Paläont. Z.	70	3/4	325–365	18 Abb.	Stuttgart, November 1996

Some heterostrophic gastropods from Triassic St. Cassian Formation with a discussion on the classification of the Allogastropoda

KLAUS BANDEL, Hamburg*

With 18 figures

Kurzfassung: Fünfzehn Schneckenarten der Unterklasse Heterostropha werden beschrieben, hiervon 12 neu. Sie werden in ein System der Heterostropha gestellt, welches in weiten Bereichen neuartig ist. Einige moderne Gruppen lassen sich mit den Streptacidoidea des Paläozoikums in Verbindung bringen. Hier leben Vertreter der Donaldinidae noch heute fort, deren vier triassische Arten in die Gattungen *Donaldina* und *Neodonaldina* eingegliedert werden. Der Protoconch scheidet die Cassianebalidae mit den Gattungen *Cassianebala* und *Loxebala* von den Ebaliden, deren Geschichte vom Devon bis in die Jetztzeit verfolgbar wird. Die Gattung *Ebala* wird schon für die Trias belegt. Für die Architectonicoidea ergibt sich eine reiche Aufsplitterung in Familien, deren Nachkommen mehr oder weniger abgewandelt noch heute leben, für die aber kein paläozoischer Bezug genannt werden kann. Den Architectonicidae können zwei Arten der Gattung *Rinaldoconchus* zugeordnet werden. Die Cassianaxidae mit *Cassianaxis* sind mit den modernen Vertretern der Gattung *Episcynia* in Verbindung zu bringen. Für die Stuoraxidae mit *Stuoraxis* und *Ampezzogyra* ist eine Verbindung zu den winzigen Omalogyridae der heutigen Meere zu vermuten. *Alexogyra* wird den modernen Vertretern der Hyalogyrinidae der Tiefsee zugeordnet. *Amphitomaria* wiederum ist in der mesozoischen und tertiären *Neamphitomaria* wiederzuerkennen und lebt wohl heute noch in bisher nicht beschriebenen Nachfahren in der Südsee. Architectonicoidea und Mathildidae sind schon vor längerer Zeit voneinander getrennte Einheiten als man vermutete. Die Valvatoidea sind mit ihren marinen Vertretern – den Cornirostridae – mit *Carboninia* und *Bandellina* vertreten. Die möglichen taxonomischen Zusammenhänge innerhalb der Heterostropha werden diskutiert.

Abstract: Fifteen species of Heterostropha are described, 12 of them for the first time. All are newly interpreted with regard to their taxonomic relation to fossil and living gastropods. The Streptacidoidea with long Paleozoic history are represented in the Late Triassic St. Cassian Formation by several genera that can be differentiated into four families. The Ebalidae are represented by *Ebala,* with smooth protoconch, Cassianebalidae by *Cassianebala* and *Loxebala* with axially ornamented protoconch. The Donaldinidae of St. Cassian are represented by one species of *Donaldina* and two of *Neodonaldina* that stand in the continuation of Paleozoic species of *Donaldina.* Architectonicoidea with shells coiled in a plane and Valvatoidea appear in the St. Cassian fauna without known Paleozoic relation. In the former superfamily the Architectonicidae can be recognized in the genus *Rinaldoconchus* with two species. Cassianaxidae with *Cassianaxis,* Amphitomariidae with *Amphitomaria,* Stuoraxidae with *Stuoraxis* and *Ampezzogyra* have a sinistral protoconch and planispirally coiled dextral teleconchs. They all resemble different modern species that have similarly small shells. Modern Hyalogyrinidae have with *Alexogyra* a new representative from the Triassic. The Valvatoidea are represented with the genera *Carboninia* and *Bandellina* of the Cornirostridae in the Triassic representatives. The relation of described species in the system of the Heterostropha is discussed.

* Address of the author: Prof. Dr. KLAUS BANDEL, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstraße 55, 20146 Hamburg, Germany.

0031–0220/96/0070-0325 $ 10.25

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. Light is also shed on the evolution of distinct lineages within the subclass. Heterostrophic protoconchs can be recognized on quite a number of species that have been found in the marls of the St. Cassian Formation of the Italian Dolomites near Cortina d'Ampezzo (ZARDINI 1978, 1980, 1985; BANDEL 1988a, b, 1991e, 1992, 1994a, b, 1995).

According to BIZZARINI et al. (1986) and URLICHS (1994) the St. Cassian Formation has been deposited in the time interval between the Late Ladinian and Carnian, with the described here mainly from the Cordevol Member of Early Carnian age. The gastropods lived in shallow water along the edge to deeper basins but were preserved in the sediments of the basins. BLENDINGER & BLENDINGER (1989), FÜRSICH & WENDT (1977) and WENDT & FÜRSICH (1980) demonstrated that basins and carbonate platforms existed very close to each other when the area was part of islands and banks at the margin of the tropical Palaeo-Tethys Ocean. Gastropods lived in great numbers within reefs growing on the transition from shallow warm carbonate lagoons to the open ocean. They were preserved in clay-rich, often tuffaceous sediments of the basins, into which they were slumped down more or less steep slopes. Their actual living environment – when preserved in the rock column – provides no further information since it has been transformed into coarse-grained limestone and commonly been dolomitized. During this process all smaller gastropods have disappeared, and larger ones are preserved only as undeterminable internal fills.

The gastropods thus must be collected from basin sediments that have formed alongside with the carbonate platforms, fringing reefs, and low islands. Localities rich in fossils have been described and located in an illustration by ZARDINI (1978). The localities here mentioned are Campo, above Campo di Sopra in Cortina d'Ampezzo in the forest; Dibona or Milieres, exposed slumps below the Rifugia 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. Kassian (S. Cassiano). In Alpe di Specie and Misurina fossils can be extracted from marls with slumps of carbonate debris that came down the slopes into the basin. The localities of Dibona and Stuores contain the fossils in graded beds of sorted pebbly carbonate and coarse sand that was emplaced by turbidity currents having their origin on the carbonate platform. In Campo, due to recent and subrecent sliding, the slump mixed up both types of deposits.

Dr. RINALDO ZARDINI and ROLANDO LANCEDELLI from Cortina d'Ampezzo have provided me with samples from their collecting activities of many years in the area of Cortina d'Ampezzo. The late R. ZARDINI also published on the gastropods of St. Cassian Formation and produced three beautifully illustrated guides, in which he named a large number of new species. His material is exhibited at the Community Museum of Cortina d'Ampezzo. These illustrations are a great improvement over the drawings that have been presented by MÜNSTER (1841), LAUBE (1868) and KITTL (1894). The study of the early whorls of many of the species from St. Cassian Formation provided the opportunity to revise the taxonomy of the species (BANDEL 1988a, b, 1991d, e, 1992a, b, c, 1993a, b, c, 1994a, b, 1995) that have been described by MÜNSTER (1841), LAUBE (1868), KITTL (1894) and ZARDINI (1978, 1980, 1985).

I want to thank R. ZARDINI and R. 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 help of SABRINA CRAFTON, FREDERIKE STICHERT, KLAUS HARBECK, NIKOLAUS LEHMANN, ALEXANDER NÜTZEL and FRANK RIEDEL in the field in campaigns 1989, 1991, 1993. Several people of the Department of Geology and Palaeontology at the University of Hamburg have helped in extracting the shells from the samples that had been washed with diluted hydrogen superoxide. Shells were picked under the binocular microscope to be photographed with a SEM afterwards. Financial support has come from the

University of Hamburg as well as from DFG (German Science Foundation) grant Ba 675/11. All people and organizations involved I wish to thank very much.

Systematic part

Reconstruction of phylogeny of gastropods relies on analysis of Recent species in a combination with comparison to fossil shells. While anatomical data provide much information as to the potential relation that exists between species and groups of species, it tells us little about the time that was involved in the differentiation of species. Without fossils the evolutionary history can never be reconstructed in a way that comes close to the truth. Even though fossils provide us only with a limited amount of data, they alone present us with an indication of the time involved, during which a species or genus or a group of potentially interrelated genera have existed. Some of the here described Heterostropha like the Donaldinidae and Ebalidae demonstrate relation to Palaeozoic species ranging as far back as the Lower Carboniferous and Middle Devonian (320–370 million years). They connect these with modern species, of which it has not been realized that they may have an independent history ranging back so far in time. They have in contrast been grouped together with similar species that have a totally different historical background and have probably arisen much later in the Middle Cretaceous, like the parasitic Pyramidellidae. Or they were placed in artificial groups such as the Aclididae, of which little is known anatomically and ecologically. Members of the Cornirostridae from the Triassic (230 million years back) connect up with Jurassic species that lived about 40 million years later and extant ones that live near Australia today. The Amphitomariidae can be related to Cretaceous and Tertiary forms, while their modern relation is still not known. The closeness in shape found between some of the St. Cassian species and modern species living 230 million years later may partly be due to convergence, but it is interpreted here to reflect a natural relation in most cases. Many of the modern counterparts of the Triassic species described here are not much better known than their fossil representatives. The anatomy and ecology of the modern species connected to a more complete fossil record will hopefully support the validity of the proposed taxa in the future. It is a well established understanding that the Recent is the key to the past, but in the reconstruction of gastropod evolution the reversed statement is also true, that the past can serve as the key to understand the Recent.

Order Allogastropoda Haszprunar 1985
Superfamily Streptacidoidea Knight 1931

Description: The Streptacidoidea [Strepacididae of Knight et al. (1960)] have high-spired shells with a sinistral protoconch, often rounded labral sinus high on the whorl, and a simple oval aperture. Their ornament consists of growth lines and/or spiral lirae. The protoconch is a discoidal (initially sinistral) whorl that caps the spire flatly or is deviated.

Differences: The Mathildoidea have an usually highly ornamented shell differing from the smooth Cassianebalidae and Ebalidae as well as from the spirally ornamented Donaldinidae. The Pyramidelloidea commonly bear columellar folds and have a more pronounced ornament, besides appearing in the geological record not before the Cretaceous.

Family Ebalidae Bandel 1994

Diagnosis: The diagnosis of the superfamily Streptacidoidea applies to the Ebalidae. The protoconch is sinistrally coiled and smooth. Transition into the dextral teleconch occurs at contact between protoconch and teleoconch. The family is based on the genus *Ebala* with the modern genotype *Ebala nitidissima.*

Difference: The Ebalidae differ from the Cassianebalidae by not having folds on the larval shell and by a more elongate aperture ending in a narrow posterior end, while that of the Cassianebalidae is here broader. Streptacididae have similar shell form but more sinuous growth lines that reflect the presence of a subsutural sinus on the outer lip of the aperture.

Genus *Ebala* LEACH 1847

Genotype: *Ebala nitidissima* (MONTAGU) that lives in the Mediterranean Sea and the Northern Atlantic Ocean (FRETTER et al. 1986: figs. 439, 440).

Description: The shell is a small (1–2 mm) slender cone with 6–8 post-larval whorls with a convex profile and deep markedly oblique sutures. The aperture is oval in outline and is a little pinched posteriorly. The spindle is straight and smooth. The protoconch consists of sinistral whorls forming almost a right angle with the teleconch.

Differences: The smooth shell connected to a long-oval simple aperture differentiates *Ebala* from *Strepacis* with sinuous growth lines, *Cassianebala* with an ornamented protoconch and *Donaldina* with a spirally ornamented teleoconch. Within the Pyramidellidae there are similar species, but they are usually larger in size and bear more sculpture.

Ebala cassiana n. sp.

Fig. 1g–i

Etymology: Named for its occurrence in the St. Cassian Formation.

Holotype: Specimen of Fig. 1g–i, deposited with Nr. 1994/173 at the "Naturhistorisches Museum", Vienna.

Type locality: Dibona (Milieres in ZARDINI 1978) about 100 m below Rifugio Dibona above the road from Cortina d'Ampezzo to Falzarego pass.

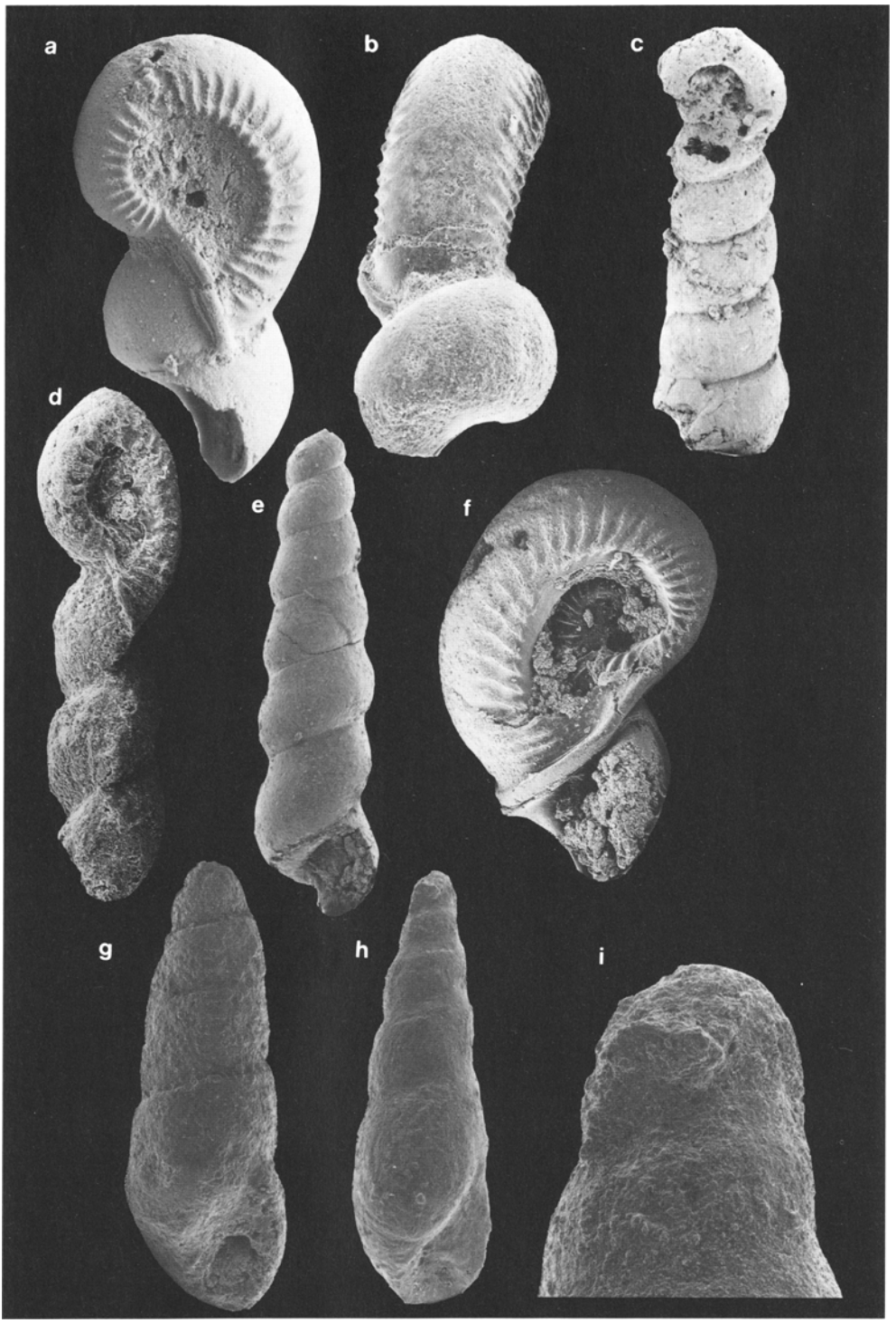
Type horizon: Early Carnian Cordevol Member of the St. Cassian Formation of the Upper Triassic of the Southern Alps (Dolomites).

Diagnosis: This Triassic *Ebala* from the St. Cassian Formation has a protoconch of 1.5 lowly coiled whorls forming an angle of almost 90° with the smooth teleoconch that consists of whorls as high as wide, separated from each other by inclined sutures.

Description: The shell is about 2 mm long with a maximum width of 0.7 mm and consists of 4.5 postnuclear whorls. Whorls are smooth and have convex flanks separated from each other by deep sutures; the apical angle amounts to about 15°. The aperture is of oval outline with narrow and pinched posterior end. The protoconch with the embryonic whorl extending above the spire consists of 1.7 sinistral whorls. It measures 0.22 mm in width and 0.2 mm in height and is lowly trochospiral in shape. Its axis of coiling is at a right angle to that of the shell (Fig. 1i).

Differences: The simple, lowly sinistrally spiral protoconch of *Ebala cassiana* resembles protoconchs as are found among species of modern *Ebala* and Carboniferous *Streptacis* and differs from the large almost planispiral protoconch of *Cassianebala*. The protoconch of *Loxebala*, in contrast, coils around the same axis as its teleoconch, while in *Ebala cassiana* almost 90° deviation occurs between axis directions. Species of *Streptacis* with smooth shell have sinuous growth lines, while those of *Ebala* are simple.

Fig. 1. Cassianebalidae with *Cassianebala speciensis* (a, b, c, d, e, f) und Ebalidae with *Ebala cassiana* from Dibona (g, h, i). a: the protoconch of *Cassianebala* is wide and was found in Alpe di Specie; b: the same protoconch as in (a) seen from the side; c: another individual with protoconch attached to the teleoconch, representing the holotype, Alpe di Specie; d: juvenile shell and protoconch, Stuores; e: teleoconch, Pralongia; f: protoconch seen from its apical side, Misurina; g: the 1.9 mm large shell of a juvenile individual; h: the almost fully grown shell of the holotype of *Ebala cassiana* is 2.2 mm long; its protoconch (i) is about 0.2 mm wide and its apex points to the right.


a
b
c
d
e
f
g
h
i

Material: Two complete individuals were studied from Dibona, several other ones with less complete shells from Misurina and Alpe di Specie.

Family Cassianebalidae n.fam.

Diagnosis: Cassianebalidae have a short and rounded aperture and are ornamented by axial folds on the sinistral protoconch. The small (1–2 mm), slender, multiwhorled teleoconch with convex flanks and well marked inclined sutures is ornamented with growth lines that reflect a slightly sinuous outline of the apertural lip, and fine spiral lirae. The family is based on the genus *Cassianebala* with *Cassianebala speciensis.*

Differences: Streptacididae and Ebalidae do not have the ornamented protoconch of the Cassianebalidae. Donaldinidae have teleoconchs with spiral ornament, while those of the Cassianebalidae are smooth.

Genus *Cassianebala* n.gen.

Genotype: *Cassianebala speciensis* n.sp.

Etymology: The teleoconch resembles that of the genus *Ebala* while the protoconch is evidence for an independent genus from the St. Cassian marls.

Diagnosis: The diagnosis of the family Cassianebalidae applies to the genus. Characteristic is the almost flatly coiled protoconch that is wider than the first whorl of the teleoconch. It is sculptured by radiating ribs that start out at the edge of the wide umbilical and apical depressions of the larval shell and end before reaching the flank. The protoconch has a thickened aperture and forms a right angle with the smooth teleoconch.

