

A Devonian member of the subclass Heterostropha (Gastropoda) with valvatoid shell shape

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With 5 figures and 1 table

BANDEL, K. & HEIDELBERGER, D. (2002): A Devonian member of the subclass Heterostropha (Gastropoda) with valvatoid shell shape. – N. Jb. Geol. Paläont. Mh., 2002: 533–550; Stuttgart.

Abstract: The new species *Palaeocarboninia jankei* from the Middle Devonian of the Eifel mountains is the oldest known representative of the gastropod subclass Heterostropha (= Heterobranchia) closely resembling *Carboninia* from the Triassic. It is also close in shape and size to the modern fresh water allogastropod *Valvata*. Regarding its protoconch it is similar to modern marine representatives of the Valvatoidea having a sinistral embryonic shell, a planispiral larval portion and the beginning of dextral coiling with the onset of the teleoconch. Other fossil and modern representatives of the Heterostropha with similar shell are compared with *Palaeocarboninia*.

Zusammenfassung: Mit der neuen Art *Palaeocarboninia jankei* wird der bisher älteste Vertreter der Unterklasse Heterostropha (= Heterobranchia) der Schnecken aus dem Mitteldevon der Eifel beschrieben. Die Zuordnung der in Größe und Form der modernen Süßwasserschnecke *Valvata* ähnelnden Art erfolgt mit Hilfe des Protoconches, dessen embryonaler Teil linksgewunden ist, und der im während der Larvenzeit gebauten Schalenabschnitt planispiral wird, um im Teleoconch rechtsgewunden zu sein. Ein solcher Protoconch charakterisiert die heutigen marinen Vertreter der Valvatoidea, aber auch die Schalen fossiler Vertreter aus dieser Gruppe, besonders die triassische *Carboninia*. Andere Heterostropha mit ähnlicher Schale werden mit *Palaeocarboninia* verglichen.

Introduction

Living gastropod species of the subclass Heterostropha FISCHER, 1885 (= Heterobranchia GRAY, 1840) with planktotrophic larva are marked by a sinistrally coiled embryonic and larval shell and the change in coiling direction into a dextral teleoconch during metamorphosis to benthic life. Heterostrophic coiling in the gastropod shell, according to existing knowledge, appears to have evolved during Devonian times and parallel to the formation of an orthostrophic coiling in the larval shell of the Caenogastropoda. Most other gastropods of that time with an ontogeny that included planktotrophic larvae appear to have had an openly coiled protoconch (FRÝDA & BANDEL 1997, BANDEL & FRÝDA 1999, FRÝDA 1999). An independent evolutionary history of the Heterostropha started a long time ago. The fossil record, for example, in Triassic times presents evidence for a high differentiation of this taxon (BANDEL 1988, 1994 a, b, 1995, 1996). DONALD (1898) described and figured the first somewhat doubtful heterostrophic protoconch of Carboniferous age. The presence of heterostrophic protoconchs has meanwhile been confirmed by KNIGHT (1931), ANDERSON et al. (1985), YOO (1988, 1994) and HERHOLZ (1992) for other Carboniferous species regarded as members of the Allogastropoda HASZPRUNAR 1985. Among these undoubted Heterostropha are the slender multiwhorled and small sized Donaldinidae and Streptacididae with a protoconch attached to the teleoconch in such a way that the axis of coiling of the former forms about an angle of 90° with the axis of coiling of the latter (BANDEL 1997, Pl. 3 fig. 1). But among the Heterostropha the orientation of the sinistral protoconch on the dextral teleoconch is variable. While the axes may deviate within larger taxa, their position on the teleoconch and the angle formed by the coiling axes is fixed within the species. Many species have a protoconch with the same orientation of the coiling axis as present in the teleoconch. In such cases the heterostrophic protoconch is more difficult to detect and, when preservation is not very good, it may not be seen at all. Therefore, KOLLMANN & YOCHELSON (1976) questioned the occurrence of Heterostropha as early as the Devonian. But a recorded protoconch (diameter 0,2 mm) of the Middle Devonian *Loxonema moniliforme* GOLDFUSS, 1844 by BANDEL (1994 a, Pl. 4, figs. 9, 10) seemed to support the thesis of the mid-Devonian existence of Heterostropha. BANDEL (1994 a, 1996, 1997) suggested that it represents the oldest member of the Streptacidoidea (Allogastropoda). But in this case the preservation left some doubts as to the heterostrophan nature of this gastropod. Similarly *Donaldina gigantea* HEIDELBERGER 2001 and *Turridina margaritata* (WHIDBORNE 1892) may represent other potential Middle Devonian members of the Heterostropha (HEIDELBERGER 2001)

because of the external similarity of their teleoconch with Carboniferous species of the Streptacidoidea.

