

Triassic Euthyneura (Gastropoda) from St. Cassian Formation (Italian Alps) with a discussion on the evolution of the Heterostropha

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with 1 Figure and 4 Plates

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Abstract

The genera *Cyndrobullina* and *Actaeonina* of the Cyndrobullinidae are described. The species *Cyndrobullina scalaris* is redescribed, and the three new species *Cyndrobullina pralongiana*, *Actaeonina stuorense*, *Actaeonina lancedellia* are presented. Two new genera *Dolomitella* and *Zardinella* are differentiated and placed into new families of the Heterostropha, the Dolomitellidae and Zardinellidae. The history of the potential earliest Opisthobranchiata is discussed. A general review of the geological history of the subclass Heterostropha (=Heterobranchia) in the class Gastropoda of the Mollusca during their Paleozoic and Mesozoic evolution is given.

Zusammenfassung

Die Gattungen *Cyndrobullina* und *Actaeonina* der Familie Cyndrobullinidae werden beschrieben. *Cyndrobullina scalaris* wird revidiert und die drei neue Arten *Cyndrobullina pralongiana*, *Actaeonina stuorense*, *Actaeonina lancedellia* beschrieben. Zwei neue Gattungen - *Dolomitella* und *Zardinella* - werden differenziert und zur Aufstellung zweier eigener Familien - Dolomitellidae und Zardinellidae - der Unterklasse Heterostropha genutzt. Die Evolutionsgeschichte der bisher ältesten, möglicherweise den Opisthobranchiern angehörigen Fossilien wird diskutiert und in den größeren Rahmen der geologischen Geschichte der Heterostropha (=Heterobranchia) innerhalb der Klasse Gastropoda unter den Mollusca während ihrer paläozoischen und mesozoischen Entwicklung gestellt.

1 Introduction

The knowledge of the morphology of the protoconch allows to place a number of gastropods from the Upper Triassic St. Cassian Formation into the gastropod subclass Heterostropha FISCHER, 1885 (=Heterobranchia GRAY, 1840). Nearly all species of this subclass with a planktotrophic larva have a protoconch that coils in the opposite direction to the teleoconch. Thus they usually change in shell coiling from left to right during their early ontogeny (BANDEL 1991d) and at or prior to metamorphosis (in contrast to the Cirroidea COSSMANN, 1916 (BANDEL 1993b)). Distinct lineages discovered among the fossil members of this subclass can be interpreted as ancestral Opisthobranchia and are here described.

According to BIZZARINI et al (1986) the St. Cassian Formation has been deposited in the time interval between Upper Ladinian and Karnian in Upper Triassic time. The gastropods here described lived in shallow water along the edge to deeper basins. They had become preserved in the sediments of the basins or on their slopes. FÜRSICH & WENDT (1977) and WENDT & FÜRSICH (1980) demonstrated that basis and carbonate platforms existed very close to each other when the area was part of islands and banks in the tropical Tethys Ocean. Gastropods lived in great numbers within reefs that existed in the transition from shallow warm carbonate lagoons to the open ocean. Their shells were not preserved in their former living environment but in clay rich, often tuffaceous sediments of the basins into which they were slumped down more or less steep slopes. The shallow water carbonate environment, when preserved in the rock column, provides no further information to the actual living place of the species involved since it has been transformed into coarsely grained limestone or even turned into dolomite. During this process all smaller gastropods had disappeared, and those species described here are all small.

Most of gastropods on which this study is based were washed from marly rock in localities described and located in an illustration by ZARDINI (1978). The localities here mentioned are that of Campo, found above Campo di Sopra in Cortina d'Ampezzo in the forrest; Dibona or Milieres exposed in slumps below the Rifugio Dibona near the road from Cortina d'Ampezzo to Falzarego pass; Alpe di Specie (Seelandwiesen) above Carbonin (Schluderbach) and close to Rifugio Vallandro (Dürrenstein Hütte); Misurina at the ski lift near the Rifugio Lago di Antorno in the Valle Popena; and Stuores (Störes-Wiesen) consisting of a landslide below the ridge of Pralongia on the way to the Settsass above St. Cassian (S. Cassiano).

I want to thank the Rinaldo ZARDINI and Rolando LANCEDELLI for material and their help in finding localities in the field and many advices on how to extract shells from the rock. Provided with this knowledge it was possible to collect material in the field and extract many small shells from it. This process was carried out with the assistance of Sabrina CRAFTON, Frederike STICHERT, Klaus HARBECK, Nikolaus LEHMANN, Alexander NÜTZEL and Frank RIEDEL in the field in campaigns in 1989, 1991, 1993. Several people of the Department of Geology and Paleontology at the University of Hamburg helped selecting the shells out of the samples, cleaning them with diluted hydrogensuperoxide and prepared the fossiles under the binocular microscope in order to take photographs by the SCAN afterwards. Material deposited in the Naturhistorisches Museum in Wien was loaned, thanks to H. KOLLMANN and O. SCHULZ. David DOCKERY (Jackson, Mississippi) and Michael SCHRÖDER (Hamburg) provided many of the new data that were utilized in the revies on evolution of the Heterostropha. Financial support has come from the University of Hamburg as well as from DFG (German Science Foundation) grants Ba 675/11. All people and organizations involved I wish to thank very much.

2 Taxonomic part

2.1 Family *Cylindrobullinidae* WENZ, 1947

Diagnosis modified from WENZ & ZILCH (1960, p.13): The shell is egg-shaped in outline with a conical or step-like spire and growth lines as the major sculptural elements. The aperture is elongated and oval, and the spindle is thickened but bears no folds. The larval shell is sinistral and twists into the teleoconch at the very end of its whorls. Its axis forms an angle from 90 degrees to less than about 45 degrees with that of the teleoconch. The type is the genus *Cylindrobullina* AMMON, 1878.

Differences: Representatives of the genera *Cylindrobullina* and *Actaeonina* differ from members of the Actaeonellidae by the absense of spindle folds and from members of the Actaeonidae by lack of a sculpture of spiral grooves and rows of pits.

Genus *Cylindrobullina* AMMON, 1878

Description: The small shell is egg shaped with a short conical spire. The whorls are separated by a flattened ramp. The wide aperture is constricted toward the posterior and widened toward the front. The inner lip rests on the slightly bent columella and forms a narrow low fold in its frontal portion and a narrow slit on the spindle. The early whorls consist of a sinistrally coiled low-spired shell attached to the teleoconch at an angle of about 90 degrees. The genotype is *Tornatella scalaris* MÜNSTER, 1841 from the St. Cassian Formation.

Differences: The shell of *Cylindrobullina* differs from that of *Actaeonina* by a more conical shape and wider, flattened ramp on whorls shoulders. *Euconactaeon* HAAS, 1953 has a shorter spire. *Consobrinella* HAAS, 1953 and *Ceritellopsis* FISCHER, 1961 show axial ribs and *Actaeon* MONTFORT, 1810 has spiral grooves as ornament.

Species *Cylindrobullina scalaris* (MÜNSTER, 1841)

Plate .1, Figures 1, 2, 3, 4, 5, 6, 7, 12

1841, *Tornatella scalaris* MÜNSTER, Beiträge IV: 103, Pl. 10, Fig. 26.

1868, *Acteonina scalaris*, LAUBE, Fauna der Schichten von St. Cassian III: 49-50, Pl. 23, Fig.6.

1868, *Acteonina subscalaris* LAUBE, Fauna der Schichten von St. Cassian, III: 50-51, Pl.23, Fig.8.

1894, *Acteonina scalaris*, KITTL, Die Gastropoden von St. Cassian, II: 241-243, Pl.11, Figs. 24-31.

1978, *Cylindrobullina scalaris*, ZARDINI, Fossili Cassiani, 1978: 55, Pl.38, Fig 14, 15.

A very extensive list of synonymies was presented by KITTL (1894).

Description: The shell is up to 6 mm high and 3 mm wide, consists of 6,5 to 7 whorls of the teleoconch. The last whorl makes up 4/5ths of the shell height. Whorls are flattened apically and form a right angle corner with the lower flank. This step-like corner may be enforced by a ridge. The aperture is pear-shaped and wider in front than at the posterior end. The inner lip is thickened where it separates from the spindle to form a narrow slit. The sinistral protoconch consists of almost two whorls with 0.22 to 0.28 mm width and nearly the same height. The first whorl belongs to the embryonic phase of development and is partly concealed by the first whorl of the teleoconch. The second whorl was formed by the planktotrophic veliger. In the final portion of the larval shell, the whorl twists into the dextral teleoconch. The open umbilicus of the protoconch points to the side. The axis of the larval shell forms a right angle with that of the adult shell.

Differences: *Cylindrobullina scalaris* differs from *C. pralongiana* by a smaller protoconch. From the species of *Actaeonina* distinguishes the stair-case like spire that is more rounded in *A. stuorense* and *A. lancedellia*. The collabral ornament of the teleoconch differs from that of *C. gracilispira* SCHRÖDER, 1993 from the Middle-Jurassic.

