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The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone

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Abstract: Many Archaeogastropoda with nacreous shell from St. Cassian Formation have a slit in the outer lip that gives rise to a selenizone. The primary objective of this study is to analyze family level characters, provide a revision of some generic classifications and compare with species living today. Members of twelve families are recognized with the Lancedellidae n. fam., Rhaphistomellidae n. fam., Pseudowortheniellidae n. fam., Pseudoschizogoniidae n. fam., Wortheniellidae n. fam. newly defined. While the organization of the aperture and the shell structure is similar to that of the living Pleurotomariidae, morphology of the early ontogenetic shell and size and shape of the adult shell distinguish the Late Triassic slit bearing Archaegastropoda from these. In the reef environment of the tropical Tethys Ocean such Archaeogastropoda were much more diverse than modern representatives of that group from the tropical Indo-Pacific Ocean. Here *Haliotis*, *Seguenzia* and *Fossarina* represent living nacreous gastropods with slit and are compared to the fossil species. All three have distinct shape and arrangement of the teeth in their radula that is not related to that of the Pleurotomariidae and also differs among each other. The family Fossarinidae n. fam. and the new genera *Pseudowortheniella* and *Rinaldoella* are defined, and a new species *Campbellospira missouriensis* is described.

Zusammenfassung: In der St. Cassian-Formation kommen zahlreiche Arten der Archaeogastropoda vor, die eine perlmutterige Schale mit Schlitz in der Außenlippe haben, welcher zu einem Schlitzband führt. In dieser Studie wird eine Gliederung in Familien vorgestellt. Die Merkmale ihrer Gattungen werden charakterisiert und mit den heute lebenden Arten der perlmutterigen Schlitzbandschnecken verglichen. Angehörige von zwölf Familien lassen sich unterscheiden, wobei Lancedellidae n. fam., Rhaphistomellidae n. fam., Pseudowortheniellidae n. fam., Pseudoschizogoniidae n. fam. und Wortheniellidae n. fam. neu definiert werden. Während die Gestalt der Schalenmündung und ihre Schalenstruktur der Arten der späten Trias jener der heute lebenden Pleurotomarioiden ähnelt, sind die Gestalt der frühontogenetischen Schale wie auch die Größe und Gestalt der ausgewachsenen Individuen von ihnen verschieden. Im Riffmilieu des tropischen Tethys-Ozeans waren Schlitzbandschnecken deutlich vielgestaltiger und artenreicher vertreten, als das heute im tropischen Indo-Pazifik der Fall ist. Unter letzteren sind die Arten von *Haliotis*, *Seguenzia* und *Fossarina* perlmutterig und haben einen Schalenschlitz. Es wird dargestellt, dass allen drei Gattungen eine charakteristische Anordnung der Zähne in ihrer Radula zu eigen ist, die auch nicht jener der Pleurotomariiden gleicht. Die Fossarinidae n. fam und die neuen Gattungen *Pseudowortheniella* und *Rinaldoella* werden definiert und *Campbellospira missouriensis* wird neu beschrieben.

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Introduction

Living environment of the gastropods of St. Cassian Formation consisted of shallow tropical reefs at the margin of islands and large shallow platforms in the tropical Tethys Ocean (Fürsich & Wendt 1977, Wendt & Fürsich 1979, Blendinger & Blendinger 1989). Here crust forming coralline algae, corals and calcareous sponges formed patch reefs on the margin of large shallow lagoons and the open sea. Most of the gastropods described here are from the St. Cassian Formation and lived on and below these patch reefs together with quite a number of different groups of gastropods, bivalves, echinoderms and brachiopods. The diversity of slit bearing Archaeogastropoda is high (about 50 species) (Münster 1841, Laube 1868, Kittl 1891, Zardini 1978, Bandel 1991, 1994, 1997). In modern tropical reefs members of the small sized Scissurelloidea, and the limpet shaped Fissurelloidea and Haliotioidea are present among the slit bearing Archaeogastropoda, with a much smaller number of species. *Pleurotomaria* and relation as well as *Seguenzia* and relation nowadays live in deeper water, while species that could have been from their stem group lived in the shallow water of St. Cassian reef. In all recognized species of St. Cassian the protoconchs have the characters as is present among the Archaeogastropoda (Bandel 1982). All here described taxa have their shell structure preserved in such a way that nacre can be documented. Among modern species with nacre and slit in their shell besides the characteristic relatives of *Pleurotomaria* spp., *Haliotis* spp. have a pair of gills, but a slit is also found among some representatives with a single gill, such as *Seguenzia* spp. and varieties of *Fossarina* spp.

The deposits of the St. Cassian Formation are of Late Triassic age belonging to the Lower Carnian stage (Bizzarini et al. 1986) and here the Cordevol (Urlichs 1994) (formed about 225 million years ago). The studied gastropod shells were found in several localities close to the towns St. Cassian in Southern Tirol and Cortina d´Ampezzo in the province Ampezzo, both in Northern Italy, and here in the mountain chain of the Dolomites. The locality Alpe di Specie (Seelandalpe) is situated west of Schluderbach (Carbonin) on the road from Cortina d´Ampezzo to Toblach (Wendt 1982, fig. 1). Here the outcrops lie on a meadow below the Rifugio Vallandro (Dürrenstein Hütte) in about 2000 m height. Locality Misurina indicates outcrops along a ski lift in about 1800 m height to the west of the Lago di Misurina situated to the east of Cortina d`Ampezzo. Campo lies about 1200 m high in the forest above Campo di Sotto, a part of the Town of Cortina d`Ampezzo and is represented by a small foxhole-like outcrop. Dibona represents strata of the St. Cassian Formation exposed in the slope and forest at about 1800 m height below Rifugio Dibona situated above the road from Cortina d`Ampezzo to the Passo Falzarego. This locality may be the same as that called Milieres by Zardini (1978) who presented a map with all mentioned localities of the Cortina d`Ampezzo area indicated. Stuores is situated near St. Cassian about 15 km to the west of Cortina d`Ampezzo. Here the outcrops lie to the northwest of Settsass Mountain southwest of St. Cassian. Their situation is illustrated by Urlichs (1994, fig. 1). Stuores is an ever changing slump outcrop at the northern side of Pralongia Ridge in about 2100 m height below which lies the town of Corvara. With exception of the Stuores locality which belongs to the *Trachyceras aon* zone, the other localities expose beds of the *Trachyceras aonoides* zone (Urlichs 1994).

Kittl (1891) described species of slit-bearing gastropods from St. Cassian Formation and placed them in the subgenera *Kokenella*, Kittl, 1891, *Temnotropis* Laube, 1868, *Worthenia* Koninck, 1883, *Pleurotomaria* Sowerby, 1821, *Zygites* Kittl, 1891, *Rhaphistomella* Kittl, 1891, *Ptychomphalus* Agassiz, 1839, *Gosseletina* Bayle, 1885, *Laubella* Kittl, 1891, *Stuorella* Kittl, 1891 and *Schizogonium* Koken, 1889. He regarded all of these to represent subgenera of *Pleurotomaria*. This changed drastically when Wenz (1938) placed *Sisenna* Koken, 1896 in the Lophospirinae Wenz, 1938 (Lophospiridae by Knight et al. 1960), *Schizodiscus* Kittl, 1891, *Temnotropis, Laubella*, *Euzone* Koken, 1896 in the Gosseletininae Wenz, 1938 (= Gosseletinidae by Knight et al. 1960), *Stuorella*, *Codinella* Kittl, 1899, *Schizogonium*, *Zygites*, *Kokenella* in the Pleurotomariinae Swainson, 1840, *Rhaphistomella*, *Ptychomphalus* in the Ptychomphalinae Wenz, 1938 (Eotomariidae Wenz, 1938 by Knight et al. 1960).

Knight et al. (1960) regrouped again and regarded *Kokenella* to represent a member of the Porcelliidae Koken, 1895, *Laubella* was placed in the Laubellidae Cox 1960 and *Zygites* in the Zygitidae Cox, 1960. Bouchet & Rocroi (2005) distinguished four superfamilies into which these genera from St. Cassian can be fitted, Pleurotomarioidea Swainson, 1840, Eotomarioidea Wenz, 1938 (*Rhaphistomella* and *Ptychomphalus* for example), Haliotioidea Rafinesque, 1815 including *Temnotropis*, and Seguenzioidea Verrill, 1884 including *Laubella*.

Species closely resembling modern Pleurotomariidae can be traced to the Early Jurassic, but less well to St. Cassian Formation. Other groups such as Ptychomphalidae, Rhaphistomellidae n. fam., Pseudoschizogoniidae n. fam., Gosseletinidae, Wortheniellidae n. fam. appear closer to some Paleozoic groups and genera than to modern species. The Schizogoniidae, Temnotropidae and Laubellidae are characteristic of the Triassic St. Cassian Formation, with the two later perhaps related to modern Haliotidae and Seguenziidae. Modern Fossarinidae n. fam. present evidence for the possibility of formation of the shell slit from ancestors without such slit, here noted among individuals of a single species.

Systematic part

Superfamily Pleurotomarioidea Swainson 1840

Here slit bearing Vetigastropoda with nacreous inner aragonitic shell layer (Erben & Krampitz 1972) and rhipidoglossate radula of the *Pleurotomaria* type are included (Troschel 1856-1863).

Pleurotomariidae Swainson, 1840 include all post-Jurassic Pleurotomarioidea (Harasewych 2002). Four of their genera have living species i.e. *Perotrochus* Fischer, 1885 and *Bayerotrochus* Harasewych, 2002 from the Caribbean Sea and *Mikadotrochus* Lindholm, 1927 and *Entemnotrochus* Fischer, 1885 from the Indo-

Pacific (Okutani & Hasegawa 2000, Harasewych 2002, Harasewych & Kiel 2007). Their shell resembles that of Jurassic *Pleurotomaria* Sowerby, 1821 that is based on *Trochus anglicus* Sowerby, 1818 (Szabo 2008, fig. 34) from the Early Jurassic. The species of *Pleurotomaria* from the Jurassic usually have a broad large shell (20-40 mm width) with rounded whorls, a median selenizone and commonly coarse axial ribs above the selenizone and general ornament by fine spiral ribs (Orbigny 1852, Hudleston 1895, Gründel 2003b, pl. 1, fig. 1-11). Molecular analysis of *Perotrochus* species and several species of *Haliotis* by Geiger & Thacker (2005) provided evidence for the great distance between these genera supporting the suggestions of Wenz (1938) who regarded these slit bearing nacreous Archaeogastropoda as not closely related to each other. Relation within the living Pleurotomariidae was documented by Harasewych et al. (1997).

Family Zygitidae Cox, 1960

The lowly trochispiral shell with rounded whorls and wide umbilicus is ornamented by rectangles all over and carries the wide selenizone in the mid whorl position. The aperture is nearly vertical with deep slit on the middle outer lip. Shell structure includes a central layer of aragonitic nacre. The protoconch has granular ornament and is succeeded by first whorls of the teleoconch with ornament of undulating axial ribs. The slit begins within or at the end of the first whorl of the teleoconch. The family is based on *Zygites* Kittl, 1891 from St. Cassian Formation with shell as wide as high and wide undulating folds superimposed on the ornament. Included is also *Dictyotomaria* Knight, 1945 with similar shell shape but no superimposed folds. Early ontogenetic shell of *Kokenella* Kittl, 1891 has the first whorl of the teleoconch in a trochispiral (Koken (1896) while the later shell is plane. Koken (1896) suggested here a change of the name of the genus to *Kokeniella* which did not find approval by later authors.

The first whorl of the teleoconch of *Zygites delphinula* (Laube, 1868) is without slit and almost plane. During growth the relative shell height increases. Ornament consists of axial and spiral ribs which form a regular network of rectangles. The selenizone lies just above the suture (pl. 1, fig. 1). Undulation formed by wide axial folds is added beginning with the second whorl of the teleoconch and begin of trochispiral coiling. When fully grown the shell is as wide as high. A shell consisting of 7 whorls measures 15 mm. Whorls are rounded and the base has a deep umbilicus (Laube 1868, pl. 27, fig. 9 as *Pleurotomaria delphinula*, Kittl 1891, pl. 1, fig. 14, Bandel 1991, pl. 1, figs. 7-8).

Dictyotomaria subcancellata (Orbigny, 1849) has a conical shell with rounded apex and whorls. The selenizone begins in the second whorl in median position. The protoconch with 0.18 mm in diameter has a smooth outer lip. Ornament of the teleoconch consists of axial and spiral ribs, which form a regular pattern of rectangles with each other (pl. 1, figs. 2-5). With seven whorls the shell is about 12 mm high and 10 mm wide. The shell wall has an inner nacreous layer. The aperture is rounded and vertically arranged (Laube 1868, pl. 27, fig. 1 as *Pleurotomaria subcancellata*, Zardini 1978, pl. 3, fig. 11, pl. 10, fig.2 a-c, Bandel 1991, pl. 1, figs. 1-6, pl. 2, figs. 3-4, 8).

Dictyotomaria has the type species *D. scitula* (Meek & Worthen, 1861) from the Late Carboniferous of Texas. A similar species from the Early Carboniferous of Australia has been determined as *Glabrocingulum* Thomas, 1940 (Yoo 1994, pl. 6, figs. 4-12) which was placed in the Eotomariidae Wenz, 1938. Similar species lived in the Late Carboniferous of North America (Sloan 1955). The juvenile shells of *Glabrocingulum* sp. from the St. Louis Outlier, Henrietta Shale in Missouri (Pennsylvanian) has rounded whorls of the early teleoconch. Ornament is spiral in the first whorl and axial ribs are added on the second whorl forming a pattern of small rectangles. The selenizone inserts in the third whorl and is accompanied by marginal spiral ribs. The protoconch is about 0.27 mm in diameter and the selenizone lies at the upper peripheral bulge of the whorls (pl. 1, figs. 6-8). Similar juvenile shells from the Late Carboniferous were documented to have nacre (Bandel et al. 2002, pl. 1, fig. 5) as had also been documented from other shells of similar age by Batten (1972) from other localities in the USA.

Dictyotomaria gondwanaensis Bandel, Gründel & Maxwell, 2000 from the Jurassic of New Zealand has a narrower umbilicus and more spiral lines on the apical whorl between selenizone and suture but resembles *D. subcancellata.* Here the 0.3 mm wide protoconch is succeeded by about one whorl of the teleoconch without slit and an ornament of evenly bend axial ribs. The slit begins in the middle of the whorl and remains in this position in a shallow concavity (Bandel et al. 2000, pl. 1, figs.1-3). *D. gondwanaensis* differs from the Carboniferous *Glabrocingulum* as well as the Triassic *D. subcancellata* by flatter shape of the juvenile shell and predominance of axial ribs on the first whorl of the teleoconch. Jurassic *Leptomaria* Etudes-Deslongchamps, 1865 has similar shape and ornament, but its fully grown shell is much larger (Szabo 2008, fig. 44) and has the type *Pleurotomaria amoena* Etudes-Deslongchamps, 1849 from the mid Jurassic of France

(Orbigny 1852, pl. 389, figs. 1-5). It could be interpreted as transitional from the Zygitidae to the Pleurotomariidae. Also *Anodomaria* Szabo, 1980 with the type species *Pleurotomaria scacchi* Gemmellaro, 1874 from the Pliensbachian of Sicily that occurs also in the Hungarian Bakony Mountains (Szabo 2008, fig. 31) is about 12 mm high and a little less wide. The shell has a narrow ramp below the suture, a rounded periphery below it and a corner is present to the flattened base with umbilicus. Shell shape resembles that of *Pleurotomaria*. Szabo (2008, fig. 29) found in Early Jurassic Hierlatz Limestone with *Anodomaria stojaspali* Szabo, 2008 a species with lower shell shape and *Anodomaria anodosa* (Szabo, 1980) with larger shell and more flattened whorl sides. While the type species of *Anodomaria* resembles *Dictyotomaria subcancellata* from St. Cassian Formation, the other species included in the genus by Szabo (2008) are larger. Thus *Glabrocingulum* from the Carboniferous, *Dictyotomaria subcancellata* from the Triassic and *Anodomaria* from the Early Jurassic can be interpreted to belong in a relationship connecting these species that lived across a time of 150 million years.

The shell of *Kokenella* Kittl, 1891 is coiled within a plane and has the selenizone on the side of the round whorls (pl. 1, fig. 9). *Kokenella costata* (Münster, 1841) from St. Cassian is better known than the type *Kokenella fischeri* (Hoernes, 1855) from the Hallstätt Limestone of the Northern Alps. It has a dextral twist and more excavated base than top. Shell structure consists of an outer prismatic layer underlain by a thick layer of nacre, as was documented in thin sections. Ornament of narrow axial and spiral ribs is arranged to form a regular pattern of rectangles. With 4.5 whorls the shell is 11 mm wide and 5 mm high. The protoconch measures 0.3 mm in diameter and has a thickened margin succeeded by the early teleoconch with collabral ribs to which later spiral ribs are added. The slit begins on the periphery of the first teleoconch whorl and migrates to the side (pl. 1, figs. 10-12). Later whorls of the teleoconch may have undulations as in *Zygites* (Zardini 1978, pl. 3, fig. 8, Bandel 1991, pl. 2, figs. 2, 11) or may be evenly rounded (Laube 1868, pl. 28, fig. 10 as *Porcellia costata*, Zardini 1978, pl. 3, figs. 9-10, Bandel 1991, pl.2, fig.1). Kittl (1891) suggested the existence of several species which was accepted by Broili (1907). A species from the Late Triassic of Iran that grew to 31 mm in diameter has been placed with *Kokenella costata* by Nützel & Senowbari-Daryan (1999, pl. 1, figs. 1-4). *Kokenella mackayi* Begg & Grant Mackie, 2003 from the Middle Triassic of New Zealand has a wide umbilicus and shell with flat spire with the early teleoconch protruding. The whorls have a flattened upper side and a corner to the base and a broad selenizone slightly above the middle of the sides (Begg & Grant Mackie 2003, fig. 3). It resembles in shape *Kokenella fischeri* as illustrated in Wenz (1938, fig. 222).

In case of *Cyclostomaria* Szabo, 1980 from the Early Jurassic of the Northern Alps and the Hungarian Bakony Mountains with discoid shell and low spire the selenizone has its position high on the whorl close to the peripheral corner without migrating onto the side as is the case in *Kokenella costata*. Szabo (2008, fig. 21) suggested to place *Cyclostomaria* with the Gosseletinidae Wenz, 1938. Knight et al. (1960) united the slit bearing Paleozoic *Porcellia* with almost plane shell with Triassic *Kokenella* and Jurassic *Talantodiscus* Fischer, 1885 in the Porcelliidae Broili, 1924. But *Porcellia* Leveillé, 1835 with type species from the Early Carboniferous of northern France holds very similar species also in the Devonian (Bandel 1993, pl. 2, fig. 3-13, pl. 3, figs. 1-12, pl. 4, figs. 1-4, 6) with the dextral early teleoconch while the later teleoconch has a slight left coiled arrangement after appearance of the narrow slit. Bandel (1993) suggested a separate place for the three genera, *Talantodiscus* near *Pleurotomaria, Kokenella* near *Zygites*, while *Porcellia* is related to the Agnesiinae Knight, 1956 with dextral early juvenile shell and twist into the later left coiled teleoconch. They are part of the Porcellioidea Koken, 1895 with species documented from the Silurian to the Cretaceous (Bandel 1993, Frýda 1997, Bandel & Frýda 2004, Bouchet & Rocroi 2005).

Family Stuorellidae Bandel, 1991 (newly defined)

Diagnosis: The conical shell with flattened whorl side consists of up to 13 whorls. Its size may reach 17 mm in height, less in width with differing apical angle among the species. Apical angle changes from smaller in the juvenile to larger in the adult shell. The base is flattened or concave and the aperture is vertical with lowly trapezoidal outline. The early teleoconch has rounded whorls and the slit appears relatively late (third or fourth whorl). The selenizone lies near the peripheral edge to the base (*Stuorella*) or near the centre of the flattened side (*Codinella*). Ornament consists of collabral and spiral lines with collabral elements forming rows of nodules or short ribs. The selenizone is flat and bordered by cords. The inner shell wall is formed by nacre while the outer layer has prismatic structure. The family is based on *Stuorella* Kittl, 1891 with the type species *Trochus subconcavus* Münster, 1841 from St. Cassian Formation (Kittl 1891, pl. 4, figs. 2-4).

Stuorella subconcava (Münster, 1841) has an acutely conical shell with apical angle of about 50° with flattened whorl profile and indistinct sutures (pl. 1, figs. 13-15, pl. 2, figs. 16-18). The selenizone lies just above the peripheral edge. The protoconch of about 0.15 mm in width has a straight thickened margin of the aperture. The early teleoconch with rounded whorls is ornamented by two spiral ribs and growth lines and fine tubercles in the first, three spiral ribs on the second and six ribs in the third whorl. Here the sides become flattened and a row of short axial folds appears. In the fourth whorl the slit originates near the basal corner and creates a selenizone with regular curved increments of growth (Zardini 1978, pl. 7, figs. 3-4, pl. 40, fig. 11a-b, Bandel 1991, pl. 9, figs. 7-8, pl. 10, figs. 1-5, 7). Thin section of the shell wall documented that the aragonitic outer layer is relatively thicker as found in living Pleurotomariidae. It resembles that found in modern *Haliotis*, and is succeeded by nacre. The shell of *Stuorella toffanae* Leonardi & Fiscon, 1959 has a larger apical angle of about 60°, consists of about 11 whorls and is 11 mm high and 9 mm wide. Here the ribbon of folds below the suture begins in the first whorls of the teleoconch (Zardini 1978, pl. 6, figs. 15-17, pl. 7, figs. 5, 14, Bandel 1991, textfig. 5, pl. 10, fig. 6). *Stuorella costalaricensis* Zardini, 1978 has a more acute shell with apical angle about 40°, consisting of 12 whorls and about 13 mm high and 10 mm wide. The flanks are slightly concave and have less ornament than the other two species (Zardini 1978, pl. 7, figs. 1-2, Bandel 1991, pl. 10, fig. 8, pl. 11, figs. 1-4).

The position of the selenizone in *Codinella* Kittl, 1899 is slightly higher up on the whorls in a more central position as is the case in *Stuorella*. *Trochus generellii* Stoppani, 1858 from the Late Triassic Esino Limestone (Wenz 1938, fig. 211) represents the type species and *Codinella zardini* Bandel, 1991 from St. Cassian has an apical angle of about 50° changing from more acute to less acute during shell growth of 10 mm in height is about 8 mm in width. Ornament is only by growth lines, the aperture is angular and the flattened base has no umbilicus (Zardini, 1978 pl. 4, figs. 2-3, Bandel 1991, pl. 11, figs. 5-6).