In the newly described taxon there can be no doubt that the protoconch is sinistrally coiled. The embryonic whorl is also quite small as is usually the case in species of the Heterostropha that have a larval shell. In addition, the sinistral protoconch is preserved on a lowly rounded conical small shell of the type that is usually described to belong to the Valvatoidea and more or less closely related allogastropod gastropods but also among the Amphiboloidea of the archaeopulmonate Heterostropha. To date the earliest Valvatoidea are known from the Late Triassic (BANDEL 1996), and the Amphibolidae are known only from extant species.

Material

During the last years, the classical locality "Am Wachtberg" near Soetenich in the Eifel Mountains (Rheinisches Schiefergebirge, Germany), described earlier by KIRCHNER (1915), provided the opportunity to study micromorph gastropods belonging to a Middle Devonian, (Givetian) fauna. It yielded, among other interesting material (HEIDELBERGER & BANDEL, 1999; HEIDELBERGER, 2001), a well preserved specimen that demonstrates the heterostrophic protoconch in good preservation.

The studied micromorphic gastropods from the quarry "Am Wachtberg" (Sötenicher Mulde, Nordeifel, MTB Mechernich, R ²⁵40 000 / H ⁵⁵98 700) were collected from the limestone of the Cürten strata, Scheid Member, Set γ (PAULUS, 1961; BECKER, 1969; LÜTTE 1991; LÜTTE, pers. comm.). They were photographed with a Scanning Electronic Microscope (SEM). The material is deposited at the Senckenberg Museum in Frankfurt/M.

Table 1. Subdivisions of Givetian strata in the quarry "Am Wachtberg" near Soetenich (simplified, according to the stratigraphical nomenclature in RIBBERT, 1985; WEDDIGE, 1996).

Middle Givetian	Kerpen stata
Lower Givetian	Rodert strata Dreimühlen strata Cürten strata Loogh strata
Upper Eifelian	

Systematic paleontology

Subclass Heterostropha FISCHER 1885
Order Allogastropoda HASZPRUNAR 1985

Based on Recent gastropods the following taxa are considered:

Superfamily Valvatoidea GRAY 1840

Description: The shell is trochiform to discoidal, variously ornamented with a heterostrophic protoconch that coils sinistrally around the same axis as the dextral teleoconch. The aperture is simple.

Included are the fresh water Valvatidae and their fossil counterpart the Provalvatidae, as well as the marine Cornirostridae with a possible relation to the similarly shaped Hyalogyrinidae and Xylodisculidae, and the also marine but planispirally shaped Orbitestellidae.

Family Cornirostridae PONDER 1990

Description of the shell: In the marine cornirostrids a small (about 2 mm diameter), depressed trochiform smooth, usually umbilicate "valvatiform" teleoconch with simple aperture is connected to a sinistrally coiled protoconch. The sinistral protoconch is smooth, consists of embryonic and larval shell and is coiled along the same axis as the dextral teleoconch. The family is based on *Cornirostra* PONDER 1990 from the shallow sea of Australia.

Genus *Palaeocarboninia* n. g.

Derivatio nominis: Named after the Triassic genus *Carboninia* BANDEL 1996 and its occurrence in the Palaeozoic

Diagnosis: The shell is rather small (up to 2 mm). The valvatiform, smooth teleoconch is dextrally coiled along the same axis as the sinistrally coiled smooth proto-

Fig. 1. *Palaeocarboninia jankei* n.g. n.sp., apertural view of a paratyp (1,2 mm high, 1,08 mm wide) from Soetenich.

Fig. 2. *Palaeocarboninia jankei* n.g. n.sp., apical view of the holotyp (1 mm high, 0,9 mm wide) from Soetenich.

Fig. 3. *Palaeocarboninia jankei* n.g. n.sp., apical view, detail of the heterostrophic protoconch (diameter 0,07 μ m); same specimen as on fig. 2.

