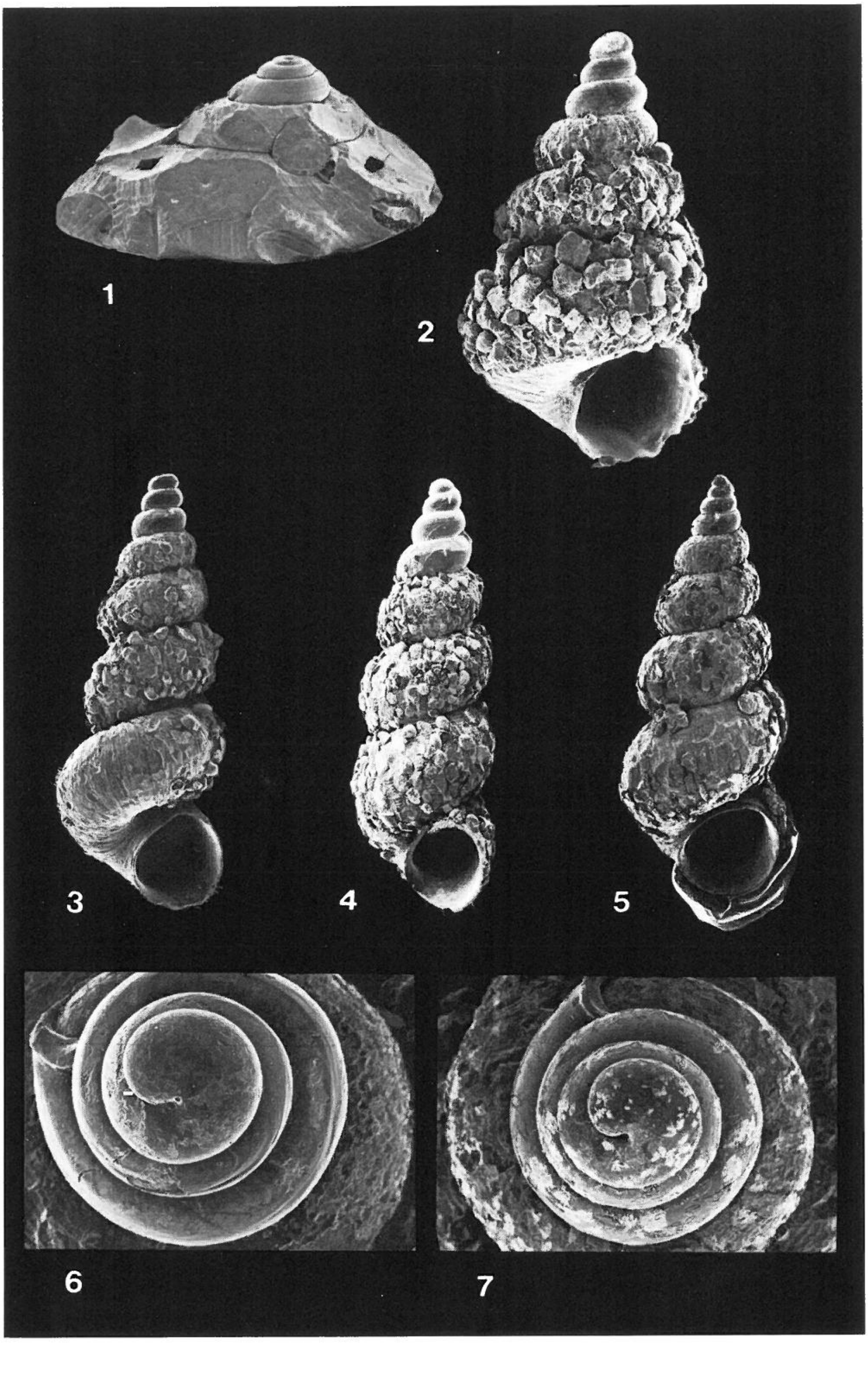
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Plate 2:

Fig. 1: The larval shell of *Scaliola bella* from Indonesia is about 0,24 mm high and owns a strongly hooked outer lip of the aperture that is thickened in the fully grown pediveliger-stage.

Fig. 2: The larval shell of *Scaliola bella* from the Southern Chinese Sea is about 0,3 mm high and the hooked margin of the outgrown shell of the pediveliger is thickened.

Fig. 3: The larval shell of *Scaliola jansseni* the Eocene of the Paris Basin is about 0,5 mm high and the margin of the shell of the outgrown pediveliger is strongly thickened.

Fig. 4: The outgrown shell of *Scaliola bella* from the Red Sea at Jemen. × 35.

Fig. 5: The outgrown shell of *Scaliola jansseni* from the Eocene of the Paris Basin. × 16.

Fig. 6: *Scoliola cotteaui* from the Oligocene of the Aquitaine, southern France. × 32.