Permian *Lamellospira* (Batten, 1972) and Carboniferous *Glyptotomaria* Knight, 1945 (Knight et al. 1960, figs. 130, 10) have similar shell shape. Among Jurassic species *Laevitomaria* Conti & Monari, 1987 has a similar conical shell shape (Szabo 2008, figs. 39-43) but commonly grew to larger size. Here the selenizone lies in a more central position on the flat whorl sides as in *Codinella*. Mid Jurassic *Pyrgotrochus* Fischer, 1885 (type is *Pleurotomaria bitorquata* Etudes-Deslongchamps, 1849 from the Jurassic of France) has conical shape and a selenizone in position just above the suture (Gründel 2000, pl. 1, figs. 1-3). Ornament consists of fine spiral lines and the selenizone is accompanied by a node bearing ridge. *Pyrgotrochus macrocephalus* (Quenstedt, 1857) from the Bajocian of Southern Germany with conical shell of more than 6 whorls is wider (60 mm) than high (less than 40 mm) with flat base (Gründel, 2003c, pl. 2, figs. 1-8). Similar species are known from northern Germany and NW France (Fischer & Weber 1997, Gründel 2003a). Several species from the Jurassic of England have a conical shell resembling that of *Stuorella* but are usually larger (Hudleston 1895). Kittl (1891) interpreted *Stuorella* as subgenus of *Pleurotomaria* and its continuation in Jurassic species such as *Pleurotomaria bitorquata* and others but also remarked on the smaller size of the Triassic *Stuorella*.

From the Campanian of the Tremp Basin in Northern Spain the small *Stuorella cretacea* Kiel & Bandel, 2000 with backward sloping lines on the upper half and lower quarter of the whorls and a trapezoid aperture closely resembles *Stuorella costalaricensis*. The conical shell consists of about eight whorls is about 7 mm high and 8 mm wide with ornament of fine spiral lines above and below the selenizone and on the concave base (Kiel & Bandel 2000, pl. 1, figs. 3-4). *Stuorella cretacea* lived on the tropical coast of the same Tethys Ocean but about 130 Million years later than the St. Cassian species.

Family Lancedelliidae n. fam.

Diagnosis: The elongate conical shell with rounded whorls and deep sutures is higher than wide, has a median selenizone and lower and upper keel on its sides. Inner shell layer is nacreous. The selenizone appears late in the juvenile shell and is accompanied by an angle above with a keel and an angle below with or without keel. Selenizone width changes with ornament and is wider where strong axial ribs come close to its margin. Ornament consists of axial ribs with alternating fine and few coarse ones. The aperture is oval with anterior funnel (pl. 2, figs. 19-22). The family holds the genus *Lancedellia* Bandel, 1991 from St. Cassian Formation.

Lancedellia with the type species *Paleunema costata* Zardini, 1978 from St. Cassian has a shell composition with an inner nacre layer as was checked in thin section of *Lancedellia costata.* A shell with 7.5 whorls is about 10 mm high and 6 mm wide. The rounded protoconch is 0.2 mm wide and succeeded by the first teleoconch with axial ribs. In the third whorl two spiral ribs insert and increase in number to four until in the fifth whorl of the teleoconch the slit begins. In the succeeding whorls the selenizone lies next to the periphery and is accompanied by spiral ribs on both sides. Ornament consists of fine axial ribs and at irregular distance coarser collabral lamellar ribs. Where stronger ribs contact the margin of the selenizone its width increases. The base is rounded and axial ribs continue into its umbilicus. The aperture has a straight inner and a rounded and notched outer lip with the slit in its middle (Zardini 1978, pl. 13, figs. 4-5, Bandel 1991, pl. 17, figs. 5-8).

The selenizone of *Lancedellia* has undulating margins. Its shell shape resembles that of the slit bearing *Murchisonia* Archiac & Verneuil, 1841 with Devonian type species. Bandel (2002) documented that the Devonian species close to the type are not related to Carboniferous species with similar shell shape, which, in addition, have no nacre but crossed lamellar structure in their shell walls (Bandel & Geldmacher 1996). The Carboniferous *Polytremaria* Orbigny, 1850 has an undulating slit as in *Lancedellia*, but the shell is of comparatively lower shape (25 mm long and 30 mm wide according to Koninck 1883, pl. 33, figs.1-5) and shell structure is unknown. A high spire as in *Lancedellia* is also found in *Apachella* Winters, 1956 and *Peruspira* Chronic, 1941 from the Permian (Knight et al. 1960). They differ from *Lancedellia* by having a simple selenizone and have been regarded to represent Neilsoniinae Knight, 1956 of the Eotomariidae, a group with more elongate shell as in the *Eotomaria* Ulrich & Scofield, 1897 relation.

Superfamily Ptychomphaloidea Wenz, 1938

The shell is low with disc-like shape and low spire. Upper side of whorls is flat and ornamented only by weak spiral lines. The selenizone lies peripheral on the shell margin and is the result of a relatively wide slit. Increase in whorl width is rapid and the base may have an umbilicus that can be closed by callus of the inner lip (Wenz 1938 for Ptychomphalinae).

Here the Ptychomphalidae with Jurassic type and the Rhaphistomellidae with Triassic type can be included both with connections to Paleozoic genera and with last representatives in the Early Jurassic. Ptychomphalinae have been included with the Eotomarioidea by Bouchet & Rocroi (2005). This placement is not accepted even though the Ordovician type of *Eotomaria* resembles somewhat that of *Ptychomphalus* with Jurassic type (250 million years later), as is discussed below.

Family Ptychomphalidae Wenz, 1938

The biconical to lens-like shell is wider than high with selenizone at or just above a marginal keel. The umbilicus is closed. Whorls on their upper side are flattened and almost smooth in *Ptychomphalus* Agassiz, 1839 that has the Early Jurassic type *Helicina compressa* Sowerby, 1813 from France. Members of the genus are also present in the St. Cassian Formation.

Ptychomphalus protei (Laube, 1868) from St. Cassian with biconical shell is relatively high in shape with peripheral selenizone that in succeeding whorls comes to lie next to suture. The inner shell layer is nacreous. With 4.5 whorls the shell is 4 mm wide and 3 mm high and with about 5.5 whorls it is 11 mm high shell is 10 mm wide. Ornament consists of collabral and very fine spiral lines. The first two whorls of the teleoconch are rounded, and in the slit starts in the third whorl which become more flattened. The aperture is almost vertical and the slit lies in the upper part of the rounded outer lip. The rounded base is covered by callus of the inner lip (pl. 2, figs. 23-26) (Laube 1868, pl. 26, fig. 7 as *Scalites protei*; Zardini 1978, pl. 2, fig. 7, Bandel 1991, pl. 12, fig. 8). A very closely related form from St. Cassian had been determined as *Euzone alauna* Koken (Zardini 1978, pl. 2, figs. 8-9).

The type *Ptychomphalus compressa* (Sowerby, 1813) (Knight et al. 1960) is very close in shape with *P. expansus* (Sowerby, 1821) from the Hierlatz Limestone (Early Jurassic) (Szabo 2008, fig. 17). *Ptychomphalus theodorii* (Schrüfer, 1861) in Gründel (1999, pl. 1, figs. 1-6, pl. 2, fig. 1) from the Early Jurassic of northeastern Germany resembles *P. expansus* but is larger (17 mm wide and 11 mm high) and relatively higher (as high as wide). The 0.4 mm wide protoconch is succeeded by smooth, later spirally lined teleoconch with the narrow slit inserting on the peripheral edge in the second whorl. It resembles a species described by Gründel & Koppka (2007, pl. 1, figs. 6-7, pl. 2, figs. 1-2, 5) as *Ptychomphalus* sp. that has the early teleoconch well preserved. The Jurassic species of this genus are either somewhat variable, or there are several similar ones (Gründel & Nützel 1998, Gründel 2007b, pl. 1, figs. 1-2) and differ from *Ptychomphalus protei* by having a lower shell and a more indistinct selenizone.

Ptychomphalidae do not continue into younger strata than Liassic. Rather close to *Ptychomphalus protei* is *Ptychomphalina* Fischer, 1885 from the Early Carboniferous of Belgium based on *Helix striatus* Sowerby, 1817 (Wenz 1938, fig. 204, Knight 1941, pl. 29, fig. 3). *Ptychomphalina striata* has a large body whorl and the selenizone on the mid-whorl (Koninck 1883, pl. 22, figs. 19-22 as *Ptychomphalus striatus*). The ornament consists of lamellar growth lines and very fine spiral lines, as is the case in *Ptychomphalus protei*. Also species of *Tropidostrophus* Longstaff, 1912 from the Early Carboniferous of the USA are similar in shape and ornament (Batten 1966, pl. 3, figs. 10-13). The latter of which differs strongly from the smooth surface present in *Rhaphistomella radians* from St. Cassian (see below).

Family Rhaphistomellidae n. fam.

Diagnosis: The shell has a low conical top, rounded sides and a rounded base with umbilicus. It is wider than high. Shell wall consists predominantly of nacre. A slit appears within the third whorl of the teleoconch and lies at the periphery producing a very indistinct but wide selenizone. Shell surface is smooth and ornament consists of a row of rounded nodules or short rounded ribs below the suture that appears with begin of the selenizone. The family is based on the Triassic *Rhaphistomella* Kittl, 1891 with type from the St. Cassian Formation.

Rhaphistomella radians (Wissmann, 1841) is 8 mm high and 11 mm wide with 5.5 whorls. The protoconch measures 0.25 mm in width and is succeeded by 2.5 whorls with fine spiral lines crossed by growth lines. The selenizone begins within the third whorl and is accompanied by a narrow ridge at its lower margin (figs. 27-28). The flattened ramp above the selenizone is smooth and ornamented by low short rounded radial ribs as soon as the slit appears. The large and vertical aperture has only a short open slit (Laube 1868, pl. 26, fig. 9 as *Pleurotomaria radians*, Zardini 1978, pl. 3, fig. 3, Bandel 1991, pl. 11, figs. 7-8, pl. 12, figs. 1-3). The outer layer of the shell is fine- grained and almost homogeneous while the inner layer is formed by thick nacre that is covered by a layer of crossed acicular structure, as was documented by thin sections.

Rhaphistomella Kittl, 1891 has an open umbilicus and flattened, smooth shell top. *Rhaphistomella* spelled *Raphistomella* by Wenz (1938) resembles the Carboniferous *Angyomphalus* Cossmann, 1915 that has the type *Angyomphalus radians* (Koninck, 1881) from the Early Carboniferous of Belgium (Knight 1941, pl. 31, fig. 3). Very similar shape and ornament is found in *Angyomphalus radianodosus* Yoo, 1994 from Australia that has a ridge of rounded nodules next to the suture and smooth shell surface with indistinct selenizone on the rounded periphery (Yoo 1994, pl. 4, figs. 4-10). Knight (1933, pl. 8, fig. 5) found a species placed with *Angyomphalus* from the Late Carboniferous Henrietta Shale of Missouri as close to *Anomphalus* Meek & Worthen, 1867 since he did not detect the selenizone. In case of the type of the genus, *Euomphalus radians* Koninck 1843, he observed the selenizone (Knight 1941). Shells from the Saint Louis Outlier of Missouri have a broad and indistinct selenizone at the corner of the shell (pl. 2, figs. 29, 30, pl. 3, fig. 31), and a shape that is very close to that of *Rhaphistomella radians* from St. Cassian. *Angyomphalus* from the Early Carboniferous of Belgium and Australia resembles the species of this genus from the Late Carboniferous of USA as well as *Rhaphistomella* from the Late Triassic. The later resembles *Ptychomphalus kericserensis* Szabo, 2008 from the Early Jurassic Hierlatz Limestone in shape and ornament but its umbilicus is closed by a plug or not present (Szabo 2008, fig. 18). *Angyomphalus minutus* from the Carboniferous also has the umbilicus filled with deposits of the inner lip.

Knight et al. (1960) suggested that *Angyomphalus* is subgenus to *Trepospira* Ulrich & Scofield, 1897 which is also similar to *Rhaphistomella* from the Triassic but may have a higher spire. They placed *Trepospira* in the subfamily Liospirinae Knight, 1956 which is based on an Ordovician type without the characteristic row of nodes just below the upper suture in the Rhaphistomellidae. *Liospira* Ulrich & Scofield, 1897 is based on badly preserved material (Knight 1941, pl. 31, fig. 1) and it cannot be evaluated with any certainty aside from being much older, living about 150 million years before the Carboniferous species *Angyomphalus* and 220 million years before *Rhaphistomella*. *Liospira* may be more related to *Raphistoma* Hall, 1847 that is from about the same time (Ordovician) and placed in the Raphistomatidae Koken, 1896.

Superfamily Schizogonioidea Cox, 1960 (newly assigned)

The shell is slit bearing with nacreous wall. The first whorls of the teleoconch without selenizone are ornamented by strong axial ribs. The position of the slit lies on the periphery of whorls or just above it. Included are the families Schizogoniidae Cox, 1960 and Pseudowortheniellidae n. fam. with species of *Schizogonium* and of *Pseudowortheniella* from Cassian Formation and Triassic age.

Family Schizogoniidae Cox, 1960

The family holds species with small and spiny shell with flat apex and the juvenile whorls coiled in a plane. The protoconch is succeeded by a rounded early teleoconch of about two whorls, and the slit bearing teleoconch is angular. The slit lies on the upper side. The periphery carries a keel and gutter-like spines. Shell wall has an inner nacreous layer as was documented in case of *Schizogonium subcostatum* by thin section. The family is based on the genus *Schizogonium* Koken, 1889 from St. Cassian Formation. An independent group around *Schizogonium* had also been recognized by Kittl (1891) and Bandel & Geldmacher (1996). Bouchet & Rocroi (2005) accepted the Schizogoniidae as members of the Vetigastropoda without assigning them to a certain superfamily. The similarity of the early teleoconch with that of *Pseudowortheniella* indicates a relation with other nacreous slit bearing gastropods that have no marginal keel and groove with spines.

The shell of *Schizogonium* is wider than high and the whorls of the teleoconch without slit are rounded and ornamented by axial ribs. The slit begins in the third whorl with the selenizone in a ridge or corner of the shell. Alongside or a little earlier a marginal keel appears that consists of gutter-like spines which may later fuse to form a continuous keel. The aperture is oval and arranged in vertical or inclined position, with the slit in its apical portion and a gutter leading into the keel at its side. The base is more or less flattened and bears a wide umbilicus in the species with low shell, and it may be closed in the fully grown species with high shell. The type is *Schizogonium scalare* (Münster, 1841) from St. Cassian Formation. Its shell consists of 5 whorls and is 7.5 mm wide and 5 mm high. The protoconch representing the embryonic whorl differs in shape and ornament from the first whorls of the teleoconch and is ornamented by spiral lines (Bandel 1991, pl. 3, fig. 7). The first 1.5 whorls of the teleoconch are ornamented by about 20 axial ribs. With initiation of the slit on the corner of the upper side also the marginal spines appear. Shell growth is allometric, with the first three whorls with wide umbilicus and low spire with flat base, and with higher body whorl that has a rounded base and a narrow umbilicus (Bandel 1991, pl. 3, figs. 1-8) (pl. 3, figs. 32-33).

Nine species of *Schizogonium* have been recognized from St. Cassian Formation (Bandel 1991). Of these *Schizogonium subcostatum* (Münster, 1841) resembles *Schizogonium scalare* but has axial ribs on the base of the juvenile shell. The shell is relatively low with oblique and round aperture. The selenizone lies on a ridge and the marginal keel has open spines only in the early whorls. The umbilicus remains open but it is relatively narrower in the fully grown shell that is with whorls 9 mm wide and 7 mm high. Ornament of the body whorl consists only of growth lines (Zardini 1978, pl. 8, fig. 20, Bandel 1991, pl. 4, figs. 1-5).

Schizogonium elevatum Kittl, 1891 has the flat base connected to a steep spire and represents the relatively highest of the species. With 5 whorls the shell is about 9 mm high and 8 mm wide. The early shell with 15 strong axial ribs resembles that of *Schizogonium scalare.* The slit begins in the third whorl as well as the margin a keel with hollow spines. These fuse in the body whorl to form a continuous keel. Juvenile shells therefore are spinier than the last one. The flat base in the fully grown shell has the umbilicus closed by callus of the inner lip. The aperture is oblique and the slit open for about one fourth whorl. On the aperture of juvenile individuals the marginal keel has an open groove leading into a spine (Zardini 1978, pl. 9, figs. 11, 14, 17, Bandel 1991, pl. 9, figs. 2-6).

Schizogonium gracilis (Münster, 1841) with flat shell base resembles *Schizogonium subdentatum* (Münster, 1841) and *Schizogonium serratum* (Münster, 1841). The embryonic whorl is succeeded by 1.8 whorls ornamented by strong axial ribs. First whorls with slit have marginal thorns and in the fourth whorl the keel of the selenizone as well as the marginal keel consists of nodes. The top of the shell is plane, while the base has the wide umbilicus with rounded sides. The aperture has vertical orientation with a narrow slit on its upper side and a groove to the keel. With 4.5 whorls the shell is fully grown and 2.3 mm wide and a little more than 1 mm high (Zardini 1978, pl. 9, figs. 7-8, Bandel 1991, pl. 5, figs. 1, 3).

Schizogonium serratum with 4.5 whorls of its shell is about 6 mm high and 10 mm wide (pl. 3, figs. 34-35). Growth of the shell is allometric and whorls of the juvenile shell are relatively flatter than later whorls. The body whorl forms and almost plane coil. Juvenile whorls are rounded and ornamented by curving axial ribs and fine spiral lines. The slit initiates in the top of the third whorl and simultaneously hollow spines appear on the marginal keel. The base has a wide umbilicus. Ornament consists of axial ribs and scaly surface, and the marginal keel can have a regular pattern of triangular serrations. The aperture is almost vertical with angular outline (Zardini 1978, pl. 9, figs. 6, 9-10, 1980, pl. 2, figs. 13-14, Bandel 1991, pl. 5, figs. 2, 4-8).

Schizogonium subdentatum has a flat shell and elevated spire. With 5 whorls it is about 6 mm wide and 1.5 mm high. The early teleoconch is ornamented by axial ribs for 1.5 whorls and in the following whorl the selenizone lies on an upper ridge while a keel forms the margin with the axial ribs ending in tubercles. The base is almost flat and has a wide umbilicus into which the axial ribs continue. The aperture in the juvenile shell is almost vertical and later shell oblique with a slit in the apical outer lip and a deep slit-like groove on its side (Zardini 1980, pl. 2, fig. 12).

Schizogonium lamellosum Bandel, 1991 is disc-like but early teleoconch with rounded whorls (pl. 3, fig. 36). With 5 whorls the shell is about 7 mm wide and 2 mm high. The whorls of the early teleoconch are ornamented by strong axial ribs. The slit begins in the second whorl of the teleoconch and forms a ridge. The marginal keel consists of gutter-like lamellar spines, whereas in later whorls spines unite to form a wide and low lamellar keel. The base is flat and has a wide umbilicus. The aperture is nearly vertical with the slit high up in the outer lip which has a narrow groove leading into the marginal lamella (Bandel 1991, pl. 6, figs. 1-6).

Schizogonium ampezzanum Bandel, 1991 with 5 whorls is 9 mm wide and only 3 mm high (pl. 3, figs. 40-41). The early teleoconch with rounded whorls has more numerous and lamellar axial ribs than *S. lamellosum* and also fine spiral lines. The slit initiates in the third whorl and the marginal keel develops hollow spines. Later whorls are flattened and the spiny carina changes into a lamellar one. The aperture is inclined and has the outer lip with the upper slit and the marginal groove to the carina. The base has a spiral keel around the wide conical umbilicus (Bandel 1991, pl. 7, figs. 4-8, pl. 8, figs. 1-2).

Schizogonium tamarinum Bandel, 1991 has its rounded base with wide umbilicus and ornament of 14 strong axial ribs which may branch towards the keel (pl. 3, figs. 37-38). A shell with 4 whorls is almost 3 mm wide and 1 mm high. The embryonic whorl is 0.18 mm wide and the following 2.2 whorls of the teleoconch are rounded and ornamented by strong axial ribs. In the third smooth whorl the slit initiates forming a keel on the upper whorl and a nodular marginal keel composed of short gutter like spines appears. In the last whorls shell shape changes from plane to trochispiral coiling. The aperture is as wide as high and has the slit in the upper part of its outer lip and a gutter on the marginal keel (Bandel 1991, pl. 8, figs. 3-8, pl. 9, fig. 1).

Spinulichospira Blodgett & Rohr, 1989 with type *S. cheeneetnukensis* Blodgett & Rohr, 1989 from the Early Eifelian of Alaska has a shell that resembles that of *Schizogonium.* It also has moderately high spire and narrow umbilicus and tube-like spines just below mid whorl height. The selenizone above the spines is not well known and original shell structure is also unknown (Blodgett & Rohr 1989). Among the non-slit nacreous Archaeogastropoda from St. Cassian *Coelocentrus* Zittel, 1882 has similar shell shape and size and a keel formed by hollow thorns. In contrast to *Schizogonium*, *Coelocentrus* has no slit and the early teleoconch is smooth and not ornamented by axial ribs as is the case in all species of *Schizogonium* (Bandel 1993, pl. 15, figs. 6-9, pl. 16, figs. 1-9). Knight et al. (1960) included here also *Pseudoschizogonium* Kutassy, 1937 which differs from *Schizogonium* and the Schizogoniidae by having no marginal keel and less ornamented early teleoconch.

Family Pseudowortheniellidae n. fam.

Diagnosis: The shell is wider than high with flatly rounded apex that has not concavely rounded whorls. The selenizone appears in the upper third at begin of the third whorl of the teleoconch. Ornament consists of strong axial ribs on the early teleoconch and later fine axial and spiral ribs. The family is based on the genus *Pseudowortheniella* from St. Cassian Formation.

The ornament of the early teleoconch, the presence of nacre in the shell wall and the position of the selenizone on the upper whorl connect Pseudowortheniellidae with *Schizogonium* and the Schizogoniidae. In contrast to the latter the shell periphery has no keel and no row of gutter-like spines.

Genus *Pseudowortheniella* n. gen.

Diagnosis: Rounded shell shape is connected to the axial and fine spiral ornament of the shell beginning right behind the protoconch. The selenizone initiates in the middle of the apical whorl side in the third whorl of the teleoconch and migrates to the side forming a ridge above the peripheral edge. The base is rounded with umbilicus that is open in the juvenile and filled with callus in the adult. The type is *Worthenia rarissima* Kittl, 1891 from St. Cassian Formation.

The name is based on the similarity to *Wortheniella* regarding ornament of the shell but differs by having a more rounded early ontogenetic shell without depression in the apex and a selenizone above the peripheral corner (pseudo).