Material: Over 20 individuals from the locality Stuores near St. Kassian, 10 from Alpe di Specie and 3 from Misurina were studied. Specimen are deposited with Nr 1994/0038 in the NHM Wien.

Species *Cylindrobullina pralongiana* n. sp.

Plate .1, Figures .8, 9, 13, 14

Plate 2, Figure 2

Diagnosis: The generic definition applies to this species. The most characteristic feature of the shell is the large protoconch measuring up to 0,4 mm in diameter and consisting of 2,5 whorls.

Description: A shell with a little more than three whorls of the teleoconch is about 3 mm high and 1,7 mm wide. The upper whorl is flattened and carries a spiral ridge that accompanies the suture. The flank forms a sharp corner with the upper ramp. Ornament consists of indistinct growth lines. The protoconch axis forms a right angle with teleoconch axis. Its embryonic whorl is partly concealed by the first whorl of the teleoconch and measures 0.08 mm in diameter. The whorls formed by the planktotrophic larva have collabral growth increments and end in an apertural rim that marks the end of larval growth. This apertural thickening of the pediveliger shell covers the narrow umbilicus that is accompanied by axial folds on the umbilical side of the larval shell. A protoconch of 0.35 mm in width is 0.28 mm high and has rounded whorls with rapid increase in shell diameter.

Differences: *Cylindrobullina pralongiana* differs from *C. scalaris* only by the larger size of its protoconch that measures 0,4 mm, while that of *C. scalaris* is never larger than 0,3 mm.

Holotype and locus typicus: *Cylindrobullina pralongiana* comes from the western slope of Pralongia ridge, from which it derived its name, and its eastern slopes, the Stuores meadows, above St. Kassian. The holotype is deposited in the NHM Wien Nr. 1994/0039. The material consists of 19 individuals from Pralongia and 6 individuals from Stuores and is deposited with Nr. 1994/0040 in the NHM Wien.

Description: The slender egg-shaped shell consist of whorls with rounded flanks forming a narrow angular ramp accompanied by a spiral groove below it. The aperture is high ovoid in outline with a curving course of the inner lip. The protoconch forms an angle of about 90 degrees with the teleoconch, and the embryonic shell is totally or partly covered by the first whorl of the teleoconch. Genotype is *Actaeonina acuta* ORBIGNY, 1847 from the Jurassic Oxfordian (SCHRÖDER, 1993) and not *Actaeonina carbonaria* (KONINCK, 1843) from the Lower Carboniferous (KNIGHT, 1941).

Differences: The shell of *Actaeonina* resembles that of *Cylindrobullina* in general shape, the type of protoconch and simple ornament consisting of growth lines. *Actaeonina* differs by its ovoid shape and slender spindle-like outline in contrast to the stair-like and more cylindrical shape of *Cylindrobullina*.

Species *Actaeonina stuorensis* n. sp.

Plate 1., Figures 10, 11

Plate 2, Figures 3, 10, 11

Diagnosis: The generic diagnosis applies to this species. The sinistral protoconch is almost planispiral and 0.15-0.18 mm in diameter and attached to the dextral teleoconch forming an angle of about 90 degrees with it. The teleoconch bears a narrow ramp on its upper flank.

Description: The small, egg-shaped shell with last whorl slightly larger than the spire consists of 5 teleoconch whorls with rounded, angular corner accompanied by a narrow groove that represents a small indentation in the posterior portion of the outer lip. The suture is accompanied by a narrow ramp below it. The aperture is pear shaped with a sigmoidal twist reflecting the sigmoidal shape of the outer lip. The inner lip is formed by a callus that shows a plica at the anterior end. The protoconch has 1.7 sinistral whorls, measures about 0,15-0,18 mm in diameter, is less high than wide, almost planispirally coiled and umbilicate. The twist into the dextral shell occurs between margin of the smooth pediveliger shell and the begin of the teleoconch with its grooved narrow apical ramp just below the suture. Protoconch axis forms a right angle with the axis of the teleoconch.

Differences: The smaller protoconch and more slender teleoconch differentiates *Actaeonina stuorensis* from *A. lancedellia*. Its shell bears a ramp which distinguishes it from *A. malzi* SCHRÖDER, 1993 and *A. abdominiforme* SCHRÖDER, 1993 from the Lower Jurassic (SCHRÖDER 1993).

Holotype and locus typicus: *Actaeonina stuorensis* from the outcrops of the St. Cassian Formation below the Pralongia ridge and the Stuoeres meadows above St. Kassian is deposited in the NHM Wien Nr. 1992/ . *Actaeonina stuorensis* derived its name from the Stuoeres (Störes-Wiesen) meadows below Pralongia Ridge and above St. Kassian where most of the representatives of the species have been found. Material: Numerous individuals have been extracted from samples collected 1991 from Stuoeres and Alpe di Specie. Material is deposited under Nr. 1994/0042 in NHM Wien.

Species *Actaeonina lancedellia* n. sp.

Plate 2, Figures 4, 6, 7, 8, 9, 12, 13

Diagnosis: The generic diagnosis applies to this species. The shell is about twice as high as wide. The teleoconch carries a protoconch with 1.5 whorls and about 0.2 mm width and height. It deviates from teleoconch axis by about 90 degrees.

Description: The shell closely resembles that of *Actaeonina stuorensis* but is broader and has a larger protoconch. A shell with 2.5 whorls of the teleoconch is about 1 mm long and 0.5 mm wide, with 3.5 whorls it is 1.2 mm high and 0.6 mm wide. Its protoconch forms almost an angle of 90 degree with the teleoconch and consists of about 1.5 to 1.6 whorls with a diameter of about 0.2 mm and about the same height. Sutures are deep and accompanied by a narrow ramp on the upper whorl flank. Whorl flanks are flattened, even concave and of rather variable shape among different individuals of this species resulting in quite some shell variation.

Differences: *Actaeonina lancedellia* can be differentiated from *A. stuorensis* by its larger protoconch and wider and less slender teleoconch. From the two species of *Cylindrobullina* it is distinguished by slender shape,

smaller size and higher spire.

Material: The holotype is deposited with Nr. 1994/0043 in the NHM Wien. It was selected from samples washed from the slumped marls of St. Cassian Formation at the locality Alpe di Specie near Seelandalpe north of Cortina d'Ampezzo during the campaigns 1989, 1991 and 1993. The species is named in honour of Rolando LANCEDELLI who has collected a lot of the material that was described by Rinaldo ZARDINI and helped us in locating several of the good collecting sites. The studied material consists of numerous individuals from Alpe di Specie, 5 individuals from Misurina and 13 from Pralongia Ridge. Material is deposited with Nr. 1994/0044 in the NHM Wien.

Remarks: Members of the Cylindrobullinidae are common in the Upper Triassic for the Dolomites (ZARDINI 1978, BANDEL 1992, Fig.32) as well as from the Pucara Formation in Peru (HAAS, 1953, BANDEL, 1994c). The Peruvian formation holds members of the genera, *Cylindrobullina* as well as *Euconactaeon* HAAS, 1953 with shorter spire and *Consobrinella* HAAS, 1953 with axial ribs (HAAS 1953). Members of the genus *Actaeonina* from Peru may be hidden among names like *Spirostylus peruvianus* HAAS, 1953 and *Ramina ? andina* HAAS, 1953 (BANDEL 1994c). The species *Coelostylina cylindrata* HAAS, 1953 was renamed into *Actaeonina cylindrata* (HAAS, 1953) by BANDEL (1994c). *Actaeonina* can be traced to Jurassic time as was documented by SCHRÖDER (1993). Similar species in the Jurassic are *Actaeonina malzii* SCHRÖDER, 1993 with well rounded flanks. Upper Jurassic *Ceritella* shows some similarity in general shell shape but its spire is smoother since sutures are less pronounced and the aperture is shorter than that of *Actaeonina* (HUCKRIEDE 1967, Pl.18, 19). *Ceritelopsis* FISCHER, 1961 from Upper Jurassic and Lower Cretaceous also resembles *Actaeonina*, but lived in a different more brackish influenced environment (BANDEL 1991a). Its young hatched crawling and did not swim off to live as planktotrophic veligers before settling to the bottom, so that the heterostrophic protoconch is less clearly developed and shows fewer whorls.

2.2 Family Dolomitellidae n. fam.

Diagnosis: The shell has a high conical shape with a rounded anterior and an egg-shaped aperture that is narrow posteriorly and rounded and wide anteriorly. The larval shell is of the *Mathilda* type, sinistral and placed at an angle of up to 90 degrees on top of the teleoconch. Sculptural elements consist of spiral ribs and almost straight growth lines, which become opisthoclinal on the upper part of the whorl. The spindle is straight and has no folds. The family is characterized by the genus *Dolomitella* from the St. Cassian Formation.

Differences: The flattened flanks ornamented by spiral lirae connected to indistinct suture and flat base characterize *Dolomitella* and distinguish it from mathildoids (BANDEL 1994a). The mathildid protoconch differentiates Dolomitellidae also from *Zardinella* and the Zardinellidae that have an ampezzanildid protoconch with axial ribs and spirally grooved teleoconch.