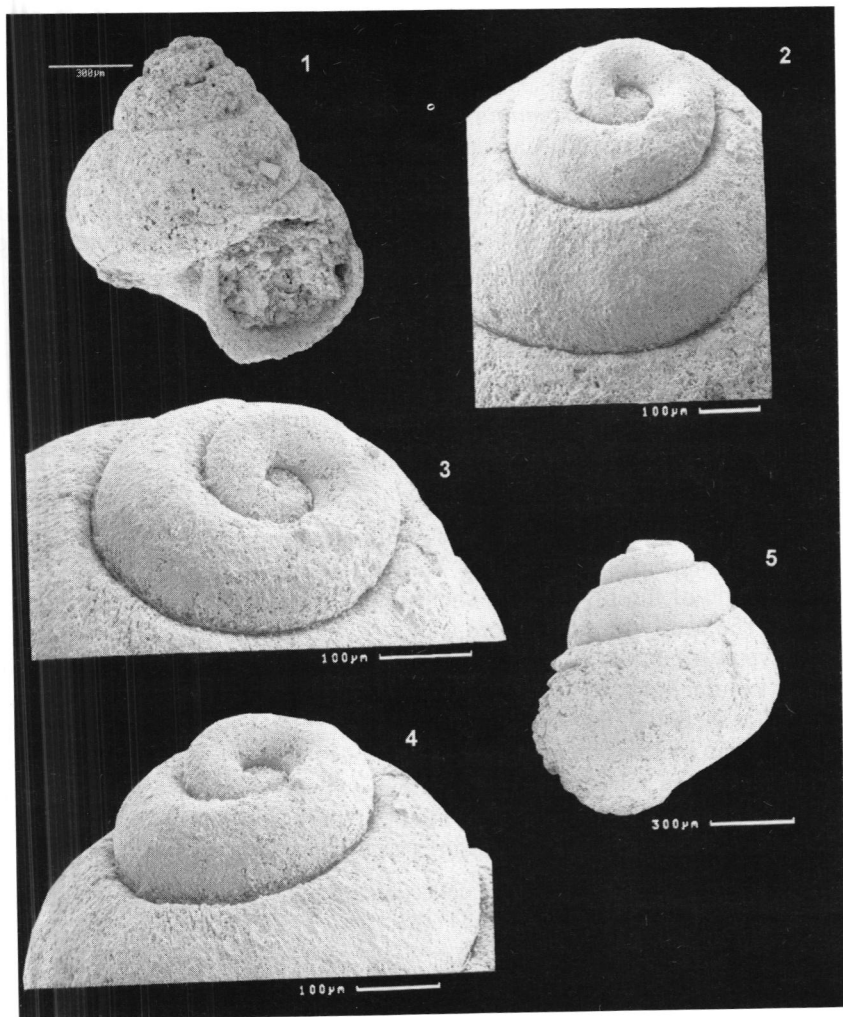


Fig. 4. *Palaeocarboninia jankei* n.g. n.sp., apical view, different view on the apex; same specimen as on fig. 2.

Fig. 5. *Palaeocarboninia jankei* n.g. n.sp., lateral view of the protoconch; same specimen as on fig. 2.

conch consisting of an embryonic and a larval shell of about 1,5 whorls. The diameter of the first protoconch whorl is less than 0,1 mm. The genotype is *Palaeocarboninia jankei* n. sp.

Discussion: *Palaeocarboninia* is distinguished from *Carboninia* BANDEL 1994 from the Triassic St. Cassian Formation by a less elevated spire and a deeper impressed embryonic whorl. *Bandellina* SCHRÖDER 1995 from the Cretaceous of Poland has a much more depressed shell. *Palaeocarboninia* may represent the oldest genus of the family Cornirostridae and one of the first Heterostropha observed in Devonian times.

Palaeocarboninia jankei n. sp.

Derivatio nominis: Named in honour of Eberhard JANKE (Elsdorf, Germany) who made his excellent collection of Devonian microgastropods available to us.

Diagnosis: The diagnosis of the genus applies.

Description: The littoriniform shell is 1 mm high and 0,9 mm wide. It has 4,5 convexly rounded smooth whorls sculptured only by indistinct growth lines. The rounded apex occupies half the height of the last whorl. The pleural angle of the fully grown shell is about 70°. The sutures are clearly incised. The nearly round aperture is only slightly wider than high. Its outer lip is evenly rounded, the inner lip consists of a short parietal part and a straight columellar part. The umbilicus is narrow and bordered by the raised columellar section of the inner lip. The sinistral smooth protoconch measures about 0,2 mm in diameter and consists of about 1,5 whorls coiling around the same axis as the teleoconch. It is immersed within the apex and its end is demarcated by a slight increase in shell width and the begin of dextral coiling. The embryonic whorl measures a little less than 0,1 mm in width.