Difference: The ornament and shape of the early teleoconch distinguish *Pseudowortheniella* from *Wortheniella.* The early teleoconch surround the protoconch that lies in a depression in case of *Wortheniella* while it lies on weakly rounded apex in *Pseudowortheniella*. The ornament of the first whorl of the teleoconch of *Bandelium* consists of more spaced axial folds on basically smooth background and the concave first whorls lies in a more conical shell shape. *Worthenia* Koninck, 1883 differs by having two angulations on its whorls which in *Pseudowortheniella* are rounded. *Gosseletina* Bayle, 1885 differs by having a more evenly rounded shell and no axial ornament on the early teleoconch. *Stenoloron* Oehlert, 1888, *Euryzone* Koken, 1896 and *Coelozone* Perner, 1907 from the Middle Devonian of France and Germany resemble *Pseudowortheniella* in shape but differ in not well known details and lived more than 150 million years earlier (Knight 1941, pl. 27, figs. 1, 5, Heidelberger 2001, pl. 2. figs. 1-6).

Pseudowortheniella rarissima (Kittl, 1891) has broadly conical shape. The base with wide umbilicus is ornamented with fine spiral lines (pl. 4, figs. 50-54). Axial ribs of the juvenile later change into coarse growth line pattern. The adult shell is wider than high with rounded spire and base (Zardini 1978, pl. 4, fig. 14, pl. 5, figs. 11, 14, pl. 6, fig. 1). The selenizone forms a raised ribbon with spiral lines and knobby increments of growth. The protoconch measures 0.17 mm and is ornamented with a fine network of tubercles. The juvenile shell without slit forms a plane spiral for 1.25 whorls before turning trochispiral (Schwardt 1992, pl. 1, figs. 1-3). A shell with 4.5 whorls is about 6 mm wide. The adult shell of *Schizogonium subcostatum* has similar ornament and shape, but the marginal keel has scaly spines, and the early teleoconch has stronger axial ribs (Bandel 1991, pl. 4, figs. 1-5).

Difference: *Pseudowortheniella rarissima* differs from all other species of the genus from St. Cassian resembling only *Wortheniella spuria* to some degree regarding the general rounded shell shape, but not the early juvenile shell. The early ornament of the teleoconch and also the general shell shape resemble that found in *Schizogonium.*

Luciellina Kittl, 1900 based on *Luciellina contracta* Kittl, 1900 from the Triassic of Hungary has a disc-shaped bi-conical shell with prominent carina at mid-height that holds the selenizone (Kittl 1900). The ornament consists of spiral ribs present on top as well as the rounded base. *Luciellina* was suggested to be related to *Luciella* Koninck, 1883 from the Early Carboniferous (Koninck 1883, pl. 32, figs. 1-20, Wenz 1938, fig. 174) that has a marginal spine bearing fringe. A species assigned to *Luciellina* by Batten (1966, pl. 4, figs. 5-8, 10-11) from the Early Carboniferous of the USA resembles *Pseudowortheniella* in ornament and shape but has more concave whorl sides. In case of *Luciella eliana* (Koninck, 1843) from the Visé of Belgium the selenizone lies below the margin of the frill (Knight 1941, pl. 36, fig. 1d). This position of the slit differs strongly from that of *Pseudowortheniella* that has no marginal frill and from *Schizogonium* with the selenizone above the frill. The position of the selenizone of *Luciella eliana* has been confirmed with specimens that have been determined by Koninck (1883) (personal observation).

Superfamily Eotomarioidea Wenz, 1938

The superfamily unites several groups with slit bearing shells of conical shape and nacre in its walls that connect to Early Paleozoic groups. The type of *Eotomaria* Ulrich & Scofield, 1897 lived during the Ordovician and has the slit just above the peripheral edge of the angular lowly conical shell that is wider than high (Knight 1941, pl. 31, fig. 5). A relation of the ancient *Eotomaria* with *Pseudoschizogonium*, *Rhaphistomatella*, *Sisenna*, *Ptychchomphalus* and *Euzone* from the Triassic, in contrast to the opinion of Knight et al. (1960) repeated by Bouchet & Rocroi (2005), is very much in doubt. A placement of Eotomariinae as subfamily of the Pleurotomariidae as had been suggested by Wenz (1938) can also be doubted due to the first presence of the latter not before the Jurassic. Here provisionally included in the Eotomarioidea are the Pseudoschizogoniidae that have rather distinct angular shape, and the Gosseletinidae with rounded shell shape.

Family Pseudoschizogoniidae n. fam.

Diagnosis: The shell has a nacreous inner layer and angular shape with a stair-like spire. The selenizone lies in a keel on the upper corner and the side is concave with a rounded corner to the base. The aperture is as wide as high and oriented vertically and the base is the juvenile shell has a narrow umbilicus and is later closed. Ornament consists of fine spiral lines and fine growth lines. The whorls of the early juvenile shell have ornament of fine spiral lines.

Pseudoschizogonium Kutassy, 1937 with the type species *Pseudoschizogonium turriculatum* Kutassy, 1937 from the Late Triassic of Hungary is represented by *Pseudoschizogonium elevatum* (Kittl, 1891) among the species of the St. Cassian Formation (Bandel 1991, pl. 13, figs. 4-5, pl. 17, fig. 5) (pl. 3, figs. 42-45, pl. 4, fig. 46). This may be *Pleurotomaria scalari* of Laube (1869, pl. 8, fig. 6). The shell wall is nacreous in its inner part as was checked by thin section. Shell shape is stair-like with rounded whorls before the slit begins. The slit initiates on the third whorl of the teleoconch and continues as selenizone on the peripheral edge in a ridge forming the corner to the concave side that forms a rounded edge with the base. The juvenile shell has a narrow umbilicus and later whorls have no umbilicus.

Pseudoschizogonium differs from *Schizogonium* by the shell that has no row of marginal spines forming a keel. The early whorls of the teleoconch have no ornament of strong axial ribs as are characteristic to the species of *Schizogonium*. The apex of *Pseudoschizogonium* is conical and rounded and thus distinct from the concave and flat apical shell of the Wortheniellidae. *Worthenia* Koninck, 1883 with the type *Turbo tabulatus* Conrad, 1835 from the Late Carboniferous (Pennsylvanian) of the USA (Pennsylvania) (Knight 1941, pl. 34, fig. 1a-c) has its trochispiral shell with turreted spire with a slit on the outer lip that leaves a selenizone in the corner of the apical ramp. It grew to more than 30 mm in size, with the shell a little higher than wide. The whorls have two angulations as in *Pseudoschizogonium* of which the upper contains the selenizone and the lower more rounded one connects to the rounded base. The early teleoconch is simple and dextral with rounded whorls and resembles that of *Pseudoschizogonium*, as does the ornament that consists of spiral ribs of which the stronger ones can have nodules. *Worthenia* may represent a Carboniferous relative of Triassic *Pseudoschizogonium*.

A family Kittlidiscidae Cox, 1960 of the Pleurotomariidae had been proposed by Knight et al. (1960) to include *Schizodiscus* Kittl, 1891 (= *Kittlidiscus* Haas, 1953) with the type species *Pleurotomaria plana* Klipstein, 1843 from St. Cassian (Kittl 1891, textfig. 2, Wenz 1938, fig. 177). This is *Solarium planum* of Laube (1868, pl. 25, fig. 10). *Kittlidiscus planus* has a low shell with rapid increase in diameter and deep sutures with two keels on the side (pl. 4, figs. 55-57). It was thought that a wide selenizone is present between the keels on the vertical shell margin. But actually the shell has no slit and selenizone and its wall not nacreous but composed of crossed lamellar structure (Bandel 1991). A relation to *Pseudoschizogonium* Kutassy, 1937 is therefore impossible even though there is a similar marginal keel. Kittlidiscidae represent Caenogastropoda, and can also not be included in the Gosseletininae as was suggested by Wenz (1938).

Family Gosseletinidae Wenz, 1938

The shell has rounded conical shape with the selenizone in the corner that lies on the peripheral margin closer to the upper than the lower suture. The protoconch is connected to the trochispiral early teleoconch. Besides *Gosseletina* also *Sisenna* and *Euzone* can be included among the taxa from St. Cassian.

Gosseletina Bayle, 1885 (= Fischer, 1885) is based on *G. callosa* (Koninck, 1843) from the Early Carboniferous (Koninck 1883, pl. 23, figs. 13-16, Knight 1941, pl. 27, fig. 1). The globular shell has a selenizone relatively high on the whorls which are evenly rounded. *G. callosa* has a 22 mm high and 27 mm wide shell with the inner lip of the aperture expanded to cover the umbilicus. Ornament of the early teleoconch and the onset of the slit in it are unknown.

Gosseletina fasciolata (Münster, 1841) from St. Cassian Formation has a spherical shell that with 5 whorls is 11 mm high and 8 mm wide. It reached 17 mm in height and 16 mm in width when fully grown (pl. 4, figs. 58-59). The protoconch measures 0.3 mm in width and the slit inserts in the second whorl of the teleoconch. The selenizone generated by the short slit is flat and wide and half covered by the succeeding whorl. Ornament consists of low spiral ribs separated by fine grooves. The rounded aperture has the inner lip expanded onto the umbilicus that is wide in the juvenile and narrow in the adult shell (Kittl 1891, pl. 1, figs. 23-25, Bandel 1991, pl. 12, fig. 4-7).

Sisenna Koken, 1896 has a conical shell with rounded whorls and narrow apical ramp. The protoconch is succeeded by rounded whorls of the teleoconch before the slit begins and whorls become more angular. The selenizone lies on the upper corner in a groove with marginal keels. The base is rounded and ornamented with spiral ribs continuous into the umbilicus. The type species is *Pleurotomaria turbinata* Hoernes, 1855 from the Late Triassic of the Northern Alps.

Sisenna venusta (Münster, 1841) from St. Cassian has a rounded conical shell with narrow umbilicus (pl. 4, figs. 59-60, pl. 5, figs. 61-62). Ornament consists of fine spiral lines and a ribbon of short rounded axial ribs from the fourth whorl of the teleoconch onward. The protoconch is 0.19 mm wide and ornamented by a pattern of flattened grooves surrounded by a network of ridges. It is succeeded by two rounded whorls forming a lowly dextral trochespiral shell with fine spiral ornament. With onset of the slit in the third whorl the apical flank is flattened and greatest width of the shell formed on the rounded sides. The selenizone is smooth, positioned on the peripheral edge and consists of a raised ridge with regular increments of growth. The sides are rounded below and also the transition to the base. Both are ornamented by fine spiral lines and low axial folds. A shell consists of more than 5 whorls and reaches a size of about 9 mm in width and height (Münster 1841, pl. 12, fig. 13, Zardini 1978, pl. 6, figs. 2, 6, 12, pl. 39, fig. 8a-c, 1980, pl. 6, fig. 6, 1985, pl. 4, fig. 4, Bandel 1991, pl. 14, fig. 7 as "*Ptychomphalus*" *neumayri*). Schwardt (1992, pl. 2, figs. 2, 3a-d) noted that in contrast to the other members of *Wortheniella*, the species determined by her as *W. venusta* (Münster, 1841) has a protoconch that does not lie in a depression of the first whorl of the teleoconch but is positioned at the top of a low trochispiral shell. The same species had been documented by Zardini (1978, pl. 3, figs. 4-6) as *Sisenna ampezzana* (Leonardi Fiscon, 1960). The species described as *Gosseletina fasciolata* (Münster, 1841) by Kittl (1891, pl. 1, figs. 23-25) could also represent *Sisenna venusta*.

Gründel & Nützel (1998, pl. 1, figs. 3-5) determined from the Early Jurassic of southern Germany *Sisenna canalis* (Münster, 1844) with shell slightly wider than high and small (about 5 mm). As in *S. venusta* the slit appears to initiate in the spiral rib that features the first rounded whorls of the teleoconch, but a selenizone is not clearly described. Among Jurassic species those of the genus *Obornella* Cox, 1956 based on *Pleurotomaria plicopunctata* Etudes- Deslongchamps, 1849 that has been described by Gründel (1997, pl. 1, figs. 4-7) based on well preserved specimen with the protoconch preserved, have a low trochispiral shell with wide umbilicus and convex base. It resembles *Sisenna,* but usually has a larger size (up to 50 mm). In *Obornella* the selenizone lies between suture and peripheral corner or near the corner, and the whorls are less angular. Species are known from the Early to Late Jurassic from Europe, Madagascar and India (Benfrika 1984, Fischer & Weber 1997, pl. 36, figs. 8, 9, Jaitly et al. 2000, pl. 1, figs. 5-8, pl. 2, figs. 1-2, Gründel 2000, pl. 1, figs. 4-8, 2003a, fig. 1, 2003b, 2003c, pl. 3, figs. 10-16; pl. 4, figs. 1-10, Hägele 2003, Harasewych & Kiel 2007, figs. 5-12).

The Early Carboniferous *Campbellospira* Yoo, 1994 from Australia has the early teleoconch whorls rounded and ornamented with spiral ribs. As soon as the slit begins the whorl develops a corner and ornament of short axial ribs is present on the apical shoulder (Yoo 1994, pl.5, figs.1-10). It resembles *Sisenna venusta* and a similar species is described below.

Campbellospira missouriensis n. sp.

Diagnosis: The shell from the Pennsylvanian Henrietta Shale of the St. Louis Outlier of Missouri has the protoconch of about 0.13 mm in width succeeded by 2.5 rounded whorls of the teleoconch with fine spiral ornament. The even low trochispiral coiling continues in the third whorl but ornament changes with short radial ribs added to the spirals on the apical whorl, a keel appears on the periphery and here a selenizone is found with indistinct regular growth increments. Its lower side is formed by a further keel below which the whorl is evenly rounded and continuous into the rounded base that has a narrow umbilicus into which the inner lip expands. The aperture is rounded with less curvature on the inner lip (pl. 5, figs. 63-65).

Deposition of the holotype (pl. 5, fig. 63): Museum of the Geologisches und Paläontologisches Institut and Museum, Hamburg.

Description: Only juvenile shells are represented of which the largest consists of 5 whorls, is 2 mm high and slightly less wide (1.5 mm in holotype). Ornament of the protoconch is not preserved and the early teleoconch has fine spiral ribs which become more distinct in the first whorl, amounting to about 6 in the visible part of the spire. The second whorl of the teleoconch has 7 visible spiral ribs and they have increased in strength and width. Within the third whorl the upper of the spiral ribs forms nodules which in continuation transform into short axial curving ribs. They end before reaching the spiral keel that indicated the apical edge of the selenizone that inserts here. It occupies the peripheral margin.

The early teleoconch has fine spiral ornament, consists of rounded whorls, with insertion of the slit within the third whorl. Alongside a corner is formed below which the selenizone has its position and axial folds appear, as in *Sisenna*. Yoo (1994) suggested that *Cambellospira* differs from other genera of the Eotomariidae by having a planktotrophic protoconch that in the type species *C. conica* Yoo, 1994 is interpreted to consist of two whorls. *C. missouriensis* has in the early teleoconch also growth intermissions in the end of the second whorl, as is the case in one of the specimens from Australia, but also after 2.3 whorls in a second and third individual. The existence of a larval shell can thus clearly be excluded.

Euzone Koken, 1896 is based on *E. alauna* Koken from the Late Triassic of the Northern Alps (Koken 1896, figs. 1-3, Wenz 1938, fig. 183). *Euzone calypso* (Laube, 1868) is up to 11 mm wide and not quite as high with well rounded whorls which increase rapidly in width. The protoconch is 0.35 mm wide and succeeded by 1.5 whorls of the early teleoconch before the slit inserts. The selenizone lies on the middle of the rounded whorl and in the whorls of the spire just above the suture. It is quite indistinct merging with the fine spiral ribs of the ornament. The evenly rounded base has a wide umbilicus (Laube 1868, pl. 28, fig. 2, Bandel 1991, pl. 13, figs. 1-3). *Euzone alauna* is similar in shape and also resembles *Gosseletina fasciolata* that has a relatively wider selenizone.

Family Wortheniellidae n. fam.

Diagnosis: The conical shell has angular whorls and flattened apex. The embryonic whorl is weakly left coiled and lies below the surface of the first whorl of the teleoconch. The slit inserts within or later than the second whorl of the teleoconch. It lies on the corner of the apical ramp to the flattened or concave sides. A spiral ridge forms the corner with the rounded base that is ornamented by spiral elements. In wide shells an umbilicus may be present in high shells it is closed. The shell is composed of an outer layer with complex crossed acicular structure and inner nacre. The family is based on the genus *Wortheniella* Schwardt, 1992 with the type species *Worthenia coralliophila* Kittl, 1891 from St. Cassian Formation.

Included are *Wortheniella* and *Bandelium* as proposed by Schwardt (1992) and the new *Rinaldoella* n. gen. Of the 17 species placed in the *Wortheniella* relation by Schwardt (1992), 7 are here regarded to belong to *Wortheniella*, one is included within *Bandelium* and 7 are placed in the new *Rinaldoella.* Two species are excluded from the group due to a different morphology of their early teleoconch such as *Worthenia rarissima* Kittl, 1891 (as *Pseudowortheniella)* and *Pleurotomaria venusta* Münster, 1841 (as *Sisenna).*

In the genus *Wortheniella* Schwardt, 1992 the shell is conical to trochispiral with one to one and half plane whorls of the early teleoconch succeeding the protoconch that lies in a depression. The slit begins after at least 1.5 whorls of the early teleoconch have formed without slit and after coiling in one plane ended. *Wortheniella* has –newly- few strong spiral ribs on the first whorl of the teleoconch and a ribbon of nodules or axial folds below the suture in later whorls of the teleoconch with a predominance of spiral lines or ribs in the general ornament of the shell. The slit lies in the upper portion of the outer lip of the aperture. Below the corner with the selenizone the flank may be concave. Ornament consists of spiral ribs and there may also be axial elements besides the growth line pattern. The shell has an inner nacreous layer. The ornament of the early teleoconch initiates with spiral ribs or lines as is the case in the type species *Wortheniella coralliophila* (Kittl, 1891) as defined by Schwardt (1992).

Wortheniella coralliophila, *W. canalifera* (Münster, 1841), *W. subpunctata* (Laube, 1868) have a relatively slender shell, while the shell of *W. tenera* Schwardt, 1992, *W. cassiana* (Kittl, 1891), *W. spuria* (Münster, 1841), and *W. toulai* (Kittl, 1891) is relatively wide.

Wortheniella coralliophila with conical shell has concave sides and a flattened base without umbilicus. With five whorls it is about 3.5 mm high and 2.5 mm wide (pl. 5, figs. 66-70). To the ornament of spiral lines nodule-like ribs appear below the suture (Schwardt 1992, pl. 7, figs. 1-2, Zardini 1978, pl. 4, figs. 8-9). The protoconch with 0.18 mm in diameter is ornamented by fine axial wrinkles and two fine spiral ribs. It ends with a thickened outer lip while the spiral lines continue in spiral ridges on the plane early teleoconch, later there are three spiral ribs. The slit begins after 2.5 whorls of the teleoconch along with shell changes to conical shape. *Wortheniella canalifera* has similar shape but in contrast to *W. coralliophila* the ornament of the first whorl of the teleoconch has more spiral lines. The protoconch measures 0.19 mm in diameter, has ornament of granular wrinkles and thickened aperture. It lies in the depression formed by the early plane whorls of the teleoconch with granular surface ornament between ribs. With almost five whorls the shell is 3 mm high and 2.6 mm wide. The selenizone appears within the third whorl of the teleoconch along with an apical row of tubercles. Two spiral keels form the corner to the rounded base (Schwardt 1992, pl. 8, figs. 2-3, Zardini 1980, pl. 1, fig. 11).

Wortheniella subpunctata has its protoconch very deeply immersed into the apex of the teleoconch (pl. 5, figs. 71-74). The early plane whorl of the teleoconch has six spiral ribs and beyond 1.5 whorls the trochispiral coiling begins. The upper of the spiral ribs ends in the slit that appears in the third whorl of the teleoconch (Schwardt 1992, pl. 8, fig. 1). *Wortheniella tenera* resembles *W. coralliophila* in regard to the ornament and the mode of insertion of the selenizone, but the fully grown shell is relatively broader and spiral ribs on the flanks are stronger and fewer in number. The protoconch is about 0.16 mm wide and is ornamented with fine tubercles. First ornament of the teleoconch consists of four spiral ribs of which the two upper ones continue in the keels that accompanies the slit (Schwardt 1992, pl. 7, fig.3 a-d, Zardini 1978, pl.

6, fig. 4). *Wortheniella cassiana* has a broad and smooth selenizone that inserts in the third whorl. The protoconch is 0.2 mm wide and ornamented with several spiral ribs ending in its raised margin of the aperture (Schwardt, 1992, pl. 3, fig. 2). *Wortheniella spuria* with rounded shell and umbilicus is ornamented by axial ribs on the apical whorl side. A fully grown shell is about as high as wide, has concave flanks and rounded base (Zardini 1978, pl. 5, fig. 12) (pl. 6, figs. 76-77). The concave selenizone is ornamented by spiral lines and begins on the peripheral edge with the onset of the third whorl. The protoconch is 0.19 mm wide and is ornamented by a dense pattern of fine tubercles. The first 1.5 rounded whorls of the teleoconch are plane. Grooves accompany the selenizone on both sides (Schwardt 1992, pl. 1, figs. 4-5). *Wortheniella toulai* (Kittl, 1891) resembles *W. spuria*. Its protoconch measures 0.5 mm in maximal width and is ornamented by a fine tubercles and is deeply immersed in the center of the following early teleoconch with 1.5 rounded whorls which are ornamented by spirally arranged rows of tubercles. The rows grade into spiral ribs the upper of which include between them the selenizone that begins after 1.75 whorls of the teleoconch are present. A spiral keel lies on the rounded flank and 5-7 strong spiral ribs form the rounded base with umbilicus (Schwardt 1992, pl. 2, fig. 1).

Genus *Rinaldoella* n. gen.

Diagnosis: The shell has a similar general shape as is found in *Wortheniella* but ornament of the first whorls of the teleoconch consists of fine spiral ribs crossed by collabral ribs that may form rows of granules or tubercles at crossing points. The ornament of the slit bearing teleoconch is dominated by spiral and axial ribs forming a cancellation. The type to the genus is *Wortheniella rinaldoi* Schwardt, 1992 from St. Cassian Formation (Schwardt 1992, pl. 3, fig. 1a-d).

Rinaldoella rinaldoi (Schwardt, 1992) has a conical shell that is a little higher than wide with whorls flattened on top and concave on the sides between selenizone and corner to the base. The base has an umbilicus. The protoconch is 0.17 mm wide and smooth. It lies deeply immersed in the center of the succeeding 1.25 rounded whorls of the early teleoconch. Here ornament consists initially of three subsequently five spirally arranged rows of tubercles formed at crossing point with collabral ribs. The selenizone inserts at 1.5 teleoconch whorls and lies within a depression accompanied by two lateral keels. The angular whorls of the teleoconch have two spiral ribs at the corner to the base that is ornamented by several spiral ribs. All these are transected by fine collabral axial ribs. The aperture has a straight inner lip and an evenly rounded outer lip, With about three whorls of the teleoconch the shell is 2.4 mm high and 2 mm wide (Schwardt 1992, pl. 3, fig. 1a-d).