Genus *Dolomitella* n. gen.

Diagnosis: General diagnosis of the genus is that of the family. The shell is only a few mm long, elongated conical with nuclear whorls obliquely immersed into the apex. The whorls of the teleoconch are almost flat sided and bear few strong spiral ribs below the impressed suture. Spiral ribs of smaller dimensions are present above the angular edge to the base, which is also sculptured by spiral costae of different dimensions. The aperture has a straight inner lip that forms no umbilicus with the columella. There is a short apertural notch inclined to the left, and the outer lip is rounded. The type species of this genus is *Dolomitella semiornata* (KITTL, 1984) from the St. Cassian Formation.

Difference: Ornament of the teleoconch of *Dolomitella* consists of ribs and not grooves as is the case in *Zardinella*.

Derivatio nominis: The genus is named according to the Dolomites from where it is derived.

Species *Dolomitella semiornata* (KITTL, 1894)

Plate 3, Figures 1, 2, 3, 6, 7

1894, *Hypsipleura semiornata* KITTL, Gastropoden von St. Cassian: 202, Pl. 8, Fig. 30.

1978, *Hypsipleura semiornata*, ZARDINI, Fossilis Cassiani: 49, Pl.33 Fig. 12,15.

1980, *Hypsipleura semiornata* f. giovanile ZARDINI, Fossilis Cassiani : 10, Pl. 4, Fig. 22-25.

1980, *Promathildia bifasciata* ZARDINI, Fossilis Cassiani : 10, Pl.4, Fig. 32,33.

Description: The generic diagnosis applies to this species. KITTL (1894) based his original description on a single individual found at the Seelandalpe. ZARDINI (1978) found many individuals at the same locality and at Misurina and presented a more extended description. He noted that the whorls are sculptured by three stronger spiral ribs at the upper portion, have only faint spiral striae in the central portion, and have three weak ribs at the lower portion just above the suture. The base is almost flattened and covered by about 10 spiral cords, the upper three are the strongest, and the third may be pronounced. There is no umbilicus, and the inner lip is straight and thickened. Growth lines are straight but slightly inclined since the plane of the aperture is not vertical. The aperture has an almost round outline and is slightly higher than wide with a short siphonal notch at its anterior position. A shell with 10 postnuclear whorls measures about 9 mm in length and 2.5 mm in width. This shell was that of a fully grown adult as indicated by the stunted growth lines of the last whorl. Representatives of this species from Campo commonly have especially strong growth lines and were called *Promathildia bifasciata* by ZARDINI (1980).

The heterostrophic protoconch consists of an about 0.15 mm large embryonic shell that is almost totally covered by the first whorl of the teleoconch. The shell secreted by the planktotrophic larva forms an additional whorl of more than 0.3 mm in width that twists into planspiral coiling near the end of its shell. A deep umbilicus is present, surrounded by large folds that do not continue across the rounded flanks. The margin of the aperture of the pediveliger is thickened, and its rim extends into the umbilicus.

Differences: The ornament of fine, noded spiral ribs and the aperture with siphonal notch separates *Dolomitella* from *Zardinella cingulata*. The smooth whorl flanks and indistinct sutures distinguish from members of *Promathida*.

Material: More than 15 individuals from Alpe di Specie, 3 from Misurina, and over 20 from Campo were studied. Individuals are deposited under Nr. 1994/0045 in the NHM in Wien.

Remarks: The heterostrophic protoconch of this species was neither noted by KITTL (1894) nor by ZARDINI (1978), but by ZARDINI (1980, p.10, Figs. 22-24). Due to its presence "*Hypsipleura*" *semiornata* can not represent a member of the genus *Hypsipleura* KOKEN, 1892 since this genus is based on the type species *H. cathedralis* KOKEN from the Raibler Formation, a member of the Zygopleurida (fide WENZ 1938, Fig. 927) with quite a different shell form. This shell form is also found in *H. subnodosa* (KLIPSTEIN, 1841) as described by KITTL (1894, Pl.7, Fig.12-16) and ZARDINI (1978, Pl.33, Fig.21). Zygopleuridae have a characteristically sculptured orthostrophic protoconch (BANDEL 1991b). The protoconch of the genotype of *Hypsipleura* as well as its relative from St. Cassian Formation is still unknown. *Dolomitella* resembles species of the Tubiferidae (=Ceritellidae) based on the Jurassic *Ceritella acuta* MORRIS & LYCETT, 1850. They represent ovate biconical species with smooth flanks of the whorls.

2.3 Family Zardinellidae n. fam.

Diagnosis: The shell is egg-shaped in outline with spiral rows of pits or spiral grooves regularly divided into rows of pits by collabral transverse ridges. The protoconch is of the ampezzanildid type with the initial sinistral embryonic shell immersed within the larval shell. Change from sinistral to dextral coiling occurs within the whorls of the protoconch and well before the onset of the teleoconch. The family is based on the Upper Triassic *Zardinella* from the St. Cassian Formation of the Dolomites in Italy.

Differences: The rounded aperture, short spire and incised spiral sculpture distinguishes from members of the Ampezzanildidae with similar protoconch (BANDEL 1991e, 1994a). The radially sculptured protoconch differentiates from other Mathildoidea but also from cephalaspidean opisthobranchs with similar shell shape and ornamental patterns of the teleoconch as for example found among Acteonidae and Ringiculidae.

Genus *Zardinella* n. sp.

Diagnosis: The general diagnosis is that of the family. The minute ovate shell has weakly convex whorls sculptured by flat-topped cords of unequal size and intervening angular grooves. Regularly spaced axial, collabral elements cross the spiral grooves forming a pattern of pits. The aperture is oval with straight columella and an indistinct anterior notch. Within the protoconch coiling changes from sinistral to dextral and the larval shell is ornamented by axial ribs. The genotype is *Zardinella cingulata* from the St. Cassian Formation.

Differences: As mentioned in the family differences of Zardinellidae the protoconch is of the ampezzanildid type (BANDEL 1994a). *Nonactonina* STEPHENSON, 1941 and the shorter *Troostella* WADE, 1926 from the Upper Cretaceous of the USA have similar teleoconchs with *Zardinella* but smooth larval shell.

Derivatio nominis: The genus is named in honor of Dr. Rinaldo ZARDINI from Cortina d'Ampezzo.

Species *Zardinella cingulata* (ZARDINI, 1978)

Plate 3, Figures 10, 11, 12, 13, 14

1978, *Coelostylina cingulata* ZARDINI, Fossili Cassiani 1978: 44, Pl.10, Fig.3; Pl.26, Fig.15-16.

Description: The diagnosis of the genus applies to this species. With five whorls, the shell is about 2.4 mm long and 1.2 mm wide. The whorls are weakly rounded and covered by three grooves of similar width, separated from each other by flat ridges of different width. Growth lines are indistinct on the ridges and well visible as lamellae within the grooves, producing a regular reticulated pattern. The base is evenly rounded and also covered with about eight grooves and ridges of similar pattern. The aperture is a bit higher than wide and of oval outline with a short, shallow canal at the frontal end. The inner lip simply covers the outside of the former whorl, and the spindle is solid.

The protoconch measures 0.33 mm in width and consists of almost two whorls. The embryonic shell is sinistral, and the twist into the dextral coil occurs within the begin of the larval shell. The apertural rim of the fully grown shell of the pediveliger is thickened, and the larval shell is ornamented by rounded, large, axial ribs with a fine pattern of spiral lirae between them.

Material: Several individuals from Campo and five individuals from Alpe di Specie were studied. Material is deposited in NHM Wien 1994/0046 .

2.4 Family Misurinellidae n. fam.

Diagnosis: The left-handed fusiform, high spired shell has a dextral protoconch. The aperture is oval with posterior notch. The family is based on the genus *Misurinella* from St. Cassian Formation.

Difference: From other heterostrophic species of the St. Cassian Formation *Misurinella* is the only one where the teleoconch is dextrally coiled, while the protoconch is sinistral. It is convergent to the modern genus of the Ellobiidae *Blauneria* SHUTTLEWORTH, 1854.

Genus *Misurinella* n. gen.

Diagnosis: The adult shell is left-handed and of fusiform shape with a high spire and a body whorl of about half shell height. The whorls are flattened and separated by shallow sutures. The aperture is narrow and elongated. The anterior portion of the inner lip is detached and separated from the body whorl to form a narrow umbilicus at the spindle. The early ontogenetic shell is right-handed and is immersed in the apex at an inclined position. The genotype is *Misurinella sinistrorsa* (KITTL, 1894) from Misurina, St. Cassian Formation.

Derivatio nominis: Named for Misurina were Rinaldo ZARDINI found the small shells of some individuals of this species in the St. Cassian shallow water slump deposits.

1894, *Euchrysalis sinistrorsa* KITTL, *Gastropoden von St. Cassian*: 205, Pl. 6, Fig. 30, 31.