Difference: The Paleozoic *Streptacis* MEEK 1872 closely resembles *Cassianebala* in general shell shape and orientation of the protoconch. *Streptacis* differs by having a more prominent sinus in its pattern of growth lines and by having a protoconch without the characteristic axial rib pattern of *Cassianebala.*

Cassianebala speciensis n.sp.

Figs. 1a–f

Etymology: Named after the Alpe di Specie (Seelandalpe) near Rifugio Vallandro (Dürrensteinhütte).

Holotype: The specimen in Fig. 1c is the holotype, which is deposited (No. 1994/174) at the "Naturhistorisches Museum", Vienna.

Type locality: Seelandalpe (Alpe di Specie) near Rifugio Vallandro (Dürrensteinhütte), north of Cortina d'Ampezzo.

Type horizon: Cordevol Member of the early Carnian marls of the St. Cassian Formation, Upper Triassic of the southern Alpes (Dolomites), derived from slumped shallow water sediments.

Diagnosis: The diagnosis of the genus applies to this species. Whorls of the teleoconch are wider than high.

Description: When the shell is about 1 mm long it has a maximum width of 0.4 mm and consists of 5 postnuclear whorls. The whorls are smooth and have convex flanks separated from each other by deep, strongly inclined sutures. The apical angle of the teleoconch amounts to about 12°. The aperture is nearly round in outline, and its inner lip is folded upward and almost straight. The protoconch consists of almost 2.5 whorls with the larval shell portion forming a planispiral coil around the sinistral embryonic whorl. Protoconch axis of coiling is at a right angle to that of the teleoconch. Width of protoconch spire is larger than that of the first whorl of the teleoconch. The protoconch measures 0.45 mm in width, has a height of 0.22 mm and is nearly planorboid with depressed umbilicus and apex. The embryonic whorl is only about 0.08 mm wide and bears an ornamental pattern of pits surrounded by narrow raised rims. The

larval whorl is rounded with smooth flank and ornamented sides. Sculpture consists of about 30 axial ribs on one whorl. Ribs begin at the angulation, of which the umbilical one forms a thickened spiral ridge. Ribs end when reaching the rounded margin of the flank. The aperture of the fully grown larval shell is thickened by a solid rim. It demonstrates that during the ontogeny of *Cassianebala speciensis* the larval existence continued after completion of the protoconch for some time and that there was an extended period of life as planktotrophic veliger.

Differences: The simple protoconch of the type found in *Ebala* and *Streptacis* differs from the large almost planispiral and strongly ornamented protoconch of *Cassianebala.* The protoconch of *Loxebala* coils around the same axis as its teleoconch. This contrasts with *Ebala cassiana* and *Cassianebala speciensis* with almost 90° difference between axis directions.

Material: Three individuals with teleoconch and three with larval shell were studied. Besides the holotype further material is deposited (No. 1994/175 from Misurina, No. 1994/176 from Stuores and 1994/177 from Pralongia) at the NHM, Vienna.

Genus *Loxebala* n. gen.

Etymology: This species from the St. Cassian Formation resembles the small Mid-Devonian *Loxonema moniliforme* GOLDFUSS from the Eifel. The name indicates a combination of a simple "loxonematoid" teleoconch with a sinistral protoconch as found among ebalids.

Genotype: *Loxebala vallandroensis* n. sp.

Diagnosis: A teleoconch like that of *Cassianebala* is connected to a protoconch that coils sinistrally around the same axis as the dextral teleoconch.

Difference: *Cassianebala* differs from *Loxebala* by the deviate shape of the protoconch that twists a dextral direction upon contact with the teleoconch, while in *Loxebala* the change from sinistral to dextral coiling occurs within the last portion of the larval shell. The ornamented protoconch of *Loxebala* differentiates it from *Streptacis* and *Ebala,* both of which have a smooth protoconch.

Loxebala vallandroensis n. sp.

Figs. 2a–d

Etymology: Named for the locality of its occurrence near Rifugio Vallandro and Alpe di Vallandro.

Holotype: The specimen in Fig. 2a (No. 1994/178) deposited at the Naturhistorisches Museum Vienna.

Type locality: Seelandalpe (Alpe di Specie), north of Cortina d'Ampezzo.

Type horizon: Cordevol Member of the St. Cassian Formation, Upper Triassic of the southern Alpes (Dolomites), from slumped shallow water sediments.

Diagnosis: The generic diagnosis applies to the species. The transition from protoconch to teleoconch is connected with axial folds on the larval shell. The aperture is about as wide as high.

Description: A 1.5 mm high shell has about 8 whorls and an apical angle of about 5°. The whorls are rounded and almost twice as wide as high, with sutures inclined. The aperture is of almost round outline with a somewhat widened and channelled anterior end and a short, almost straight, raised inner lip. Growth lines are simple and reflect the well rounded outer lip. The protoconch measures about 0.25 mm across and consists of two whorls. It is a little wider than the first whorl of the teleoconch. The embryonic shell is smooth and strongly sinistrally coiled, while the larval shell turns into the planispiral and dextral whorl in the last quarter of its whorl. It has folds forming axial ribs in the last half whorl before onset of the teleoconch. The outer margin of the pediveliger shell may have a thickened rim.

Difference: The flat protoconch with same axis as the teleoconch differentiates *Loxebala vallandroensis* from the very similar *Cassianebala speciensis,* where the protoconch forms an

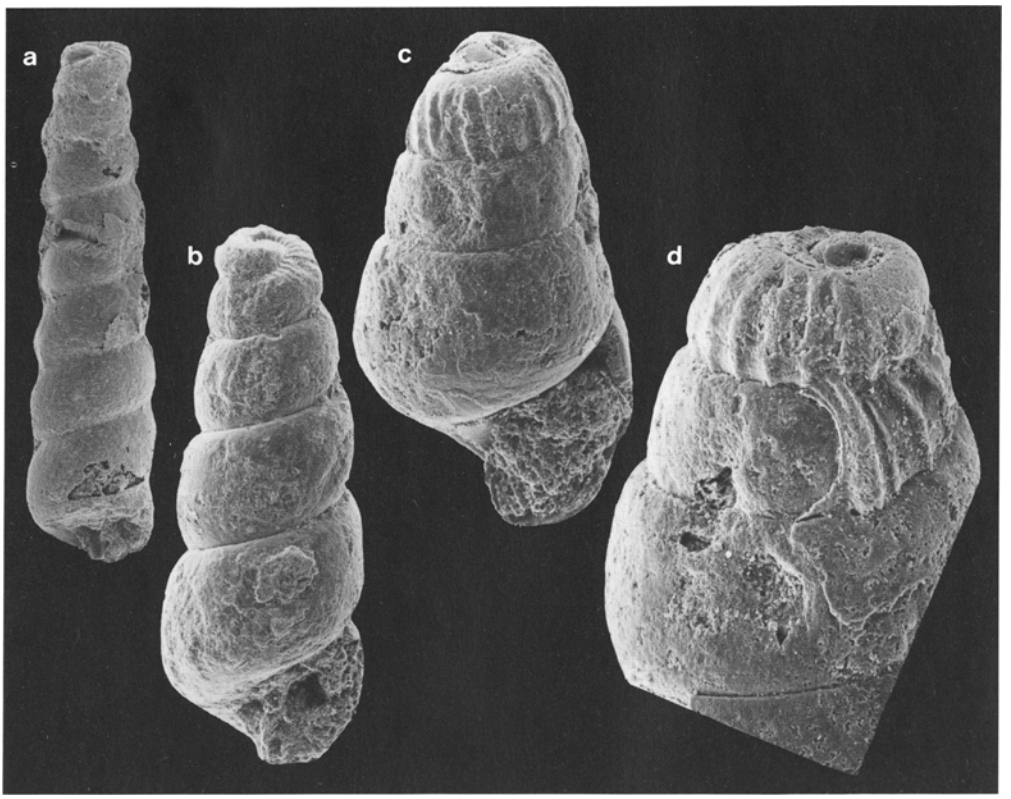


Fig. 2. *Loxebala vallandroensis* from Alpe di Specie with 1.6 mm high shell (a), and Misurina (b, c, d). b: juvenile shell of about 1.1 mm height; c: ornamented protoconch, seen in detail in (d) and having a maximum diameter of 0.26 mm.

angle of almost 90° with the teleoconch (Fig. 3). This feature also separates it from the species of *Ebala* where, in addition, the protoconch is not sculptured. A similar protoconch as in *Loxebala* is found among the Ampezzanildidae BANDEL 1994 of the Mathildoidea (BANDEL 1995), but here the teleoconch is ornamented in all the members of this family.

Material: Besides from the holotype 2 individuals from Specie, 1 from Campo and 5 from Misurina were studied. Further material from Misurina has been deposited at NHM Vienna (No. 1994/179).

Family Donaldinidae BANDEL 1994

Diagnosis: In members of the Donaldinidae the teleoconch is ornamented with prominent spiral ribs. The protoconch is sinistrally coiled. The family is based on the genus *Donaldina.*

Difference: The other Streptacidoidea (Streptacididae, Ebalidae, Cassianebalidae) are not ornamented by prominent spiral ribs. Ornamentation of Mathildoidea includes also axial ribs, while morphology of teleoconch and protoconch may be quite similar (Fig. 4a–c). Anoptychiidae have a change of ornament in their teleoconchs, but juvenile teleoconchs may resemble those of Donaldinidae (BANDEL 1994b, 1995).

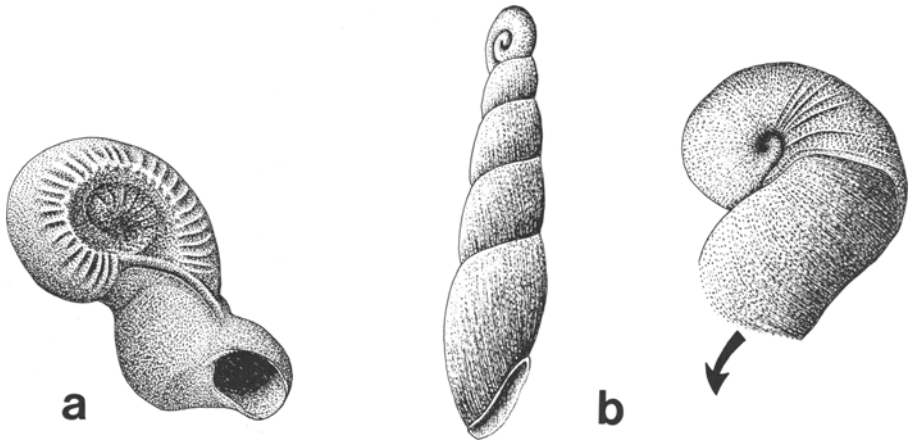


Fig. 3. Sketches of *Cassianebala speciensis* with 0.4 mm wide protoconch and begin of teleoconch (a) and of reconstructed *Ebala cassiana* with protoconch and about 1 mm high teleoconch (b).

Genus *Donaldina* KNIGHT 1933

Genotype: *Donaldina* is based on the Carboniferous *Donaldina grantonensis* (DONALD 1898) from Scottland.

Description: The high spired shell is ornamented with spiral threads confined generally to the lower part of the whorl.

Difference: *Donaldina* differs from *Neodonaldina* by the presence of a subsutural ramp, which is not developed in the teleoconch of the later.

Donaldina zardinii n. sp.

Fig. 4d–g

Etymology: Named in honour of Dr. RINALDO ZARDINI from Cortina d'Ampezzo.
Holotype: The specimen illustrated in Fig. 4f, g, deposited at NHM, Vienna (No. 1994/180).
Type locality: Dibona near the road from Cortina d'Ampezzo to Falzarego pass.
Type horizon: Cordevol Member of the Lower Carnian St. Cassian Formation; in marls into which the gastropods were transported by turbidity currents.

Diagnosis: The generic diagnosis also applies to this species. *Donaldina zardinii* has a sinistral protoconch with an almost 90° deviation from the axis of coiling of the teleoconch. Ornament of the teleoconch consists of a smaller subsutural ramp with one spiral lira and at least 3 lirae on the flanks. Whorl profile is rounded below and flattened above.

Description: Slender shell with an apical angle amounting to about 22° in the first 5–7 whorls, later decreasing to about 10°. A shell of 3.5 mm height consists of about 10 postnuclear whorls. The upper whorl flanks are flattened and here ornamented by one lira in central position and growth lines that reflect the presence of a small recess near the suture. The lower whorl flank is ornamented by three, later four spiral ribs. The flattened base is covered by four somewhat weaker spiral ribs. The aperture is as wide as it is high, and the columellar portion of the inner lip is thin and slightly arcuate. The protoconch is smooth and consists of about one and a half whorls of lowly trochispiral shape with sinistral coiling. Its axis forms almost a right angle with the axis of the teleoconch, so that its umbilicus and apex point sideways. It measures about 0.25 mm in width and its transition into the teleoconch is connected to the twist into the dextral coil.

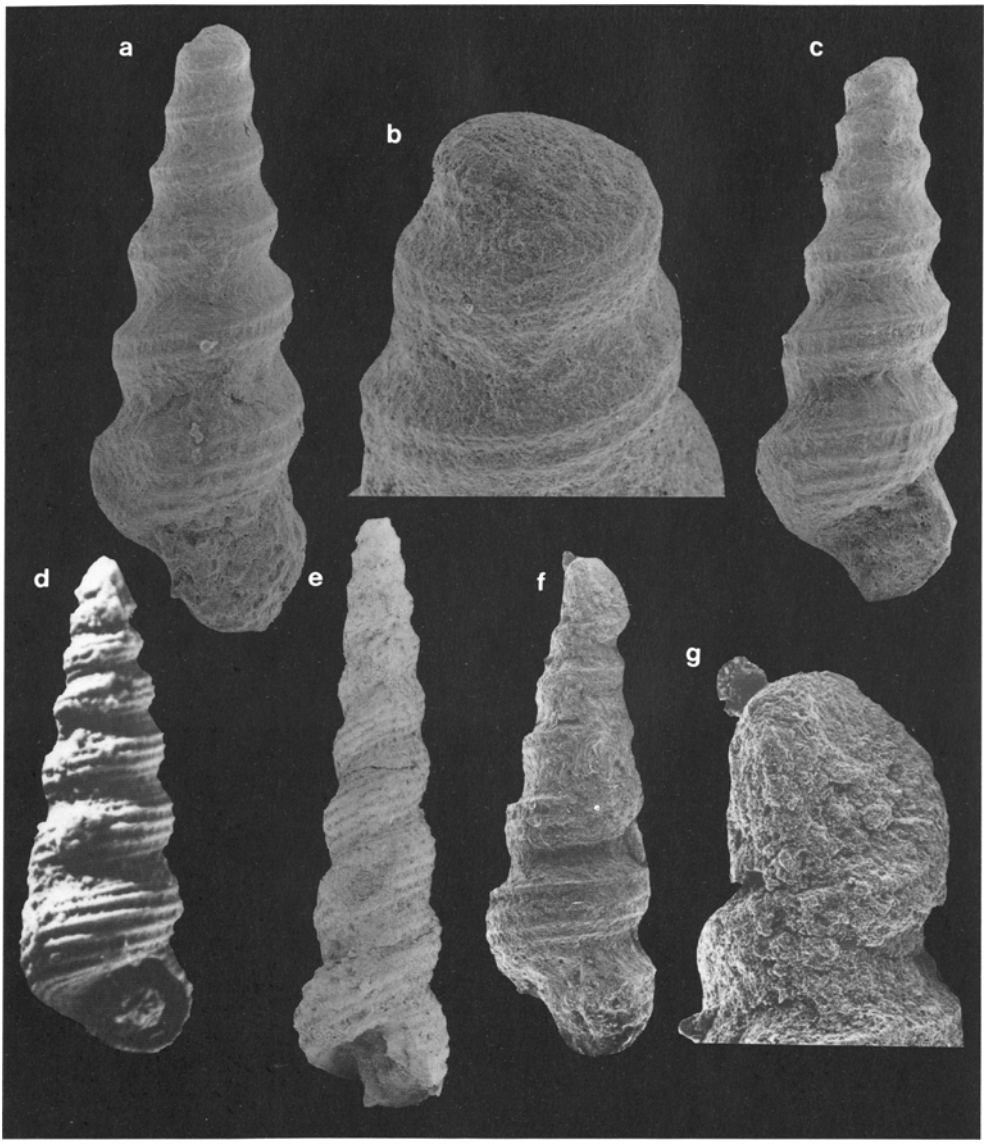


Fig. 4.a–c: *Turrithilda cassiana* from Dibona with 2 mm high shell (a, c) and details of the almost flat protoconch (b); d–g: *Donaldina zardinii* from Campo (d, e) and Dibona (f, g). d: a 2 mm high shell; e: 4 mm high. The holotype (f) measures 2 mm in height and its protoconch (g) is 0.25 mm wide.

Differences: *Donaldina zardinii* differs from *Turrithilda cassiana* BANDEL (1995: figs. 4a–c) by the ornament of the teleoconch, which in the latter has fewer spiral ribs and a smooth upper flank. In addition the protoconch lies flat on the teleoconch, while that of *D. zardinii* forms a right angle with it. Sculpture is much more pronounced in *Donaldina zardinii* than in *D. grantonensis*, which has a weaker ornament and more rounded whorl flanks (KNIGHT 1941).

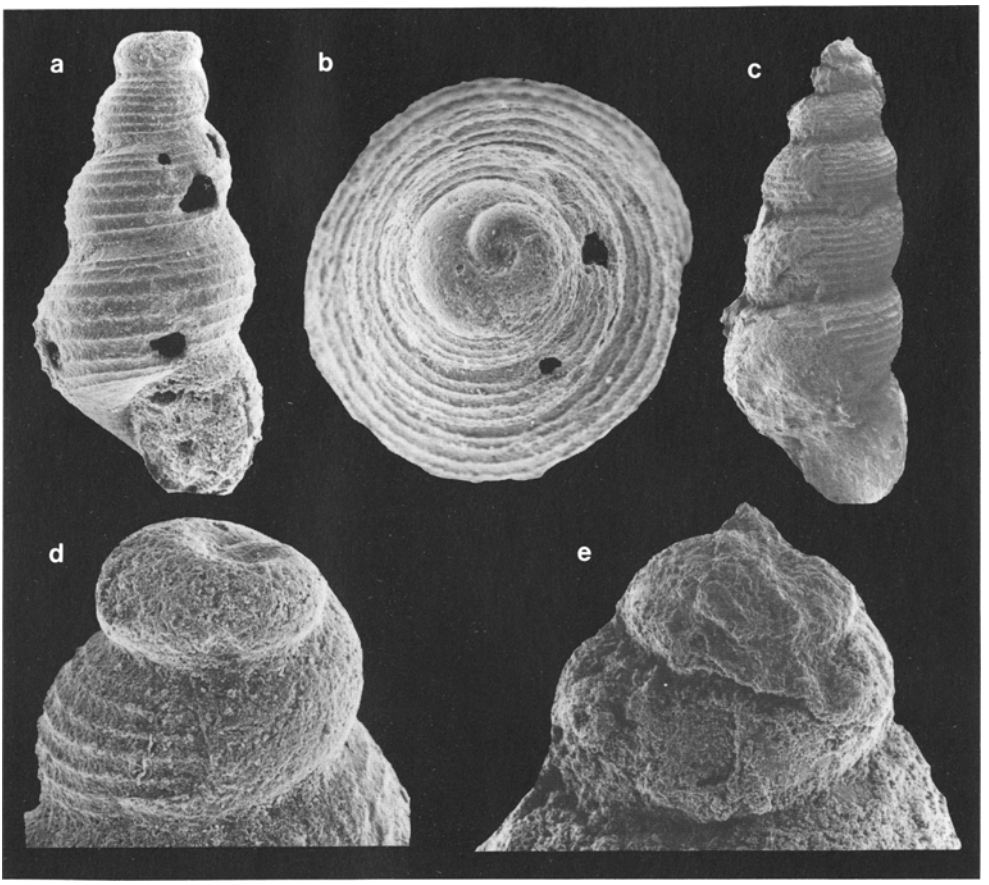


Fig. 5.a–e: *Neodonaldina elongata* from Specie (a, b, d) and from Dibona (c, e). (a) is about 1 mm high and its protoconch (b, d) is a little more than 0.2 mm wide and provided with an apertural projection (d). The more grown but not adult shell measures 1.8 mm in length and its protoconch (e) also has the apertural projection.