Rinaldoella muensteri (Klipstein, 1843) has the ornament of the early teleoconch as fine spiral lines, and the embryonic shell is 0.22 mm wide with sinuous outer lip (pl. 5, fig. 75, pl. 6, figs. 88-89). The slit inserts in the second whorl of the teleoconch (Schwardt 1992, pl. 5, fig. 2a-d, Zardini 1978, pl. 5, fig. 13a-d). Rounded axial folds are present on the apical ramp and crossed over by finer spiral ribs. Below the selenizone ornament consists of a cancellation produced by spiral ribs and collabral growth increments. A keel accompanies the edge to the base with spiral ribs. *Rinaldoella muensteri* (Klipstein, 1843) and *Rinaldoella johannisaustriae* (Klipstein, 1843) have a more angular shape than found among the species of *Wortheniella* and fine spiral ornament on the early teleoconch. The shell of *R. johannisaustriae* is a little wider and has an umbilicus in its flattened base with ornament of many fine spiral ribs (Schwardt 1992, pl. 5, fig. 1a-d, Zardini 1978, pl. 5, fig. 8a-c). The protoconch measures 0.19 mm in diameter and is surrounded by the first whorls of the teleoconch with slit inserting after about 1.25 whorls. *Rinaldoella subgranulata* (Münster, 1841) has a stepped conical shell that is a little higher than wide (pl. 6, figs. 78-80). Ornament consists of a reticulation and a row of tubercles next to the suture that increases in strength on the later whorls of the shell (Zardini 1978, pl. 5, figs. 6-5, 1985, pl. 5, fig. 1 as *Worthenia crenata*). The protoconch is 0.15 mm wide, smooth and has a lobed outer lip. The plane first whorl of the teleoconch is ornamented by two spirals and wrinkles and axial ribs appear after 0.25 whorls. The slit inserts after 2.5 whorls of the teleoconch with the selenizone forming a nodular raised ribbon on the peripheral corner of the succeeding whorls (Schwardt 1992, pl. 4, figs. 4-5). *R. subgranulata* differs from *R. crenata* (Münster, 1841) by a more concave flank and a finer granulated ornament. The ornament of the shell of *R. crenata* is a regular pattern of rectangles to which on the apical side of later whorls sharp axial ribs are added (Zardini 1978, pl. 6, fig. 9). The protoconch is nearly smooth, about 0.16 mm wide and has a lobed margin of its aperture. The plane first whorl of the teleoconch has four spiral ribs which transform to fine nodular growth increments and axial ribs are added (pl. 6, figs. 81-84). The selenizone begins at the end of the third whorl and forms the corner of the apical ramp with narrow groove below it (Schwardt 1992, pl. 4, figs. 1-3).

Rinaldoella coronata (Münster, 1841) with stepped conical shell is almost as wide as high and has a reticulate ornament with few spiral ribs. The protoconch is 0.19 mm wide and smooth and lies in a depression formed by the juvenile teleoconch ornamented by collabral ribs and later with one spiral line. The selenizone begins in the third whorl and forms a raised nodular ribbon with spiral lines on the peripheral corner and the side below is concave up to the keel which forms the edge to the base (Zardini 1978, pl. 4, fig. 13, Schwardt 1992, pl. 6, figs. 1-3). *R. coronata* has coarser ornament than *R. beaumonti* (Klipstein, 1843) with lowly conical stepped shell that is about as wide as high, has a reticulate ornament with few fine spiral ribs and strong collabral ribs (Zardini 1978, pl. 4, figs. 4-6). Here the protoconch is 0.19 mm wide and lies in a shallow depression of juvenile teleoconch with rounded whorls and ornament of fine spiral lines and some collabral growth lines. The selenizone begins in the third whorl and forms a nodular raised ribbon that lies at the peripheral corner. The apical whorl side is flattened and the base has an umbilicus (Schwardt 1992, pl. 6, figs. 4-5) (pl. 7, figs. 93-96). *R. beaumonti* has a more flattened base than *R. subgranulata* and *R. crenata* and a wider umbilicus than *R. coronata*.

The rounded shape and the smooth ornament of the early juvenile shell distinguishes from *Rinaldoella beaumonti* with concave apex and strong ornament on the second whorl of the teleoconch is clearly distinct from *Pseudoschizogonium elevatum* while adult shells are similar to each other (compare pl. 3, figs. 42-45 with pl. 7, figs. 93-96).

A species from the Late Triassic of Iran determined as *Worthenia* cf. *crenata* by Nützel & Senobari-Daryan (1999) resembles *Rinaldoella*, and a similar but even more badly preserved species from the Late Triassic was determined as *Worthenia* cf. *rhombifera* Körner, 1937 by Nützel & Erwin (2004). Both lack the needed information of their early ontogenetic shell to be successfully compared with the species from St. Cassian.

The genus *Bandelium* Schwardt, 1992 has a conical shell with its protoconch in a depression of the plane first whorl of the teleoconch that is ornamented by axial ribs (Schwardt 1992, pl. 1, figs. 4-5). The type is *Worthenia campensis* Zardini, 1980 from the St. Cassian Formation (Zardini 1980, pl. 1, fig .8). The juvenile, non slit shell of *Bandelium* is ornamented by axial ribs on a smooth background, which differs from *Wortheniella* that has here only spiral ornament and from *Rinaldoella* with narrow axial and spiral ribs crossing and forming rows of nodules.

Bandelium campense (Zardini, 1980) has a slender conical shell that is ornamented by axial ribs (pl. 7, figs. 97-99). The fully grown shell is angular and has concave flanks. A triangular furrow formed by the suture is bordered by the selenizone below and the corner to the base above. The embryonic shell measures about 0.19 mm in diameter and is smooth with sinuous margin of the aperture. It is surrounded by 1.25 plane teleoconch whorls which are ornamented by acute coarse axial ribs with a fine median spiral rib crossing them and forming tubercles, which in the later trochispiral whorls move closer to the suture. The convex selenizone inserts just before the end of the third whorl close to the suture and is covered by tubercles. The aperture has an anterior notch (Zardini 1980, pl. 1, fig. 8, Schwardt 1992, pl. 9, fig. 3).

Bandelium ruedigeri (Schwardt, 1992) has similar shell shape and ornament of axial ribs on the early teleoconch (pl. 7, fig. 100). The embryonic shell measures about 0.18 mm in diameter and is smooth with sinuous margin of the aperture. With begin of the nodular selenizone axial ribs become obsolete, in contrast to *B. campense*. Below the selenizone flanks are slightly concave, vertical to the angular corner to the spirally ornamented base. The flattened base has no umbilicus and the aperture has an anterior notch (Schwardt 1992, pl. 9, figs. 1-2).

Remarks: *Eymarella* Cossmann, 1897 with the type *Pleurotomaria subscalariformis* Hörnes, 1855 from the Late Triassic (Hallstätt) of the Northern Alps has a small trochispiral shell with blunt apex and discoid coiled early whorls. The selenizone near the basal edge is ornamented by spiral ribs. The selenizone lies lower on the whorls but otherwise comparison with the Wortheniellidae is difficult since the early teleoconch is badly known. Similarly *Tahua* Begg & Grant-Mackie, 2003 proposed by Begg & Grant-Mackie (2003: fig. 15), based on *Tahua waipiro* Begg & Grant-Mackie, 2003 is not well preserved. It has a conical shell with upper and lower corner and a narrow upper ramp with the selenizone at about mid position on the sides of the whorls. This Norian species from New Zealand is based on casts of moulds. A second species called *Tahua tairoa* Begg & Grant Mackie, 2003 has ornament with nodular spiral lines and appears to have a flat or even concave early teleoconch (Begg & Grant-Mackie 2003, fig. 16) and resembles in shape that of *Wortheniella*. But the species of *Tahua* are not so well preserved that they may be connected to *Wortheniella* with any certainty. Species resembling *Wortheniella* from the Triassic of China (Yin & Yochelson 1983) and from the Triassic of Peru (Haas 1953) have early teleoconch badly preserved. ?*Worthenia rhombifera* Körner, 1937 from Peru has been restudied by Bandel (1994). Not much is known about the continuation of Wortheniellidae in the Jurassic even though Szabo (2008: fig. 20) described *Worthenia superstes* Szabo, 1980 from the Early Jurassic based on one rather fragmentary specimen of a pagodiform shell with the selenizone in a ridge but neither early ontogenetic shell nor body whorl known.

Triassic *Wortheniella* resembles Carboniferous *Worthenia* regarding ornament of the teleoconch and position of the selenizone. It differs in regard to the shape and coiling mode of the early whorls which are dextral and conical in *Worthenia,* as documented from the Early Carboniferous of Australia that closely resembles that of the type species (Yoo 1994). *Baylea* Koninck, 1883 with the type *Trochus yvonni* Léveillé, 1835 from the Tournai of Belgium (Koninck 1883, pl. 27, figs. 1-5) resembles *Wortheniella,* but the rounded whorls of the early teleoconch are conical. According to Batten (1966) *Baylea* occur widespread from the Early Carboniferous to the close of the Permian. The selenizone in case of *Baylea spirolirata* Batten, 1966 from the Early Carboniferous of the USA inserts in the 3.5 whorl and it is described to have a unique plane early teleoconch with the protoconch in its centre (Batten 1966). In case the protoconch would lie in a pit, *Baylea spirolirata* closely resembles *Wortheniella subpunctata* (Laube, 1868).

Superfamily Haliotioidea Rafinesque, 1815

The ear-shaped shell has a slit and consists largely of nacre. Haliotidae may have their ancestors in the Temnotropidae (Laube 1868, Koken 1897, Bandel 1991, Kiel & Bandel 2000). The genus *Haliotis* Linné, 1758 is not clearly recognizable before Late Cretaceous time (Sohl 1992) and it differs from all other Rhipidoglossa by the arrangement of the teeth in the radula (Troschel 1856-1863), and also its molecular composition (Geiger & Thacker 2005).

Family Temnotropidae Cox, 1960

The low shell has a wide aperture and few whorls which rapidly increase in diameter. The slit lies in the keel on the apical ramp. The base is concave and the aperture strongly oblique. Shell structure is with an inner layer of nacre. *Temnotropis* Laube, 1870 has the type *Sigaretus carinatus* Münster, 1841 from St. Cassian Formation (Bandel 1991, Bandel & Geldmacher 1996).

The shell of *Temnotropis carinata* (Münster, 1841) consists of an outer complex prismatic to spherulitic layer and an inner layer of nacre, as was documented by thin sections from specimens from the localities Misurina and Alpe di Specie. Its shell is 15 mm wide with about three whorls and resembles that of a *Haliotis* with ear-like shape (fig. 101). The protoconch is about 0.25 mm wide and is distinct from the teleoconch. The first whorl of the teleoconch has spiral ribs and after 1.5 whorls a slit forms. The base is concave with narrow umbilicus that may become filled with callus and ornamented by growth lines and indistinct spiral ribs (Zardini 1978, pl. 3, fig. 1, Bandel 1991, pl. 13, figs. 6-8, pl. 14, figs. 1-2). *Temnotropis fallax* Kittl, 1891 probably represents the juvenile of *Temnotropis carinata* with relatively smaller aperture (Kittl 1891, pl. 1, figs. 26-27, pl. 5, figs. 18-19), and *T. carinata* as described by Kittl (1891) is probably the same as *Temnotropis bicarinata* (Laube, 1868) (Broili 1907, fig. 22).

The Campanian *Temnotropis frydai* Kiel & Bandel, 2000 from the Tremp Basin in Northern Spain has rounded early whorls, an umbilicus and a narrow, lens-shaped aperture. The low conical shell has flat but convex whorls with rapid increase in diameter. The first 1.5 whorls are convex and smooth and later 15 spiral ribs appear and the slit near the outer margin. The base is concave with umbilicus and ornament of four spirals ribs (Kiel & Bandel 2000, pl. 1, figs. 5-7). *T. frýdai* is distinct from *T. carinata* by a narrower aperture and resembles *Haliotis antillesensis* Sohl, 1992 from the Maastrichtian of Puerto Rico that also lived at the shore of the tropical Tethys Ocean but had the slit transformed to a row of tremata.

Praestomatia Cox, 1960 based on *Stomatia acuteangulata* (Koken, 1897) from the Late Triassic of the Alps is very close in shape to *Temnotropis carinata* and may be the same or a similar species. Knight et al. (1960) placed *Praestomatia* with the *Stomatellidae* Gray, 1840 based on the living *Stomatella auriculata* Lamarck, 1816 from the tropical Pacific. *Stomatella* has a similar shell shape as *Haliotis* but no slit and its radula places it in the Trochoidea close to the Trochidae (Hickman & McLean 1990, fig. 67).

Zardinitrochus suessi (Klipstein in Kittl, 1891) described as *Temnotropis* by Kittl (1891) (Zardini 1978, pl. 2, fig. 11) has been interpreted a stem group representative of the Scissurellidae (Bandel 1998, pl. 7, figs. 3-4). It resembles *Temnotropis* with regard to its ear-like shell shape and differs from it by the ornament of the early whorls with strong axial ribs (pl. 7, figs. 101-102). *Triassurella carnica* Nützel & Geiger, 2006 could also represents a member of the Scissurellidae from St. Cassian with rather unusual shape (Nützel & Geiger 2006, fig .1). Its shell composition is still unknown.

Family Haliotidae Rafinesque, 1815

Haliotis Linnè, 1758 has a series of respiratory holes which are formed during the growth of the shell. The youngest holes are open (pl. 7, figs. 103-104). In the Red Sea at Aqaba *Haliotis pustulata* Reeve, 1846 and *H. unilateralis* Lamarck*,* 1822 are found sympatrically under stones near the coral reef. From the Red Sea they are documented by Sharabati (1984, pl. 2, figs. 1-2), Geiger & Poppe (2000, pl. 17, 19), Zuschin et al. (2009, pl. 1, figs. 6-8) and from Australia by Wilson (1993). *H. pustulata* has a rough sculpture of nodules and fine spiral cords and in the grown individuals four raised holes remain open. In case of *H. unilateralis* the shell is elongate ovate and dorsally rounded with ornament of irregular radiating folds crossed by low, rounded spiral ribs of variable thickness. In both species the slit appears after about one whorl of the teleoconch without slit. The protoconch is elongate and almost 0.18 mm in diameter and has a very prominent lateral fold with pointed apical folded part. Ornament of the first teleoconch consists of spiral ribs. The open holes of the anterior slit are utilized by the animal to blow out water, usually through the posterior ones, also to expel the fecal pellets and to extend mantle tentacles, often in the two anterior ones. The margin of the broad foot carries many tentacles which in the mobile animal are expanded to the sides while the head carries long tentacles with large eyes at their base.

The shell is also similar in case of *Haliotis tuberculata* Linné, 1758 from the Mediterranean (pl. 7, fig. 105, pl. 8, fig. 106). The first whorl of the teleoconch has a rapid increase in width and the protoconch measures about 0.23 mm in width. In the teleoconch posterior holes are closed by a selenizone.

Superfamily Seguenzioidea Verrill, 1884

A superfamily Seguenzioidea was proposed by Quinn (1993) and accepted by Bouchet & Rocroi (2005). The independent status of Seguenziidae and its place among the Vetigastropoda had been confirmed by Sasaki (1998) and supported by molecular analysis of *Seguenzia* and several other genera by Kano (2008). Laubellidae were compared with *Seguenzia* Jeffreys, 1876 (Bandel 1991, Bandel & Geldmacher 1996). Accordingly they resemble each other by the small shell that is around 2 to 5 mm high, the slit and selenizone just below the suture and ornament of spiral ribs crossed by fine regular axial ribs.

Family Laubellidae Cox, 1960

The small ovoid conical shells have a slit in their upper whorl flank close to the suture. They are ornamented with fine axial and spiral lines. The inner lip of the aperture has a tooth. Shell composition is largely of aragonitic nacre. The family is based on *Laubella* Kittl, 1891 with the type species *Pleurotomaria delicata* Laube, 1868 from St. Cassian Formation (Laube 1868, pl. 27, fig. 5, Kittl 1891, pl. 4, figs. 6-10).

Laubella delicata (Laube, 1868) with 5.5 whorls is 4 mm high and 2.5 mm wide with rounded base and deep umbilicus. The body whorl is as large as the spire. The last whorl of the shell deviates a little and its aperture is narrowed. Whorls of the spire have five spiral ribs and the rounded last whorl has 28 spiral ribs, which are crossed by fine collabral ribs, forming a delicate net. The rounded protoconch is 0.16 mm wide. The slit appears in the second whorl of the teleoconch and lies on the upper part of the rounded outer lip. It is open for one third of a whorl. The inner lip of the aperture has a median fold (Zardini 1978, pl. 7, figs. 7-8, Bandel 1991, pl .15, figs. 1-4). The shell consists of a thin outer layer that bears the ornament and which is underlain by the thicker inner layer composed of well stacked nacre. A most amazing feature of the fully grown shell is the presence of a septum at about half of the body whorl that has an open slit. Such a feature is not known from other Archaeogastropoda.

Similar species from St. Cassian are *Laubella bella* Bandel, 1991 with egg-shaped shell has 5.5 whorls, is 5 mm high and about 4 mm wide. In contrast to *L. delicata* it has the selenizone accompanied by marginal depressions and has finer ornament (Zardini 1978, pl. 6, fig .6, 1985, pl. 6, fig. 7, Bandel 1991, pl. 16, figs. 1-2, 7, pl. 17, figs. 1-2, 4). *Laubella minor* Kittl, 1891 with 6.5 whorls is 4 mm high and 2.5 mm wide. Here the early teleoconch has spiral and fine regular axial ornament as *L. bella* and *L. delicata* (Bandel 1991, pl. 15, fig. 8, pl. 16, figs. 3-6, 8). *Laubella texturata* (Münster, 1841) is larger than the others with the selenizone on a keel accompanied by a depression on either side. The margin to the base has a corner and the umbilicus is narrow. The inner lip has a swelling (Bandel 1991, pl. 15, figs. 5-7).

Family Seguenziidae Verrill, 1884

Seguenzia Jeffreys, 1876 has the shell with a deep sinus in the apical portion of its outer lip (pl. 8, fig. 113) and only one gill. *Seguenzia megaloconcha* Rokop, 1972 from the Pacific has a 0.3 mm large protoconch ornamented by irregular fine ridges and with thickened simple margin of the outer lip (pl. 8, fig. 114). The early whorls of the teleoconch have three spiral ribs crossed by axial ribs. In the third whorl axial ribs reflect the formation of a slit. In case of *Seguenzia floridana* Dall, 1927 from the Atlantic the sinus below the suture also appears in the third whorl. Similar shape in the juvenile and fully grown shell is also documented on species from the New Zealand region (Marshall 1983). The open slit may reach back for one third of a whorl. The shell wall of *Seguenzia monocingulata* (Seguenza, 1876) was determined to be composed of an acicular prismatic outer layer, a central layer of nacre and a dissected crossed acicular layer covering the interior of the shell (Bandel 1979, pl. 1, figs. 2, 4, confirmed by Hedegaard 1990, 1997). The aperture has a fold on its inner lip that extends into the shell interior and lobed outer lip with deep apical sinus, a central concave lobe and a rounded short anterior lobe. *Seguenzia mirabilis* Okutani, 1964 from Japan also has these characters (Sasaki 2008, fig. 4A-B). *Seguenzia* lives on soft bottom below the wave base and feeds on Foraminifera (McLean 1981, Marshall 1983, 1988, Okutani 2000).

Remarks: *Laubella* with its small trochispiral shell is ornamented with axial and spiral lines which have a swelling on their inner lip as in modern *Seguenzia* and *Ancistrobasis* Dall, 1889 (Marshall 1983, 1988; Quinn 1983). A slit in the outer lip is only found in *Seguenzia*. The Seguenzioidea have since been suggested by Bouchet & Rocroi (2005) to include Seguenziidae as well as the Chilodontidae Wenz, 1938 among the living species and also the fossil predominantly Jurassic and Cretaceous Eucyclidae Koken, 1896 and the Triassic Laubellidae. Here it is preferred to interpret *Seguenzia* and similar gastropods with slit just next to the suture to belong in an independent family Seguenziidae. *Laubella* appears morphologically related to *Seguenzia.* It lived side by side with several species which are related to the Eucyclidae such as *Eucycloscala* Cossmann, 1895. *Laubella* as potential counterpart of the Seguenziidae lived alongside with *Eucycloscala* as possible counterpart to the Chilodontidae in St. Cassian reef environment thus documenting that about 220 million years ago both groups were distinct from each other, Seguenziidae and Chilodontidae may thus have a considerable taxonomic and phylogenetich distance from each other.

Superfamily Trochoidea Rafinesque, 1815

Most species considered to belong in that superfamily have nacre in the shell, an organic operculum, no slit in the outer lip and a radula with a central zone of 11 teeth (Hickman & McLean 1990 as Trochidae). Within this superfamily species belonging to the Trochidae Rafinesque, 1815, Tegulidae Kuroda, Habe & Oyama, 1971, Gibbulidae Stoliczka, 1868, Monodontidae Cossmann, 1916, Cantharididae Cotton, 1959, Stomatellidae Gray, 1840 and Umboniidae Adams & Adams, 1854 usually have these characters.

Family Fossarinidae n. fam.

Diagnosis: The small nacreous shell can have a slit on its outer lip or not. The shell is as wide as high and consists of about 3.5 whorls. The protoconch has ornament of fine axial ribs crossed by two spiral ribs with distinct marginal fold attached and next to the outer lip. Ornament of teleoconch consists of growth lines and more or less distinct spiral ribs. A characteristic species of the family is *Fossarina mariei* (Fischer, 1890) as here described living in shallow water of the Gulf of Aqaba (Red Sea).

Genus *Fossarina* Adams & Angas, 1864

The small shell has fine spiral ornament and the aperture entire in subgenus *Fossarina* (*Fossarina*) and with a notch of the aperture in *Fossarina* (*Clydonochilus*) Fischer, 1890 as in Wenz (1938, figs. 635, 636). A species belonging here has been determined as *Fossarina mariei* (Fischer, 1890) by Zuschin et al. (2009, pl. 6, figs. 2-4) from the northern Red Sea with the typical sinus at the posterior margin of the aperture as illustrated on Fischer's (1890, pl. 3, fig. 3) original figure. They found shells in sand on and around the reef. This species from Aqaba clearly has both types of aperture, some individuals with slit and others without slit. *Fossarina mariei* could be the same or a similar species as *Fossarina rimata* (Hutton, 1884) from Australia.

Fossarina mariei has the small shell with thin wall and nacreous inner layer. It consists of 3.5 whorls and measures about 1.2 mm in width and height. The protoconch of about 0.2 mm in diameter has the characteristic folded side that is attached to the outer lip of the aperture. Its ornament consists of fine axial ribs crossed by two spiral ribs. The adult shell may or may not develop a slit at the lower part of its outer lip. This slit can be connected to clear selenizone behind it. But there are other individuals with no indication of a slit but an uninterrupted outer lip. The slit develops at begin of the second teleoconch whorl of the teleoconch. Ornament may consist of wide and low spiral ribs which may be quite indistinctly developed, and growth increments. The aperture is rounded and can be closed with an organic operculum with central disc surrounded by spiral growth additions of which there may be up to 10 (pl. 8, figs. 116-120).