1985, *Euchrysalis sinistrorsa* ZARDINI, *Fossili Cassiani* 1985: 14, Pl. 5, Fig. 3, 4.

Description: The shell resembles a grain of wheat (KITTL, 1894) in its size and shape and measures about 5 mm in length with 6-7 whorls. The last whorl is about as high as the spire above. Shell surface is smooth, and the spindle is hollow. Growth lines are straight and indistinctly seen on the otherwise smooth whorl surface. The aperture is suboval in shape with a pointed posterior end, a rounded anterior end, and a shallow siphonal depression. The dextral protoconch is smooth, almost 0.2 mm wide and lies inclined on the apex of the sinistral teleoconch. Its umbilicus opens in the apex of the teleoconch, and its axis forms an angle larger than 90 degrees with the axis of the teleoconch. The sinistral protoconch twists in the transition from the larval shell into the dextral juvenile teleoconch.

Material: 3 individuals from Misurina were studied. Material is deposited in NHM, Wien 1994/0047.

Remarks: The genus *Euchrysalis* LAUBE, 1869 is based on *Euchrysalis fusiformis* (MÜNSTER, 1841) from the St. Cassian Formation which has an orthostrophic shell (BANDEL 1993a). Thus, *Euchrysalis* is a member of the Caenogastropoda and not of the Heterostropha, as *Misurinella*. WENZ (1938, p. 367) assumed that *Euchrysalis* represents a member of the Subulitoidea, which according to KOLLMANN & YOCHELSON (1976) included gastropods of Paleozoic age that have unornamented fusiform to globose shell with a nonsinuate outer lip. Several Carboniferous species of subulitid gastropods were analysed and demonstrated protoconchs of caenogastropod type (BANDEL & NÜTZEL, in prep.). Thus *Misurinella* can not be related to these.

The smooth sinistral shell connected to an elongate aperture resembles that of the modern *Blauneria*. This amphibious member of the archaeopulmonate family Ellobiidae lives above the high water mark in intertidal areas along modern tropical shores. The extreme rarity of specimen of *Misurinella sinistrorsa* could indicate a similar living environment as that of modern *Blauneria*. A relationship to modern *Blauneria*, which has the same sinistral adult shell and dextral early ontogenetic shell, can not be proved and convergence is a reasonable assumption. The possibility of this species representing merely a sinistral variety of *Coelochrysalis fusiformis* as considered by KITTL (1894) can be excluded. In such a case the protoconch should also be sinistral, as is the case among the triphorids and other sinistral Caenogastropoda.

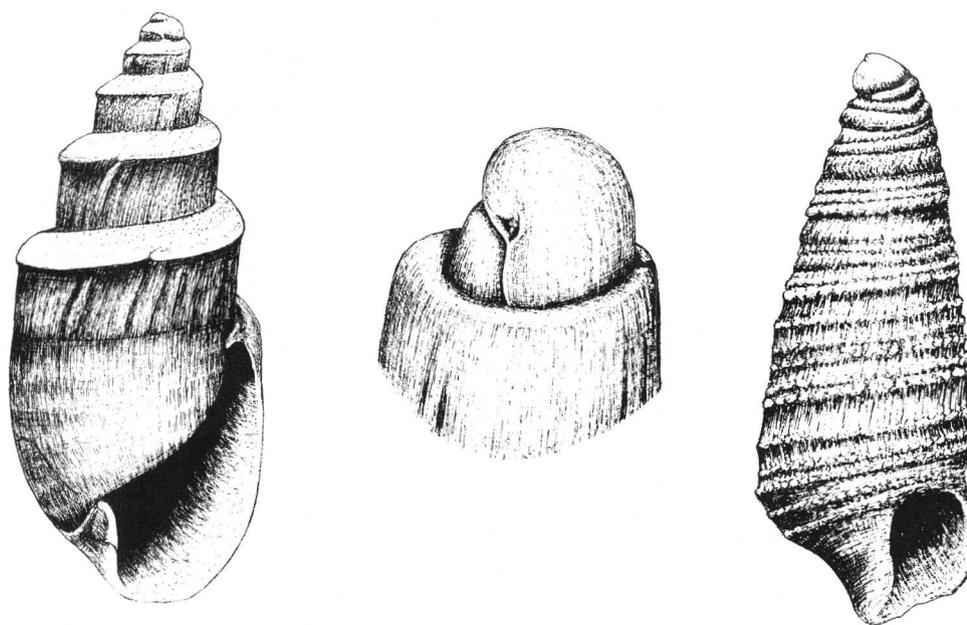


Figure 1 a, b, c

Cylindrobullina scalaris with the fully grown shell (a) and apex with protoconch (b) and fully grown *Dolomitella semiornata* (c)

3 Classification and evolutionary history

The origin of the subclass Heterostropha FISCHER, 1885 can probably be traced back to the Ordovician. First clearly recognized members of the group with preserved sinistral protoconch come from Mid-Devonian strata of Sötenich in the Eifel mountains. Here "*Loxonema*" *moniliforme* GOLDFUSS has a sinistral protoconch that lies flatly on the slender teleoconch (Pl.4., Fig. 9). In the Carboniferous the Streptacididae KNIGHT, 1931 have small, very slender, multiwhorled shells that have a different axis of coiling in the sinistral protoconch than present in the dextral teleoconch (Pl.4, Fig. 8). Carboniferous and Permian species of the Streptacididae are usually minute (KNIGHT, 1931) and differ from the contemporaneous Donaldinidae BANDEL, 1994 by the absence of a prominent spiral ornament. Donaldinidae commonly have the upper whorl flank flattened and protoconch position is flat on the apex (YOO 1988, 1989). This is the case in the figured species of *Donaldina* from the Pennsylvanian of Texas (Pl. 4, Fig. 10, 11) and among Triassic and modern representatives of the Donaldinidae (BANDEL 1991c, Pl.8, Fig.5, 1992c; Fig.28, 1994b). Some of the members of this family produce wider shells and reach larger size as found among the Streptacididae (ERWIN, 1988).

Still within the Carboniferous and among minute slender shells, species make their appearance that have a smooth shell surface, a sinuous outline of the outer lip and elongated aperture. They can probably be included into the family Ebalidae BANDEL, 1994. Triassic and Jurassic representatives of this family (SCHRÖDER 1993, BANDEL 1994b) connect with the extant genotype. A special branch with ebalid teleoconch morphology and protoconch with ornament of strong axial ribs characterized the Cassianebalidae BANDEL, 1994.

KOLLMANN & YOCHELSON (1976) interpreted representatives of the Lower Carboniferous *Acteonina* and *Girtyspira* KNIGHT, 1936 as the oldest known representative of the Opisthobranchia. Similar species of *Girtyspira* from Upper Carboniferous of the USA that have been discussed by KNIGHT (1936, 1941) have since been analysed by us (BANDEL & NÜTZEL in prep.). They bear orthostrophic protoconchs of the caenogastropod type. Also Carboniferous gastropods named *Acteonina* from the Visé and Tournai of Belgium have not provided a heterostrophic shell and probably represent convergent shells to Triassic *Cylindrobullina* but of subulitid and thus caenogastropod relation.

Members of the superorder Euthyneura SPENGLER, 1881 and the order Opisthobranchia MILNE EDWARDS, 1848 can not be clearly differentiated among those Paleozoic Heterostropha that are known up to now. Those with still extant species as in Ebalidae and Donaldinidae have to be placed with the order Allogastropoda HASZPRUNAR, 1985. Opisthobranchia of the suborder Cephalaspidea FISCHER, 1883 (Architectibranchia HASZPRUNAR, 1985) are recognizable in the representatives of the superfamily Cylindrobullinoidea WENZ, 1947, family Cylindrobullinidae WENZ, 1947. Here genera like *Cylindrobullina* AMMON, 1878, *Consobrinella* HAAS, 1953 and *Acteonina* from the Upper Triassic represent species with a shell that resembles modern forms as well as those of fossil groups. The shells of modern *Acteocina* Gray, 1847 (Pl. 4, Fig.6,7) and *Retusa* BROWN, 1825 look very much like those of *Acteonina* and *Cylindrobullina* from Triassic and Jurassic times (SCHRÖDER, 1993). *Retusa* closely resembles the Triassic *Conactaeon peruviana* HAAS, 1953. But there is also a close resemblance with Jurassic and Cretaceous *Ceritellopsis* FISCHER, 1961 which was connected to the archaeopulmonates by BANDEL (1991a).

The family Actaeonellidae ZILCH, 1959 appeared with *Trochactaeon* MEEK, 1863 in the Barremian and gave rise to the convolute *Actaeonella* ORBIGNY, 1843 in the Aptian (SOHL & KOLLMANN 1985), and both genera disappeared by the end of the Cretaceous. *Trochactaeon* is convergent with some ellobiids like *Melampus* MONTFORT, 1810 and there may be confusions in Upper Cretaceous fossil communities where shallow sea meets coastal swamp environment (STOLICZKA 1865, HARBECK 1993, MUSTAFA & BANDEL 1992). *Ptychostylus* SANDBERGER, 1870 may represent an early Purbeckian precursor to *Trochactaeon* (BANDEL 1991a). KOLLMANN (1967) related the Middle Jurassic *Cylindrites* SOWERBY, 1824 with *Trochactaeon* which may also connect to *Cylindrobullina*- like precursors.