Material: From the locus typicus of Dibona three individuals were studied, among them the holotype. The other individuals from Campo are deposited at NHM, Vienna (No. 1994/181).

Genus *Neodonaldina* n. gen.

Etymology: Combination of a new Triassic gastropod that resembles the older Carboniferous *Donaldina.*

Genotype: *Spirocyclina elongata* ZARDINI 1978 from the Upper Triassic of the Italian Alps.

Diagnosis: The small, slender and high-spired shell has rounded whorls sculptured with spiral costae. The protoconch consists of a sinistral embryonic and larval shell.

Differences: *Neodonaldina* resembles *Donaldina* KNIGHT 1933 but spiral costae are evenly distributed over the whorl-flank, while they cover only the lower flank in the latter

(KNIGHT 1941: pl. 48, fig. 3). The juvenile teleoconch of Anoptychiidae resembles the teleoconch of *Neodonaldina* but in contrast to the latter in *Anoptychia* and *Camponella* the sculptural ornament is lost on later whorls (BANDEL 1995).

Neodonaldina elongata (ZARDINI 1978)

Figs. 5a–e; 6a

1978 *Spirocyclina elongata* sp. nov. – ZARDINI: 55, pl. 40, fig. 5.

Description: The specimen described by ZARDINI (1978) from the locality Tamarin right outside and NE of Cortina d'Ampezzo is about 4 mm high, shows about 8 whorls of the teleoconch and an oval, anteriorly flattened aperture. The whorls are convex and increase rapidly in their diameter. The ornament consists of spiral costae. New material from Misurina, Specie, Campo and Dibona represent not fully grown shells. They have a maximum of seven whorls, are up to 2 mm high and have an apertural angle of 25° at first that later decreases to about 15°. The protoconch consists of two smooth whorls coiling around the same axis as the teleoconch, but in opposite direction in the first whorl. Change into planispiral coiling occurs within the last half of the larval whorl. The larval shell is about 0.2 mm high and wide with the embryonic shell measuring 0.1 mm across. The aperture of the fully grown larval shell is provided with a hook-like basal projection. Thus the pediveliger had a large posterior sinus on its outer lip and a strong lobe near its lower centre, with a smaller sinus probably present between the lobe and the umbilicus, but covered by the shell of the teleoconch.

The onset of the teleoconch goes along with a drastic change in ornament consisting of 7–8 spiral ribs on the flanks. These do not increase in number but in distance from each other with further growth of whorls of the teleoconch. On the base, which is not umbilicate, 3–4 further spiral lirae are present, which become covered by the next whorl. The aperture is simple and about as wide as high with rounded outer and inner lip and somewhat flattened flanks on the parietal part of the inner lip and the anterior portion of the outer lip. Growth lines form fine lirae crossing the spiral ribs regularily and reflecting a simple vertical arrangement of the apertural margin.

Difference: *Promathilda* (?*Clathrobaculus*) *gracillima* HAAS (1953: pl. 13, figs. 55–58, 64, 65) from the Upper Triassic of Peru resembles *Neodonaldina elongata* closely and its protoconch is also heterostrophic, but it seems to have formed a larger angle with the teleoconch than in the related species of the St. Cassian Formation (BANDEL 1994b).

Material: 7 individuals from Campo, 1 from Misurina, 3 from Dibona, and 1 from Alpe di Specie were studied. Specimen from Campo (No. 1994/182), from Dibona (No. 1994/183) and from Alpe di Specie (No. 1994/184) are deposited at the NHM, Vienna.

Neodonaldina ampezzana n. sp.

Fig. 6b–g

Etymology: After the Ladinian region Ampezzo.

Holotype: Specimen illustrated in Fig. 6e, together with additional material deposited at NHM, Vienna (No. 1994/185).

Type locality: In the forest above Campo close to Cortina d'Ampezzo.

Type horizon: Marls of the Cordevol Member of the Upper Triassic St. Cassian Formation.

Diagnosis: The many-whorled turriform shell has a change in whorl profile from rounded to flattened. With teleoconch growth whorl height increase in relation to width. Ornament consists of weak spiral ribs that increase in number during growth of shell. The protoconch is smooth, sinistral and its axis deviates a little from that of the teleoconch.

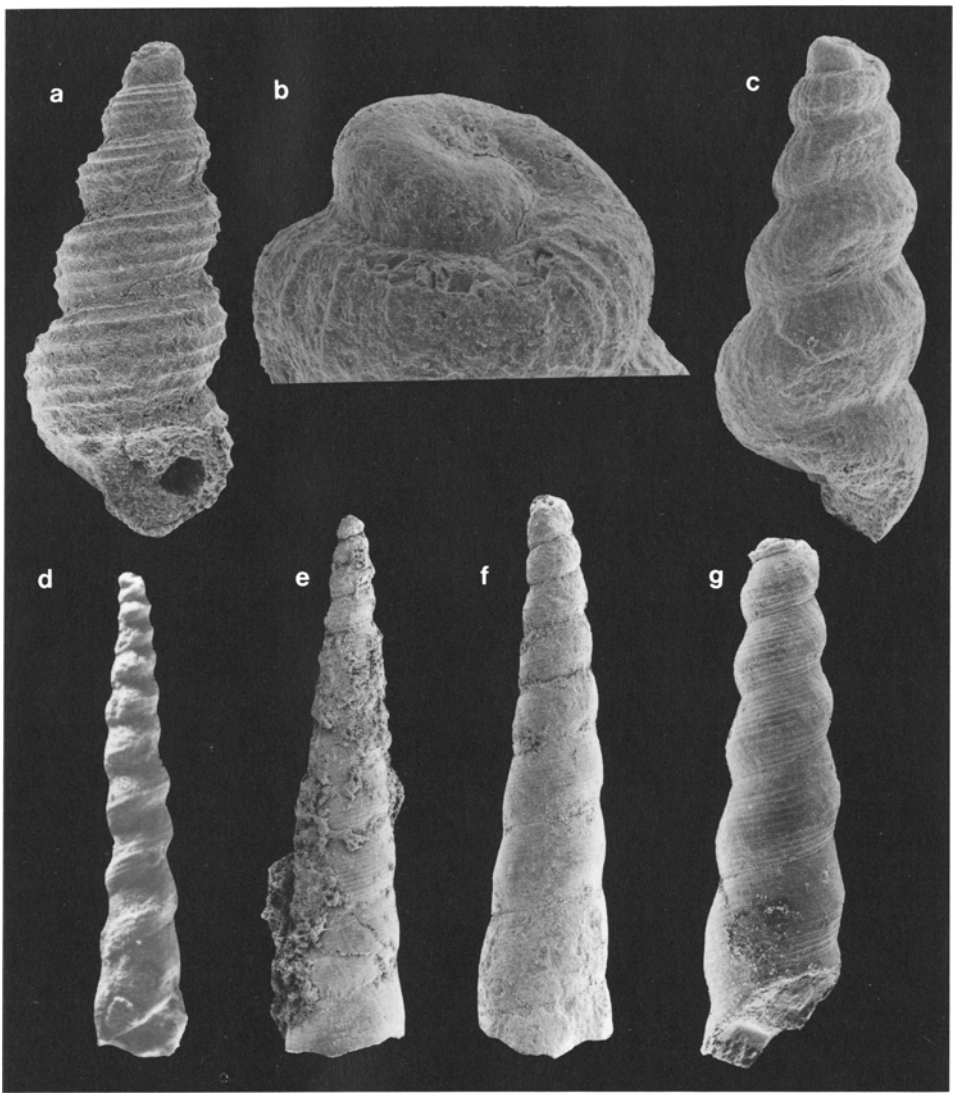


Fig. 6. *Neodonaldina elongata* (a) and *Neodonaldina ampezzana* (b–g) from Campo. a: 1.6 mm high; b: protoconch, 0.18 mm in width, belonging to a juvenile shell (c) of *N. ampezzana* with 1.7 mm length; d: individual photographed by ZARDINI; e: 5.7 mm long shell with transition from angular to flattened flanks (holotype); f: 5.9 mm long shell with flattened flanks; g: 3.7 mm long fragment of juvenile shell.

Description: A shell with 11 whorls and 7 mm height and 1.3 mm width has an apical angle of 12°. In earlier whorls the angle is a little larger. The protoconch consists of 1.3 whorls and has a sinistral first whorl that grades into planispiral coiling before begin of the teleoconch. Transition into the teleoconch may be accompanied by strong axial folds that follow the straight growth line pattern. The teleoconch ornament consists of delicate spiral ribs, which appear clearly with the second whorl of the teleoconch. Here about 6 ribs are present, while in the

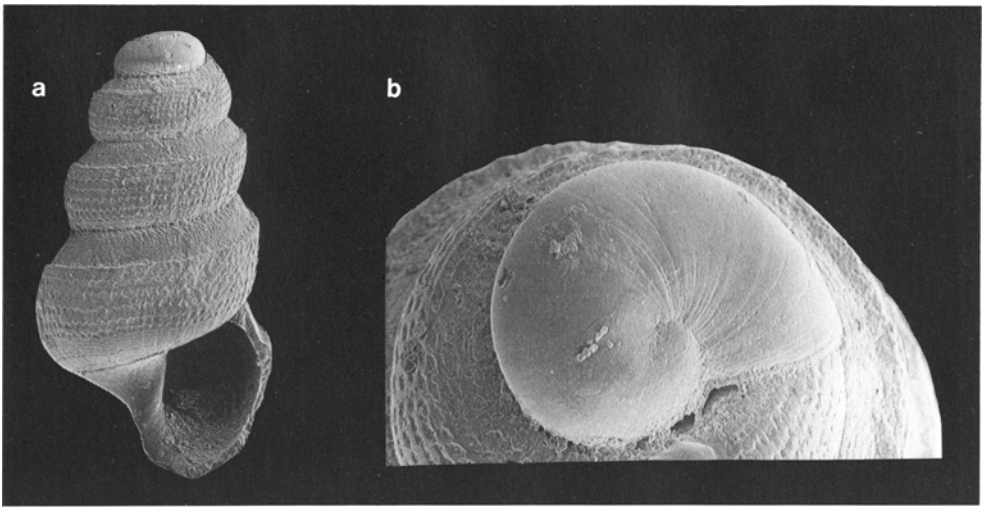


Fig. 7. Modern *Donaldina* sp. with 0.8 mm high shell (a) from the shallow sea at Cebu (Philippines) has a protoconch of 0.18 mm width with initial whorl dipping below the apical surface (b).

seventh whorl they have increased to 18. While the first teleoconch whorls are wider than high, later ones become increasingly higher, until they are about of equal width and height. At the same time the evenly regular, lowly convex curvature of whorl flanks changes to a more flattened profile with indistinct angulation at mid-whorl.

Material: 9 individuals from Campo.

Remarks: *Ebala liassica* SCHRÖDER 1995 (SCHRÖDER 1992: pl. 10, figs. 18–21), from the Lower Jurassic of northern Germany is very similar to *E. cassiana.* The larval shell differs from *Cassianebala* and *Loxebala* reaching in *E. liassica* only 0.18 mm in maximum width. The modern type species of the genus *Ebala* differs by having fine spiral sculpture on the whorls, but the protoconch is of similar dimensions as in *Cassianebala* having 1.5 whorls with a width of 0.43 mm.

Modern gastropods with a shell fitting into the diagnosis of *Donaldina* and the Donaldinidae live among coralline algae in the environment of tropical coral reefs. Specimens belonging to the same genus were found in shallow water of the Caribbean Sea at Isla Cozumel near Yucatan by LEHNERT (1989), among coral rubble of shallow bays near Santa Marta, Colombia (pers. observ.), transported from the reef into deeper water near Cebu in the Philippines (BANDEL 1991a) (Fig. 7a, b) and collected from shallow coral reefs at Lizard Island in the great Barrier reef of Australia.

At Lizard Island living individuals of *Donaldina* were observed under the microscope. The organization of the visible soft body differs from that of all other known gastropods, including the pyramidellids. Two prominent ciliated pallial tentacles extend from the labral sinus culminating high in the whorl and featuring the outer lip of the aperture. The cilia of the frontal pallial tentacle continue into a cilated band of the pallial cavity that extends to its apical end at about three quarters of the body whorl. The head is also of characteristic shape with small simple eyes close to each other in the back and triangular flattened tentacles extending to the sides covered by a dense fine ciliation. Between the tentacles two ciliated lobes cover the mouth, which opens in the centre below them. The ciliated mouth lobes are mobile and search about when the animal is active aided by sense cilia on their frontal end. The propodium is also densely ciliated, and the

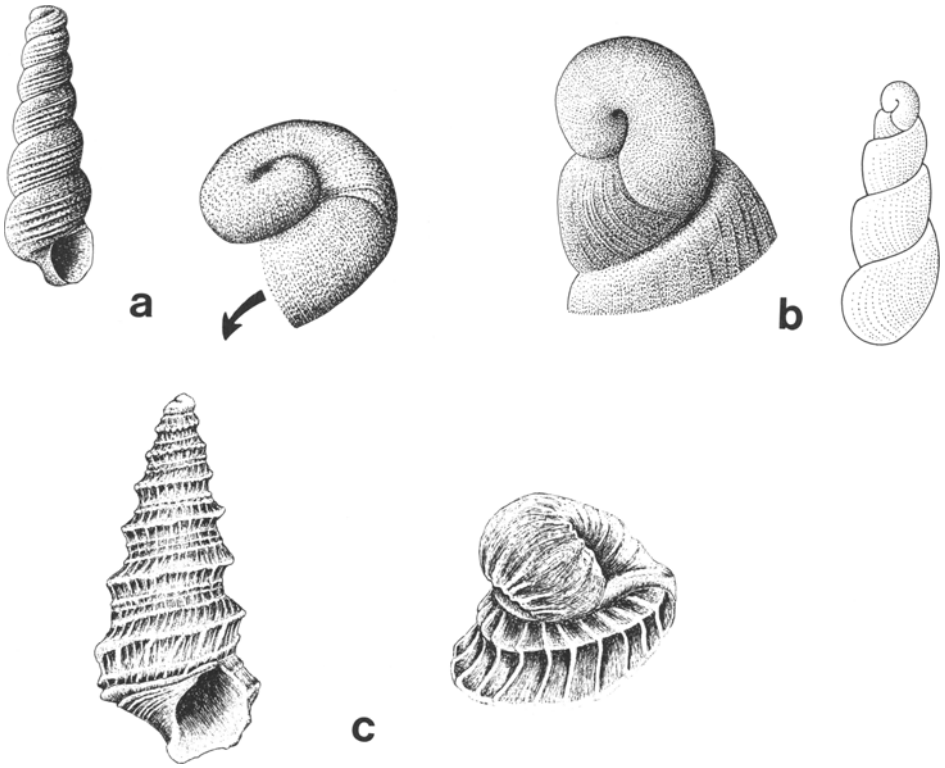


Fig. 8. Drawings of *Donaldina filosa* YOO 1988 from the Lower Carboniferous of Australia (shell about 0.7 mm high) (a), *Ebala* sp. with 0.6 mm high shell from the Indo Pacific (b), and *Promathilda decorata* (KLIPSTEIN 1834) from the St. Cassian Formation (c) (shell about 1.5 mm high).

cilia are in rapid motion as the animal moves about. Motion of the foot is continuous and rapid, while the shell is dragged behind and periodically pulled foreward in short jerks by contraction of the retractor muscle. The foot carries a large transparent operculum that is able to seal the aperture tightly. More details of the anatomy are found in BANDEL et al. (in prep.).

Superfamily Architectonicoidea GRAY 1850
Family Architectonicidae GRAY 1850

Description: The conically to planspirally coiled shell is usually of low profile with different types of ornamentation present. Its aperture is round or angular and about as wide as high. The umbilicus is usually open. The whorls of the protoconch coil sinistrally along the same axis as the normally dextral teleoconch. The modern genus *Architectonica* RÖDING 1798 represents the base for the family.

Genus *Rinaldoconchus* BANDEL 1988

Genotype: *Rinaldoconchus ampezzanus* (ZARDINI 1980) from the Upper Triassic St. Cassian Formation.

Diagnosis: The diagnosis of the family Architectonicidae applies. The small shell is of low conical shape with rounded whorls. It has a wide open umbilicus and is ornamented by few spiral ribs and numerous fine spiral lirae. Its aperture is vertically arranged. The protoconch twists from sinistral coiling into the planispiral coiling mode. Larvae and adults coil around the same axis but in opposite directions.

Differences: Spiral ribs as major element of the ornament differentiate *Rinaldoconchus* from other lowly spired or planispirally coiled Heterostropha from the St. Cassian Formation. The sinistral protoconch separates it from the archaeogastropod *Fredericella* BANDEL 1993. *Rinaldoconchus* resembles in shape modern members of the genera *Philippia* GRAY 1847 and *Heliacus* ORBIGNY 1842 but is of smaller size (BIELER 1985: figs. 1, 7). The whorls of *Heliacus* are ornamented by similar spiral ribs on the upper surface and fine ribs on the basal side.

Rinaldoconchus ampezzanus (ZARDINI 1980)

Figs. 9c, f; 14b

1980 *Euomphalus ampezzanus* n. sp. – ZARDINI: 4, pl. 2, fig. 2.
1988 *Rinaldoconchus ampezzanus* ZARDINI – BANDEL: 11, pl. 2, fig. 3; pl. 5, figs. 1, 2, ill. 4.

Diagnosis: The generic description applies to this species. The small shell is wider than high (5:4) and of trochiform shape. Usually only two spiral ribs remain visible on the whorls of the spire while the others become covered by the following whorl. The umbilicus is conical. The aperture is round and uninterrupted.