Fossarina mariei represents one of the most common species from the reef flat at Aqaba and lives from tidal pools into the very shallow water on rocks covered by algae and protected somewhat next to the lagoon of the reef platform. A very similar protoconch is found in *Broderipia irridescens* (Broderip, 1834) as described by Sasaki (1998, fig. 59a-d). The adult in that case is a limpet and the same or a similar species also lives in Aqaba on stones together with or close to *Fossarina* but occurs less commonly. Its protoconch closely resembles that of *Fossarina*.

Differences of the radula of Pleurotomariidae, Haliotidae, Seguenziidae and Fossarinidae

Distinct groups of slit bearing Archaeogastropoda document their independent evolutionary history also by the shape of their radula. Troschel (1856-1863) and Troschel & Thiele (1865-1893) noted this difference for example when comparing the radula of *Scissurella* with that of *Pleurotomaria* and *Haliotis*. Pleurotomarioidea are distinguished from the Scissurelloidea also by the composition of their shell that is nacreous in the first and crossed lamellar in the second. The Scissurellidae had been living in the St. Cassian reefs along with slit bearing nacreous species (Bandel 1999).

The radula of Pleurotomariidae is quite distinct among the Archaeogastropoda in general. The radular teeth of *Perotrochus teramachii* Kuroda, 1955 from Taiwan have elongate shape with hooked anterior end and each row of the ribbon consists of about 150 teeth. A median zone forms an inner arc consisting of the central tooth and 12 larger pairs of lateral teeth (pl. 9, fig. 123). This median zone is included in an arc formed by the numerous teeth of the outer zone. Teeth of the outer margin of the inner zone decrease in size and merge in shape with the inner teeth of the marginal zone. These intermediate smaller teeth number about 25 on each side of the central arc. The marginal teeth are long and pointed with broader base and on each side there are about 40 (pl. 9, figs. 121-123). Such a mode of arrangement of teeth in the radula is found in neither of the discussed groups, nor within the Scisurellidae or Fissurellidae.

A radula of similar construction of related species has been described by Fretter (1964), Hickman (1981, 1984) and Harasewych (2002, fig. 7). In case of *Entemnotrochus adansonianus,* Harasewych (2002) characterized the central zone to consist of many lateral teeth on each side of a small pointed elongate central tooth. It has no cutting edge and expanded base. It is accompanied by one pair of inner lateral teeth with similar shape. The more outer lateral pairs according to his observation increase in length to the outside. He distinguished from them the marginal teeth which have slender tips that may be lamellar brushes.

The teeth of the radulae of modern Pleurotomariidae are used to feed on sponges (Woodward 1901). Hickman (1984) suggested that a basic design may have disappeared due to the adaptation to this source of food. Beck (1995), in contrast, assumed a development of the rhipidoglossan radula from a basic design as is present in the radula of *Perotrochus*.

Troschel & Thiele (1865-1893, pl. 26, figs. 1-13) and Thiele (1931) noted that the radula of the Haliotidae differs strongly from that of *Pleurotomaria*. *Haliotis* has the arrangement of its teeth also different from that commonly found within the Trochoidea, including *Fossarina*.

The two species of *Haliotis* from Aqaba have an almost identical radula (pl. 9, figs. 124-126). *Haliotis pustulata* Reeve, 1846 has a more elongate shell than *Haliotis unilateralis* Lamarck, 1822 (pl. 9, figs. 124-125 is from the first and fig. 126 from the second). The central tooth is wide and short with simple broad cutting edge. It appears to be flatter from above than it actually is, when seen from the side and succeeding teeth in a row are attached quite distant from each other. The first lateral pair of the central zone is almost as wide as the central tooth, while the next lateral pair is smaller. The inner pair closely resembles in shape that of the central tooth. They are inclined toward the front of the radula, while the following ones are arranged in a row inclined to the back. Three pairs of intermediate teeth follow of which the inner is the largest. Many marginal teeth next to them have thin elongated shafts and finely serrated cusps. The marginal ones are narrowest and there are about 45 of them on each side in each row of the ribbon.

Haliotis rugosa Lamarck, 1822 from the Indian Ocean as illustrated by Herbert (1990, figs. 6-8) fits that description and also some other species documented by Hickman (1981, 1984). They resemble that of *Haliotis diversicolor* described by Sasaki (1998, fig. 32). Regarding the shape of the teeth of the radula *Haliotis* resembles *Angaria* Röding, 1798 as described by Hickman & McLean (1990, fig. 14), and both genera may be related according to the interpretation of Beck (1995).

The radula of *Seguenzia megaloconcha* Rokop, 1972 from the Pacific Ocean has the rows of teeth in tight position and forming an arch with all teeth bearing cutting edges. It is characteristic with few teeth in a row compared with other nacreous Vetigastropoda (Bandel 1979, pl. 3, fig. 8). The central tooth is tongue like with triangular cusped cutting edge. The pair of lateral teeth has a triangular base and a cutting edge with the elongate and pointed margin with many cusps. The marginal teeth form only five pairs of similar shape, elongate and with curved narrow pointed cutting edge (pl. 9, figs. 127-129). Quinn (1983) assembled drawings of the radula of different species of Seguenziidae and noted that all resemble each other as had been noted by Schepman (1908).

The radula of *Fossarina mariei* resembles that found in the *Trochus* relation. The central tooth has a narrow anterior part and wide angular base. Its cutting edge is in line with the cutting edges of the 11 teeth composing the central zone. These are interlocking with their bases overlapping onto each other. The fourth pair is the largest and all cutting edges have a triangular main cusp and several inner and outer cusps. The marginal teeth are long, numerous and form rows with the outer ones more delicate than the inner ones. The innermost marginal tooth resembles the outermost lateral tooth that has a basal lamellar shoulder onto which the inner marginal tooth is bedded. About 16 teeth form each of the marginal zones and are tightly connected to each other and becoming smaller from the inner to the outer (pl. 9, figs. 130-132).

Fossarina was suggested to represent a member of the subfamily Fucariinae Warén & Bouchet, 1993 based on *Fucaria* Warén & Bouchet, 1993 that lives on hydrothermal vents and was classified to be close to the Halystylinae Keen, 1958 (Warén & Bouchet 1993) and later with the Trochidae with uncertain relation (Warén & Bouchet 2001). The shell of *Fucaria* resembles that of *Fossarina* in shape and ornament, but the radula of *Fucaria mystax* Warén & Bouchet, 2001 (Warén & Bouchet, 2001, fig. 11c) differs by the number of teeth in the median row. It amounts to 23 in *F. mystax*, while there are 11 teeth here in the case of *Fossarina*. Their arrangement is similar but the shape of the central tooth along with the cutting edges of the lateral teeth differs from that among the *Gibbula* Risso, 1826 relation. *Fossarina*, therefore, does not fit into the Gibbulidae as had been suggested by Hickman & McLean (1990). The small limpet *Broderipia iridescens* (Broderip, 1834) with nacreous shell has a radula that resembles that of *Stomatella* Lamarck, 1816 and also that of *Fossarina*, and all three have a similar ornament of their protoconch (pl. 8, fig. 120). Margaritidae Stoliczka, 1868 may have more and Solariellidae Powell, 1951 fewer teeth in the central zone of their radula. In both groups small species with shell shape as in *Fossarina* occur. Confirmation of the independence of the Solariellidae and the Margaritidae has come from molecular analysis as discussed by Williams et al. (2008) confirming the importance of differences present in the construction of their radula.

Conclusions

Gastropods with a slit in the outer lip of their shell appeared in the geological record during the Ordovician and can be traced for more than 450 million years through the geological record (Wenz 1938, Bandel 1997). Species living in the tropical reef during deposition of St. Cassian Formation could thus be related with species that had lived during the time before for about 225 million years up to the Carnian stage and with those that lived during about the same period afterwards up to nowadays. When attempting to classify species from the St. Cassian Formation the long distance in time that may have separated them from morphologically similar species that lived before and later should be taken into consideration.

Modern *Fossarina* with its species *F. mariei* documents that a slit in the outer lip of its shell can be present and can give rise to a selenizone but in other individuals of that species living in the same environment a slit can be absent. The radula of *Fossarina* resembles that found commonly among species of the Trochoidea. It is quite different from that of the other nacreous slit bearing gastropods of the genera of the Pleurotomariidae, *Haliotis* and *Seguenzia*. The later is related with genera belonging to the Seguenziidae that have no slit in their outer lip. With regard to their radula, the shape and ornament of their early ontogenetic shell these Seguenziidae without shell slit resemble *Seguenzia* with slit and selenizone. Thus species with a slit and selenizone and such without slit here from a group of interrelated genera. In contrast, *Haliotis* with its many living species has a shape of its shell that has apparently remained similar and provided with the same type of selenizone since more than 80 million years. In case of *Pleurotomaria* as characteristic genus of the Pleurotomariidae the organization of the shell has not changed much from begin of the Jurassic onward. The many species and genera of the family which occurred since that time have changed to a more restricted living environment but are clearly connected to the modern genera and species of the family. The fossil record gives evidence for a continuous evolution of slit bearing interrelated species of Pleurotomaiidae for about 200 million years.

Members of the Zygitidae and the Stuorellidae n. fam. with 7 species from St. Cassian can be interpreted as stem Pleurotomarioidea. *Lanzedellia* in contrast, has a slenderer shell than any modern representative and is regarded as of the Lancedellidae n. fam. Its relation to the Pleurotomariidae is in doubt, while there are similar Paleozoic species known. Small and more lentil-shaped shells as in the Ptychomphalidae resemble Paleozoic species in case of *Ptychomphalus* and continue into the Early Jurassic. Rhaphistomellidae n. fam. based on *Rhaphistomella* existed with very similar species since the Early Carboniferous and up to the Early Jurassic. The long ranging history of Ptychomphalidae and Rhaphistomellidae from the mid-Paleozoic to begin of the Jurassic indicates the independence of these and their superfamily status as Ptychomphaloidea. The 10 recognized species of the Schizogoniidae from St. Cassian in shape and ornament differ strongly from all Modern slit-bearing gastropods. Pseudowortheniellidae n. fam. based on *Pseudowortheniella* n. gen. resembles them in regard to the early teleoconch but no marginal groove and keel is present here. Both families can be interpreted as members of one superfamily, the Schizogonioidea, which appear to have only a Triassic time range in their existence. Pseudoschizogoniidae n. fam. with *Pseudoschizogonium* has angular shape with stair-like spire, the selenizone in a peripheral keel and spiral ornament on its juvenile shell. Here a relation to Paleozoic *Worthenia* is plausible. Gosseletinidae are represented in the St. Cassian reefs by *Gosseletina, Sisenna* and *Euzone* with related species in the Early Jurassic and species of similar shape in the Paleozoic. They could be placed with the Eotomarioidea, but that superfamily is based on an Ordovician species about which few details are known and thus such placement needs to be confirmed by more detailed study of older genera. Wortheniellidae n. fam. has numerous species characteristic to the Triassic with left-handed early ontogenetic shell forming a groove in the plane first whorl of the teleoconch. The genera *Wortheniella*, *Bandelium* and *Rinaldoella* n. gen. are distinguished by characteristic ornament of the early teleoconch. Wortheniellidae could connect with Paleozoic *Worthenia* with similar shell shape among Carboniferous species from similar tropical reef environments, but the Wortheniellidae differ by the early ontogenetic whorls with sinistral shell coiling. Temnotropidae resemble *Haliotis* in having ear-like shape and can be traced to the Cretaceous, and thus to a time in which *Haliotis* makes its appearance. Both families can be connected to each other in the Haliotioidea. Laubellidae with the slit high up on the outer lip have four species that resemble modern *Seguenzia* but a relation to the Seguenziidae is doubtful.

During Late Triassic slit bearing Archaeogastropoda from reef environment of the tropical Tethys Ocean were much more diverse than modern representatives of that group from the tropical Indo-Pacific Ocean. Here *Haliotis* and *Fossarina* represent living nacreous gastropods with slit and are compared to the fossil species, while members of the Pleurotomariidae live on the deep reef slope and *Seguenzia* has species on soft bottom substrate in deeper water. Haliotidae, Fossarinidae (Trochoidea) and Seguenziidae are not closely related to Pleurotomariidae and also not to each other, as is documented not only by the shape and arrangement of the teeth in their radula but also their molecular composition.

Genera of 12 families have representatives which lived in the tropical reef of the St. Cassian Formation. These are the Zygitidae, Stuorellidae, Lancedelliidae, Ptychomphalidae, Rhaphistomatidae, Schizogoniidae, Pseudowortheniellidae, Pseudoschizongoniidae, Gosseletinidae, Wortheniellidae, Temnotropidae and Laubellidae. Their relation with living species is difficult to document since the characters of shell structure is also found among different groups in the Archaeogastropoda in general and the character seen as decisive, the selenizone, has obviously evolved several times during evolution of the Rhipidoglossa as is documented by Seguenziidae and Fossarinidae. A selenizone can also have become obsolete among species in a group of related species, even though a case of a slit bearing gastropod evolving into one without slit has only been documented in case of the Scissurellidae which have no nacre.

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References

Bandel, K. (1979): The nacreous layer in the shells of the gastropod family Seguenziidae and its taxonomic significance.- Biomineralisation, **1:** 49-61.

Bandel, K. (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken.- Fazies, **7:** 1-198.

Bandel, K. (1991): Schlitzbandschnecken mit perlmutteriger Schale aus den triassischen St. Cassian- Schichten der Dolomiten.- Ann. Naturhist. Mus. Wien, **92(A):** 1-53.

Bandel, K. (1993a): Trochomorpha aus der triassischen St. Cassian Formation (Gastropoda, Dolomiten).- Ann. Naturhist. Museum Wien, **95:** 1-99.

Bandel, K. (1993b): Evolutionary history of sinstral archaeogastropods with and without slit (Cirroidea, Vetigastropoda).- Freiberger Forschungshefte, Paläontologie, **C450:** 41-82.

Bandel, K. (1994): Comparison of Upper Triassic and Lower Jurassic gastropods from the Peruvian Andes (Pucará Group) and the Alps (Cassian Formation).- Palaeontographica, **233A:** 127-160.

Bandel, K. (1997): Higher classification and pattern of evolution of the Gastropoda. A synthesis of biological and paleontological data.- Courier Forschungsinstitut Senckenberg, **201:** 57-81.

Bandel, K. (1999): Scissurellidae als Modell für die Variationsbreite einer natürlichen Einheit der Schlitzbandschnecken (Mollusca, Archaeogastropoda).- Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **81:** 1-120.

Bandel, K. (2002): Reevaluation and classification of Carboniferous and Permian Gastropoda belonging to the Caenogastropoda and their relation.- Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **86:** 81-188.

Bandel, K. & Frýda, J. (1996): *Balbinipleura*, a new slit bearing archaeogastropod (Vetigastropoda) from the Early Devonian of Bohemia and the Early Carboniferous of Belgium.- N. Jb. Geol. Paläont. Mh., 1996, **6:** 325-344.

Bandel, K. & Frýda, J. (2004): *Sasakiela*, a new slit Early Carboniferous porcelliid genus (Porcellioidea, Gastropoda) with unusual shell ontogeny.- N. Jb. Geol. Paläont. Mh., 2004, **3:** 135-150.

Bandel, K. & Geldmacher, W. (1996): The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda.- Freiberger Forschungshefte **C464:** 1-71.

Bandel, K., Gründel, J. & Maxwell, P. (2000): Gastropods from the upper Early Jurassic/Middle Jurassic of Kaiwara Valley, North Canterbury, New Zealand.- Freiberger Forschungshefte, **C490:** 67-132.

Bandel, K., Nützel, A. & Yancey, T.E. (2002): Larval shells and shell microstructures of exceptionally well-preserved Late Carboniferous gastropods from the Buckhorn Asphalt Deposits (Oklahoma, USA).- Senckenbergiana lethaea, **82:** 639-689.

Batten, R.L. (1966): The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset (Parts I and II).- Palaeontographical Society Monographs, **119:** 53-109.

Batten, R.L. (1972): The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of Eastern United States.- American Museum Novitates, **2501:** 1-34.

Beck, L.A. (1995): Zur Systematik und Evolution europäischer Trochiden (Kreiselschnecken) unter besonderer Berücksichtigung der Gattung *Gibbula* Risso, 1826, *Osilinus* Philippi, 1847 und *Jujubinus* Monterosato, 1884 (Gastropoda, Prosobranchia).- Dissertation am Fachbereich der Philipps-Universität Marburg.

Begg, J.G. & Grant-Mackie, J.A. (2003): New Zealand and New Caledonian Triassic Pleurotomariidae (Gastropoda, Mollusca).- Journal of the Royal Society of New Zealand, **33:** 223-268.

Bizzarini, F., Laghi, R., Russo, F. & Urlichs, M. (1986): Preliminary biostratigraphic correlation between Ampezzo Basin sections and their Cordevolian stratotype (Late Triassic, Italian Dolomites).- Lavori Soc. Ven. Sc. Nat, **11:** 151-158.

Blaschke, F. (1905): Die Gastropodenfauna der Pachycardientuffe der Seiseralpe in Südtirol nebst einem Nachtrag zur Gastropodenfauna der roten Raibler Schichten vom Schlernplateau.- Beitr. Pal. Österr.-Ungar. Orients, **17:** 161-222.

Blendinger, W. & Blendinger, E. (1989): Windward-leeward effects on Triassic carbonate bank margins in the Dolomites, northern Italy.- Sedimentary Geology, **64:** 143-166.

Blodgett, R.B. & Rohr, D.M. (1989): Two new Devonian spine-bearing pleurotomariacean gastropod genera from Alaska.- Journal of Paleontology, **63:** 47-52.

Böhm, J. (1895): Die Gastropoden des Marmolatakalkes.- Palaeontographica, **42:** 211-308.

Bouchet, P. & Rocroi, J.-P. (2005): Classification and nomenclator of gastropod families.- Malacologia, **47:** 1-397.

Broili, F. (1907): Die Fauna der Pachycardientuffe der Seiser Alp. Scaphopoden und Gastropoden.- Palaeontographica, **54:** 69-138, pl. 6-11.

Erben, H.K. & Krampitz, G. (1972): Ultrastruktur und Aminosäuren-Verhältnisse in den Schalen der rezenten Pleurotomariiden (Gastropoda).- Biomineralisation, **6:** 12-31.

Fischer, P. (1880-1887): Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles.- Savy, Paris, 1369 pp.

Fischer, J.-C. & Weber, C. (1997): Volume II, Gastéropodes Jurassiques.- In: Fischer, J.-C (ed.): Révision critique de la Paléontologie Francaise, incluant de rédition de la original.- pp. 300-622. Paris, Masson & Muséum national d'Histoire naturelle.

Fretter, V. (1964): Observations on the anatomy of *Mikadotrochus amabilis* Bayer.- Bull. mar. Sci. Gulf Caribb., **14:** 172-184.

Frýda, J. (1997): Oldest representatives of the superfamily Cirroidea (Vetigastropoda) with notes on their early phylogeny.- Journal of Paleontology, **71(5):** 839-847.

Frýda, J. (1998): Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia).- Vestnik Ceskeho Gologickeho Ustavu, **73:** 41-47.

Fürsich, F.T. & Wendt, J. (1977): Biostrationomy and palaeocology of the Cassian Formation (Triassic) of the Southern Alps - Palaeogeography, Palaeoclimatology, Palaeoecology, **22:** 257-321.

Geiger, D.L. & Poppe, G.T. (2000): The family Haliotidae.- In: Poppe, G. T. & Groh, K. (eds.): A Conchological Iconography: 135 pp., 83 pls.; Hackenheim (ConchBooks).

Geiger, D.L. & Thacker, C.E. (2005): Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea.- Molluscan Research, **25:** 47–55.

Gründel, J. (1998): Archaeo- und Caenogastropoda aus dem Dogger Deutschlands und Nordpolens.- Stuttgarter Beiträge Naturkunde, (B) **260:** 1-39.

Gründel, J. (1999): Gastropoden aus den höheren Lias von Grimmen, Vorpommern (Deutschland).- Archiv für Geschiebekunde, **2:** 629-672.

Gründel, J. (2000): Archaeogastropoda aus dem Dogger Norddeutschlands und des nordwestlichen Polens.- Berliner geowissenschaftliche Abhandlungen, **E34:** 205-253.

Gründel, J. (2003a): Gastropoden aus dem unteren Lias (Ober-Hettangium bis Unter-Sinemurium) Südwestdeutschlands.- Stuttgarter Beiträge zur Naturkunde, (B) **340:** 1-55.

Gründel, J. (2003b): Gastropoden aus dem Bajocium und Bathonium von Sengenthal und Kinding, Franken (Süddeutschland).- Zitteliana, **A43:** 45-91.

Gründel, J. (2004): Gastropoden aus dem oberen Bathonium von Luc-sur-Mer/Calvados (Normandie, Frankreich): I Archaeogastropoda und Neritimorpha.- Freiberger Forschungshefte, **C502:** 15-50.

Gründel; J. (2007): Jurassische Gastropoden aus der Betakalkbank (oberes Sinemurium, obere Obtusum-Zone) Südwestdeutschlands.- Stuttgarter Beiträge zur Naturkunde, (B) **370:** 1-29.

Gründel, J. & Koppka, J. (2007): Gastropoden aus einem Lias-Geschiebe von Lentschow bei Lassan (Vorpommern, Nordostdeutschland).- Archiv für Geschiebekunde, **4:** 643-658.

Gründel, J. & Nützel, A. (1998): Gastropoden aus dem oberen Pliensbachium (Lias d2, Zone des *Pleuroceras spinatum*) von Kalchreuth, östlich Erlangen (Mittelfranken).- Mitteilungen Bayrische Staatssammlung Paläontologie historische Geologie, **38:** 63-96.

Haas, O. (1953): Mesozoic invertebrate faunas of Peru.- American Museum of Natural History, Bulletin, **101:** 3-328.

Harasewych, M.G. (2002): Pleurotomarioidean gastropods.- Advances in Marine Biology, **42:** 237-294.

Harasewych, M.G., Adamkewicz, S.L., Blake, J.A., Saudek, D., Spriggs, T. & Bult, C.J. (1997): Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18 S rDNA and cytochrome c oxidase I sequences.- Molecular Marine Biology and Biotechnology, **6(1):** 1-20.

Harasewych, M. G. & Kiel, S. (2007): Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagaskar.- The Nautilus, **121(2):** 76-89.

Hedegaard, C. (1990): Shell structures of the Recent Archaeogastropoda.- Thesis University of Aarhus, 148 pp.

Hedegaard, C. (1997): Shell structures of recent Vetigastropoda.- Journal of Molluscan Studies, **63:** 369-377.

Heidelberger, D. (2001): Mitteldevonische (Givetische) Gastropoden (Mollusca) aus der Lahnmulde.- Geologische Abhandlungen Hessen, **106:** 1-291.

Hickman, C.S. (1981): Evolution and function of asymmetry in the archaeogastropod radula.- The Veliger, **23:** 189-194.