Members of the superfamily Actaeonoidea ORBIGNY, 1842 with family Actaeonidae ORBIGNY, 1842 and its name giving genus *Actaeon* MONTFORT, 1810 can be traced from the Middle Jurassic (SCHRÖDER 1993) in a continuous line to the modern species. The Upper Cretaceous of the Gulf coast of the United States has a characteristic form with *Eactaeon* STEPHENSON, 1955 (Pl. 4, Fig. 4, 12). *Sulcoactaeon* COSSMANN, 1891 (SOHL 1964) may represent a continuation of the *Acteonina*-*Cylindrobullina* group into the Jurassic. *Bullopsis* CONRAD, 1858 from the Upper Cretaceous is somewhat intermediate to members of the Actaeonellidae. The family Ringiculidae FISCHER, 1883 with genus *Ringicula* DESHAYES, 1838 has been traced to the Lower Cretaceous (Valangien of Poland) by SCHRÖDER (1993) and has since been common and diversified into several genera like *Ringinella* ORBIGNY, 1843, *Avellana* ORBIGNY, 1843, *Biplica* POPENOE, 1957,

Eriptycha MEEK, 1867, present in the Apt / Alb of Japan (KASE 1984) and *Olygoptycha* MEEK, 1876 by the end of the Cretaceous.

The family Zardinellidae is based on the genus *Zardinella* from the St. Cassian Formation. The combination in *Zardinella* of an ampezzanildid larval shell (BANDEL 1994a) and an ovoid teleoconch with incised spiral gooves having a pit-row pattern, as is found among many cephalaspidean and archaeopulmonate species, is unique. Among Upper Cretaceous cephalaspideans such as *Nonacteonina* STEPHENSON, 1941 and *Troostella* WADE, 1926 a teleoconch with similar ornamental pattern but more ovate shell shape is found, but the protoconch also twists into the dextral coil long before begin of the teleoconch. But here the protoconch is smooth while in *Zardinella* the larval shell is of the axially ribbed ampezzanildid type. SCHRÖDER (1993) demonstrated that true *Actaeon*, which has a mathildid larval shell, is present in the Jurassic. From such early Acteonidae the Nonacteoninidae as well as the Ringiculidae developed, both with tofanellid type (BANDEL 1994a) of protoconch morphology.

The family Nonacteoninidae n. fam. contains elongated to subovated shells with spire of a little more than one third total shell length and sutures in narrow channels. The sculpture consists of narrow incised spiral grooves or rows of pits crossed by simple growth lines. The aperture is narrow posteriorly and rounded anteriorly and has a smooth columellar lip (SOHL 1964). The protoconch consists of three smooth whorls with sinistral coiling very indistinctly present only in the embryonic whorl. Here the earliest part of the shell with a hammered ornament is covered by the first whorl of the larval shell. The larval shell is evenly and dextrally coiled, and its aperture is simple. Begin of the teleoconch sculpture is abrupt with spiral rows of pits appearing. The family is based on the genus *Nonacteonina* which has the genotype *N. graphoides* STEPHENSON, 1941 from the Upper Cretaceous of Texas (Navarro Group). Nonacteonidae differ from Acteonidae by the shape of the protoconch (Pl. 4, Fig. 2, 5) that is sinistrally coiled in the later (Pl. 4, Fig. 3, 4, 12) while it is almost completely dextral in the former (Pl. 4, Fig. 2). From the Ringiculidae they are distinguished by the simple aperture, while the protoconch of both families is similar.

Members of the superfamily Diaphanoidea ODHNER, 1922 have not been confirmed from Mesozoic rocks. It would probably be quite difficult to recognize them if they are found as fossils because of the convergence among the bullomorph species with short spire and thin shell. Retusidae THIELE, 1926 with *Goniocylichna* WADE, 1926 from the Upper Cretaceous of Mississippi are very similar to modern members of that family with an operculum. The presence of an operculum indicates that the Retusidae have retained some old characters and can be considered to represent an old group (RUDMAN, 1971, own data). But also other groups of the opisthobranchs, like the socoglossans and the anaspideans have genera that resemble *Cylindrobullina* in shell shape, like *Cylindrobulla* FISCHER, 1857 and *Akera* O.F. MÜLLER, 1776. The suborder Tectibranchia hold Bullomorpha, Sacoglossa, Aplysiomorpha, Thecosomata and Gymnosomata, most of which differentiate after begin of the Tertiary. *Ellipsoscapa* STEPHENSON, 1941 from the US Gulf Coast Upper Cretaceous was placed in the Scaphandridae by SOHL (1964) but it could also be placed within several other groups of the opisthobranchs. According to WENZ (1938) Atyinae and Philinidae are also present from the Lower Cretaceous onward.

Family Dolomitellidae n. fam. with Triassic *Dolomitella* may be related to early representatives of the Tubiferidae. Dolomitellids have much in common with members of the mathildids as well, so that their place in the system of the Heterostropha has to remain in question.

The Jurassic family Tubiferidae COSSMANN, 1895 with genera like *Ceritella* MORRIS & LYCETT, 1850 have been considered as members of the Nerineoidea ZITTEL, 1873, (WENZ 1938; VAUGHAN 1988; PONDER & WARÉN 1988). Members of the genus *Ceritella* with conical shape, rounded base, and a variety of sculptural patterns are quite common in the European Jurassic (HUCKRIEDE 1967). However, apart from the heterostrophic protoconch and their disappearance with the Cretaceous, the egg-shaped Tubiferidae have very little in common with the slender acicular Nerineidae and Nerinellidae. HUCKRIEDE (1967) included also species in the genus *Ceritella* that looks like an *Acteonina* with radial ribs and folds. BANDEL (1991a) extracted this subgenus *Ceritelopsis* FISCHER, 1961 from *Ceritella* and placed it among the Cylindrobullinidae. *Zikkuratia* SOHL, 1963 which was considered to represent a member of the Retusidae from the Upper Cretaceous (SOHL 1964) may form a link between the Tubiferidae and the Bullomorpha.

The allogastropodan branch Pyramidelloidea GRAY, 1840 as characteristic parasitic gastropods (FRETTER & GRAHAM, 1986), appear quite late in the geological record. SCHRÖDER (1993) interpreted *Kleinella* ADAMS, 1860 from the Lower and Middle Jurassic of Northern Germany as member of the Pyramidellidae, but probably it belongs to the Donaldinidae. True pyramidellids are found in the Campanian and Maastrichtian Gulf Coast fauna of the USA with the genera *Creonella* WADE, 1917 and *Lacrimiformia* SOHL, 1960. The neritiform Amathinidae PONDER, 1987 are considered to represent close relatives of the

Pyramidellidae. They appear with *Damesia* HOLZAPFEL, 1888 an Upper Cretaceous of Europe and North America (DOCKERY, 1993).

Mathildidae DALL, 1889 have changed little since Triassic times but are unknown from rocks older than Ladinian age. *Mathilda* SEMPER, 1865, *Promathilda* ANDREAE, 1887 *Tirolthilda* BANDEL, 1994, *Schroederilda* BANDEL, 1994 and *Turrithilda* SCHRÖDER, 1993 are closely related genera occurring in the Upper Triassic St. Cassian Formation (BANDEL 1994a) and the same time in Peru (HAAS, 1953) as well as in the Jurassic of Northern Germany (SCHRÖDER 1993). In the Lower Cretaceous of Poland representatives of *Gymnothilda* SCHRÖDER, 1993 and *Gegania* JEFFREYS, 1884 make their first appearance (SCHRÖDER 1993).

Members of the family Nerineidae ZITTEL, 1873 may have developed from similar species as present in the Anoptychiidae BANDEL, 1994 from the St Cassian Formation. Anoptychiidae with genera *Anoptychia* KOKEN, 1892, *Turristylus* BLASCHKE, 1905 and *Camponella* BANDEL, 1994 have a mathildid protoconch, highly ornamented juvenile shell of mathildid type and later a smooth and slender adult shell. In respect to the outer shell morphology they resemble the Nerineidae which together with the Itieriidae COSSMANN, 1896 have plicae on the inner side of their whorls. *Nerinea* DESHAYES, 1827 appeared in the Lower Jurassic and both families disappear at the end of the Cretaceous.