Fig. 7: The larval shell of *Scaliola bella* from Indonesia looks very similar to that of the Eocene member of the genus (fig. 8) but is less wide (0,21 mm).

Fig. 8: The larval shell of *Scaliola jansseni* from the Eocene of the Paris Basin is 0,32 mm wide.

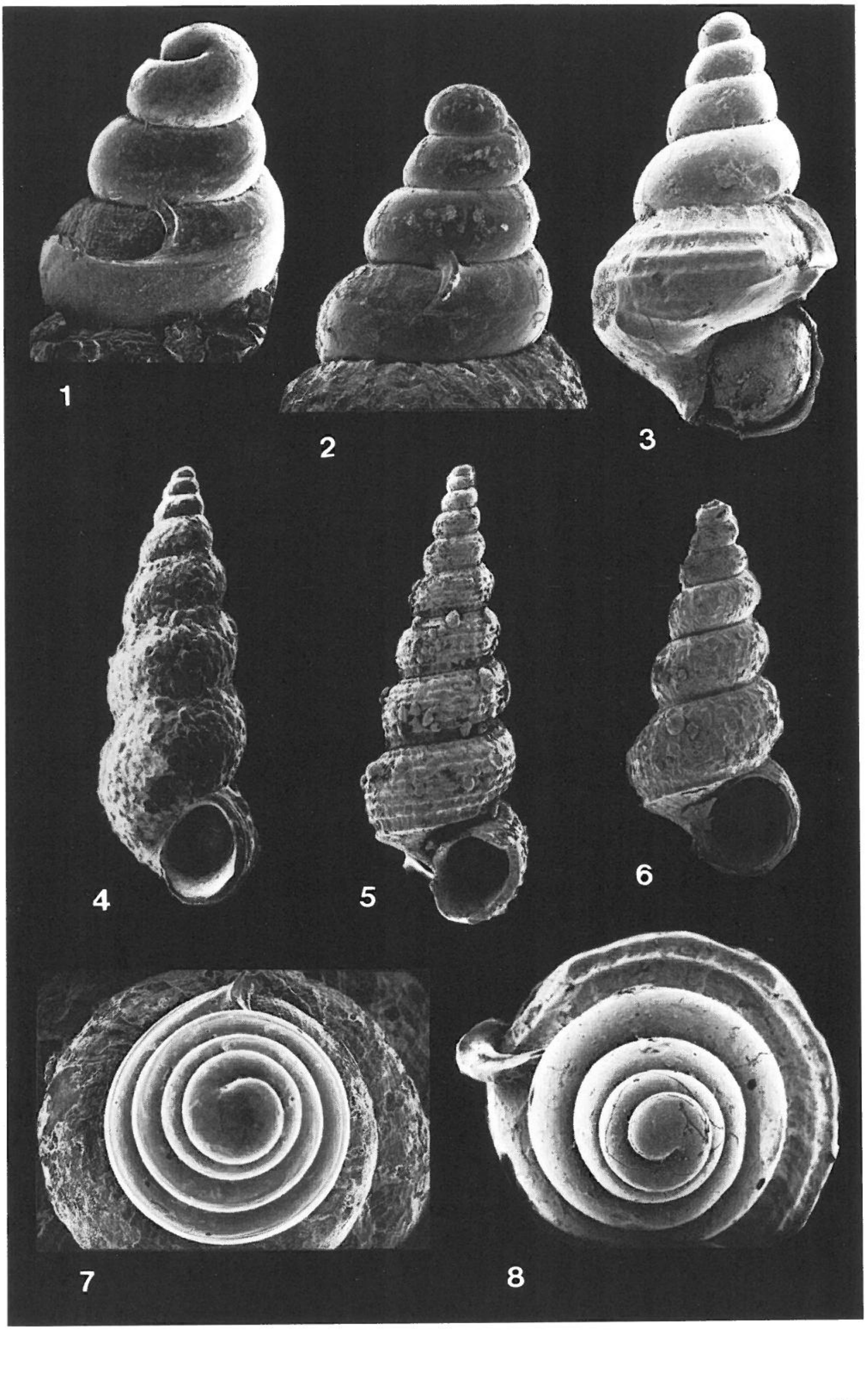
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Plate 3:

Fig. 1: The larval shell of *Bittium reticulatum* washed from algae in the littoral zone of the western Mediterranean is about 0,31 mm high and has a strong projection of the apertural margin along with a sculpture of nodules similar to the Triassic species in fig. 7.

Fig. 2: The 0,27 mm high larval shell of *Cerithium atratum* from the Colombian Caribbean Coast is strongly sculptured.

Fig. 3: The 0,27 mm high larval shell of *Finella dubia* that has been living on littoral seaweed in the Colombian Caribbean Coast is very similar to that of *Scaliola*.

Fig. 4: The teleoconch of *Bittium spina* from the Middle Miocene of the Dingden Sands in western Germany look like that of modern *Bittium*.