Description: The shell is small and with 3.3 whorls of the teleoconch measures 2 mm in width and a little more than 1 mm in height. The rounded whorls are ornamented by a variable number of low spiral ribs of which only the uppermost two, rarely three, are visible on the spire, while the others become covered by the following whorl. The ribs on the upper whorl are larger than those found on the base and in the umbilicus. Fine spiral striae are present between ribs and in the widely open umbilicus. The umbilicus forms a conical depression with flattened sides and in it all whorls are visible. The protoconch consists of about 1.5 whorls and measures 0.16 mm in diameter. Its larval part has radial folds where it twists from its sinistral coiling into the planispiral coiling mode.

Differences: *Rinaldoconchus ampezzanus* differs from *R. bieleri* by its larger size, relatively higher shell and conical umbilicus.

Material: 23 specimens from the Alpe di Specie and 4 from Misurina NHM Wien, No. 1994/186 – Alpe die Specie specimens and No. 1994/187 – Misurina specimens. The holotype is housed at the Community Museum in Cortina d'Ampezzo.

Rinaldoconchus bieleri n. sp.

Figs. 9a, b, d, e, g, h; 11b

Etymology: This small species is named after RÜDIGER BIELER (Chicago) who untangled the complex classification of the Architectonicidae.

Holotype: The holotype is deposited in the NHM Vienna (No. 1994/188).

Type locality: Dibona, above the road from Cortina d'Ampezzo to the Falzarego pass and on the slope below Rifugio Dibona.

Type horizon: Cordevol Member of the early Carnian marls of the St. Cassian Formation.

Diagnosis: The generic description applies. The small, low, trochiform shell is about twice as wide as high. Three spiral ribs sculpture each whorl. The umbilicus is wide exposing the rounded whorls, and the aperture is round with part of the inner lip resting on the whorl surface.

Description: The shell is small and with 2.5 whorls of the teleoconch and measures almost 1.2 mm in width and about 0.4 mm in height. The rounded whorls are ornamented with a

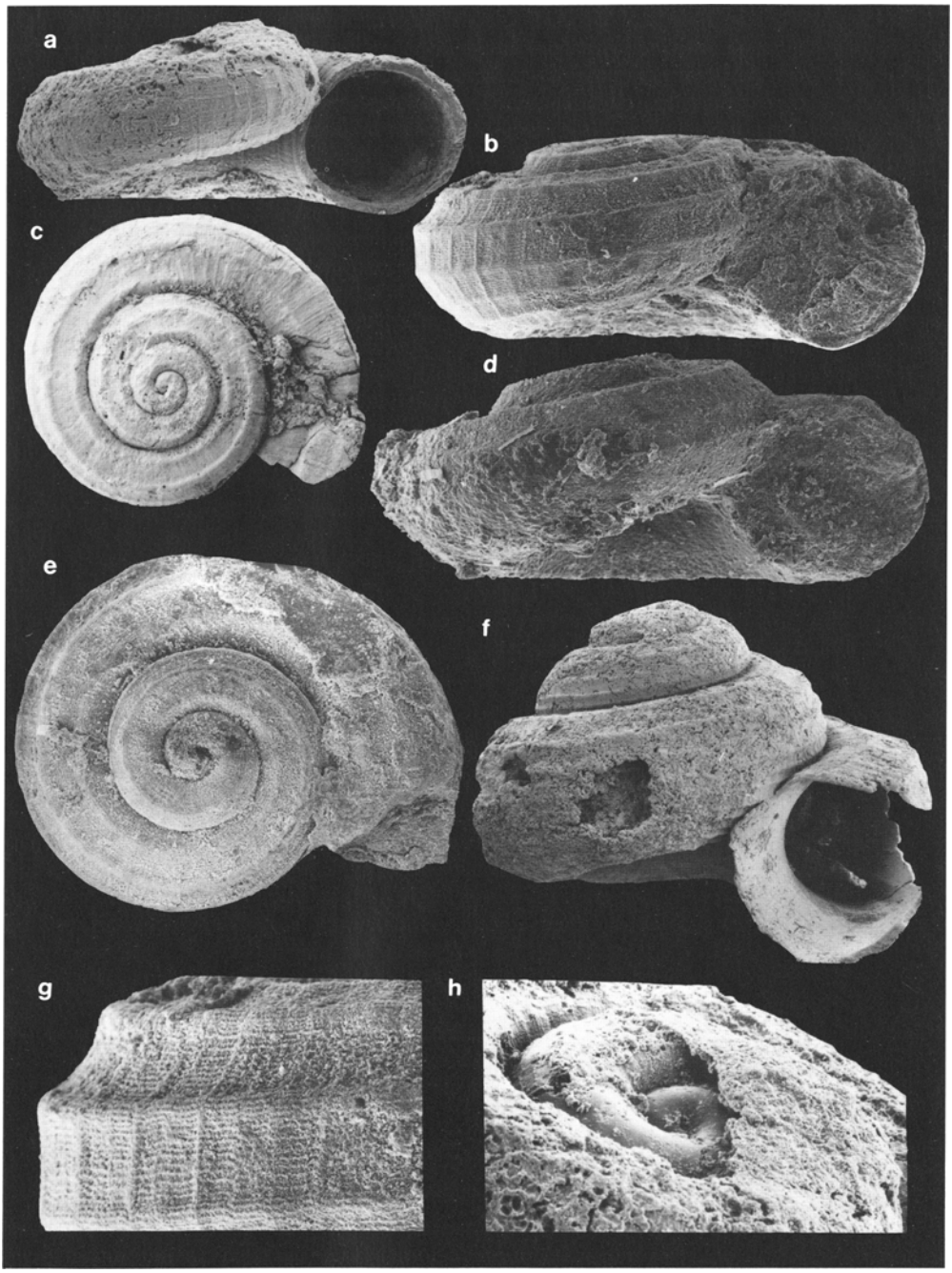


Fig. 9. *Rinaldoconchus bieleri* (a, b, d, e, g, h) and *Rinaldoconchus ampezzanus* (c, f). a: *R. bieleri* with 0.8 mm wide shell has a 0.2 mm wide smooth and sinistral protoconch (h) from Alpe di Specie. b: 1 mm wide shell from Dibona seen from the side; g: detail; e: viewed from above. c, f: *R. ampezzanus* from Alpe di Specie is 1.6 mm wide.

small number of low spiral ribs with numerous spiral threads between them. Growth lines transect the ribs and reflect the vertical orientation of the simple aperture. Spiral ornament varies individually but usually three ribs remain on the upper flank, of which the second is the most prominent one. The base is rounded, and the umbilicus is wide and displays all former whorls. The protoconch consists of about 1.2 whorls and measures about 0.20–0.22 mm in diameter. Its larval part has some coarse growth lines or collabral folds where it twists from its sinistral coiling into the planispiral coiling mode. Larvae and adults have the same axis but coil in opposite directions.

Differences: *Rinaldoconchus bieleri* is smaller and lower than *R. ampezzanus*, and its umbilicus is wider and not flat-sided. *Rinaldomphalus cassianus* BANDEL 1993 has nacreous shell structure and the characteristic embryonic shell of the archaeogastropods. The archaeogastropod *Fredericella cancellata* is also of closely similar shape and ornament (BANDEL 1993a: pl. 2, figs. 2, 3; pl. 6, figs. 7–9) but differs with regard to the protoconch.

Material: 22 specimen from Alpe di Specie, 6 from Dibona and 10 from Misurina. Material from the Alpe di Specie is deposited at NHM Vienna (No. 1994/189).

Family Cassianaxidae n. fam.

Diagnosis: The small (about 1–2 mm) planorboid shell is ornamented only by very delicate spiral striae and growth lines or collabral folds. It has a rounded upper whorl surface connected by an angular lower corner with the flattened and umbilicated base. The protoconch coils around the same axis as the teleoconch but is sinistral, while the teleoconch is dextral. The initially sinistral shell becomes planispirally coiled early in the development of the larval shell. The family is based on *Cassianaxis riedeli* from the St. Cassian Formation, which is close in shape to modern *Episcynia inornata* (D'ORBIGNY 1842) that represents the genotype of *Episcynia* MÖRCH 1875. This species lives in the Caribbean Sea along with two related species (ABBOTT 1974).

Genus *Cassianaxis* n. gen.

Etymology: Modern *Pseudomalaxis* and Tertiary *Dinaxis* resemble this new gastropod from the St. Cassian Formation. Its name represents a combination of the name endings of these genera with that of the formation.

Genotype: *Cassianaxis riedeli* from St. Cassian Formation.

Diagnosis: The characters of the family are present in this genus. The depressed shell is less than 2 mm large and has a low conical spire of about 4 whorls and a low peripheral keel. The umbilicus is wide with coarse axial folds and fine collabral lines. The protoconch consist of an embryonic shell that dips below the larval shell.

Differences: *Cassianaxis* differs from the other Heterostropha of the St. Cassian Formation by its rounded upper shell surface and the flattened base with folded sharp edge at the open umbilicus.

Cassianaxis riedeli n. sp.

Figs. 10a–h; 13a, b

Etymology: Named after FRANK RIEDEL (Berlin) who assisted in collecting gastropods in June 1989 in the Dolomites.

Holotype: The figured individual (Figs. 10a, b) deposited at MNH Vienna (No. 1994/190).

Type locality: Outcrops on the steep flank of the Praelongia ridge above St. Cassian in the Dolomites.

Type horizon: St. Cassian Formation in the area of the Stuores meadows at Pralongia; Cordevol Member of the early Carnian.

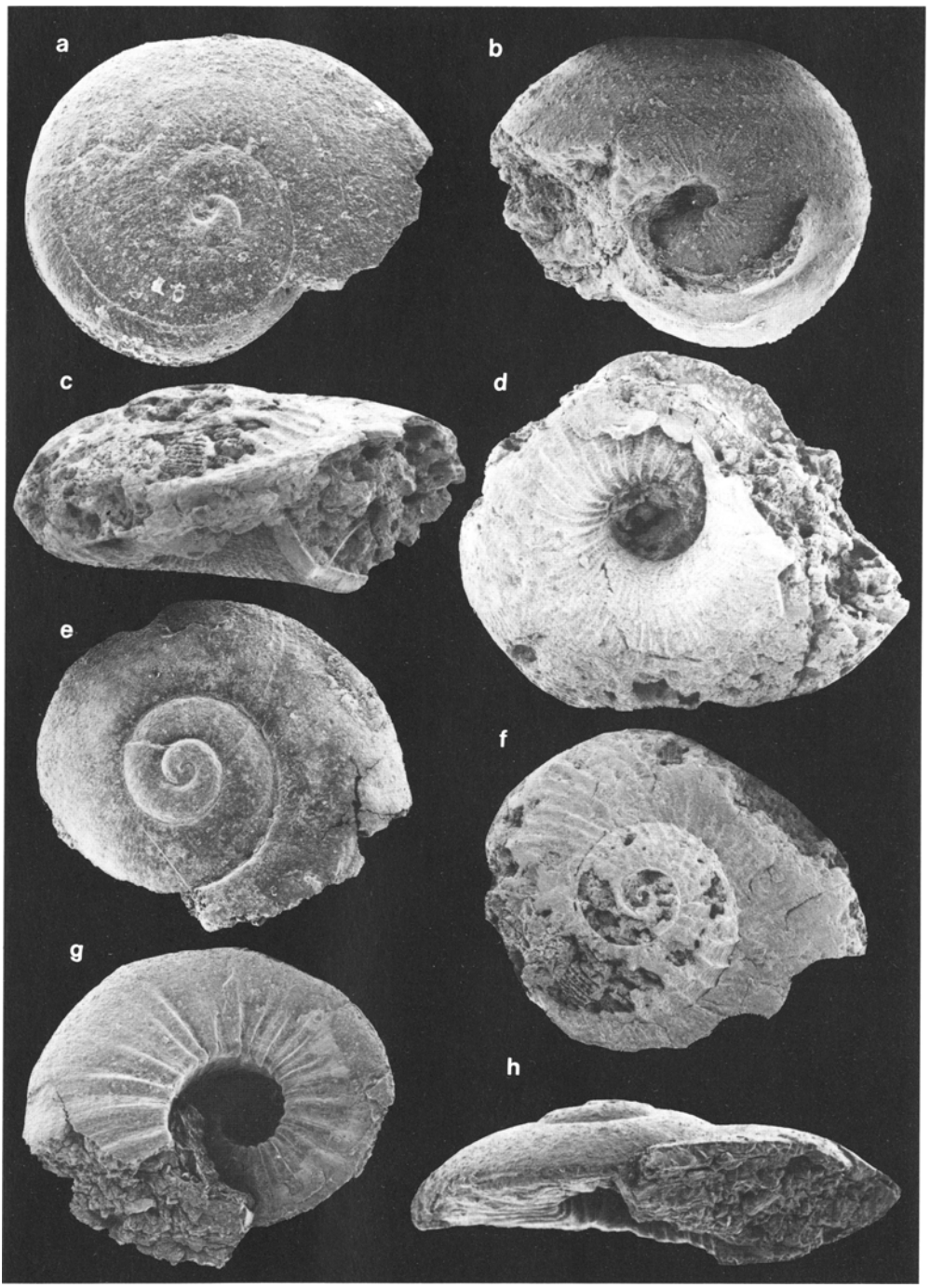


Fig. 10. *Cassianaxis riedeli* from Pralongia. a, b: 0.85 mm wide individual in apical view (a) and umbilical view (b); c, f: 1.2 mm wide invividual in lateral view (c), seen from above (f) and from below (d) with wider umbilicus than younger shell (b); e, g, h: 1.1 mm wide shell (protoconch figured in Fig. 13b) in apical view (e), umbilical view (g) and viewed from the side (h), showing slightly compactional distortion.

Diagnosis: The generic diagnosis applies to this species. The small shell with a low conical spire and rounded whorl surfaces has a flattened base with an open and conical umbilicus. Diameter of protoconch and teleoconch whorls increases rapidly with growth. The ornament consists of growth lines and collabral folds, which are more prominent on the base than on the spire. The protoconch consists of a little more than two whorls with the embryonic part sinistrally coiled and the larval shell becoming planispirally coiled.

Description: A shell with 3.5 whorls measures less than 0.5 mm in height and slightly more than 1 mm in width. The upper flank of each whorl is evenly rounded and sculptured by faint growth lines and sometimes with low collabral folds. The marginal flank forms a rounded corner on its lower part where it continues into the flattened base. The latter is wrinkled by strong axial folds, which cross the sharp margin of the deep umbilicus and continue onto the vertical umbilical flanks, in which all whorls are visible. A very fine spiral liration is present and especially well visible on the whorls in the umbilicus. The aperture is wider than high and of angular outline. Its plane is slightly inclined so that the outer lip projects somewhat beyond the inner lip. The latter covers half of the base of the body whorl and forms the vertical inner flank of the umbilicus. The protoconch measures about 0.3 mm across and consists of 2 whorls. It shows the characteristic twist of the Cassianaxidae that is also found in modern *Epsiscynia.* It takes place from the sinistral embryonic portion into the planispiral, and the begin of dextral coiling within the larval part of the protoconch. The embryonic whorl measures about 0.1 mm in diameter.

Differences: *Cassianaxis riedeli* differs from *Episcynia inornata* by the rounded flank without keel. From the other Heterostropha of the St. Cassian Formation with basically smooth planorboid shell, as present in *Rinaldoconchus, Amphitomaria, Alexogyra* and *Stuoraxis, Cassianaxis* is distinguished by the rounded upper surface connected to a flattened base.

Material: Four individuals from the Pralongia outcrop.

Family Amphitomariidae n. fam.

Diagnosis: The small, planispirally coiled architectonicoids have a sinistral protoconch and one or two angular keels on the flanks of the teleoconch. When there is no free larval stage present within the ontogeny of a species the embryonic shell aquires a planispirally coiled shape like that of the teleoconch. The family is based on the genus *Amphitomaria.* Cretaceous and Tertiary *Neamphitomaria* (BANDEL 1988b) resembles species of the more modern genus *Anomalorbis* PAUL 1991 from the Eocene (PAUL 1991) and unnamed extant species from the sea near Cebu, Philippines (BANDEL 1991a).

Differences: The sinistral protoconch differentiates the Amphitomariidae from the Paleozoic Euomphalidae, where the protoconch is dextral and planispiral and commonly openly coiled. With regard to the teleoconch, shapes of Euomphalidae and Amphitomariidae are very close to each other. Amphitomariidae differ from other Heterostropha from St. Cassian by their planispiral coiling connected to the presence of two keels on the upper and lower flanks.

Genus *Amphitomaria* KOKEN 1897

Genotype: *Euomphalus cassianus* KOKEN 1889 from the St. Cassian Formation.

Diagnosis: The small shell is about 3 mm wide and has planispirally coiled whorls with angular outline and keeled margins. The protoconch consists of an about 0.1 mm wide embryonic shell and a following sinistral larval shell that goes into planispiral coiling in its final portion. The smooth larval shell ends abruptly where the sculptured teleoconch begins.

Differences: The angular outline of the whorls separates *Amphitomaria* from the other Heterostropha of the St. Cassian Formation. *Neamphitomaria* BANDEL 1988 from the Upper

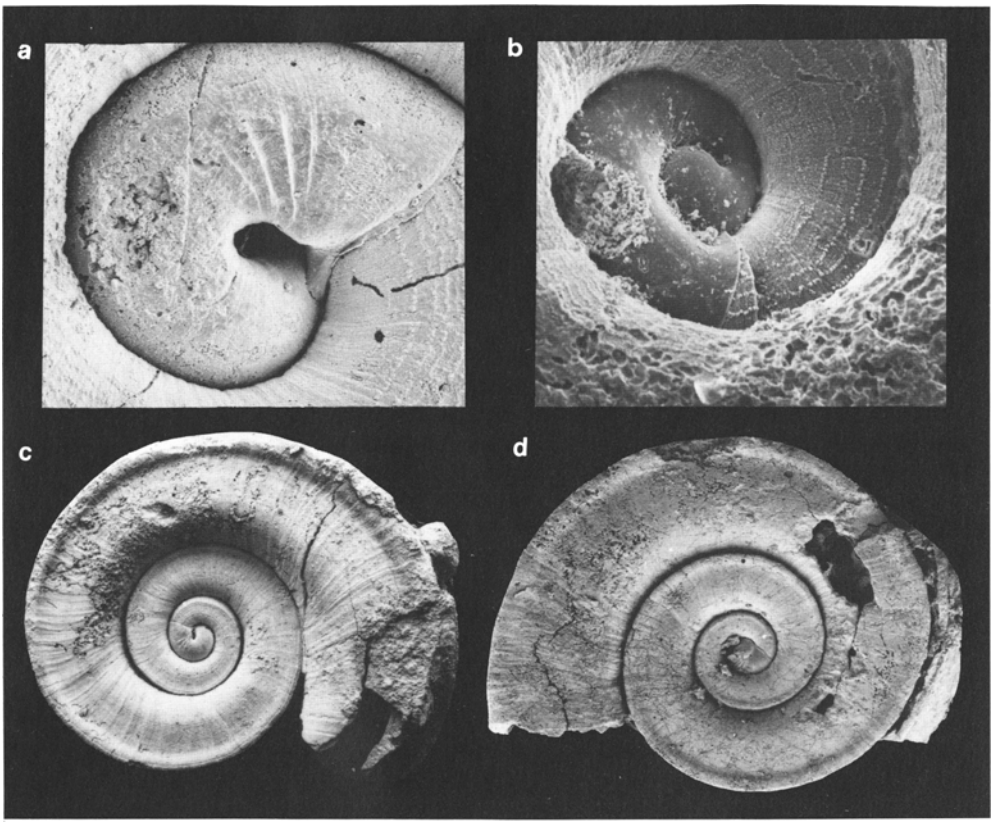


Fig. 11. *Amphitomaria cassiana* (a, c, d) and *Rinaldoconchus bieleri* (b) from Alpe di Specie. a: protoconch, 0.2 mm wide, is sinistral with its umbilicus in the apex of the teleoconch; c: teleoconch with a wide and low umbilicus (width of shell 1.8 mm), d: teleoconch, 1.7 mm wide, with a plane apical side.