Tofanellidae BANDEL, 1994 are based on the genus *Tofanella* BANDEL, 1994 and holds the genera *Cristalloella* BANDEL, 1994 and *Camponaxis* BANDEL, 1994. Similar species are united in the genus *Chevallieria* COSSMANN from the Jurassic (SCHRÖDER, 1993) as well as later times. In the Lower Cretaceous of Poland *Wonwalica* SCHRÖDER, 1993 represents the group. Probably some members of this group still live in the Indopacific Ocean (BANDEL 1991c). The family Trachoeocidae BANDEL, 1994 contains the genera *Trachoeocus* KITTL, 1894, and *Vallandroella* BANDEL, 1994, the family Ampezzanildidae BANDEL, 1994 has genera like *Ampezzanilda* BANDEL, 1994, *Cassianilda* BANDEL, 1994, *Stuorilda* BANDEL, 1994. These three families are connected to each other by the morphology of their protoconch. Here the sinistral larval shell changes into dextral coiling before metamorphosis, and an apertural projection may be present.

Members of the family Rissoellidae GRAY, 1850 anatomically represent Allogastropoda intermediating between Architectonicoidea and Pyramidelloidea (PONDER 1983, HASZPRUNAR 1988) but their embryonic shells show no trace of sinistral coiling. They would thus be very difficult to detect in the fossil fauna and are not known from Mesozoic strata.

Valvatidae GRAY, 1840 live in fresh water and still have extant marine relatives united in the family Cornirostridae PONDER, 1990. The later is based on *Cornirostra* PONDER, 1990 from the shallow sea of Australia which is very similar to the genera *Carboninia* BANDEL, 1994 and *Bandellina* SCHRÖDER, 1993 of the St. Cassian Formation and the Lower Cretaceous of Poland. Provalvatidae BANDEL, 1991 represent transitional species that lived in brackish water during Upper Jurassic times. *Provalvata* BANDEL, 1991 from the Purbeck is provided with a sinistral protoconch, while in the Valvatidae based on the genus *Valvata* O.F. MÜLLER, 1774 the protoconch is planispiral. This is also the case in the genus *Ariomphalus* BANDEL & RIEDEL, 1994 from the Campanian fresh water deposits of Ajka in Hungary (RIEDEL 1993, BANDEL & RIEDEL, 1994). The members of the family Orbitestellidae IREDALE, 1917, according to PONDER (1990), are connected with Cornirostridae. Like these and the Valvatidae they have a characteristic pallial tentacle. This unusual feature is utilized to channel exhalent water and faeces from the pallial cavity away from the inhalent stream. *Orbitestella* IREDALE, 1927 can be traced to the Paleocene of Denmark (own data). The Glacidorbidae PONDER, 1986 represent planispiral, operculate fresh water gastropod from Australia that could be interpreted to be related to the Provalvatidae from the Purbeckian of Europe. Anatomically they intermediate between Rissoellidae and Pyramidellidae (Pers. communication HASZPRUNAR 1991).

BIELER (1988) derived Mathildidae and Architectonicoidea from a common ancestral group living in the Cretaceous. In the Upper Triassic Mathildoidea and Architectonicoidea, in contrast, are present without any transitional forms between them (BANDEL 1988b, 1991e, 1994c). This is evidence for a much longer independent history of both groups quite separate from each other. Representatives of the families Architectonicoidea, Stuoraxidae, Cassianaxidae, Amphitomariidae, Omalogyridae and Glacidorbidae may be interrelated and are united by a low to planispirally coiled shell.

Among the Triassic relatives to the family Architectonicoidea GRAY, 1850 the genera *Stuoraxis* BANDEL, 1994 and *Ampezzogyra* BANDEL, 1994 form the family Stuoraxidae BANDEL, 1994. *Alexogyra* BANDEL, 1994 is interpreted to be related to modern species of the Hyalogyrinidae WARÉN & BOUCHET, 1993 which live in deep water and have a radula with a large number of teeth in each row (WARÉN & BOUCHET 1993).

This contrasts to *Xylodiscula* MARSHALL, 1988 with similar shell that lives on sunken driftwood and has only few teeth in each row of the radula. The shell resembles that of the Hyalogyrinidae and was placed in the family Xylodisculidae WARÈN, 1992 by WARÈN (1992).

Rinaldoconchus BANDEL, 1988 is similar to the modern *Heliacus* (BANDEL 1988a). Genera of the architectonicids like the flatly coiled *Pseudomalaxis* FISCHER, 1850 and the trochiform *Lemniscolittorina* SOHL, 1960 are known from the Campanian and Maastrichtian of Tennessee and Mississippi (DOCKERY 1993). The family Cassianaxidae BANDEL, 1994 with the genus *Cassianaxis* BANDEL, 1994 is close to the modern genus *Episcynia* MÖRCH, 1975. The Amphitomariidae BANDEL, 1994 with *Amphitomaria* continue with Cretaceous and Tertiary members of *Neamphitomaria* BANDEL, 1988 which may connect with the Family Omalogyridae SARS, 1878. A possible relation may exist in the genus *Anomalorbis* PAUL, 1991 with the type species *Planorbis hemistoma* SOWERBY, 1816 from the Eocene of England with very similar and still undescribed Upper Cretaceous species from the Gosau (Northern Alps) and the Isona Formation (Southern Pyrenees) (HARBECK 1989, BANDEL 1988a, PAUL, 1991) and modern species from the shallow sea near Cebu (BANDEL 1991c, Pl.7, Fig.2).

Misurinellidae BANDEL, 1994 with *Misurinella* BANDEL, 1994 is similar to modern *Blauneria* SHUTTLEWORTH, 1854 and differs only by the absence of a columellar fold. If *Misurinella* is not a relative of *Blauneria* and thus to the Ellobiidae H. & A. ADAMS, 1855, it is certainly a very nice example of close convergence of shell form. The Ellobiidae represent the modern core group of the Archaeopulmonata MORTON, 1955 (=Mesommatophora HUBENDICK, 1947), and are the least specialized of the three suborders of the order Pulmonata CUVIER, 1817 within the Euthyneura. The Archaeopulmonata have marine species, while the Basommatophora KEFERSTEIN, 1864 live in fresh water and the Stylommatophora SCHMITT, 1855 live ashore.

Archaeopulmonates with the Ellobiidae are usually found in the intertidal mud flats, rubble zones and coastal forests and swamps. They can be traced to the Upper Jurassic (BANDEL 1991a). *Melampoides* YEN, 1951 from the Oxfordium of Portugal and *Juramarinula* BANDEL, 1991 and *Proauriculastra* BANDEL, 1991 from the Purbeckian of central and western Europe also lived in this environment. The Upper Cretaceous species of *Auriculinea* TAUSCH, 1886 lived at the far end of the estuarine zone in the coastal swamps at Ajka in Hungary (BANDEL & RIEDEL 1994).

A similar environment in the Eastern Pacific area and most abundantly in Australian and New Zealand is occupied by the Amphibolidae GRAY, 1840, of which the genus *Salinator* HEDLEY, 1900 had a representative in Europe (Dudar, Hungary) during the Eocene (HARBECK, 1993). The limpet-like Siphonariidae GRAY, 1840 and Trimusculidae ZILCH, 1959 may be represented by a number of genera from the Jurassic and Cretaceous as there are *Rhytidopilus* COSSMANN, 1895, *Ptychogyra* HABORT, 1905, *Brunonia* G. MÜLLER, 1898, *Anisomyon* MEEK & HAYDEN, 1860, *Pseudohercynella* KAUNHOWEN, 1898 along with the modern *Siphonaria* SOWERBY, 1823. While some of these probably belong here, others may not represent gastropods at all, but may even represent the floats of siphonophoran hydroids. These limpets settle in the upper tidal regime of rocky shores and their characteristic sinistral protoconch has been recognized from the Campanian of Mississippi by (DOCKERY, 1993).

Two groups of the archaeopulmonated have entered the fresh water with the Chiliniidae H. A. ADAMS, 1855 in wave or current swept hard substrated in southern South America and on the Falkland Islands and their limpet-like relatives the Latiidae HANNIBAL, 1912 in river rapids of New Zealand. The Carychiidae JEFFREYS, 1828 may even be present on land since Upper Carboniferous time with the genera *Anthracopupa* WHITFIELD, 1881, *Maturipupa* PILSBRY, 1926 and *Dendropupa* OWEN, 1861. According to SOLEM (1981) they represent 3 of the 7 modern orders of the Stylommatophora. Modern *Carychium* O.F. MÜLLER, 1774 is very similar in shell shape. A relation with the Carboniferous species is also documented in the special ontogeny of *Carychium* that lives in wet litter and moss in springs and forrests. Here the ellobiid ontogeny has been modified with sinistral protoconch (DOLL & SANDER 1985), reduced velum and lost operculum, but is clearly different from that of the Basommatophora (BANDEL, 1982, own observations). The ancestral archaeopulmonates that gave rise to the Carboniferous pulmonates should thus have resembled modern ellobiids in regard to shell and environmental requirements. These again are not unlike the cylindrobullinids of the Triassic, or resemble in some way the ebalid forms of the marine streptacidoid allogastropods of the Devonian and Early Carboniferous.