Hickman, C.S. (1984): Form and function of the radulae of pleurotomariid gastropods.- The Veliger, **27:** 29-36.

Hickman, C.S. & McLean, J.H. (1990): Systematic revision and suprageneric classification of trochacean gastropods.- Science Series No. 35, Natural History Museum of Los Angeles County, Los Angeles, 169 p.

Hudleston, W.H. (1895): A monograph of the British Jurassic Gasteropoda. Part 1.No.8, The Inferior Oolite Gasteropoda.- Palaeontographical Society, London, Monograph, 391-444.

Kano, Y. (2008): Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in deep-sea habitats.- Zoologica Scripta, **37:** 1-21.

Kiel, S. & Bandel, K. (2000): New slit-bearing Archaeogastropoda from the Late Cretaceous of Spain.- Berliner geowissenschaftliche Abhandlungen, **E34:** 269-277.

Kittl, E. (1891): Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. Teil I.- Annalen des k.k. naturhistorischen Hofmuseums, **6:** 166-262.

Kittl, E. (1900): Trias-Gastropoden des Bakonyer Waldes. Palaeontologie der Umgebung des Balatonsees.- Result. der wissenschaftlichen Erforschung des Balatonsees., Bd. 1, Teil 1, Paleont. Ang. B. 2, T. 5, 1912, pp. 1-58.

Knight, J.B. (1941): Paleozoic gastropod genotypes.- Geological Society, Special Papers 32, 510 pp., 96 pls., 32 figs.

Knight, J.B., Cox, L.R., Myra, A., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960): Systematic descriptions (Archaeogastropoda).- Treatise on Invertebrate Paleontology, Pt.1, Mollusca 1.- Geological Society of America, Inc. and University of Kansas Press: 310-324, Lawrence, Kansas.

Koken, E. (1896): Die Leifossilien, ein Handbuch für den Unterricht und das Bestimmen von Versteinerungen.- Leipzig, 1-848.

Koninck, L.G. de (1883): Faune du calcaire carbonifére de la Belgique, quartiéme partie. Gastéropodes.- Musée Royal d'Histoire Naturelle de Belgique Annales, Série Paléntologique, **8:** 1-240.

Kutassy, A. (1927): Beiträge zur Stratigraphie und Paläontologie der alpinen Triasschichten in der Umgebung von Budapest.- Magyar kir. Földt. intéz. Evk., **27:** 103-177.

Laube, G.C. (1868): Die Fauna der Schichten von St. Cassian.- Kaiserliche Akademie der Wissenschaften, Denkschrift, **28:** 29-94.

Leonardi, P. & Fiscon, F. (1958): La fauna cassiana di Cortina d'Ampezzo, Parte IIIa Gasteropodi.- Mem. Inst. Geol. Min. Univ. Padova, **21:** 1-103.

Marshall, B.A. (1983): Recent and Tertiary Seguenziidae (Mollusca; Gastropoda) from the New Zealand region.- New Zealand Journal of Zoology, **10:** 235-262.

Marshall, B.A. (1988): New Seguenziidae (Mollusca: Gastropoda) from the Tasman, south Pacific, and Southern Antilles Basin.- New Zealand Journal of Zoology, **15:** 235-247.

Münster, G.G. zu (1841): Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen.- In Wissmann and Münster, Beiträge zur Geognosie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. In Münster, Georg Graf zu, Beiträge zur Petrefacten-Kunde, Heft 4, Bayreuth, Buchner, pp. 25-152, pls. 1-16.

Nützel, A. & Erwin, D.H. (2004): Late Triassic (Late Norian) gastropods from the Wallowa Terrane (Idaho, USA).- Paläontologische Zeitschrift, **78:** 361-416.

Nützel, A. & Geiger, D.L. (2006): A new scissurelloid genus and species (Mollusca; Gastropoda) from the Late Triassic Cassian Formation.- Paläontologische Zeitschrift, **80:** 277-283.

Nützel, A. & Senowbari- Daryan, B. (1999): Gastropods from the Late Triassic (Norian-Rhaetian) Nayband Formation of central Iran.- Beringeria, **23:** 93-132.

Okutani, T. (2000): Marine mollusks in Japan.- Tokai University Press. Tokyo, 1174 pp.

Okutani, T. & Hasegawa, K. (2000): Superfamily Pleurotomarioidea.- In: Okutani, T. (ed): Marine Mollusks of Japan: 37-44, Tokai University Press, Tokyo.

Orbigny, A. de (1852): Prodrome de paleontology stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paleontologie, vol. 3, Paris.

Quinn, J.F. (1983): A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). I. Summary and evaluation of the super family.- Proceedings of the Biological Society of Washington, **96:** 725 757.

Sasaki, T. (1998): Comparative anatomy and phylogeny of the recent Archaeogastropoda (Mollusca: Gastropoda).- The University Museum, The University of Tokyo, Bulletin, **38:** 224 pp.

Schepman, M.M. (1908): The Prosobranchia oft the Siboga Expedition. Part I Rhipidoglossa and Docoglossa.- Siboga Expedition. Monographie, **49:** 1-107.

Schwardt, A. (1992): Revision der *Wortheniella* Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten).- Ann. Naturhist. Mus. Wien, **94:** 23-57.

Sharabati, D.P. (1984): Red Sea Shells.- Law Book Co., London, 128 pp.

Sloan, R.E. (1955): The Carboniferous gastropod genus *Glabrocingulum* Thomas.- Fieldiana, Geol., **10:** 275-281.

Sohl, N.F. (1992): Upper Cretaceous gastropods (Fissurellidae, Haliotidae, Scissurellidae) from Puerto Rico and Jamaica.- Journal of Paleontology, **66:** 414-434.

Szabo, J. (1980): Lower and Middle Jurassic gastropods from the Bakony Mountains (Hungary) Part II Pleurotomariacea and Fissurellacea (Archaeogastropoda).- Annales historio naturalis Musei nationalis hungarici, **72:** 49-71.

Szabo, J. (2008): Gastropods of the Early Jurassic Hierlatz Limestone Formation; part 1: a revision of type collections from Austrian and Hungarian localities.- Fragmenta Palaeontologica Hungarica, **26:** 1-108.

Thiele, J. (1931): Handbuch der systematischen Weichtierkunde.- Jena, Gustav Fischer Verl.

Troschel, F.H. (1856-1863): Das Gebiß der Schnecken, zur Begründung einer natürlichen Classifikation. 1.- 252 p. Berlin, Nicolaische Verlagsbuchhandlung.

Troschel, F.H. & Thiele, J. (1865-1893): Das Gebiss der Schnecken zur Begründung einer natürlichen Classification 2.- 217-246, Berlin, Nicolaische Verlagsbuchhandlung.

Urlichs, M. (1994): *Trachyceras* Laube, 1869 (Ammonoidea) aus dem Unterkarn (Obertrias) der Dolomiten (Italien).- Stuttgarter Beitr. Naturk., (B) **217:** 55 pp.

Warén, A. & Bouchet, P. (1993): New records, species genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps.- Zoologica Scripta, **22:** 1-90.

Warén, A. & Bouchet, P. (2001): Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records.- The Veliger, **44:** 116-231.

Wendt, J. (1982): The Cassian patch reefs (Lower Carnian, Southern Alps).- Facies, **6:** 185-202.

Wendt, J. & Fürsich, F.T. (1979): Facies analysis and paleogeography of the Cassian Formation, Triassic, Southern Alpes.- Riv. Ital. Paleont., **85:** 1003-1028.

Wenz, W. (1938): Gastropoda, Teil I.- In: Schindewolf, O.H. (ed): Handbuch der Paläozoologie, Bd. 6:1-1639; Berlin (Borntraeger).

Wilson, B.R. (1993): Australian marine shells, prosobranch gastropods. Pt.1 (Prosobranch gastropods).- Odyssey Publishing: Kallaroo Western Australia, 408 pp.

Yoo, E.K. (1994): Early Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia.- Records of the Australian Museum, **46:** 63-120.

Zardini, R. (1978): Fossili cassiani (Trias Medio-Superiore) atlante dei gasteropodi della formazione di S. Cassiano raccolti nella regione dolomitica attorno a Cortina d'Ampezzo.- 1-58; Ed. Ghedina, Cortina d'Ampezzo.

Zardini, R. (1980): Fossili cassiani (Trias Medio-Superiore), prima aggioramento all'atlantei dei gasteropodi della formazione di S. Cassiano raccolti nella regione dolomitica attorno a Cortina d'Ampezzo.- 1-16, Ed. Ghedina, Cortina d'Ampezzo.

Zardini, R. (1985): Fossili cassiani (Trias Medio-Superiore) atlante dei gasteropodi della formazione di S. Cassiano raccolti nella regione dolomitica attorno a Cortina d'Ampezzo.- 1-15; Cortina d' Ampezzo.

Zuschin, M., Janssen, R. & Baal, C. (2009): Gastropods and their habitats from the Northern Red Sea (Egypt, Safaga). Part I Patellogastropoda, Vetigastropoda and Cycloneritimorpha.- Annalen Naturhistorisches Museum Wien, **111a:** 73-158.

Plate 1

Fig. 1: Juvenile shell of *Zygites delphinula* (Laube, 1868) from Alpe di Specie has the protoconch succeeded by a little more than one rounded whorl before insertion of the slit. The shell is about 0.7 mm wide.

Fig. 2: *Dictyotomaria subcancellata* (Orbigny, 1849) from Misurina, St. Cassian Formation has an about 7 mm high shell.

Fig. 3: Juvenile shell of *Dictyotomaria subcancellata* (Orbigny, 1849) with slightly crushed shell from St. Cassian (Campo) and appearance of angular shape and higher position of the selenizone on the whorls. Shell height about 3 mm.

Fig. 4: Apical view of *Dictyotomaria subcancellata* with not-deformed shell and regular pattern of axial and spiral ribs interrupted by the selenizone, from loc. Campo at Cortina d'Ampezzo and shell-size about 3 mm.

Fig. 5: Juvenile shell of *Dictyotomaria subcancellata* with apical angle larger than that of the fully grown shell (fig. 2). The shell from Campo is 3 mm high.

Fig. 6: *Glabrocingulum* from Late Carboniferous Henrietta Shale, St. Louis Outlier Missouri with the selenizone on the mid-whorl. The shell is about 1.3 mm wide.

Fig. 7: Apical view onto *Glabrocingulum* from Henrietta Shale with smooth protoconch, fine spiral lines on the early teleoconch and begin of axial ornament on its second whorl. The shell is about 1.5 mm wide.

Fig. 8: Juvenile shell of *Glabrocingulum* seen from the side with beginning of the selenizone and about 2 mm high shell.

Fig. 9: *Kokenella costata* (Münster, 1841) from Alpe di Specie, St. Cassian Formation, with juvenile shell seen from the side and shell about 0.8 mm wide.

Fig. 10: Protoconch of *Kokenella costata* and early insertion of the slit on the upper whorl and its rapid migration to the side within half a whorl with protoconch about 0.3 mm wide.

Fig. 11: Early teleoconch of *Kokenella costata* without folds and evenly spaced folds superimposed on the pattern of rectangles in later shell that is about 2 mm wide.

Fig. 12: Early shell of *Kokenella costata* (Münster, 1841) from St. Cassian (Alpe di Specie) with begin of the selenizone early in the first whorl of the teleoconch, detail to fig. 11.

Fig. 13: *Stuorella subconcava* (Münster, 1841) with 2.5 mm high juvenile shell is from Alpe Specie.

Fig. 14: *Stuorella subconcava* from St. Cassian Formation locality Costellaresc at Cortina d'Ampezzo is 6 mm high.

Fig. 15: *Stuorella subconcava* from locality Rumerlo at Cortina d'Ampezzo of St. Cassian Formation is 10 mm wide at its base and slightly deformed.


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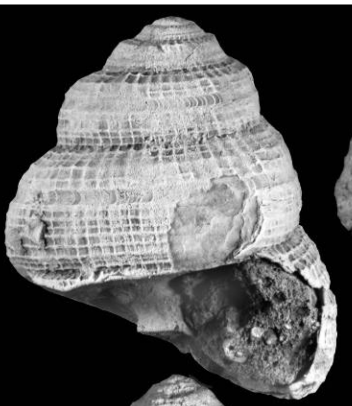
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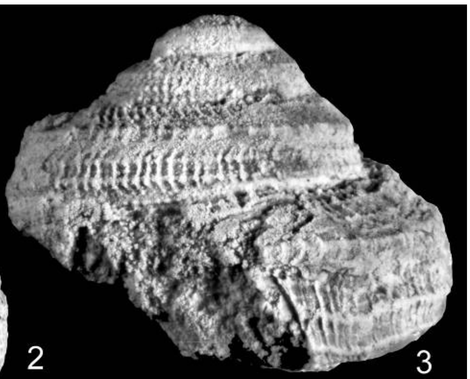
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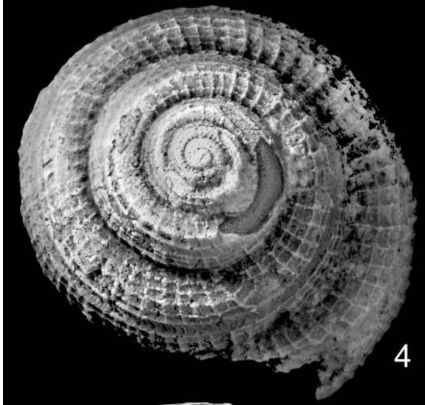
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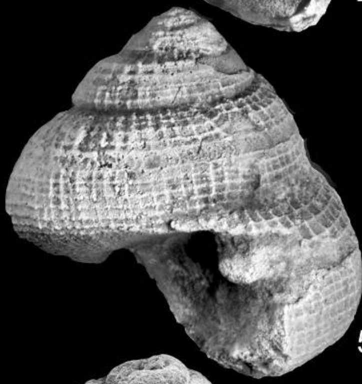
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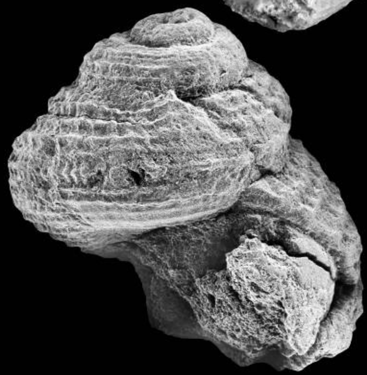
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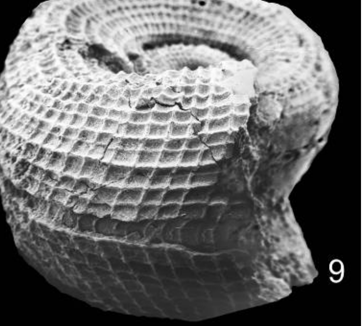
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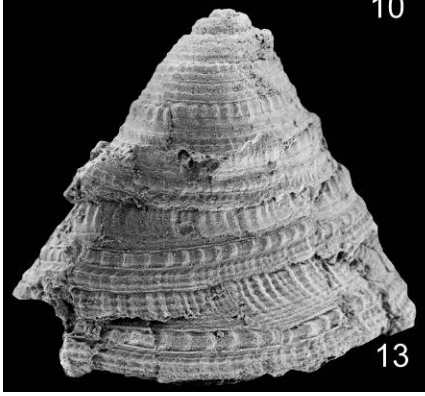
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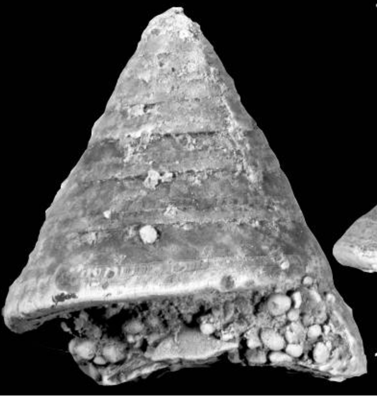
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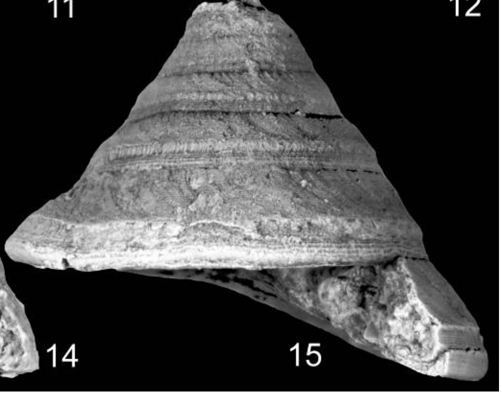
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Plate 2

Fig. 16: *Stuorella subconcava* with 10 mm wide shell from Rumerlo, St. Cassian Formation.

Fig. 17: *Stuorella subconcava* as in fig. 17 seen from the side.

Fig. 18: *Stuorella subconcava* with about 1 mm wide shell, about 0.15 mm wide protoconch and the begin of the slit later than the begin of a row of nodules below the suture in the third whorl of the teleoconch, from Cortina d'Ampezzo-Campo, St. Cassian Formation.

Fig. 19: *Lancedellia costata* (Zardini, 1841) with grown shell that is 10 mm high from Cortina d'Ampezzo-Campo, St. Cassian Formation.

Fig. 20: Apical view of *Lancedellia costata* of the shell in fig. 19.

Fig. 21: Undulating selenizone of *Lancedellia costata* on the 5 mm high sixth whorl of the teleoconch.

Fig. 22: Early shell of *Lancedellia costata* with 0.2 mm wide protoconch and 0.5 mm wide first whorl.

Fig. 23: *Ptychomphalus protei* (Laube, 1868) with 11 mm wide shell from St. Cassian Formation, locality Costalaresc, Cortina d'Ampezzo.

Fig. 24: *Ptychomphalus protei* with the same shell as in fig. 23 seen from the side.

Fig. 25: *Ptychomphalus protei* from Costaleresc with 15 mm wide shell.

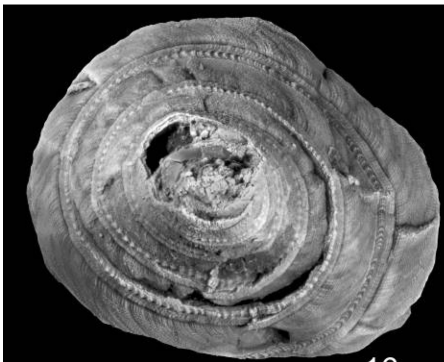
Fig. 26: *Ptychomphalus protei* same species as in fig. 25 seen from above.

Fig. 27: *Rhaphistomella radians* (Wissmann, 1841) from Stuores locality above St. Cassian with the shell about 3 mm wide.

Fig. 28: Detail of *Rhaphistomella radians* in fig. 27 with the 0.25 mm wide protoconch and begin of the slit in the third whorl.

Fig. 29: Side view of juvenile shell of *Angyomphalus minutus* from Henrietta Shale, Pennsylvanian of Missouri with begin of the slit in the third whorl of the teleoconch. The shell is 2 mm wide.

Fig. 30: Apical view of *Angyomphalus minutus* with 1.7 mm wide shell with the smooth broad selenizone at the periphery and begin of row of axial ribs below the suture.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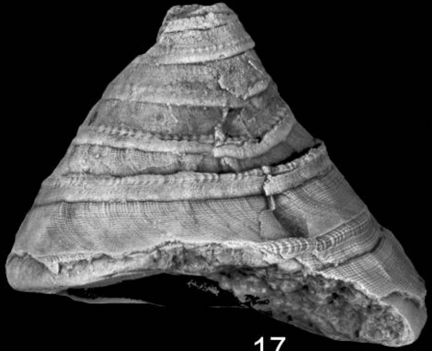
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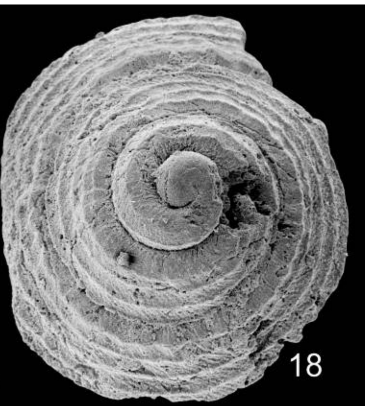
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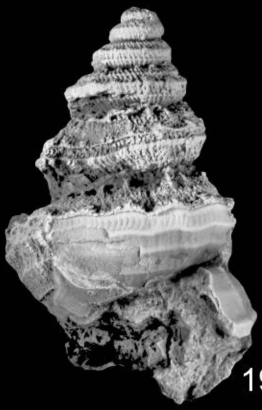
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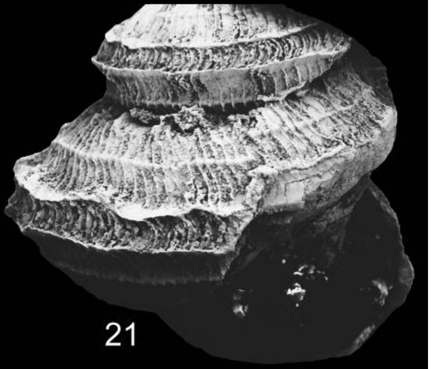
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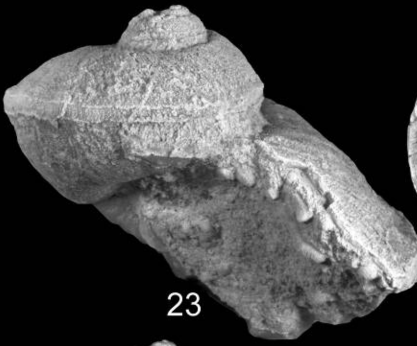
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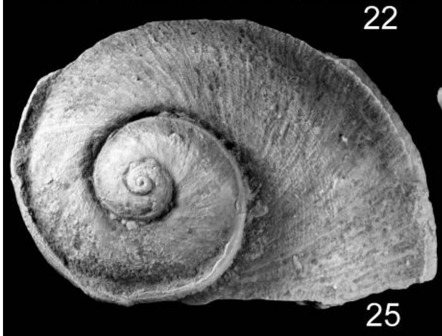
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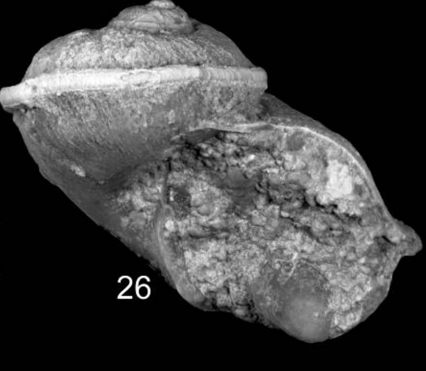
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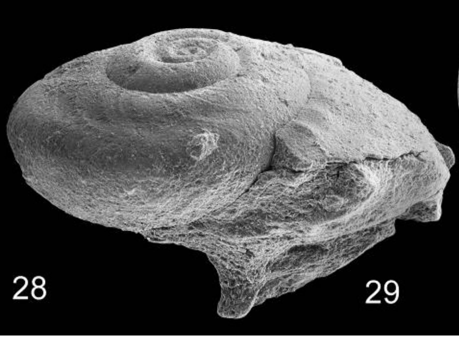
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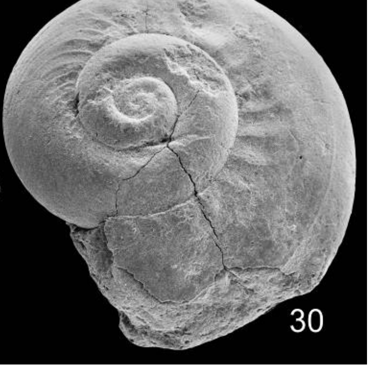
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Plate 3

Fig. 31: Side view of *Angyomphalus minutus* with 3.4 mm wide shell that displays the wide smooth selenizone on the rounded periphery.