Cretaceous (DOCKERY 1993: pl. 35, figs. 1–3) and the Eocene of the USA (BANDEL 1988b: pl. 4, figs. 7, 8) differ in the morphology of the protoconch, which is planispiral and consists of only the embryonic shell.

Amphitomaria cassiana (KOKEN 1889)

Fig. 11 a, c, d

1889 *Euomphalus cassianus* sp. nov. – KOKEN: 416, pl. 14, fig. 2.
1891 *Euomphalus cassianus* KOKEN – KITTL: 227, pl. 4, fig. 23.
1897 *Amphitomaria cassiana* KOKEN – WENZ: fig. 348.
1978 *Amphitomaria* cfr. *cassiana* – ZARDINI: 23, pl. 7, figs. 17, 18.
1980 *Amphitomaria tetracarinata* – ZARDINI: 5, pl. 2, fig. 6.
1985 *Amphitomaria ampezzana* – ZARDINI: 13, pl. 5, fig. 2.
1988 *Amphitomaria cassiana* KOKEN – BANDEL: 5; pl. 1, figs. 1–5; pl. 2, figs. 1, 2, 4.

Description: The general diagnosis of the genus fits this species. The planispirally coiled shell of 3 mm diameter consists of about three whorls of the teleoconch. The shell is biconvex and demonstrates some variability in shape and sculpture. In some individuals the last whorl detaches from earlier whorls (*Amphitomaria tetracarinata* of ZARDINI 1980). Fine spiral lines

may be present or absent, axial striae may or may not appear, and a shallow keel may be present on the basal side. The two lateral keels border the vertical and smooth flank. Growth lines are simple and straight, and whorl diameter is angular with four corners or five when an additional keel appears. The 0.1 mm wide sinistral embryonic shell lies within the larval shell and is only visible through the umbilicus of the teleoconch. The larval shell consists of almost one whorl added to it and measures about 0.2 mm across. Its sinistral coil ends near the end of its whorl and becomes planispiral. Axial folds are present near the umbilicus.

Differences: *Amphitomaria cassiana* differs from *Zardinihelix venustus* (MÜNSTER 1841) by the structure of the shell (not nacreous but aragonitic crossed lamellar) and the morphology of the protoconch (not like that of an archaeogastropod) (BANDEL 1988a, b, 1993a). Very similar euomphaloid species of *Amphiscapha* KNIGHT 1942 from the Upper Carboniferous, and the Permian have an open umbilicus and/or a bulbous protoconch, or they are provided with an archaeogastropod protoconch, quite different from the architectonicoid protoconch of *A. cassiana* (own observations).

Material: About 40 individuals from the Alpe di Specie, 25 from Misurina and over 20 from Campo. Material is deposited with NHM Vienna (1994/191 – Alpe di Specie specimens, 1994/192 – Campo specimens and 1994/193 – Misurina specimens).

Family Stuoraxidae n.fam.

Diagnosis: The teleoconch is minute (up to 1 mm), has rounded whorls and is almost planispirally coiled. It resembles modern members of the Omalogyridae G.O. SARS 1878. But in contrast to these the protoconch is of the planktotrophic type found commonly among Architectonicoidea. The embryonic shell as well as the early larval shell are sinistrally coiled, and in the larval shell coiling becomes planispiral. The larval shell is ornamented by collabral folds.

Differences: The smooth rounded whorls of the small, planispirally coiled teleoconch of Stuoraxidae are similar to that of the Omalogyridae, Hyalogyrinidae WARÉN & BOUCHET 1993 and Xylodisculidae WARÉN 1992. The axially ornamented protoconch distinguishes the Stuoraxidae from all the others.

Genus *Stuoraxis* n.gen.

Etymology: The species is common in the Stuores Alm outcrops and resembles a small *Pseudomalaxis* in general shape.

Genotype: *Stuoraxis lehmanni* from the Stuores Alm above St. Cassian.

Diagnosis: The small shell (about 1 mm) consists of rounded evolute whorls that overlap only slightly onto each other forming a shallow dextral coil with a wide umbilicus. The aperture is almost round, of simple outline and vertically oriented. The protoconch consists of a low conical larval shell of a sinistral coil that twists into the planispiral coil in the final portion of the larval whorl. Here transversal folds are present, and the apertural rim of the pediveliger is thickened.

Differences: Among the heterostrophic species of the St. Cassian Formation *Stuoraxis* and *Alexogyra* are the only almost planispiral species with round whorl diameter without sculpture of the teleoconch whorls. They are distinguished from each other by the axial ornament of the protoconch in *Stuoraxis* that is not present in *Alexogyra.*

Stuoraxis lehmanni n.sp.

Figs. 12a–e, 13c–f, 14c

Etymology: The species in named in honour of NIKOLAUS LEHMANN, who successfully washed individuals of this species from the marls at Stuores meadows in a very cold stream in June 1989.

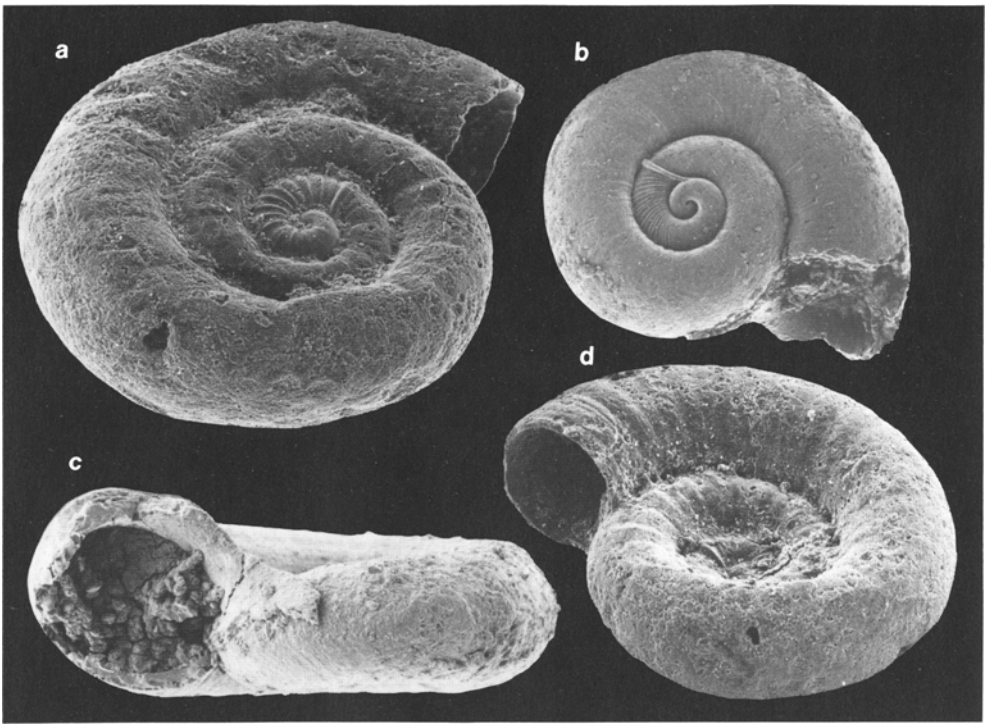


Fig. 12. *Stuoraxis lehmanni* from Misurina (a, d) and Stuores (b, c). a: Apical view with the protoconch seen in detail in Fig. 13f of a 0.9 mm wide fully grown shell seen; d: umbilical side view; b: apical view of a 0.85 mm wide shell with protoconch illustrated in Fig. 13d; c: lateral view.

Holotype: Figured specimen (Fig. 12b) from Stuores deposited in the NHM Vienna (No. 1994/194).
Type locality: Stuores meadows above St. Cassian.
Type horizon: Marls of the Cordevol Member of the early Carnian St. Cassian Formation.

Diagnosis: The generic diagnosis applies to this species. Ornament of the teleoconch consists only of indistinct growth lines. The protoconch has a sinistral embryonic shell and a larval shell that changes into the planispiral coil that is ornamented by axial folds and ends with a thickened apertural rim.

Description: A fully grown shell with three and a half whorls is not quite 1 mm wide and 0.3 mm high. The whorls are rounded and sculptured only by faint growth lines. The apical side of the shell is almost flat, while the lower side is concave with a wide umbilicus exposing all whorls. In the second whorl of the teleoconch growth lines become more irregular and coarse, indicating that the shell was fully grown and the animal had reached its adult stage. The protoconch measures about 0.28 mm across and is a flat, sinistral coil. The embryonic shell measures less than 0.1 mm in width and dips below the apical surface. In the last quarter of the larval whorl, radial folds cross the surface of the shell. They are longer on the apical side than on the umbilical side. In some individuals the axial folds of the larval shell begin earlier and are stronger than in other individuals, but they are always well developed. The aperture of the pediveliger is thickened by a rim that is broadly attached to the surface of the whorl at the inner lip.

Differences: The small size and rounded whorls of *Stuoraxis lehmanni* distinguishes it from *Amphitomaria cassiana*, its smooth teleoconch differs from *Ampezzogyra schroederi*, its

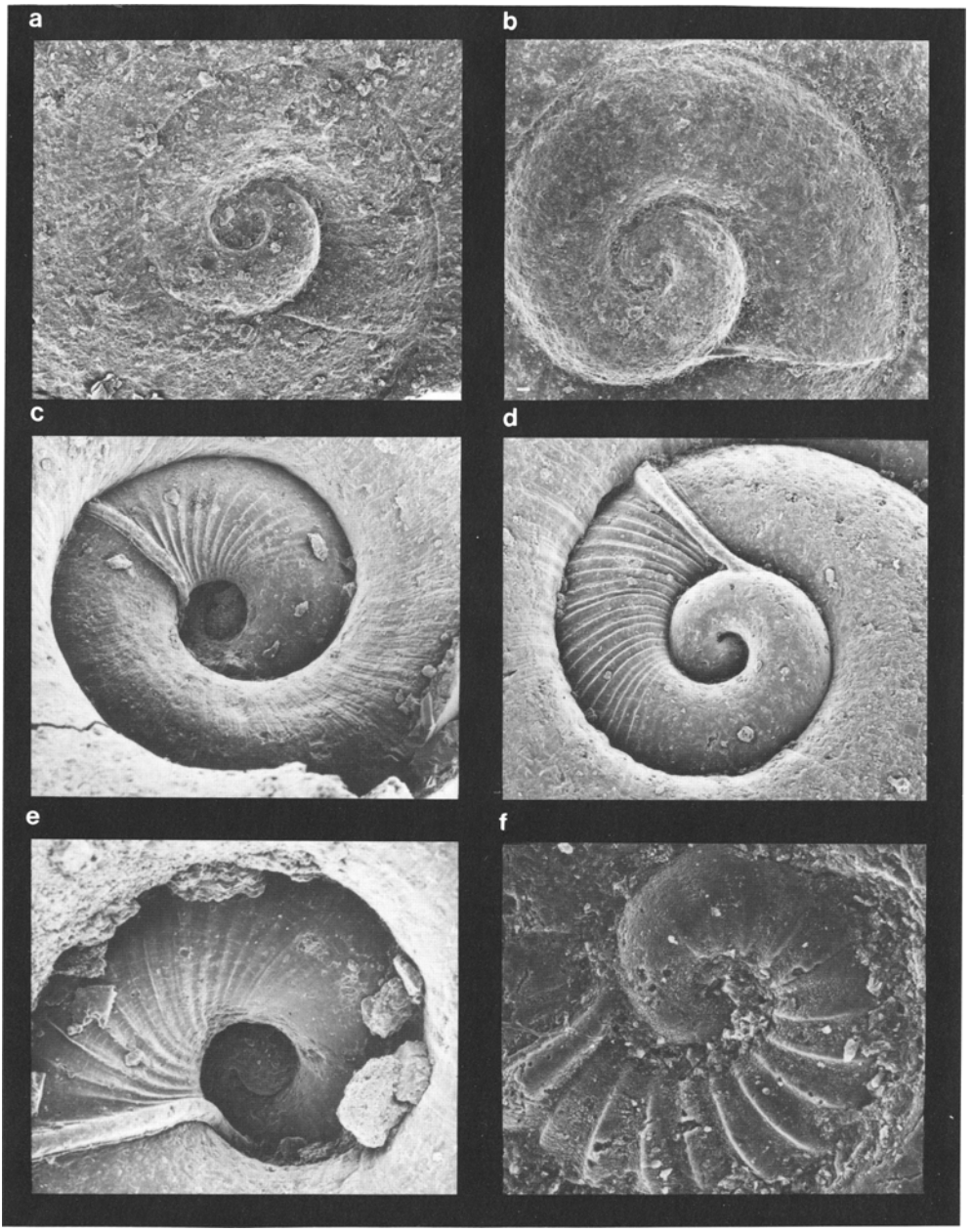


Fig. 13. The protoconch of *Cassianaxis riedeli* from Pralongia (details of Figs. 10a, e) is 0.3 mm wide (a, b). The protoconchs of *Stuoraxis lehmanni* from Stuores (c, d, e) and from Misurina (f) show more or less folds on the larval shell and measure 0.28 mm across.

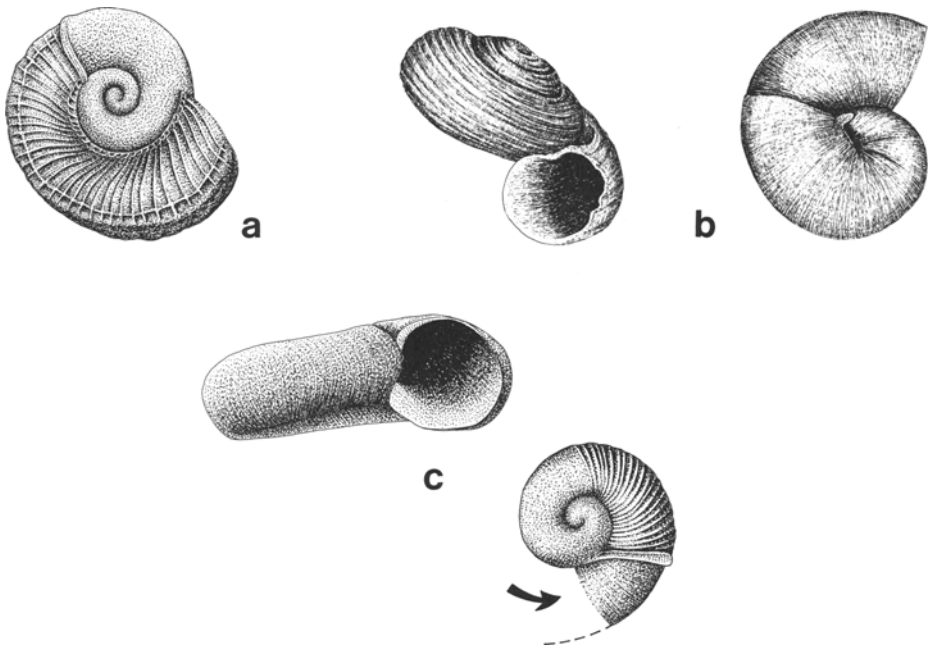


Fig. 14. Drawings of *Stuoraxis lehmanni* (c) with 0.9 mm wide teleoconch and with protoconch and *Rinaldoconchsu ampezzanus* (b) with protoconch and teleoconch (1.2 mm wide and 1 mm high) in comparison to *Pseudomalaxis pateriformis* STEPHENSON 1955 (a) with protoconch and begin of teleoconch (1 mm in diameter) from the Upper Campanian of Mississippi.

ornamented protoconch distinguishes it from *Alexogyra marshalli*, its planorboid low coiling mode differs from that of the higher-spired *Bandellina* and *Carboninia*. Smooth planispiral shells are also noted in the archaeogastropod *Triadoskenea ampezzana* BANDEL 1993 from the St. Cassian Formation, but here the protoconch is that of an archaeogastropod (BANDEL 1993a: pl. 4, figs. 5–7).

Material: About 40 individuals from the Stuores locality, 5 from Dibona, 2 from Alpe di Specie and 1 from Misurina NHM, Vienna (No. 1994/195).

Genus *Ampezzogyra* n. gen.

Etymology: The teleoconch of this small species resembles some sculptured species of *Omalogyra* and it is found near Cortina d'Ampezzo, thus explaining the combination into *Ampezzogyra*.

Genotype: *Ampezzogyra schroederi* from the St. Cassian Formation.

Diagnosis: The small (around 1 mm), planorbid dextral teleoconch has a sinistral protoconch. While the latter is basically smooth, ornament of the teleoconch consists of axial ribs crossed by fine spiral lirae.

Difference: The sinistral protoconch having more than one whorl differentiates *Ampezzogyra* from the archaeogastropod *Sorapisella* BANDEL 1993 from the St. Cassian Formation. The latter has the characteristic archaeogastropod protoconch of less than one whorl (BANDEL 1993a: pl. 4, figs. 1, 3, 4).

Ampezzogyra schroederi n. sp.

Fig. 15a–f

1993 indet. species – BANDEL: 17, pl. 3, figs. 1, 3; pl. 4, fig. 2.

Etymology: Named after MICHAEL SCHRÖDER, who performed a beautiful study of Jurassic gastropods that greatly aided in the present study.

Holotype: Specimen figured in Fig. 15b, f from the Alpe di Specie, deposited at the NHM, Vienna (No. 1994/196).

Type locality: Alpe di Specie north of Cortina d'Ampezzo, Dolomites.

Type horizon: Slump deposits in the St. Cassian Formation of the Cordevol Member, Early Carnian.

Diagnosis: The generic diagnosis applies to this species. The whorls of the small, dextral teleoconch are almost planispirally coiled. Their ornament consists of axial lamellar ribs and fine punctated spiral lirae. The protoconch is sinistral, but its larval portion grades into planispiral coiling.