Basommatophora KEFERSTEIN, 1864 with limpet-like forms as found among the modern ancyliids are present with the Upper Cretaceous *Ancylina* BANDEL & RIEDEL, 1994 in the fresh water deposits of Ajka in Hungary (BANDEL & RIEDEL 1994). The lymnaid group appears even earlier and is present since Upper Jurassic and sinistral forms like *Prophysa* BANDEL, 1991 occurs in Purbeckian deposits of Europe. Planorbis shells as in

Gyraulus CHARPENTIER, 1837 are recognized from the Lower Jurassic onward and are very evident in the Wealden facies in Europe (BANDEL, 1991a). Here also a potential precursor of *Planorbarius* FRORIEP, 1806 lived with *Proplanorbarius* BANDEL, 1991.

Stylommatophora SCHMITT, 1855 are very rare in Mesozoic rocks but become more common during the Cretaceous. In the Purbeck of Europe *Cherusiola* HUCKRIEDE, 1967 may represent a pulmonate land snail. Streptaxidae appeared in the Late Cretaceous Gosau deposits in the northern Alps with *Eoplicadomus* HRUBESCH, 1965 and *Gosavidiscus* HRUBESCH, 1965. The Camaenidae appeared in the Upper Cretaceous of Utah with *Kanabohelix* PILSBRY, 1927 (SOLEM 1978). *Protocorilla* HRUBESCH, 1965 of the Corillidae lived on the islands of the northern Tethys Ocean at the Gosau and in Hungary (Ajka) during Middle Upper Cretaceous time. Oreohelicidae according to SOLEM (1978) lived in North America since Early Cretaceous. The Clausiliidae are still dextral in the Gosau, represented by *Dextrospira* HRUBESCH, 1965 and similar to *Proalbinaria* MATHERON from France. The Andromidae are known from the Lower Cretaceous of North America and in the Upper Cretaceous of Europe are common with species of *Lychmus* MATHERON, 1832. Thus the assumption of WENZ & ZILCH (1960) and SOLEM & YOCHELSON (1979) that stylommatophoran land snails have a Paleozoic origin still needs the fossil record to bridge the long gap from Late Carboniferous *Anthracopupa* and *Dendropupa* to Early Cretaceous fossils.

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Plate 1

- Figure 1: The apex of *Actaeonina scalaris* illustrated in fig. 5 with the sinistral protoconch (about 0.25 mm wide) and its open umbilicus pointing to the side.
- Figure 2: The base of the 0.25 mm wide protoconch of *Actaeonina scalaris* on its teleoconch shows the open umbilicus.
- Figure 3: *Actaeonina scalaris* with 2 mm high juvenile shell.
- Figure 4: *Actaeonina scalaris* with 5 mm high shell from the collection of the NHM Wien, 1866/II299.
- Figure 5: *Actaeonina scalaris* with almost 5 mm high shell from the collection of the NHM Wien, 1866/II299.
- Figure 6: *Actaeonina scalaris* with 6 mm high shell.
- Figure 7: The juvenile shell of *Actaeonina scalaris* is about 1.2 mm high.
- Figure 8: *Cylindrobullina pralongiana* with about 2 mm high shell.
- Figure 9: More than 2 mm high shell of *Cylindrobullina pralongiana*.
- Figure 10: The shell of *Actaeonina stuorense* is 1.3 mm high.
- Figure 11: The shell of *Actaeonina stuorense* is almost 2 mm high.
- Figure 12: Apical view of the shell of *Actaeonina scalaris* illustrated in fig. 7 with the sinistral protoconch forming a right angle with the dextral teleoconch.
- Figure 13: Apical view of *Cylindrobullina pralongiana* with almost 2 mm high shell and protoconch forming right angle with teleoconch.
- Figure 14: Umbilical side of the protoconch of *Cylindrobullina pralongiana* of the shell shown in fig.9.

Plate 2

- Figure 1: The apex of *Cylindrobullina pralongiana* with the 2.5 whorls of the almost 0.5 mm large protoconch.
- Figure 2: The protoconch of *Cylindrobullina pralongiana* illustrated in pl. 1, fig.8 consists of 2.5 whorls and more than 0.3 mm width.
- Figure 3: Umbilical side of the protoconch of *Actaeonina stuorense* illustrated in pl. 1, fig. 10.
- Figure 4: Juvenile shell (0.8 mm high) of *Actaeonina lancedellia* with protoconch at right angle on the top of the teleoconch.
- Figure 5: The fully grown shell of *Actaeonina stuorense* is almost 3 mm high.
- Figure 6: Juvenile shell of *Actaeonina lancedellia* with the sinistral protoconch in the apex and about 1 mm height.
- Figure 7: Lateral view of a juvenile *Actaeonina lancedellia* with about 0.5 mm high shell.
- Figure 8: The umbilical side of the protoconch of *Actaeonina lancedellia* of the shell illustrated in fig. 7.
- Figure 9: Apical view of *Actaeonina lancedellia* with protoconch of 1.6 whorls and 0.2 mm width and 0.19 mm height.
- Figure 10: The protoconch of *Actaeonina stuorense* of the shell illustrated in pl. 1, fig. 10 seen from the apical side.
- Figure 11: The apex of *Actaeonina stuorense* illustrated in pl. 1, fig. 10 consists of almost two whorls and is less than 0.2 mm wide.
- Figure 12: Umbilical view of *Actaeonina lancedellia* of the shell shown in fig. 13 with the open umbilicus.
- Figure 13: Juvenile shell of *Actaeonina lancedellia* with sinistral protoconch and the first whorl of the teleoconch is 0.6 mm high.

Plate 3

- Figure 1: Shell of *Dolomitella semiornata* with about 3.5 mm length.
Figure 2: *Dolomitella semiornata* with 3.5 mm long shell.
Figure 3: The juvenil shell of *Dolomitella semiornata* is 1.5 mm high with sinistral protoconch deviating from the teleoconch.
Figure 4: The juvenile shell of *Zardinella cingulata* is 1.2 mm high.
Figure 5: *Misurinella sinistrorsa* with 5.5 mm long shell.
Figure 6: Apex of *Dolomitella semiornata* with 0.25 mm high protoconch that has folds where it twist into dextral coiling.
Figure 7: The apex of *Dolomitella semiornata* illustrated in fig. 2 is of the mathildid type with 0.35 mm wide protoconch.
Figure 8: The apex of *Misurinella sinistrorsa* illustrated in fig. 5 with the dextral protoconch twisting into the sinistral teleoconch.
Figure 9: The 5 mm long shell of *Misurinella sinistrorsa* seen from the backside.
Figure 10: Apical view of *Zardinella cingulata* illustrated in fig. 11.
Figure 11: *Zardinella cingulata* with 1.6 mm high juvenile shell.
Figure 12: A juvenile shell of *Zardinella cingulata* is 3 mm high.
Figure 13: The apex of *Zardinella cingulata* shown in fig. 12 demonstrates the change of ornament in the transition from the about 0.5 mm wide protoconch to the teleoconch.
Figure 14: The apex of *Zardinella cingulata* has a sinistral embryonic whorl and axially ornamented larval shell of about 0.5 mm width.

Plate 4

- Figure 1: The aperture of *Misurinella sinistrorsa* illustrated in pl. 3, fig. 5 in detail.
Figure 2: The protoconch (0.7 mm wide) of *Nonacteonina* of the shell illustrated in fig.4 has only a very indistinctly sinistral embryonic part and about three dextrally coiled whorls.
Figure 3: The protoconch (0.22 mm wide) of *Tornatellaea cretacea* Wade from the Ripley Formation of Mississippi closely resembles that of Donaldinidae and some other Triassic heterostropha with sinistral protoconch having the same axis of coiling as dextral teleoconch.
Figure 4: The juvenile shell (1.8 mm high) of *Nonacteonina* from the Upper Cretaceous Ripley Formation of Tennessee has a smooth protoconch and spirally ornamented teleoconch.
Figure 5: The protoconch of the about 2 mm long juvenile shell of *Eoacteon* from the Upper Cretaceous Ripley Formation of Mississippi in shape and dimensions resembles that of *Cylindrobullina*.
Figure 6: The young cephalaspidean shell (1.2 mm high) from Lizard Island (Great Barrier reef) shows the same type of protoconch as is developed in the Triassic *Cylindrobullinidae*.
Figure 7: Cephalaspidean shell (2.5 mm high) of the *Acteocina* type from Cebu, Philippines resembles *Cylindrobullina* in its shape.
Figure 8: The about 1 mm long and slender shell of *Streptacis* from the Pennsylvanian of Texas has a strongly deviating sinistral protoconch.
Figure 9: *Loxonema moniliforme* from the Mid Devonian of the Eifel Mountain is the oldest known heterostrophic species of the Strepacidoidea. The shell is 4 mm long.
Figure 10: The protoconch of *Loxonema moniliforme* (detail to fig. 9) is sinistral, measures about 0.2 mm in diameter, and resembles that of *Donaldina* (fig. 11).
Figure 11: The apex of *Donaldina* from the Pennsylvanian of Texas is formed by a sinistral protoconch (about 0.2 mm width) with the same axis as the dextral teleoconch.
Figure 12: The juvenile shell (1.2 mm high) of *Zikkuratia* from the Ripley Formation of Mississippi closely resembles Triassic *Cylindrobullina*.