Fig. 32: *Schizogonium scalare* (Münster, 1841) with shell about 3 mm wide, from St. Cassian Formation.

Fig. 33: *Schizogonium scalare* with shell about 3 mm wide, same shell as in fig.32.

Fig. 34: *Schizogonium serratum* from Campo, St. Cassian Formation, 7 mm in diameter.

Fig. 35: *Schizogonium serratum* same as in fig.34 with shell of 7 mm.

Fig. 36: *Schizogonium lamellosum* with shell of 1.2 mm in diameter from St. Cassian Formation.

Fig. 37: *Schizogonium tamarinum* from Misurina, St. Cassian Formation with 1.3 mm wide shell.

Fig. 38: *Schizogonium tamarinum* Bandel, 1991 same shell as in fig. 37.

Fig. 39: *Schizogonium ampezzanum* Bandel, 1991 from St. Cassian Formation as in fig. 40.

Fig. 40: Juvenile shell of *Schizogonium ampezzanum* is about 1.2 mm in diameter.

Fig. 41: Protoconch of *Schizogonium ampezzanum* of the shell in fig. 40.

Fig. 42: *Pseudoschizogonium elevatum* (Kittl, 1891) from Costalaresc at Cortina d'Ampezzo. Shell is 5 mm wide.

Fig. 43: Juvenile shell of *Pseudoschizogonium elevatum,* same shell as in fig. 42.

Fig. 44: *Pseudoschizogonium elevatum* from Rumerlo at Cortina d'Ampezzo with 5 mm wide shell

Fig. 45: Same shell as in fig. 44.


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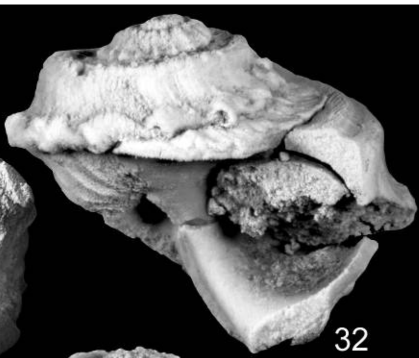
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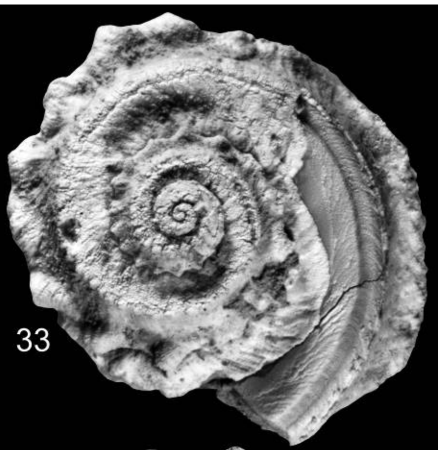
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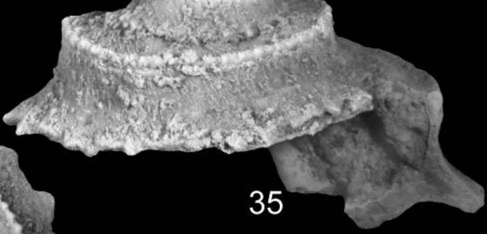
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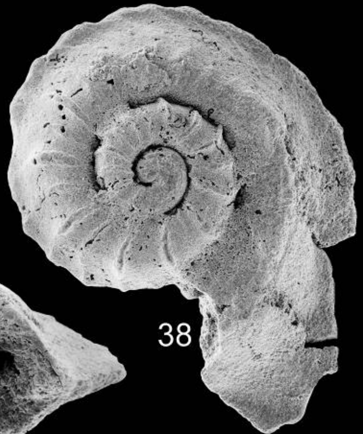
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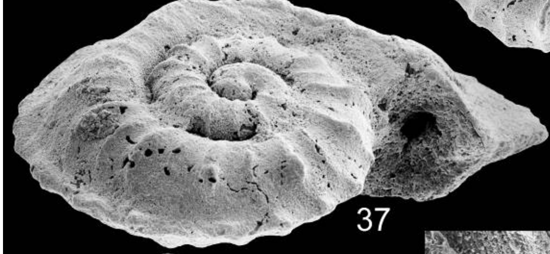
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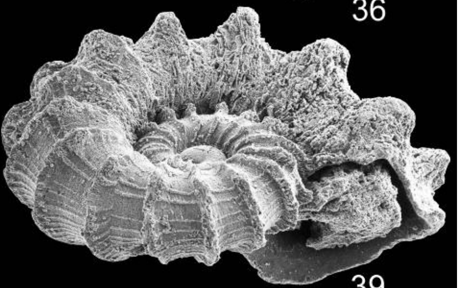
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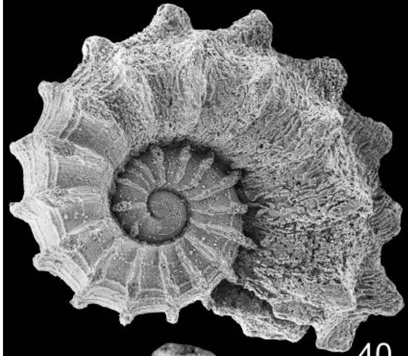
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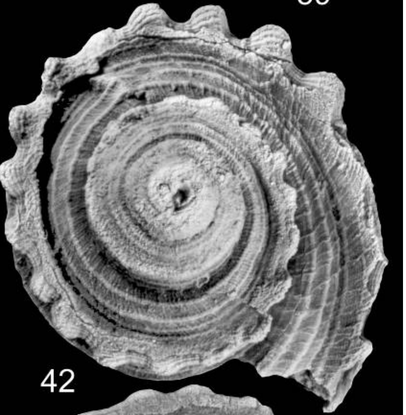
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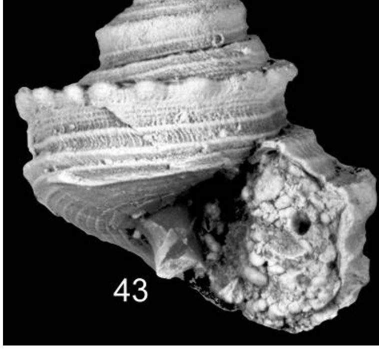
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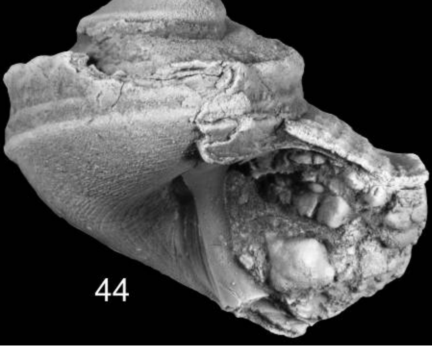
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Plate 4

Fig. 46: *Pseudoschizogonium elevatum* with 9 mm wide shell from Rumerlo at Cortina d'Ampezzo, St. Cassian Formation.

Fig. 47: *Pseudoschizogonium elevatum*, same shell as in fig. 46.

Fig. 48: Juvenile shell of *Pseudoschizogonium elevatum* with slit beginning in the third whorl of the teleoconch and the shell 2.2 mm wide from locality Dibona, St. Cassian Formation.

Fig. 49: Juvenile shell of *Pseudoschizogonium elevatum* with 1.2 mm wide shell from Dibona.

Fig. 50: Protoconch of *Pseudowortheniella rarissima* (Kittl, 1891) with pit and ridge pattern is about 0.17 mm wide.

Fig. 51: Change of ornament in the shell of *Pseudowortheniella rarissima* with about 2 mm wide two inner whorls from Alpe di Specie.

Fig. 52: First whorl of teleoconch with axial ribs as in *Schizogonium* also in *Pseudowortheniella rarissima.* Shell about 1.2 mm wide, from Alpe di Specie.

Fig. 53: Juvenile shell of *Pseudowortheniella rarissima* frm St. Cassian Formation. Shell width about 1.5 mm.

Fig. 54: Shell of *Pseudowortheniella rarissima* that is about 3 mm wide from Alpe di Specie.

Fig. 55: *Kittlidiscus planus* (Klipstein, 1843) from St. Cassian with 11 mm wide shell

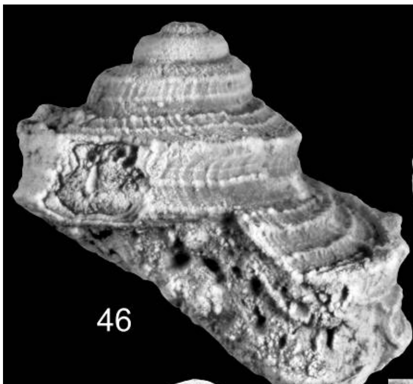
Fig. 56: *Kittlidiscus planus* as in fig. 55.

Fig. 57: *Kittlidiscus planus* from St. Cassian with 10 mm wide shell compressed.

Fig. 58: *Gosseletina fasciolata* (Münster, 1841) with 7 mm wide shell from Alpe di Specie, St. Cassian Formation.

Fig. 59: *Gosseletina fasciolata* same as in fig. 60 with the whorl attached in the position of the selenizone.

Fig. 60: Protoconch of *Sisenna venusta* (Münster, 1841) from St. Cassian Formation with 0.18 mm in diameter.



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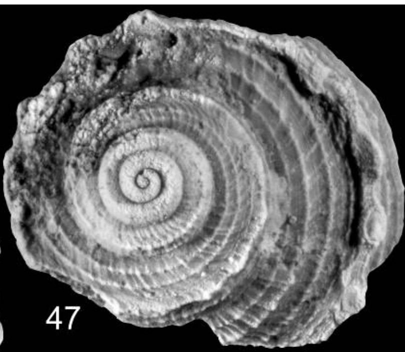

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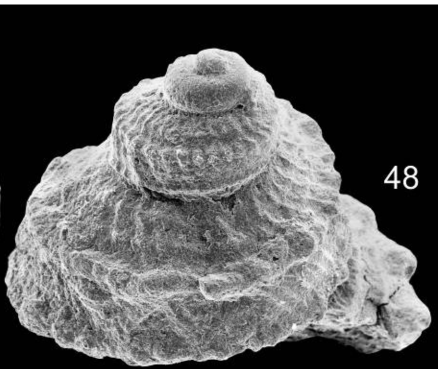

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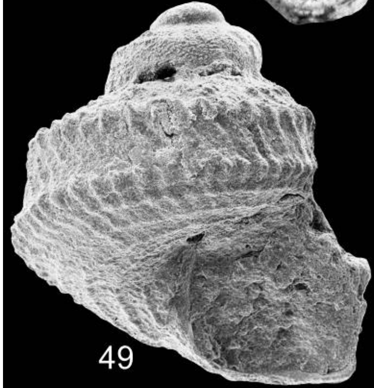

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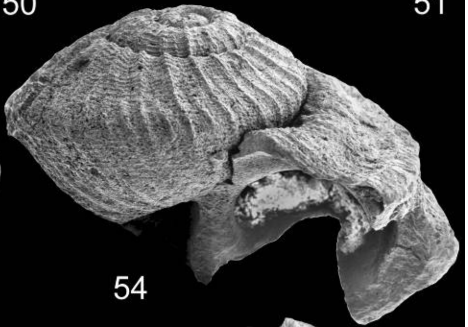

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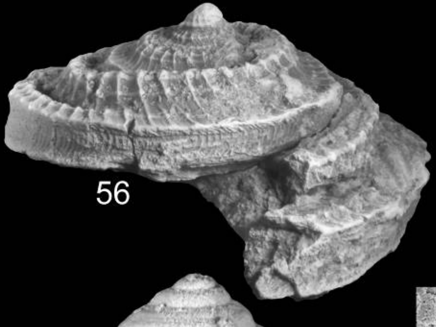

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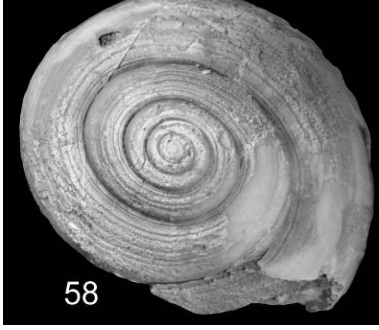

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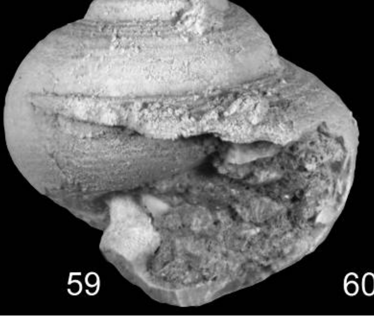

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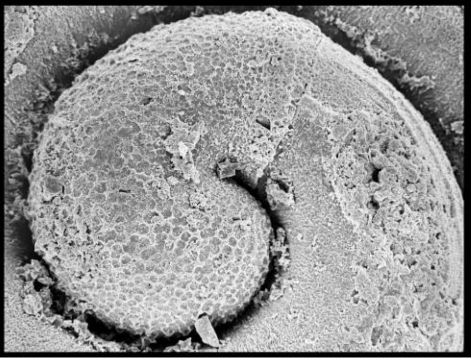

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Plate 5

Fig. 61: Juvenile teleoconch of *Sisenna venusta* with fine spiral ornament and in the fourth whorl axial folds are added. The shell from Loc. Campo is 2 mm wide.

Fig. 62: Shell of *Sisenna venusta* seen from behind is about 2 mm wide.

Fig. 63: *Campbellospira missouriensis* n. sp. with 1.5 mm wide shell from the Saint Louis Outlier, Missouri, USA.

Fig. 64: *Campbellospira missouriensis* with about 1.5 mm high juvenile shell from the Pennsylvanian of USA.

Fig. 65: *Campbellospira missouriensis* with the shell about 1.5 mm in size from the Pennsylvanian of Missouri, USA.

Fig. 66: *Wortheniella coralliophila* (Kittl, 1891) from Alpe di Specie with about 1 mm high shell and begin of selenizone in third whorl of teleoconch.

Fig. 67: Protoconch of *Wortheniella coralliophila* with ornament and about 1.5 mm in width, from Alpe di Specie.

Fig. 68: *Wortheniella coralliophila* with 10 mm high shell from Misurina, St. Cassian Formation.

Fig. 69: Juvenile teleoconch of *Wortheniella coralliophila* with rounded shape of flat whorl and protoconch in depression. Width of shell about 0.8 mm.

Fig. 70: Juvenile teleoconch of *Wortheniella coralliophila* seen in inclined position, as in fig. 69.

Fig. 71: *Wortheniella subpunctata* from Misurina with about 1.2 mm high shell.

Fig. 72: Apical shell of *Wortheniella subpunctata* as in fig. 71 with change in ornament with begin of slit.

Fig. 73: Protoconch of *Wortheniella subpunctata* with fine ornament of wrinkles and spiral line with the aperture raised. Its size is about 0.2 mm. St. Cassian Formation.

Fig. 74: Juvenile shell of *Wortheniella subpunctata* with about 2 mm high shell and predominantly spiral ornament and selenizone begin in last whorl.

Fig. 75: *Rinaldoella muensteri* with 13 mm high shell from Alpe di Specie, St. Cassian Formation.


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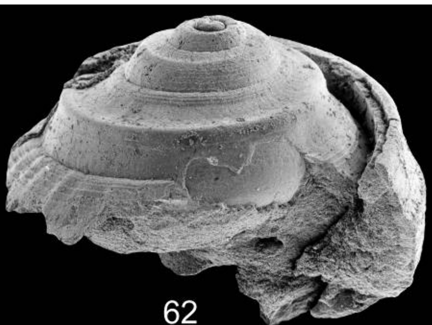
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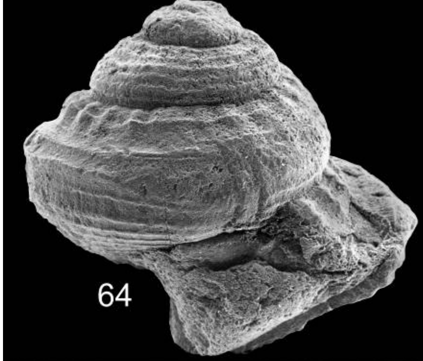
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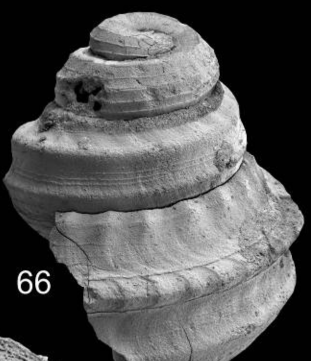
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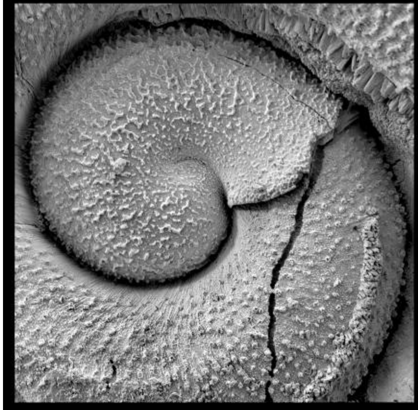
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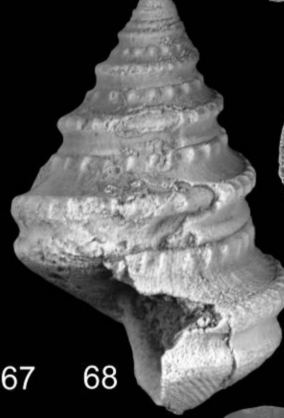
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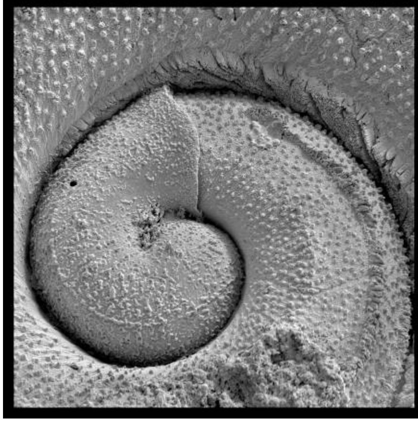
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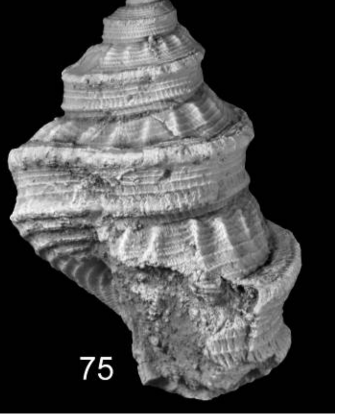
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Plate 6

Fig. 76: Juvenile shell of *Wortheniella spuria* with about 0.8 mm high shell, protoconch in apical depression and ornament of spiral lines.

Fig. 77: *Wortheniella spuria* with same shell as in fig. 76 with depression in the apex that contains the protoconch.

Fig. 78: *Rinaldoella subgranulata* with flat apex and protoconch in depression with begin of selenizone in third whorl of teleoconch. Shell about 2 mm in height.

Fig. 79: Juvenile shell of *Rinaldoella subgranulata* with change in shape and ornament in first whorls with about 1.5 mm in width.

Fig. 80: Protoconch of *Rinaldoella subgranulata* with smooth surface and sinuous margin in depression of early teleoconch, detail to fig. 79. Width of protoconch about 0.18 mm.

Fig. 81: Juvenile teleoconch of *Rinaldoella crenata* with about 1.3 mm high shell and characteristic pattern of ornament.

Fig. 82: Juvenile shell of *Rinaldoella crenata* almost 2 mm wide and with beginning slit in the third whorl of the teleoconch and protoconch in low pit of the apex.

Fig. 83: Protoconch of *Rinaldoella crenata* with about 0.18 mm in width and sinuous margin lies in low depression in the apex.

Fig. 84: Juvenile shell of *Rinaldoella crenata* with detail in fig. 83 and change of shape and ornament of the first whorls of the teleoconch that are 1.5 mm wide and slit inserting in last whorl.

Fig. 85: Shell structure with outer layer of dissected spherulite sectors and inner layer of nacre, all aragonitic in composition. The shell is about 0.25 mm thick. *Wortheniella coralliophila* from Misurina, St. Cassian Formation.

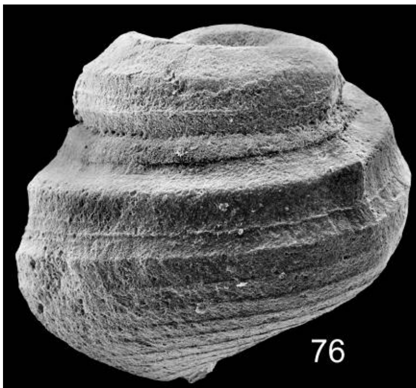
Fig. 86: Shell structure of *Wortheniella coralliophila* as in fig. 85 with outer layer composed of spherulite sectors and inner layer with stacked nacre plates.

Fig. 87: Shell structure in the selenizone of *Wortheniella* is quite the same as next to it with outer prismatic and inner nacreous layer. Misurina, St. Cassian Formation.

Fig. 88: Apical view of *Rinaldoella muensteri* with about 3 mm wide shell and protoconch in a pit and beginning of selenizone in second whorl of teleoconch.

Fig. 89: *Rinaldoella muensteri* in side view with flattened apex with depressed protoconch and selenizone in second whorl of teleoconch. Shell 2.2 mm high.