Description: A shell with 1.2 mm size consisting of a little more than three whorls and probably fully grown. Its maximum width is 0.4 mm and whorls overlap very little onto each other in the planorboid shell. The whorls are well rounded and only a little higher than wide, so that the aperture is of round shape. 20–33 rounded axial ribs ornament each whorl in quite irregular succession and with increasing number on the last whorl. They continue over the rounded flanks and end only in contact to the whorls of the younger shell. Fine spiral lines of punctae cover the shell surface throughout, including the axial ribs. The apical depression is a bit less concave than the wide umbilicus, so that dextral coiling is apparent throughout the teleoconch. The protoconch is sinistrally coiled and consists of 1.5 whorls of about 0.2 mm width. The sinistral embryonic whorl is smooth with a well rounded apex. The larval portion of the whorl may have a few weak folds on its apical side, while the umbilical side has only simple and indistinct growth lines on a smooth background. The aperture of the protoconch is round and simple and a little widened in its final end. Onset of teleoconch sculptures is abrupt.

Material: 1 individual from Dibona, 1 individual from Campo, 3 individuals from Alpe di Specie and 2 individuals from Misurina. The Misurina material is deposited at NHM, Vienna (No. 1994/197).

Family Hyalogyrinidae WARÉN & BOUCHET 1993

Description: The small gastropods have a globular or depressed featureless shell and sinistrally coiled protoconch. The family is based on *Hyalogyrina* with the type *H. glabra* MARSHALL 1988 found off New Zealand on sunken driftwood.

Genus *Alexogyra* n. gen.

Etymology: Named in honor of ALEX NÜTZEL (Hamburg), who helped to find the specimen of a Triassic shell that resembles *Hyalogyra.* The generic name is a combination.

Genotype: *Alexogyra marshalli* from the St. Cassian Formation.

Diagnosis: The protoconch is smooth and has an expanded and thickened aperture. The shell diameter increases rapidly, and the initial part is comparatively small. The teleoconch is of planorbid shape with a plane apical side and rounded umbilical side and wide umbilicus. The aperture is rounded and wider than high.

Difference: The perfectly smooth protoconch is like that found among modern Hyalogyrinidae (MARSHALL 1988: fig. 7f–j) and differs from that of the Stuoraxidae, which have axial folds or ribs. The shell diameter increase differentiates the teleoconch of *Stuoraxis,* which is also smooth. The increase in shell diameter in the protoconch is more rapid than in the Triassic Cornirostridae, which also have a larger and higher teleoconch. Xylodisculidae WARÉN 1992

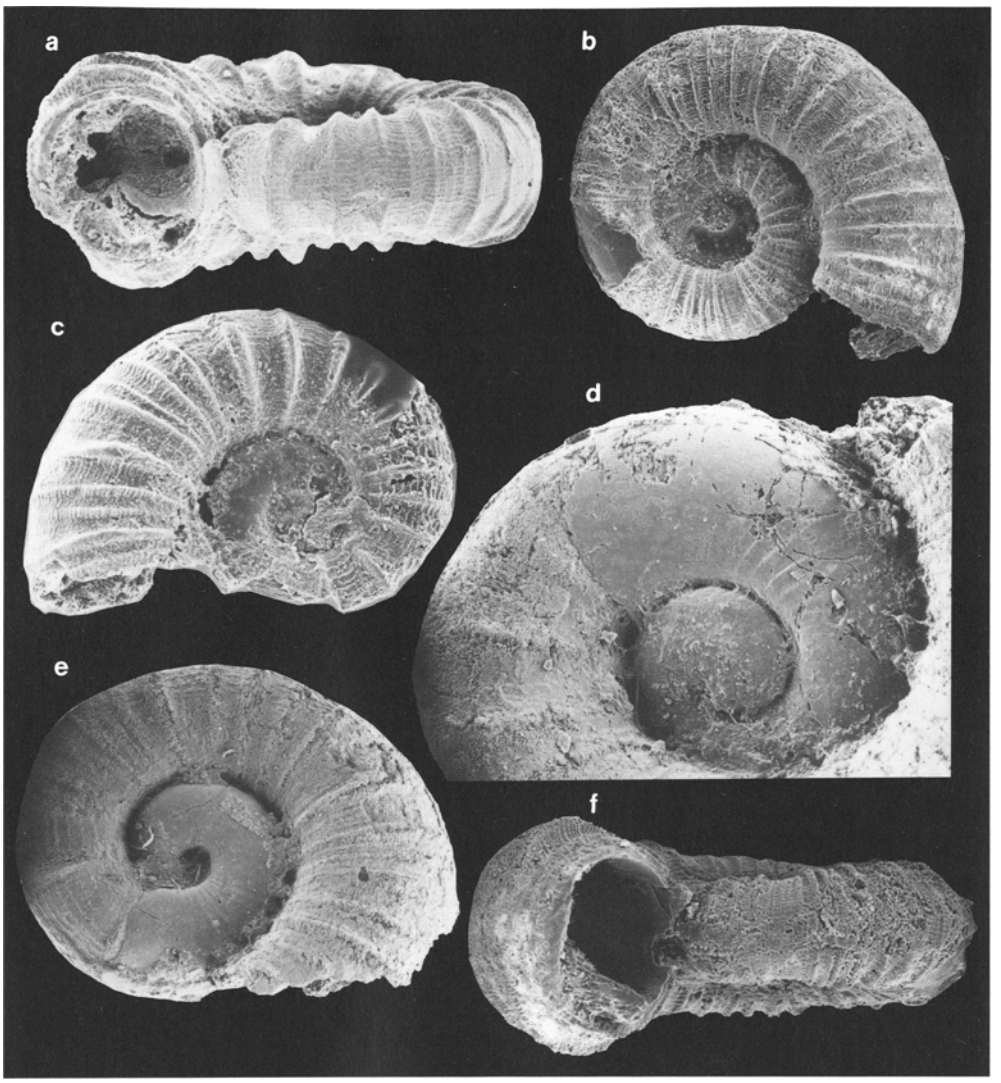


Fig. 15. *Ampezzogyra schroederi* from Specie (a–c, f) and from Misurina (d, e). The holotype (b, f) measures 0.9 mm across (b). The individual in (a) is 0.7 mm wide and the individual in (c) measures 0.5 mm across. d: the sinistral protoconch is 0.22 mm across and in (e) is seen from the umbilical side.

also have a less rapid increase in whorl diameter of the protoconch, and the teleoconch has an angular flank (MARSHALL 1988: fig. 8A–H).

Alexogyra marshalli n. sp.

Fig. 16a, c, d

Etymology: This species of *Alexogyra* is named after our friend BRUCE MARSHALL (Wellington, New Zealand), who described the first *Hyalogyra.*

Fig. 16. *Alexogyra marshalli* from Misurina (a, c, d) and *Bandellina cassiana* from Stuores (b, e, f). a: the protoconch of 0.26 mm in diameter increases rapidly in whorl diameter, has a partly covered initial sinistral portion and ends in an apertural rim. b: in *B. cassiana* the protoconch is of 0.28 mm width, has slowly increasing whorl diameter and sinistral initial portion well developed. c–d: the teleoconch of *A. marshalli* measures only 1.7 mm in width and has a wide umbilicus and flatly rounded apex. e–f: the teleoconch of *B. cassiana* is heliciform and measures about 0.8 mm across.

Holotype: An individual from Misurina deposited in NHM, Vienna (No. 1994/198).
Type locality: Misurina near Cortina d'Ampezzo, Dolomites.
Type horizon: Marls of the Cordevol Member, St. Cassian Formation, Early Carnian.

Diagnosis: The generic diagnosis applies to the species. The smooth protoconch consists of 1.8 whorls, which end in a thickened rim. The teleoconch continues in the same general shape as the protoconch forming two additional dextral whorls. Ornament consists only of growth lines, and flanks are well rounded.

Description: The planorbid shell with a 0.26 mm wide protoconch is 1.7 mm wide and 0.6 mm high with two whorls of the teleoconch. The aperture is rounded, and the inner lip coats the former whorl with a thin callus. The umbilicus is wide and exhibits all former whorls.

Difference: The smooth protoconch differs from the ribbed protoconch found in *Cassianaxis riedeli.* The extant *Hyalogyra* MARSHALL 1988 is larger (more than 2 mm wide), and its protoconch has fewer whorls. *Bandellina* is higher and has a more narrow umbilicus and a more sinistrally coiled protoconch. *Xylodiscula* (MARSHALL 1988) is very similar but has more angular whorls and a more sinistral and tightly coiled protoconch.

Material: One individual from Misurina (holotype), 3 individuals from Dibona (NHM Vienna, No. 1994/199), and 2 further specimen from Alpe di Specie.

Remarks: WARÉN & BOUCHET (1993) consider the Hyalogyrinidae to belong to the Heterobranchia, but on the other hand discuss their place among the Archaeogastropoda. This puzzling jump through the system of the Gastropoda is because of a radula present in the members of that family that they consider as rhipidoglossate since it has more than 7 teeth in each row. Among Heterostropha (= Heterobranchia) the number of teeth within a row of the radula may be regularly 7 as in the Valvatoidea or it may be variable as in the Architectonicidae (BANDEL 1984). There may also be numerous teeth in each row as is the case among many members of the Euthyneura. Since TROSCHEL's (1856) research, this convergence with the radula of the Vetigastropoda with regard to the number of teeth in each row is well known. The sinistral protoconch of the Hyalogyrinidae consists of an embryonic and a larval shell and is thus quite different from the protoconchs of archaeogastropods. A discussion on left or right coiling in archaeogastropod protoconchs, as carried out by WARÉN & BOUCHET (1993), thus, has nothing to do with sinistral or dextral protoconchs in Heterostropha, Neritimorpha, or Caenogastropoda (BANDEL 1982, 1991b, 1992a; HASZPRUNAR 1993).

Superfamily Valvatoidea GRAY 1840
Family Cornirostridae PONDER 1990

Description: A small (diameter about 2 mm) valvatiform teleoconch with simple aperture is connected to a sinistrally coiled protoconch in this group of marine species of Heterostropha. The sinistral protoconch is smooth, consists of an embryonic and a larval shell and is coiled along the same axis as the dextral teleoconch.

Difference: Members of the family Provalvatidae BANDEL 1991 have small littoriniform to almost planorboid shells, as found among the Cornirostridae. They are distinguished from the latter by the protoconch, which coils in the same axis sinistrally as the following dextral teleoconch, but has no larval shell. Provalvatidae could represent the transition from fully marine Cornirostridae to fresh water Valvatidae, which have a planispirally coiled protoconch in modern species as well as among fossil ones (BANDEL & RIEDEL 1994; RIEDEL 1993). Hyalogyrinidae have a more rapid increase in shell diameter during growth (WARÉN & BOUCHET 1993: fig. 39)

Genus *Carboninia* n. gen.

Etymology: Named after the village of Carbonin, which is located below the meadows of the Alpe di Specie (Seelandalpe) where specimens of the taxon were collected in 1989.
Genotype: *Carboninia valvatiforma* n. sp. from the St. Cassian Formation.

Diagnosis: The diagnosis of the family applies to this genus. The small littoriniform shell (2 mm high) is about half as high as wide and has an apical angle that decreases with shell growth. The ornament is formed by simple and indistinct growth lines that reflect the shape of the simple aperture. The latter has rounded anterior and posterior corners. The base is rounded and bears a narrow umbilicus formed by the raised columellar portion of the inner lip. Transition from the early shell into the teleoconch is indistinct.

Differences: *Carboninia* differs from *Bandellina* by its higher shell. Its sinistral protoconch distinguishes it from Triassic species of the Coelostylinidae with similar teleoconchs (BANDEL 1993b). The latter commonly shows fine spiral ornament, which is not found in *Carboninia*. Spiral ribs and a characteristic archaeogastropod protoconch distinguishes species of the genus *Yunnania*, which in size and morphology of the teleoconchs closely resemble *Carboninia* (BANDEL 1993a: pl. 7, figs. 6–8; pl. 8, figs. 1–8; pl. 9, figs. 1–3).

Carboninia valvatiforma n. sp.

Figs. 17a–h, 18a.

Etymology: The *Carboninia* shell is formed like the shell of a high-spired extant *Valvata*.
Holotype: From Alpe di Specie, deposited at the Naturhistorisches Museum, Vienna (No. 1994/200).
Type locality: Alpe di Specie north of the road from Cortina d'Ampezzo to Toblach (Dobbiaco) near Carbonin.
Type horizon: The shallow water slump debris of the Cordevol Member, St. Cassian Formation, Early Carnian.

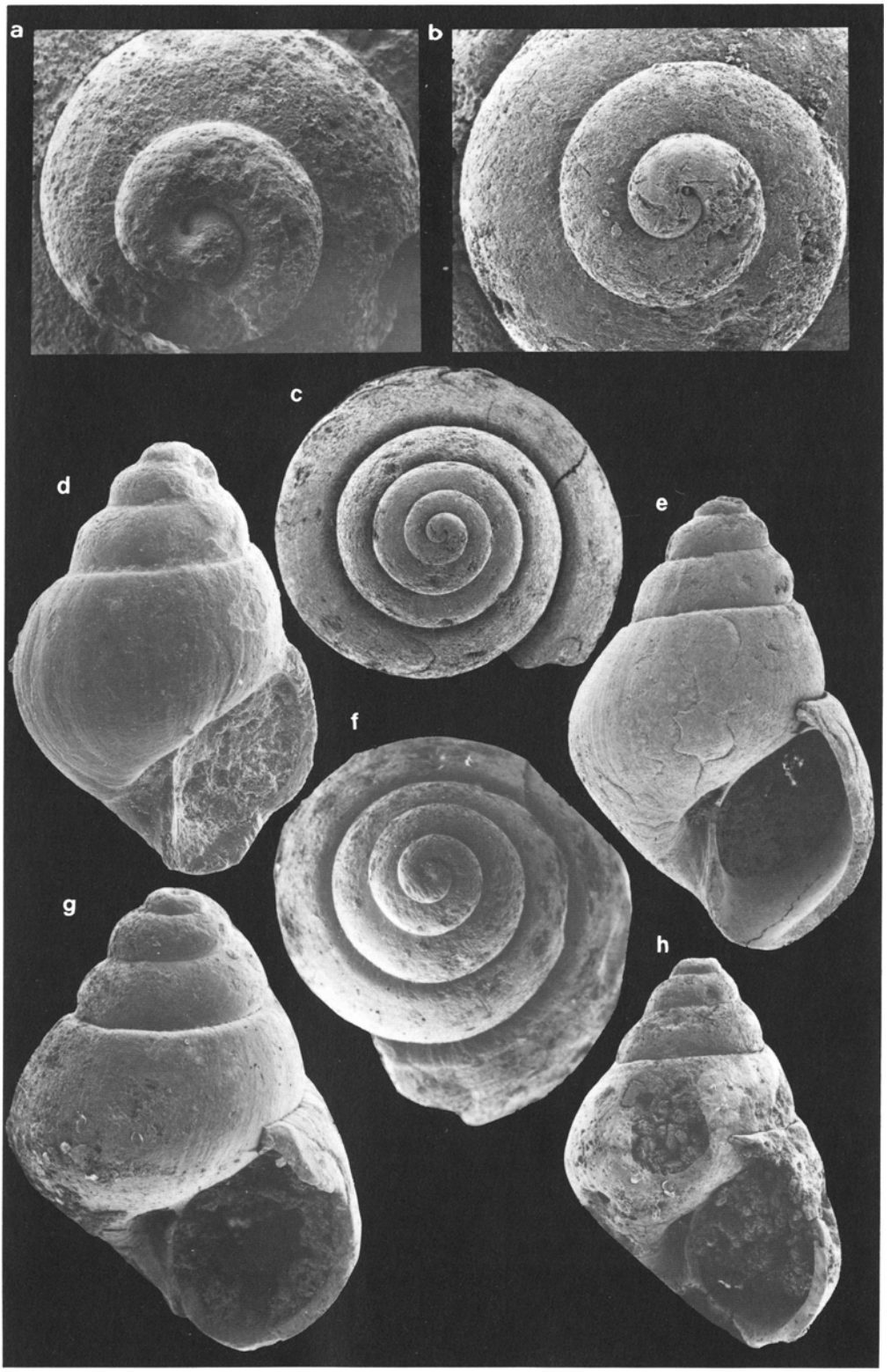
Diagnosis: As for genus.

Description: The small littoriniform shell reaches a size of about 2 mm and a width of about 1 mm. It has almost 6 rounded whorls that are sculptured by indistinct straight growth lines. The aperture is a little higher than wide, has an evenly rounded outer lip and an inner lip with flattened parietal part and straight columellar part, both forming an angle of about 125° with each other. The columellar part of the lip is raised forming a narrow umbilicus. The last whorl is almost twice as high as the spire. The apical angle of the teleoconch amounts to about 45° and is larger in younger stages. The protoconch consists of 1.8 whorls, is sinistral and coils around the same axis as the dextral teleoconch. Change from left into right coil occurs graduationally without folds. Transition form the protoconch into the teleoconch is indistinct and not accompanied by a sculptural change. The embryonic shell is smaller than 0.1 mm and clearly immersed within the apex. The larval shell measures about 0.2 mm in width and its apertural margin merges with the teleoconch and is difficult to spot on some individuals.

Differences: The same as described for the genus. The extant *Hyalogyrina* MARSHALL 1988 with species such as *H. grasslei* WARÉN & BOUCHET 1993 are rather similar, but the increase in whorl diameter is larger and the protoconch has fewer whorls in this species form hydrothermal vents in the Guayamas Basin living at about 2000 m depth (WARÉN & BOUCHET 1993).

Material: Three individuals from Alpe di Specie and 1 individual from Campo (No. 1994/201) at NHM, Vienna.

Fig. 17a–h. *Carboninia valvatiformis* from Misurina (b–e) and from Specie (a, f–h). The protoconch of about 0.2 mm in diameter ends with an indistinct thickening. a: detail of (h); b: detail of (c, e) with about 2 whorls present. d: 1.2 mm high shell; e: 1.4 mm high shell; g: 1.1 mm high shell; h: 1.7 mm high shell (holotype).


a
b
c
d
e
f
g
h

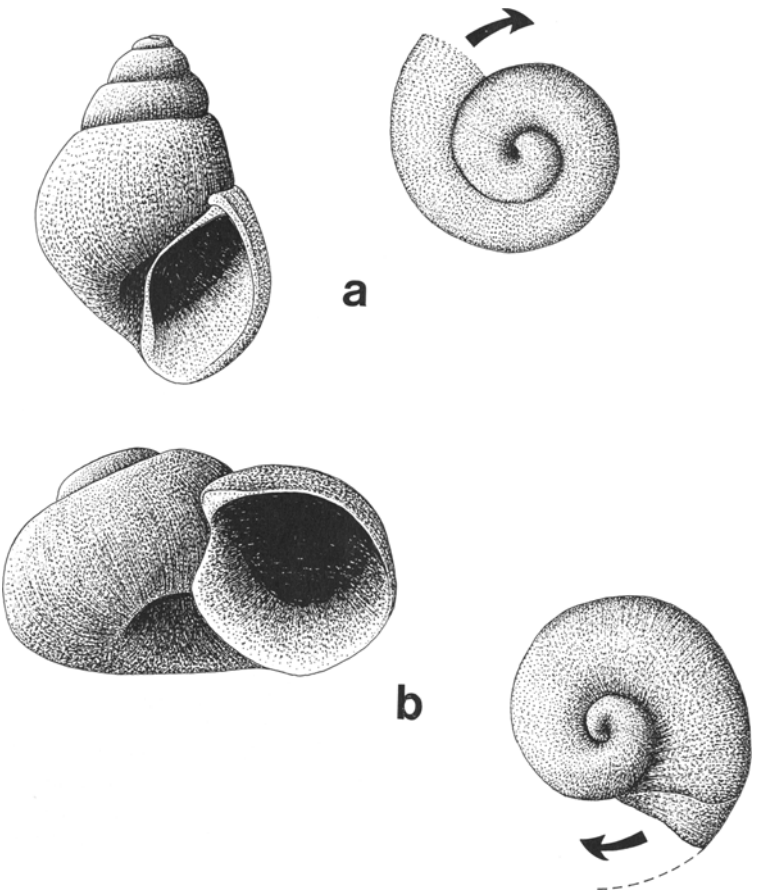


Fig. 18. Drawings of *Carboninia valvatiformis* (a) with teleoconch and protoconch and 1.2 mm high shell and *Bandellina cassiana* (b) with teleoconch and protoconch and 0.8 mm wide shell.