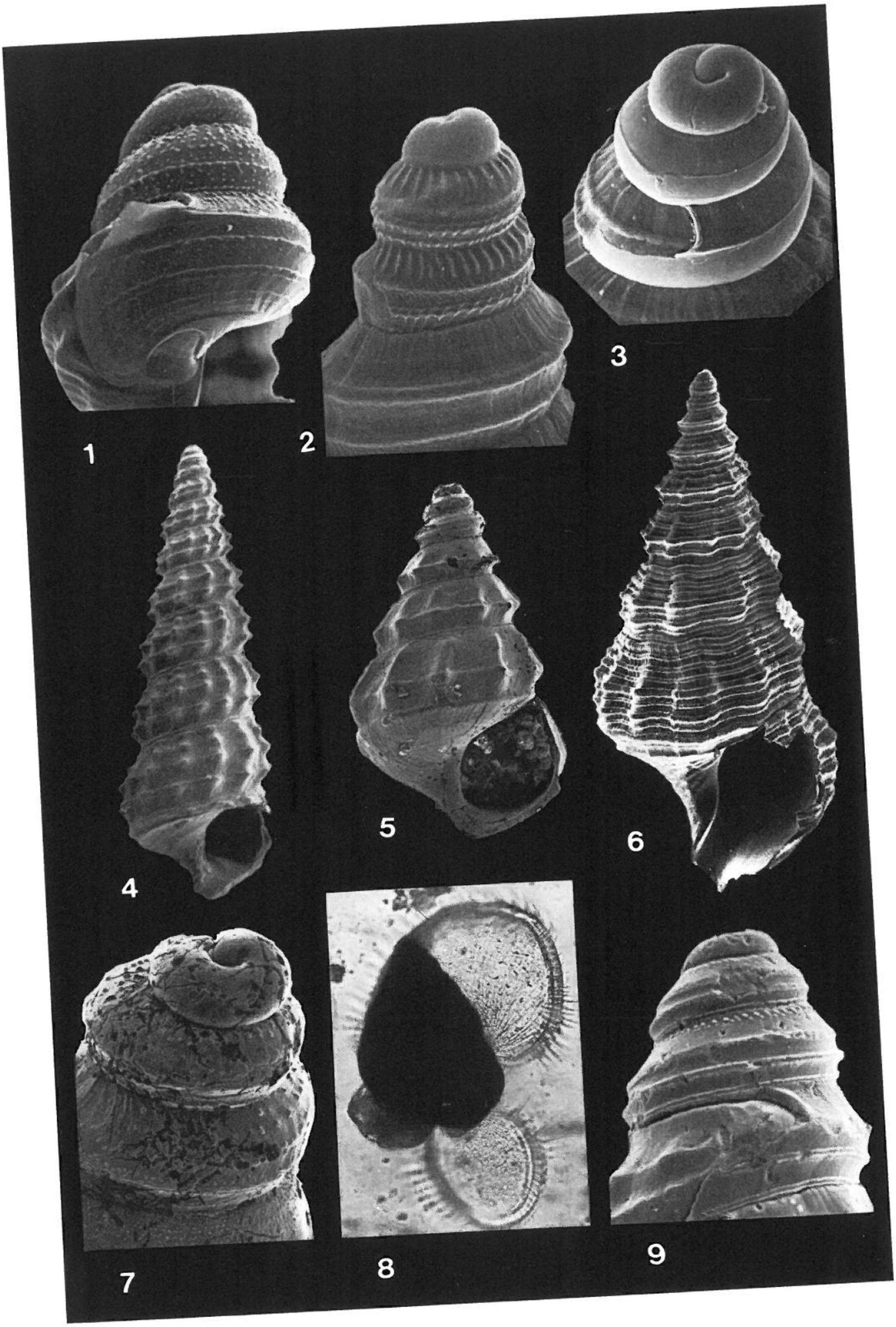
Fig. 5: Juvenile 1,2 mm high shell of *Ampezzoscala ornata* from the Upper Triassic St. Cassian Formation of the Dolomites.

Fig. 6: The juvenile shell of *Cerithium atratum* from the coastal Caribbean Sea of Colombia is shown in the details of the larval shell in fig. 2.

Fig. 7: The larval shell of *Ampezzoscala ornata* is about 0,3 mm high and sculptured by similar nodular elements as present in modern *Bittium reticulatum* (fig. 1) and also has a strong larval hook like most modern cerithioidean larvae.

Fig. 8: A larva of Cerithioidean veliger from the Red Sea photographed alive on bord of the Research Vessel Meteor during summer 1987 shows a large velar lobe held above the shell and a smaller velar lobe held in front of the shell. (Seen from below, shell about 0,3 mm high).

Fig. 9: The larval shell of *Bittium spina* from the Middle Miocene (detail to fig. 4) resembles in sculpture cerithioidean larval shell from the Jurassic and Cretaceous as found among members of the genus *Procerithium*.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