Fig. 90: Juvenile shell of *Rinaldoella beaumonti* with protoconch in depression, early teleoconch with rows of nodule and slit inserting in second whorl of teleoconch. The shell is about 1 mm wide.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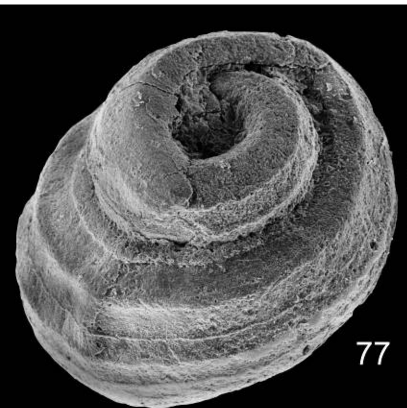
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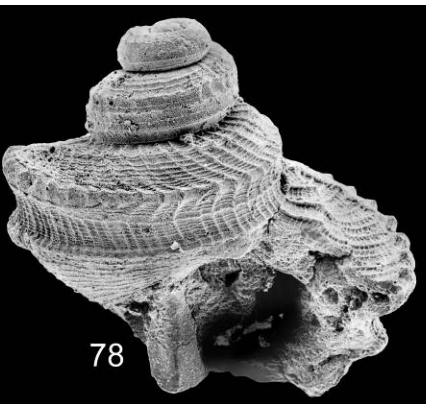
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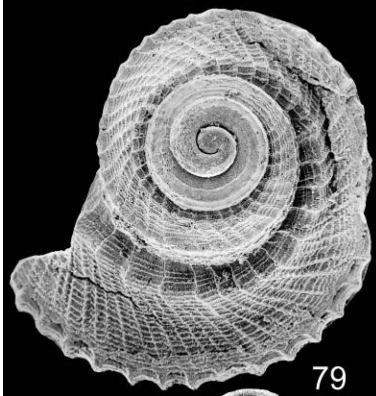
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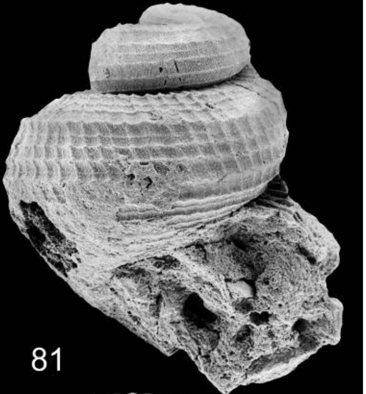
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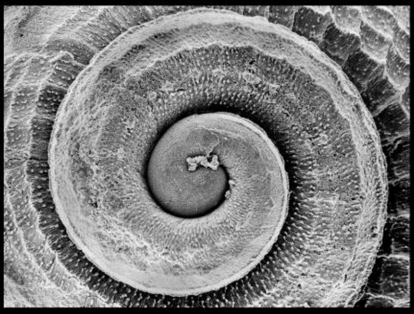
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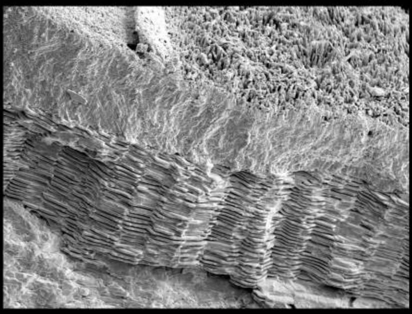
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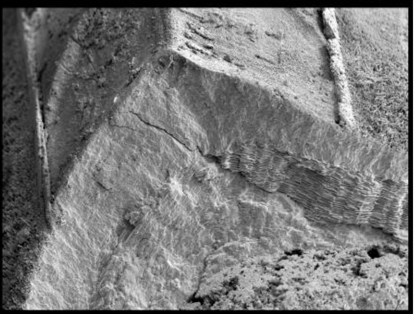
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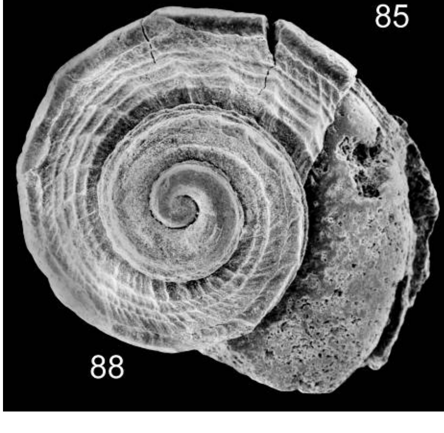
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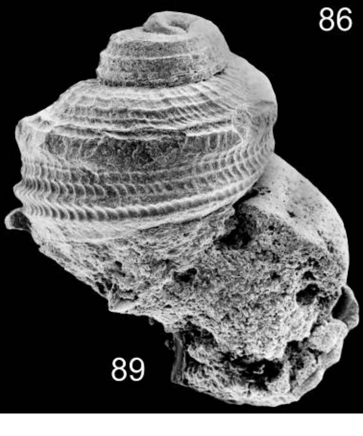
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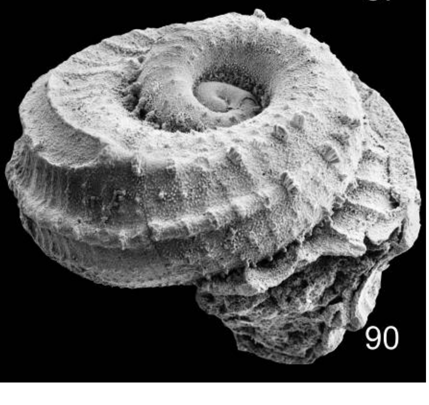
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Plate 7

Fig. 91: Same shell as in fig. 90 of *Rinaldoella beaumonti* from Campo, St. Cassian Formation.

Fig. 92: Smooth protoconch of *Rinaldoella beaumonti* with sinuous margin, detail to fig. 91.

Fig. 93: Early teleoconch of *Rinaldoella beaumonti* with rounded whorls and corner with begin of selenizone. Shell about 1 mm wide from Campo, St. Cassian Formation.

Fig. 94: Change in shape of *Rinaldoella beaumonti* from Campo with 5 mm wide shell.

Fig. 95: *Rinaldoella beaumonti* from Campo with 3 mm wide shell, same as in fig. 96 with begin of selenizone in second whorl of teleoconch.

Fig. 96: Same shell as in fig. 96 of *Rinaldoella beaumonti* seen from the side.

Fig. 97: *Bandelium campense* (Zardini, 1980) from Campo at Cortina d'Ampezzo with about 1 mm high shell.

Fig. 98: Early whorls of *Bandelium campense* from Campo with 0.6 mm wide shell.

Fig. 99: Protoconch of *Bandelium campense* is smooth with sinuous margin and about 0.2 mm in width. Campo of Cortina d'Ampezzo, St. Cassian Formation.

Fig. 100: 1.3 mm high shell of *Bandelium ruedigeri* (Schwardt, 1992) from loc. Campo, St. Cassian Formation.

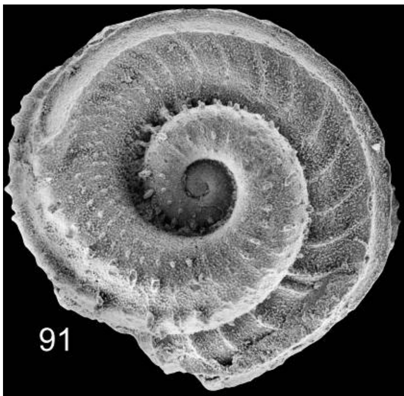
Fig. 101: Protoconch of *Zardinitrochus suessi* (Klipstein, 1841) is about 0.2 mm wide, detail to fig. 102.

Fig. 102: Juvenile shell of *Zardinitrochus suessi* from Campo, about 1.2 mm wide, St. Cassian Formation.

Fig. 103: Juvenile shell of *Haliotis pustulata* Reeve, 1846 from the Gulf of Aqaba, about 2 mm in width.

Fig. 104: Juvenile shell of *Haliotis unilateralis* Lamarck, 1822 from the Gulf of Aqaba is quite similar to that in fig. 103, but more rounded and 1.5 mm in diameter.

Fig. 105: Larval shell of *Haliotis tuberculata* from the plankton of the Mediterranean Sea at Banyuls-Sur-Mer. The shell is about 0.2 mm wide.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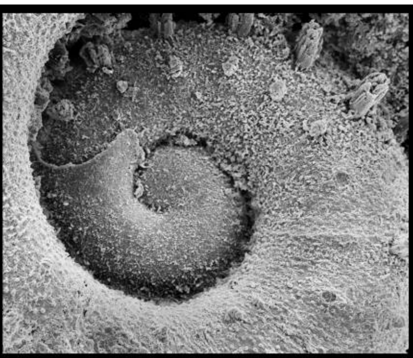
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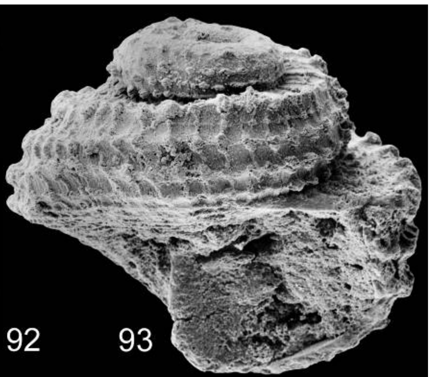
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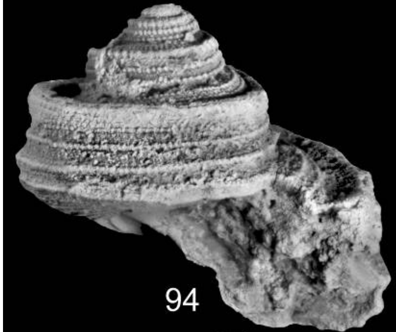
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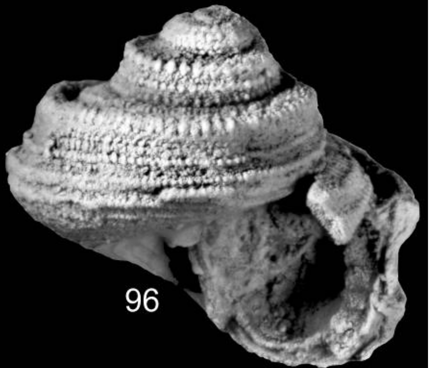
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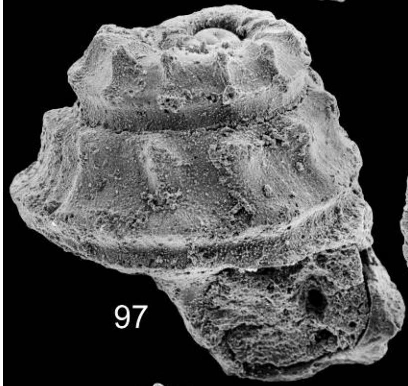
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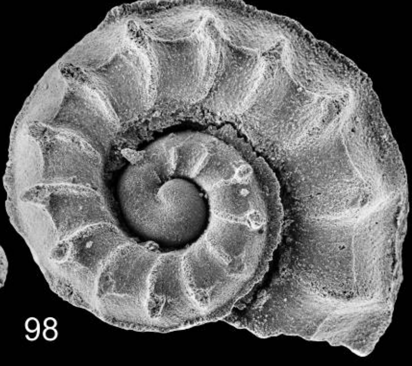
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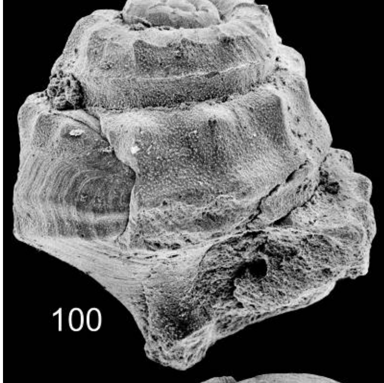
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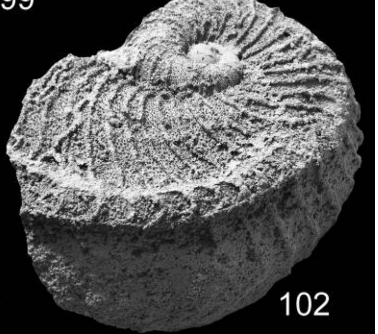
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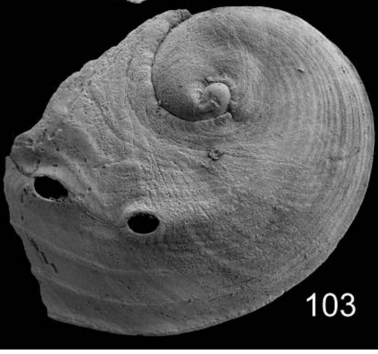
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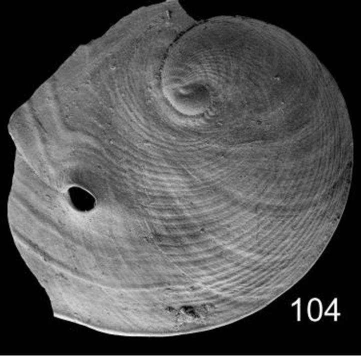
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Plate 8

Fig. 106: Juvenile shell of *Haliotis tuberculata* from the Mediterranean Sea at Banyuls-Sur Mer with first slit and closed holes. Shell about 2 mm wide.

Fig. 107: *Temnotropis carinata* from St. Cassian Formation with shell about 8 mm wide.

Fig. 108: *Laubella delicata* (Laube, 1868) with internal septum and 1.7 mm high shell. Loc. Campo, St. Cassian Formation.

Fig. 109: *Laubella delicata* as in fig. 108 documenting the position of the internal septum behind the open slit.

Fig. 110: *Laubella delicata* with the slit of the aperture that reaches far back, from St. Cassian Formation. The shell is about 2 mm high.

Fig. 111: *Laubella minor* from Alpe di Specie, St. Cassian Formation, with selenizone beginning in third whorl. 1.8 mm high shell.

Fig. 112: Apex of *Laubella minor* from Campo at Cortina d'Ampezzo with smooth protoconch and selenizone beginning in second whorl of teleoconch. Shell about 1.6 mm wide.

Fig. 113: The shell of *Seguenzia monocingulata* Seguenza, 1876 from the shelf of the US East-Coast is about 4 mm high and has the slit high up in the outer lip.

Fig. 114: Protoconch and early teleoconch of *Seguenzia*, detail to fig. 113.

Fig. 115: Protoconch and early teleoconch of *Basilissa* from the deep shelf of the SE coast of USA are very similar to that of *Seguenzia* but the adult shell has not slit. Protoconch about 0.22 mm wide.

Fig. 116: Fully grown shell of *Fossarina mariei* (Fischer, 1890) from Aqaba with slit closed by growth increments with denser frequency at end. Shell 1.2 mm high.

Fig. 117: Shell of *Fossarina mariei* from the Gulf of Aqaba with growth increments continuous in slit. Shell almost 1 mm high.

Fig. 118: *Fossarina mariei* from Aqaba with growth increments detached from slit margin. Shell about 1 mm high.

Fig. 119: *Fossarina mariei* with small sinus in outer lip and organic operculum. Shell about 1 mm high.

Fig. 120: Protoconch of *Fossarina mariei* with ornament of ribs and width of almost 0.2 mm.


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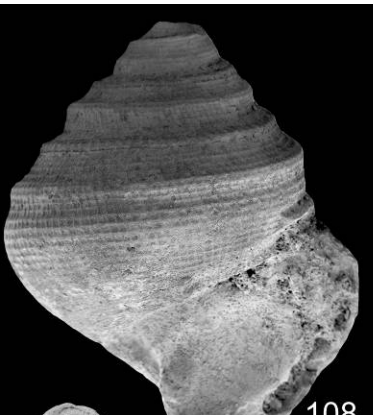
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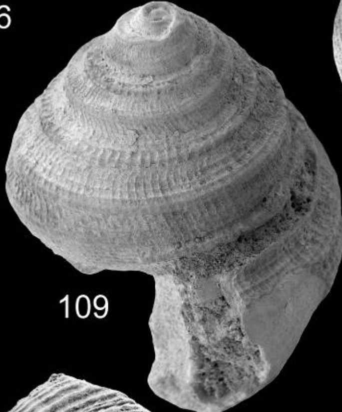
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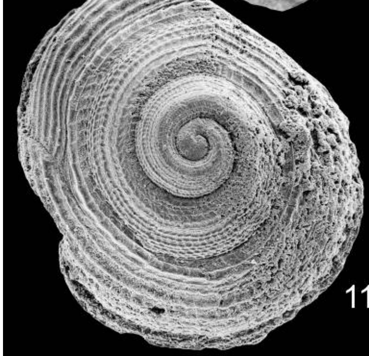
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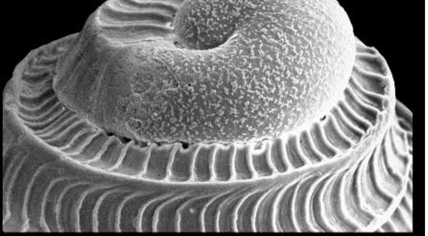
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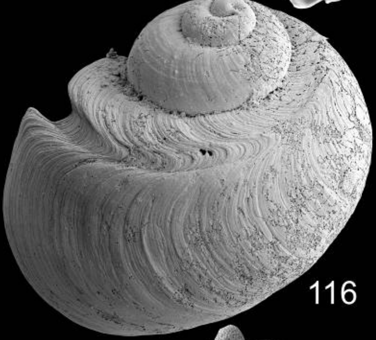
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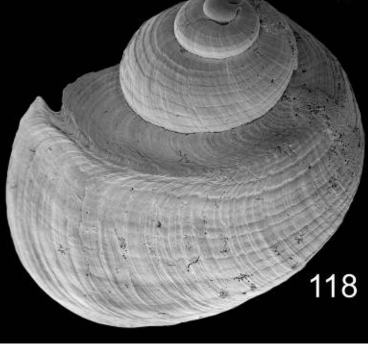
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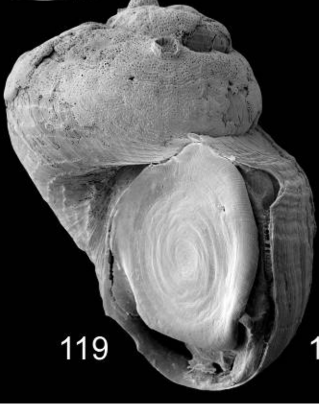
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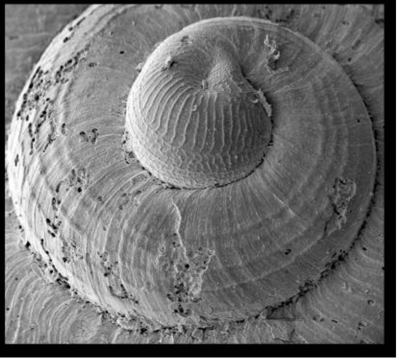
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Plate 9

Fig. 121: Radula of *Perotrochus teramachii* Kuroda, 1955 from Taiwan, half row with central teeth at right. Width of radula about 1 mm.

Fig. 122: Half radula of *Perotrochus teramachii*, central teeth at left. Same radula as in fig. 121.

Fig. 123: Radula of *Perotrochus teramachii*. Central part complete with the central tooth pointed and similar to the lateral teeth. Same radula as in fig. 121.

Fig. 124: Radula of *Haliotis pustulata* Reeve, 1846 from Aqaba with the ribbon about 0.8 mm wide.

Fig. 125: Radula of *Haliotis pustulata* Reeve, 1846 from the Gulf of Aqaba, detail to fig. 124 with central teeth at the right.

Fig. 126: Radula of *Haliotis unilateralis* Lamarck, 1822 from the Gulf of Aqaba with central teeth at the left.

Fig. 127: Complete radula of *Seguenzia megaloconcha* Rokop, 1972 from the Pacific with ribbon about 0.05 mm wide.

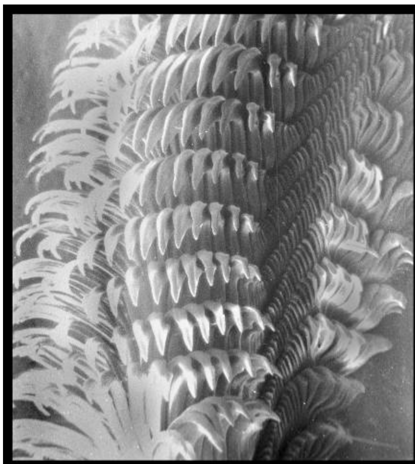
Fig. 128: Marginal teeth of the radula of *Seguenzia megaloconcha* from the same specimen as in fig. 127.

Fig. 129: Central zone in the radula of *Seguenzia megaloconcha* from the radula in fig. 127 and 128.

Fig. 130: Radula of *Fossarina mariei* (Fischer, 1890) from the Gulf of Aqaba. The radula ribbon is about 0.2 mm wide.

Fig. 131: Central zone of the radula of *Fossarina mariei* with central teeth at the right. Same species as in fig. 130.

Fig. 132: Marginal teeth of the radula of *Fossarina mariei* with transition to the central zone at left. Same radula as in fig. 130.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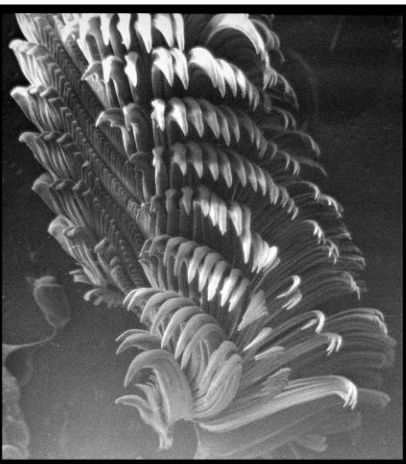
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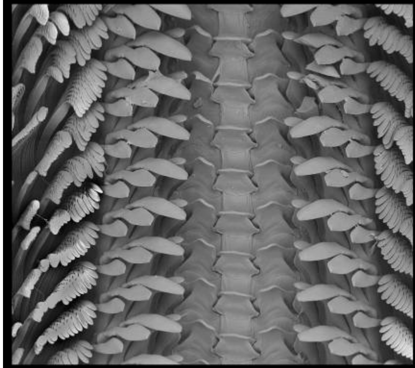

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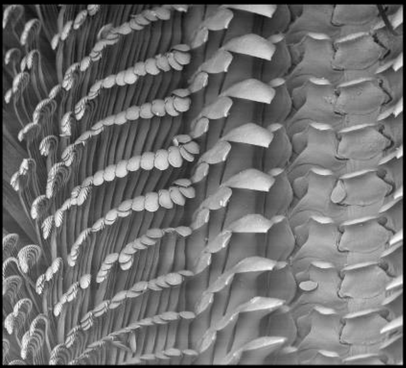

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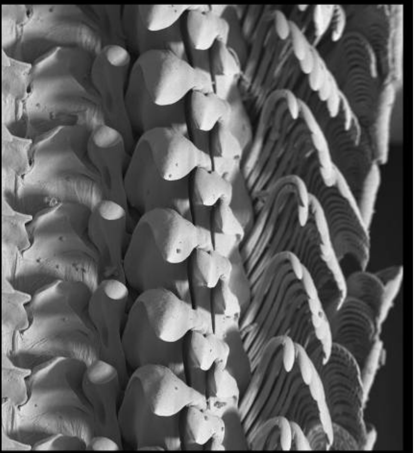


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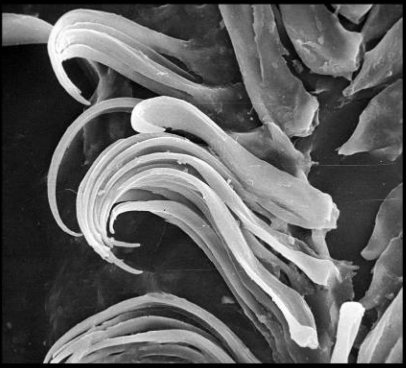
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