Genus *Bandellina* SCHRÖDER 1995

Genotype: *Bandellina laevissima* SCHRÖDER 1995 from the Lower Cretaceous of Poland.

Description: The low-spired turbinate shell bears an open umbilicus with an angular edge at the base and has convexly rounded whorls separated from each other by deep sutures. Growth lines are weakly inclined, and shell surface is smooth. The rounded aperture has an evenly curving outer and a thickened inner lip. The embryonic shell is sinistrally coiled and submerged into the almost planispiral larval shell that ends with a thickened edge of the aperture of the pediveliger.

Differences: *Bandellina* has a lower spire as *Carboninia* and resembles the extant *Hyalogyra* MARSHALL 1988 that lives on sunken wood in about 1000 m deep water of New Zealand (MARSHALL 1988) but also near hot vents in the deep sea (WARÉN & BOUCHET 1993). *Bandellina* has a protoconch with more whorls, and the increase in shell diameter of the teleoconch is less than in *Hyalogyra*.

Bandellina cassiana n. sp.

Figs. 16b, e, f; 18b

Etymology: The species is from the St. Cassian Formation.
Holotype: The individual illustrated in Figs. 16b, f has been deposited at the Naturhistorisches Museum, Vienna (No. 1994/202).
Type locality: Stuores at the Pralongia ridge above St. Cassian, Dolomites.
Type horizon: Cordevol Member of the St. Cassian Formation at Stuores (Störeswiesen).

Diagnosis: The generic diagnosis applies to this species. The shell with rounded whorls is wider than high (10: 7) and its base is pierced by an open umbilicus. The aperture is round and wide. The protoconch consists of two whorls, which are smooth and change from sinistral coiling into dextral coiling in transition to the teleoconch.

Description: The 0.7 mm wide shell consists of 3.3 whorls, of which two belong to the larval shell. The protoconch is 0.28 mm wide with an 0.1 mm wide embryonic part. A strong increment of growth distinguishes the protoconch from the teleoconch, while with regard to shape of the whorl and ornament no difference is noted. Shell diameter increases rapidly during growth and the aperture is rounded with the inner lip broadly attached to the former whorl and the remaining lip well rounded.

Differences: *B. cassiana* differs from *B. laevissima* by its larger larval shell (two whorls instead of 1 3/4) that measures 0.27 mm in diameter, which is almost the same as found in the genotype (SCHRÖDER 1992, 1995).

Material: Eight individuals from Stuores and 11 from Misurina were studied.

Integration of the data into the system of gastropods

Based on the morphology and formation of the early ontogenetic shell, the living Gastropoda can be divided into 4 subclasses. Archaeogastropoda modify their embryonic shell before it is calcified and produce no larval shell (BANDEL 1982). Neritimorpha have a cup-shaped embryonic shell as do the Archaeogastropoda, but do not modify it before adding a strongly convolute larval shell (BANDEL 1982, 1992a). Caenogastropoda produce an embryonic and larval shell with the same direction of coiling as is present in the adult shell (BANDEL 1975, 1991b). The Heterostropha differ from all these by having an embryonic and larval shell that is coiled in a different direction, usually a sinistral one, from that of the adult shell, which is usually dextral (BANDEL 1992b).

The Heterostropha of Palaeozoic times have been united under the term Opisthobranchia by KNIGHT et al. (1960). They noted a heterostrophic protoconch only in a few Palaeozoic genera such as *Donaldina* KNIGHT 1933 and *Streptacis* MEEK 1872 and placed them in the Pyramidelloidea. Another supposed heterostrophic form from the Carboniferous was placed in the genus *Acteonina* D'ORBIGNY 1850 in the Acteonoidea (= Cephalaspidea) as suggested by DE KONINCK (1842–51). KOLLMANN & YOCHELSON (1976) noted that the heterostrophic protoconch of *Donaldina* had actually only been figured and described with some certainty by DONALD (1898). Its presence in members of this genus has since been confirmed for Carboniferous species by KNIGHT (1931), ANDERSON et al. (1985), YOO (1988, 1994), and HERHOLZ (1992). But the Palaeozoic history of the Heterostropha is still poorly known. Thus *Loxonema monilifera* GOLDFUSS from the Mid-Devonian of the Eifel has a heterostrophic protoconch (BANDEL 1994b). The antiquity of the evolutionary history of the Heterostropha is thus quite evident. Still the rich diversification of this subclass in the Upper Triassic St. Cassian fauna is quite surprising (BANDEL 1994a, b; 1995). With these data in mind and based on ideas of the classification of modern Heterostropha, a taxonomic system can be proposed into which the described species from the St. Cassian Formation can be fitted:

Gastropoda Cuvier 1797
Subclass Archaeogastropoda Thiele 1925
Subclass Neritimorpha Golikov & Starobogatov 1975
Subclass Caenogastropoda Cox 1959
Subclass Heterostropha Fischer 1885

Within the Heterostropha three superorders can be differentiated: the Allogastropoda Haszprunar 1985, Opisthobranchia Milne Edwards 1848, and the Pulmonata Cuvier 1817. Allogastropoda hold the superfamilies Streptacidoidea, Mathildoidea, Pyramidelloidea, Nerineoidea, Architectonicoidea and Valvatoidea.

Of the Streptacidoidea representatives of the family Streptacididae Knight 1931 are known from the Carboniferous and Permian. The *Streptacis* relation with high-spired shell ornamented by fine spiral lirae crossed by fine or lamellar collabral threads or with smooth background is present with numerous species in the Carboniferous (own observation based on material from the USA; Bandel & Nützel in prep.). The protoconch is sinistrally coiled in all cases. The axis of coiling differs among species from more or less the same as that of the teleoconch forming a right angle with it. Change of coiling from sinistrally early portion of the protoconch into the planispiral and dextral mode of coiling occurs within the larval shell before onset of the dextral teleoconch. The aperture may be rounded or extending into a short siphonal notch. The morphology of the protoconch of *Streptacis* has been confirmed for Carboniferous species by Anderson et al. (1985), Yoo (1988, 1994) and Herholz (1992).

The family Ebalidae (Triassic-Recent) is based on *Ebala* Leach 1847 with the type species *Ebala nitidissima* (Montagu). This up to 2.5 mm high slender gastropod lives in 5–50 m depth in the Mediterranean Sea as well as in the Atlantic Ocean as far north as Norway (Rasmussen 1944; Thorson 1946). The planktotrophic larvae hatch with a shell of about 0.12 mm width from the egg mass and produces more than one whorl during larval life before it settles to the ground. It then grows another 6–8 whorls of the teleoconch onto which the protoconch is attached obliquely. Cassian representatives of the family Ebalidae such as *Ebala cassiana, Cassianebala* and *Loxebala* resemble their extant relatives. From the early Jurassic of Northern Germany *Ebala liassica* Schröder 1995 is known and a representative was also noted in the Santonian of Jordan (own observation). The presence of a sinistral protoconch on the Mid-Devonian species *Loxonema moniliforme* Goldfuss (Bandel 1994b: pl. 4, fig. 10) that has traditionally been placed with the genus *Loxonema* indicates that the Ebalidae and Cassianebalidae may represent a very ancient lineage among the Heterostropha and within the Gastropoda in general. The genus *Loxonema* is still problematic since the genotype of Silurian age is known only with a part of its teleoconch (Bandel 1991d) that belongs to a large and fully grown individual.

The family Donaldinidae in Palaeozoic time comprises members of the genera *Donaldina* Knight 1933, *Aclisina* De Koninck 1881 and *Pseudoaclisina* Yoo 1988 from the Carboniferous. They have a sinistral protoconch with axis of coiling either in the same direction or deviation up to 90° from that of the dextral teleoconch. The group is represented by the Upper Triassic *Donaldina (D. zardinii)* and *Neodonaldina (N. elongata* and *N. ampezzana).* Representatives of this ancient group with characteristic shell shape and size are still living in shallow water of modern seas and are anatomically well differentiated from the Pyramidellidae (Bandel 1991a; Bandel et al. in prep.). *Neodonaldina* resembles *Donaldina,* the only difference being that the spiral costae are evenly distributed over the whorl-flank. In *Donaldina,* spiral ornamentation is confined to the lower two-thirds of each whorl. Erwin (1988) described *Donaldina knighti,* a species with rounded whorls and evenly spaced spiral lines, which is similar to *Neodonaldina.* Another species from the same Permian strata was named *Donaldina gracilis* Erwin 1988 and has a smooth upper whorl surface. Each of these species may or may

not belong to the genus *Donaldina.* As their protoconchs are unknown they can also be placed within the caenogastropod unit of the murchisoniids with similar teleoconchs (BANDEL 1993b). Own data on Carboniferous gastropods from the USA indicate that many species of *Donaldina* with sinistral protoconch preserved are present and species resembling *Neodonaldina* can also be found (own observ.). *Donaldina filosa* YOO 1988 and *Donaldina minutissima* YOO 1988 from the Lower Carboniferous of New South Wales have fine spiral lirae and a sinistral protoconch (YOO 1988: pl. 21, figs. 1–6; pl. 22, figs. 10–14) and resemble Triassic species of *Donaldina* and *Neodonaldina.*

Neither the Carboniferous type of the genus *Donaldina* nor *Neodonaldina elongata* from the Upper Triassic can be considered members of the Loxonematoidea, as suggested by WENZ (1938). Regarding their heterostrophic shell they could represent relatives of the Pyramidelloidea as indicated by KNIGHT et al. (1960), but also of the Mathildidae as suggested by HAAS (1953). According to KOLLMANN & YOCHELSON (1976), the larval shell of *Donaldina* figured by KNIGHT et al. (1960: 215, fig. 3b) was originally illustrated by DONALD (1898). It shows an angle of about 90° between the axis of the larval shell and that of the teleoconch. In contrast, *Donaldina* sp. from the Lower Carboniferous of New South Wales has a larval shell inclined at a small angle to the axis of the teleoconch (YOO 1988: figs. 110–111). These published data along with own observations demonstrate that the protoconch of Carboniferous members of the genus *Donaldina* had a species specific morphology. In this regard the species of the Streptacidoidea are like those of the modern Pyramidelloidea (FRETTER et al. 1986).

The superfamily Architectonicoidea GRAY 1850 is here interpreted to hold the families Architectonicidae, Stuoraxidae, Cassianaxidae, Hyalogyrinidae, Xylodisculidae, Amphitomariidae, Omalogyridae and Glacidorbidae. Of all these the Architectonicidae are represented by *Rinaldoconchus (R. ampezzanus, R. bieleri),* which is similar to the modern *Heliacus* (BANDEL 1988b). A gap of knowledge exists with regard to Jurassic species; *Pseudomalaxis* FISCHER 1850 and *Lemniscolittorina* SOHL 1960 are known from the Campanian and Maastrichtian of Tennessee and Mississippi (DOCKERY 1993; own data).

Of the Triassic member of architectonicoids the genera *Stuoraxis (S. lehmanni)* and *Ampezzogyra (A. schroederi)* can not be closely related to a modern form and are thus placed in the family Stuoraxidae. Their ornamented protoconch distinguishes them from the Hyalogyrinidae and the Xylodisculidae of modern times, which live on sunken wood and near hydrothermal vents in the deep sea (MARSHALL 1988; WARÉN 1992; WARÉN & BOUCHET 1993). *Hyalogyra* MARSHALL 1988 has a minute, thin shell with convex smooth whorls and ornament only of growth lines. Teleoconch whorls expand rapidly and there is a wide umbilicus. The protoconch consists of 1.2 sinistral whorls. MARSHALL (1988) noted that *Hyalogyra* is close to *Hyalogyrina,* which has a more turbinate shell with narrow umbilicus. The radulae of these deep water species have many teeth in each row and were thus interpreted as rhipidoglossate, thus archaeogastropod-like, by MARSHALL (1988) and WARÉN & BOUCHET (1993). But within the Heterostropha and in the core group of the architectonicoids, the Architectonicidae, the radulae range from a modified taenoglossate type with 7 or less teeth in each row to a ptenoglassate type with more, sometimes many more teeth in each row (TROSCHEL & THIELE 1866–1893; BANDEL 1984). The radula of the Hyalogyrinidae is close in shape to such a ptenoglossate form.

The radula of the Xylodisculidae represents one of the reduced types with only 6 teeth in each row. *Xylodiscula* MARSHALL 1988 has a minute (less than 2 mm) subdiscoidal umbilicate shell with regularly expanding whorls of the teleoconch, which are evenly rounded or weakly angulated at the shoulders and at the periphery. The whorls are slightly to markedly flattened above the periphery and curve evenly into the umbilicus (MARSHALL 1988). Species with more rounded teleoconchs such as *X. librata* MARSHALL 1988 resemble *Alexogyra,* but the protoconch of *Xylodiscula* has less whorls (1–1.7) and an apertural rim with a varix that spreads

onto the adjacent part of the protoconch. This latter feature is not seen on *Xylodiscula major* WARÉN & BOUCHET 1993 where the protoconch grades indistinctly into the teleoconch. The Glacidorbidae PONDER 1986 represent planispiral, operculate freshwater gastropods from Australia. Anatomically they are intermediate between the Rissoellidae and Pyramidellidae (HASZPRUNAR 1988). These small freshwater species could be the descendants of an independent group of the Heterostropha with low shell shape that developed parallel to the Valvatidae.

The teleoconch of *Ampezzogyra* resembles that of members of the modern Omalogyridae SARS 1878 that have species with smooth teleoconch such as *Stuoraxis* and others with axial ribs such as *Ampezzogyra* (SLEURS 1983, 1985). With regard to the small size Orbitestellidae are also similar, but they differ in ornament and whorl angulations. From the Santonian of Jordan BANDEL (1988) described a species with similar protoconch ornament but also with sculptured embryonic shell. Among modern species no forms are known up to date that can be regarded as total match of the Stuoraxidae of the St. Cassian Formation.

The family Cassianaxidae based on the genus *Cassianaxis (C. riedeli)* is close to the modern genus *Episcynia* MÖRCH 1975 with the type *E. inornata* (D'ORBIGNY 1842) from the Caribbean. The morphology of the radula of *Episcynia* has been studied by PONDER (pers. comm.). According to his observations it distinguishes this genus from members of the other architectonicoideans. *Episcynia* of the Caribbean has a rather inconspicuously heterostrophic larval shell that is almost flat. It has a keeled teleoconch with a large umbilicus.

KOKEN (1897) transferred his *Euomphalus cassianus* KOKEN 1889 to the genus *Amphitomaria.* BANDEL (1988b) redescribed *Amphitomaria cassiana* (KOKEN 1889) and noted that it was not a member of the Euomphaloidea as had been assumed by KOKEN (1889) and repeated by WENZ (1938) and KNIGHT et al. (1960), but rather was a member of the Architectonicoidea with some similarity to the modern genus *Pseudomalaxis* FISCHER 1885. *Amphitomaria* is not related to the genus *Discohelix* as was assumed by KNIGHT et al. (1960) since the latter represents a member of the trochoids (Vetigastropoda, Discohelicidae SCHRÖDER 1995). The Amphitomariidae with *Amphitomaria cassiana* are continuous with Cretaceous and Tertiary members of *Neamphitomaria* BANDEL 1988 and their relations. Possibly related are representatives of the genus *Anomalorbis* PAUL 1991 with the type species *Planorbis hemistoma* J. SOWERBY 1816 from the Eocene of England (PAUL 1991) with very similar representatives from the Upper Cretaceous of the Gosau (Northern Alps) and the Isona Formation (Southern Pyrenees) (HARBECK 1989; BANDEL 1988b). In the shallow sea near Cebu representatives of this group are still alife (BANDEL 1991a), but have not been studied anatomically up to now.

Amphitomaria can be compared with the Upper Cretaceous and Eocene members of the genus *Neamphitomaria* BANDEL 1988, including *N. stantoni* (SOHL 1960) from the SE United States and *N. rotella* (I. LEA 1833) from the Middle Eocene of Claiborne Bluff and Texas (BANDEL 1988b). The genotype of *Neamphitomaria* is *Pseudomalaxis stantoni* SOHL 1960. Its teleoconch is quite similar to *Amphitomaria* while the protoconch differs. Here young hatched as non-planktotrophic, crawling, miniature adults. *Neamphitomaria reticulata* DOCKERY 1993 seems to have had a sinistral larval shell, which would place it nearer to *Amphitomaria* than to *Neamphitomaria* without free larvae (DOCKERY 1993: pl. 32, fig. 5; pl. 37, fig. 12). In *Neamphitomaria* no larval shell is developed, and the teleoconch is secreted right after formation of an embryonic shell. *Neamphitomaria planospira* DOCKERY 1993 has an almost planispirally coiled dextral protoconch (DOCKERY 1993: pl. 35, figs. 4–8) and represents a member of the caenogastropods, demonstrating the presence of convergent small species in the Campanian Coffee Sand fauna, as is still the case in the extant fauna. A further species of *Neamphitomaria* was discovered in the Paleocene of Mathews Landing on the Alabama River in Alabama by DAVID DOCKERY and myself.