Plate 1

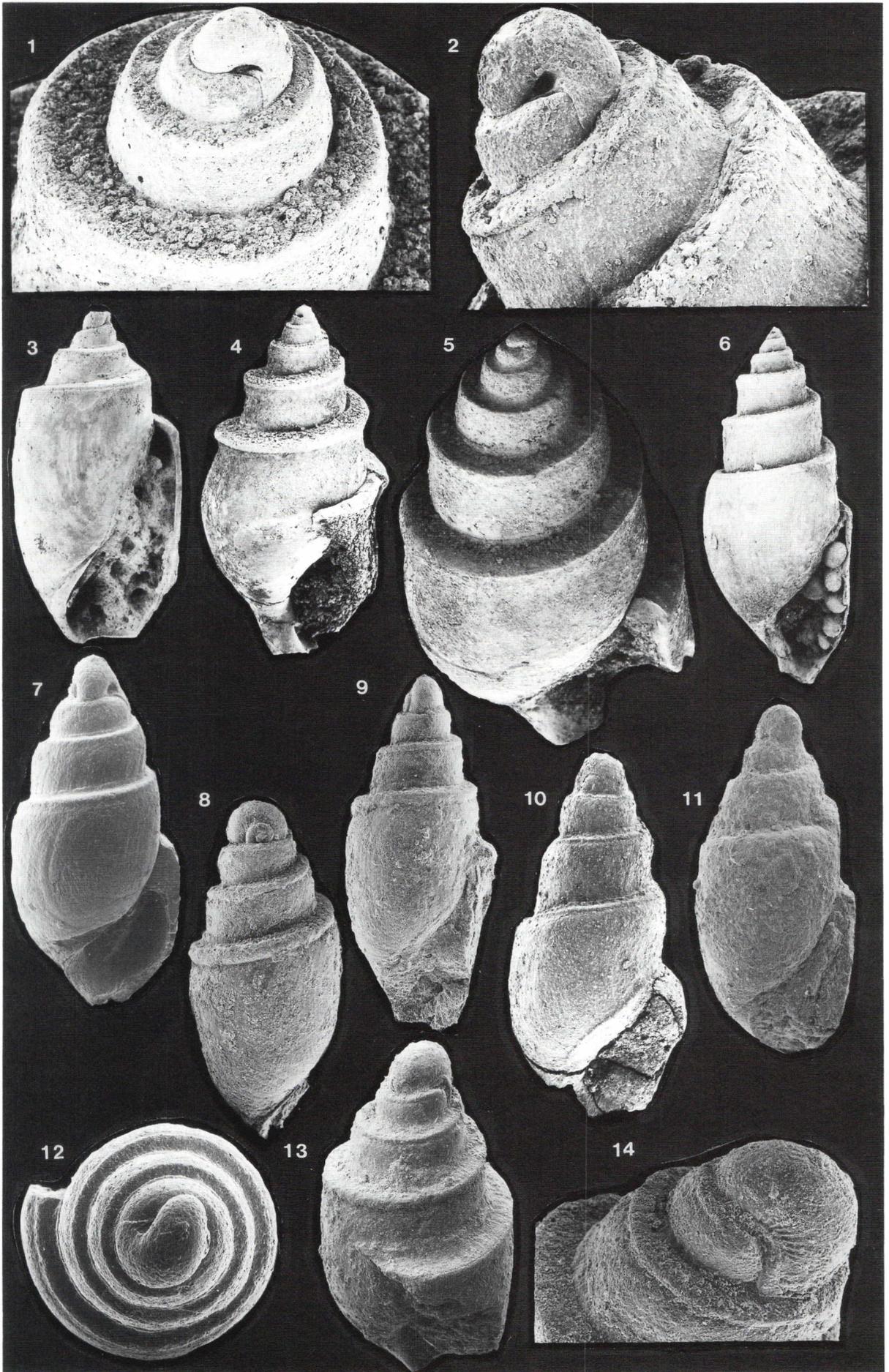


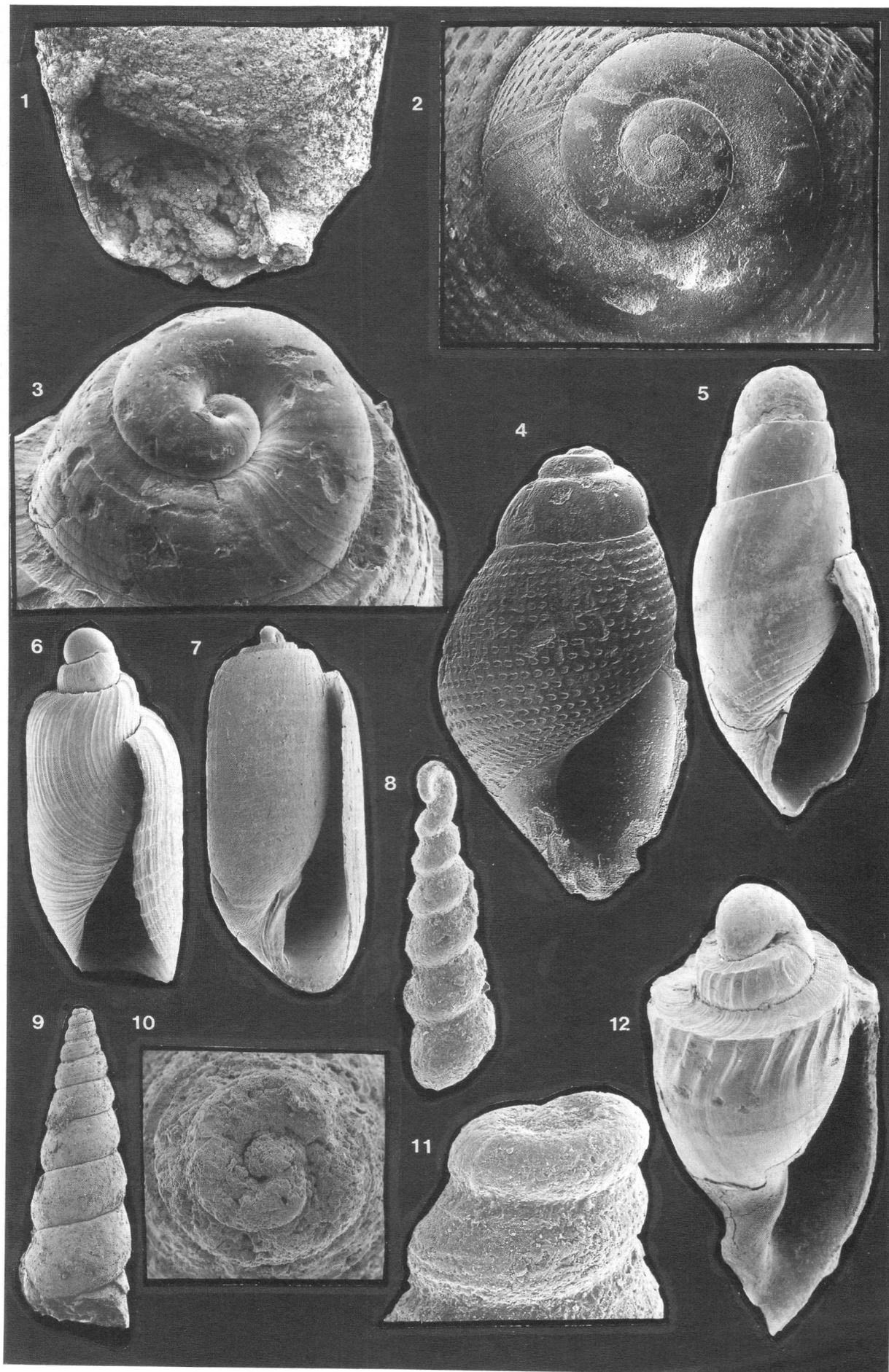
Plate 2



Plate 3



Plate 4



**Sächsisches Lehr- und Besucherbergwerk
"Himmelfahrt Fundgrube"
der
TU Bergakademie Freiberg**

- *** Die Geschichte Sachsens war vom 12. bis zum Ende des 19. Jahrhunderts eng mit dem Silberbergbau verbunden. Insbesondere im 16. Jahrhundert war der deutsche Bergbau technologisch weltweit führend.
- *** Sachzeugen dieser Epochen sind im Freiburger Raum sowohl landschaftlich als auch durch zahlreiche Bergwerke erhalten.
- *** Die Technische Universität Bergakademie Freiberg ist die älteste montanwissenschaftliche Einrichtung ihrer Art und verfügt als einzige Hochschule über ein intaktes Lehrbergwerk.
- *** Im Lehrbergwerk werden geologische, bergbauliche, markscheiderische, geotechnische und andere Praktika für Studenten durchgeführt.
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ganzjährig, werktags: 9.30 Uhr
Übertageführungen Schacht "Alte Elisabeth"
Mai-September, werktags: 13.00 Uhr