The family Cornirostridae based on the genus *Cornirostra* PONDER 1990 from the shallow sea of Australia (PONDER 1991) is considered to belong to the superfamily Valvatoidea

GRAY 1840. It is similar to the genera *Carboninia (C. valvatiformis)* and *Bandellina (B. cassiana)* of the St. Cassian Formation. *Bandellina cassiana* is very similar to *Bandellina laevissima* SCHRÖDER 1995 that lived much later in Lower Cretaceous shallow water environments of Poland. It is a bit lower and has even smoother surfaces than *Carboninia valvatiformis,* and its umbilicus is wide and surrounded by a ridge. Preservation of *B. laevissima* is very good and shows the larval shell to be set off from the teleoconch by an apertural rim and the embryonic shell to be sculptured by a fine network of ridges (SCHRÖDER 1995). The latter feature was not noted in *B. cassiana,* but preservation is not good enough to judge whether it may have been present or not. While *Carboninia* and *Bandellina* were marine gastropods, the species of the possibly related genus *Provalvata* BANDEL 1991 lived in the brackish water facies of the lowermost Cretaceous in Europe (Wealden facies). In the Provalvatidae the protoconch has no larval shell but the embryonic shell of *Provalvata* still has a distinct sinistral appearance (BANDEL 1991c). In modern *Valvata* the embryonic shell is planispirally coiled and the present-day environment is freshwater (RIEDEL 1993). The same type of protoconch is also found in fossil valvatids from the Upper Cretaceous of Ajka in Hungary (BANDEL & RIEDEL 1994). Provalvatidae represent valvatid precursors of Jurassic times, and these in turn may be the offshoots of the Cornirostridae of Triassic time. The family Valvatidae GRAY 1840 based on the genus *Valvata* O. F. MÜLLER 1774 is present with the genus *Ariomphalus* in Campanian freshwater deposits of Ajka in Hungary (BANDEL & RIEDEL 1994).

According to PONDER (1990b, 1991), the members of the family Orbitestellidae IREDALE 1917 are related to Cornirostridae. Valvatoidea of modern times have been considered to consist only of freshwater gastropods until the characteristic pallial tentacle was also discovered in *Cornirostra* and the minute marine representatives of the genus *Orbitestella.* The latter genus can be traced back to the Palaeocene of Danmark (own data).

In the superfamily Mathildoidea DALL 1850 the family Mathildidae DALL 1889 contains Cassian representatives of the genera *Mathilda, Promalthilda, Tirolthilda, Turrithilda* and *Schroederilda.* From it the family Tofanellidae BANDEL 1994 holding the genera *Tofanella, Cristalloella* and *Camponaxis* differs by the shape of the protoconch that changes into the dextral coiling still well within the larval shell and not in transition to the teleoconch. A similar protoconch as found in the tofanellids is also present in the Trachoecidae BANDEL 1994 containing the genera *Trachoecus* and *Vallandroella* but the teleoconch resembles that of a small fusinid neogastropod. In the family Ampezzanildidae BANDEL 1994 a tofanellid protoconch has strong axial ornament and may be provided with an apertural projection. It contains the genera *Ampezzanilda, Cassianilda* and *Stuorilda* (BANDEL 1995). The family Anoptychiidae BANDEL 1994 is based on the genus *Anoptychia* KOKEN 1892 and also holds the genera *Turristylus* BLASCHKE 1905 and *Camponella* from the St. Cassian Formation. In it a mathildid protoconch is connected to a juvenile teleoconch with mathildid ornament (BANDEL 1992b: fig. 27) and a later teleoconch that resembles that of species of the Nerineidae. The superfamily Nerineoidea ZITTEL 1873 appears with the Jurassic and may have developed from representatives of the Anoptychiidae. In the Nerineoidea the families Nerineidae ZITTEL 1873, Nerinellidae PCHELINTSEV 1960 and Itieriidae COSSMANN 1896 had representatives in Jurassic and Cretaceous times.

The superfamily Pyramidelloidea GRAY 1840 was interpreted to hold ancient groups (KNIGHT et al. 1960). But the bulk of the Pyramidellidae appear in the Upper Cretaceous. The Campanian and Maastrichtian Gulf Coast fauna of the USA holds several pyramidellids that have been placed in the genera *Creonella* WADE 1917 and *Lacrimiformia* SOHL 1960. Also the family Amathinidae PONDER 1987 holding limpet-like species appears during the Upper Cretaceous with *Damesia* HOLZAPFEL 1888 with heterostrophic protoconch and neritiform teleoconch (DOCKERY 1993; own data).

The superorder Euthyneura SPENGEL 1881 includes the orders Opisthobranchia MILNE

EDWARD 1848 and Pulmonata. Among the opisthobranch Cephalaspidea FISCHER 1883 Cylindobullinidae WENZ 1947 with genera such as *Cylindrobullina* AMMON 1878 and *Actaeonina* D'ORBIGNY 1847 are present in the St. Cassian Formation (BANDEL 1994a), while Actaeonoidea D'ORBIGNY 1842 and Ringiculoidea FISCHER 1883 begin their history in the Jurassic (SCHRÖDER 1995). Members of the Cylindrobullinidae resemble modern species with conoid shell as found among some of the different groups of the Opisthobranchia. BANDEL (1994a) also included the Dolomitellidae BANDEL 1994 and Zardinellidae BANDEL 1994 among the potential ancestors of the opisthobranchs.

The Pulmonata CUVIER 1797 consist of three suborders, of which only the Archaeopulmonata MORTON 1955 have marine species, while the Basommatophora live in freshwater, and the Stylommatophora live on land. The Archaeopulmonata and family Ellobiidae H. & A. ADAMS 1855 may be connected with the Upper Triassic *Misurinella* BANDEL 1994 that resembles modern *Blauneria* SHUTTLEWORTH 1854 and differs only by the absence of a columellar fold (BANDEL 1994a: pl. 3, fig. 9). If *Misurinella* is not a relative of *Blauneria*, it is certainly a very nice example of close convergence of shell form. Here the protoconch is dextral while the teleoconch is sinistral.

References

ABBOTT, R. T. 1974. American Seashells. – 663 pp., New York (Van Nostrand Reinhold Company).

ANDERSON, J. R.; HOARE, R. D. & STURGEON, M. T. 1985. The Pennsylvanian genera *Orthonema* MEEK and WORTHEN and *Streptacis* MEEK from the Appalachian Basin. – Journal of Paleontology **59**: 1011–1027, Tulsa.

BANDEL, K. 1975. Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). – Abhandlungen der mathematisch-naturwissenschaftlichen Klasse, Akademie für Wissenschaft und Literatur Mainz 1975 (1): 1–133, Mainz.

– 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – Fazies **7**: 1–198, Erlangen.

– 1984. Radulae of Caribbean and other Mesogastropoda and Neogastropoda. – Zoologische Verhandelingen **214**: 1–188, Leiden.

– 1988a. Early ontogenetic shell and shell structure as aid to unravel gastropod phylogeny and evolution. – [In:] PONDER, W. F. (ed.) Prosobranch phylogeny. – Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland. Malacological Review, Supplement **4**: 267–272, Ann Arbor/Mich.

– 1988b. Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? – Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg **67**: 1–33, Hamburg.

– 1991a. Character of the microgastropod fauna from a carbonate sand of Cebu (Philippines). – Mitteilung des Geologisch-Paläontologischen Instituts der Universität Hamburg **71**: 441–485, Hamburg.

– 1991b. Ontogenetic changes reflected in the morphology of the molluscan shell. – [In:] SCHMIDT-KITTLER, N. & VOGEL, K. (eds.) Constructional morphology and evolution: 211–230, Berlin (Springer Verlag).

– 1991c. Gastropods from brackish and freshwater of the Jurassic-Cretaceous transition (a systematic evaluation). – Berliner geowissenschaftliche Abhandlungen **134**: 9–55, Berlin.

– 1991d. Über triassische „Loxonematoidea" und ihre Beziehungen zu rezenten und paläozoischen Schnecken. – Paläontologische Zeitschrift **65**: 239–269, Stuttgart.

– 1991e. Larger gastropod units present in the Triassic of St. Cassian Formation. – [In:] MEIER-BROOK, C. (ed.) Proceedings of the Tenth International Malacological Congress (Tübingen): 497–502, Tübingen.

– 1992a. Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritomorpha. – Paläontologische Zeitschrift **66**: 231–240, Stuttgart.

– 1992b. Die Evolution der Gastropoden aus biologischer und paläontologischer Sicht. – Veröffentlichungen des Übersee Museums, Natur-Wissenschaften **11**: 17–25, Bremen.

– 1992c. Über Caenogastropoda der Cassianer Schichten (Obertrias) der Dolomiten (Italien) und ihre taxonomische Bewertung. – Mitteilungen des Geologischen-Paläontologischen Instituts der Universität Hamburg **73**: 37–97, Hamburg.

– 1993a. Trochomorpha (Archaeogastropoda) aus den St.-Cassian-Schichten (Dolomiten, Mittlere Trias). – Annalen des Naturhistorischen Museums Wien **95**: 1–99, Wien.

BANDEL, K. 1993b. Caenogastropoda during Mesozoic times. – [In:] JANSSEN, A. W. & JANSSEN, R. (eds.) Proceedings of the Symposium Molluscan Paleontology. – Scripta Geologica, Special Issue **2**: 7–56, Leiden.

– 1993c. Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda). – Freiberger Forschungshefte, Paläontologie, **(C)450**: 41–81, Leipzig.

– 1994a. Triassic Euthyneura (Gastropoda) from St. Cassian Formation (Italian Alps) with a discussion on the evolution of the Heterostropha. – Freiberger Forschungshefte, Paläontologie, Stratigraphie, Facies, **(C)452** (2): 41–81, Leipzig.

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

– 1995. Mathildoidea (Heterostropha, Gastropoda) from the Late Triassic St. Cassian Formation. – Scripta Geologica, Leiden **3**: 1–83, Leiden.

BANDEL, K. & NÜTZEL, A. (in prep.). Notes on heterostrophic gastropods from the Palaeozoic.

BANDEL, K.; NÜTZEL, A; RIEDEL, F. & TIEMANN, H. (in prep.). Anatomical notes on an extant species of the Donaldinidae (Streptacidoidea, Allogastropoda).

BANDEL, K. & RIEDEL, F. 1994. The Late Cretaceous gastropod fauna from Ajka (Bakony Mountains, Hungary): a revision. – Annalen des Naturhistorischen Museums Wien **96A**: 1–65, Wien.

BIELER, R. 1985. Die Gattungen der Architectonicidae (Gastropoda: Allogastropoda). Teil 3: *Pseudotorinia, Nipteraxis, Heliacus, Eosolarium.* – Archiv für Molluskenkunde **116**: 89–117, Frankfurt.

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 Societa Veneziana di Scienze Naturali **11**: 151–158, Venezia.

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

BOUCHET, P. & WARÉN, A. 1993. Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda. – Società Italiana Malacologia, Bolletino Malacologico, Supplemento **3**: 579–840, Milano.

DE KONINCK, L. 1842–1851. Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique. – 716 pp., Liège.

DOCKERY, D. T. III, 1993. The streptoneuran gastropods, exclusive of the Stenoglossa, of northeastern Mississippi. – Bulletin of Mississippi Department of Environmental Quality Office of Geology (Jackson) **129**: 1–191, Jackson/Miss.

DONALD, J. 1898. Observations on the genus *Aclisina* DE KONINCK, with descriptions of British species and of some other Carboniferous Gastropoda. – Quarterly Journal of the Geological Society London. **54**: 45–72, London.

ERWIN, D. H. 1988. Permian Gastropoda of the Southwestern United States: Cerithiacea, Acteonacea, and Pyramidellacea. – Journal of Paleontology **62**: 566–575, Tulsa.

FRETTER, V.; GRAHAM, A. & ANDREWS, E. B. 1986. The prosobranch molluscs of Britain and Denmark. Part 9- Pyramidellacea. – The Journal of Molluscan Studies, Supplement **16**: 556–649, London.

FÜRSICH, F. T. & WENDT, J. 1977. Biostratonomy and palaeocology of the Cassian Formation (Triassic) of the southern Alps. – Palaeogeography, Palaeoclimatology, Palaeoecology **22**: 257–321, Amsterdam.

HAAS, O. 1953. The Late Triassic gastropods from Central Peru. – Bulletin of the American Museum of Natural History **101**: 9–328, New York.

HARBECK, K. 1989. Palökologische und mikrofazielle Untersuchungen an Küstensumpfablagerungen aus dem Maastricht bei Isona (Becken von Tremp, Südpyrenäen, Spanien). – Unpubl. Diploma Thesis, Dept. of Geology and Paleontology, University Hamburg: 167 pp., Hamburg.

HASZPRUNAR, G. 1985. The fine morphology of the osphradial sense organs of the Mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). – Philosophical Trnasactions of the Royal Society London, (B) **307**: 497–505, London.

– 1985. Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). – Zoologica Scripta **14**: 25–43, Stuttgart.

– 1988. On the origin and evolution of the major gastropod groups, with special reference to the Streptoneura. – Journal of Molluscan Studies **54**: 367–441, London.

– 1993. The Archaeogastropoda. A clade, a grade or what else? – American Malacological Bulletin **10**: 165–177, Houston, Tex.

HERHOLZ, M. 1992. Mikromorphe Gastropoden aus dem rheinisch-westfälischen Steinkohlerevier (Oberkarbon). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte **1992**: 242–256, Stuttgart.

KNIGHT, J. B. 1931. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier; 2, *Aclisina* and *Streptacis*. – Journal of Paleontology **5**: 1–15, Tulsa.

– 1941. Paleozoic gastropod genotypes. – Bulletin of the Geological Society of America, Special Paper **32**: 1–510, 96 pls., New York.

KNIGHT, J. B.; BATTEN, R. L. & YOCHELSON, E. L. 1960. Systematic descriptions. – [In:] MOORE, R. C. (ed.) Treatise on Invertebrate Paleontology, Part I, Mollusca 1: I169–I351, New York (Geological Society of America), Lawrence/Kans. (University of Kansas Press).

KITTL, E. 1894. Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. Teil III. – Annalen des kaiserlich-königlichen naturhistorischen Hofmuseums **9**: 144–277, Wien.

KOLLMANN, H. A. & YOCHELSON, E. L. 1976. Survey of Paleozoic gastropods possibly belonging to the subclass Opisthobranchia. – Annalen des Naturhistorischen Museums, Wien **80**: 207–220, Wien.

KOKEN, E. 1889. Über die Entwicklung der Gastropoden vom Cambrium bis zur Trias. – Neues Jahrbuch für Mineralogie, Geologie, Paläontologie, Beilagenband **4**: 305–484, Stuttgart.

– 1897. Die Gastropoden der Trias um Hallstatt. – Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt **17**: 1–112, Wien.

LAUBE, G. C. 1868. Die Fauna der Schichten von St. Cassian. – Kaiserliche Akademie der Wissenschaften, Denkschrift **28**: 29–94, Wien.

LEHNERT, H. 1989. Gastropoden aus dem flachmarinen Schelf vor Cozumel, Mexico: Faunenbestand und Verbreitungsmuster. – Diploma Thesis, Universität Erlangen-Nürnberg: Institut für Paläontologie, 96 pp., Erlangen.

MARSHALL, B. A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depth of New Zealand and New South Wales. – Journal of Natural History **22**: 949–1004, Wellington.

MÜNSTER, G. 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. [In:] WISSMANN, H. L. & MÜNSTER, G. Beiträge zur Geognosie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. – Beiträge zur Petrefacten-Kunde, Heft **4**: 152 pp., Bayreuth.

PONDER, W. F. 1990a. The anatomy and relationship of marine Valvatoideans (Gastropoda: Heterobranchia). – Journal of Molluscan Studies **56**: 533–555, London.

– 1990b. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). – Journal of Molluscan Studies **56**: 515–532, London.

– 1991. Marine valvatoideans, implications for heterobranch phylogeny. – Journal of Molluscan Studies **57**: 21–32, London.

PONDER, W. F. & WARÉN, A. 1988. Classification of the Caenogastropoda and Heterostropha – A list of the family group and higher category names. – [In:] PONDER, W. F. (ed.) Prosobranch phylogeny. – Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh, Scotland. – Malacological Review, Supplement **4**: 88–128, Ann Arbor, Mich.

PAUL, C. R. C. 1991. The morphology, palaeoecology, and taxonomic affinities of three British Tertiary species of *"Planorbis"* (Mollusca; Gastropoda). – Tertiary Research **13**: 37–46, Leiden.

RASMUSSEN, F. 1944. Faunistic and biological notes on marine invertebrates I. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening **107**: 207–233, Kopenhagen.

RIEDEL, F. 1993. Early ontogenetic shell formation in some freshwater gastropods and taxonomic implications of the protoconch. – Limnologica **23**: 349–368, Jena, Stuttgart.

SCHRÖDER, M. 1992. Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. – Unpubl. Dissertation, Universität Hamburg.

– 1995. Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. – Palaeontographica, (A) **238**: 1–95, Stuttgart.

SLEURS, W. 1983. The marine microgastropods from the northern coast of Papua New Guinea (Mollusca: Gastropoda). 1. Family: Omalogyridae (with the description of two new species). – Bulletin Institut royal des Sciences Naturelles de Belgique **55**: 1–11, Brussels.

– 1985. Marine microgastropods from the Republic of Maledives; 1. Genus *Ammonicera* VAYSSIÈRE, 1983, with description of four new species (Prosobranchia: Omalogyridae). – Basteria **49**: 19–27, Amsterdam.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. – Meddelelser. Kommisionen for Havnundersgelser, Ser. Plankton, **4**: 1–523, Kopenhagen.

TROSCHEL, F. H. 1856. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification, **1**: 252 pp., Berlin (Nicolaische Verlagsbuchhandlung).

TROSCHEL, F. H. & THIELE, J. 1865–1893. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification, **2**: 409 pp., Berlin (Nicolaische Verlagsbuchhandung).

URLICHS, M. 1994. *Trachyceras* LAUBE 1869 (Ammonoidea) aus dem Unterkarn (Obertrias) der Dolomiten (Italien). – Stuttgarter Beiträge zur Naturkunde, (B) **217**: 1–55, Stuttgart.

WARÉN, A. 1992. New and little-known "skeneimorph" gastropods from the Mediterranean Sea and the Atlantic Ocean. – Bolletino Malacologico **27**: 149–247, Milano.

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, Stuttgart.

WENDT, J. & FÜRSICH, F. T. 1980. Facies analysis and palaeogeography of the Cassian Formation, Triassic, Southern Alps. – Rivista Italiana di Paleontologia **85**: 1003–1028, Milano.

WENZ, W. 1939. Gastropoda, Teil I. – [In:] SCHINDEWOLF, O. H. (ed.) Handbuch der Paläozoologie, Bd. 6: 1639 pp., Berlin.

YOO, E. K. 1988. Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. – Records of the Australian Museum **40**: 233–264, Sydney.

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

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. – 58 pp., Cortina d'Ampezzo.

– 1980. Fossili Cassiani (Trias Medio-Superiore). Primo aggiornamento all' atlante dei gasteropodi della Formazione di S. Cassiano raccolti nella regione dolomitica attorno a Cortina d'Ampezzo. – 16 pp., Cortina d'Ampezzo.

– 1985. Fossili Cassiani (Trias Medio-Superiore). Primo aggiornamento all' atlante dei bivalvi e secondo aggiornamento all' atlante dei gasteropodi con illustrazioni dei gusci che hanno conservato la pigmentazione originaria. Fossili raccolti nella Formazione di S. Cassiano della regione dolomitica attorno a Cortina d'Ampezzo. – 16 pp., Cortina d'Ampezzo.

Annahme des Manuskriptes durch die Schriftleitung am 27. Juli 1995.