Holotype: *Palaeocarboninia jankei* collection E. JANKE, deposited in the Senckenberg Museum Frankfurt/M (SMF XII 3472).

Locus typicus: Soetenich, quarry "Am Wachtberg", Eifel, Germany.

Stratum typicum: Cürten strata (Early Givetian, Late Middle Devonian).

Discussion: The differences between the Devonian and Triassic members of the Cornirostridae are minute. *Palaeocarboninia* is more lowly coiled and has a wider pleural angle than *Carboninia*. It unites a dextrally coiled teleoconch consisting of rounded smooth whorls with a sinistrally coiled protoconch that is immersed in the apex of the teleoconch. Also apertural shape and the narrow umbilicus are similar in *Palaeocarboninia* and *Carboninia*, as are the protoconchs with embryonic whorl measuring about 0,1 mm and larval shell of about 0,2 mm in diameter. The similarity proves definitely that heterostrophic gastropods existed at least since the Middle Devonian. The

shells are in general of a small size (1-2 mm), as are those of the modern species here considered related, *Cornirostra* and *Tomura*.

Review of fossil and Recent taxa that can be related to *Palaeocarboninia*

To analyze the position of *Palaeocarboninia* within the evolution of the Heterostropha, a comparison with similar fossil and Recent taxa is needed.

Comparison with fossil Heterostropha

Genus *Carboninia* BANDEL 1996

Carboninia is based on *C. valvatiforma* BANDEL 1996 from the Late Triassic (Ladinian-Carnian) St. Cassian Formation (BANDEL 1996, Figs. 17a-h). Its about 2 mm high littoriniform shell is about half as high as wide and has an apical angle that decreases with shell growth. It has almost 6 rounded, smooth whorls and its aperture is a little higher than wide. It has an evenly rounded outer lip and an inner lip with flattened parietal part and straight columellar part. The columellar part of the lip is raised forming a narrow umbilicus. The base is rounded. The smooth protoconch consists of 1.8 whorls, is sinistral and coils around the same axis as the dextral teleoconch, transition into the teleoconch is indistinct. The embryonic shell is smaller than 0,1 mm, clearly immersed within the apex and the larval shell measures about 0,2 mm in width. From the mid Jurassic of Poland GRÜNDEL (1998, Pl. 5, figs. 60, 61, Pl. 7, fig. 94) described *Carboninia miniperforata* GRÜNDEL 1998 with an almost 0,4 mm large protoconch that has 1,75 whorls. This Jurassic species closely resembles the Triassic type but has a larger protoconch.

Genus *Bandellina* SCHRÖDER 1995

The genus is based on *B. laevissima* SCHRÖDER 1995 from the Lower Cretaceous of Poland and consists of a low spired turbinat shell that bears an open umbilicus with an angular edge to the base. Its convexly rounded, smooth whorls are separated from each other by deep sutures. 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. From the Campanian of Jordan (Amman Formation) a *Bandellina* is preserved (own data) that is just like the Triassic and the Jurassic

species of the genus with an about 2 mm large shell that consists of four whorls and has the characteristic protoconch.

Genus *Doggerostr*a GRÜNDEL 1998

GRÜNDEL (1998, Pl. 5, figs. 56-59) noted that the Early Cretaceous type species of *Bandellina* differed from a mid Jurassic species with otherwise very similar shell shape by having an umbilical corner and, therefore, he created the new genus *Doggerostr*a GRÜNDEL 1998 with the type *D. riedeli* GRÜNDEL 1998 from the mid-Jurassic of Poland. Accordingly *Bandellina cassiana* BANDEL 1996 from the Dolomites which also has a cornered umbilicus was placed with this genus and called *Doggerostr*a *cassiana*. It has a 0,7 mm large shell wider than high and consisting of 3,3 whorls of which two belong to the larval shell. Here the protoconch consists of two whorls which are smooth and change from sinistral coiling into dextral coiling in transition to the teleoconch. It is 0,28 mm wide with a 0,1 mm wide embryonic part. A strong increment of growth distinguishes the protoconch from the teleoconch, while in regard to shape of the whorl and ornament no difference is noted (BANDEL 1996, Figs. 16, b, e, f).

Genus *Alexogyra* BANDEL 1996

Alexogyra is based on the Late Triassic *A. marshalli* BANDEL 1996 from St. Cassian Formation (BANDEL 1996, Figs. 16 a, c, d). It has a smooth sinistral protoconch in which the embryonic shell lies below the larval whorl, partly hidden by it. The protoconch consists of 1,8 whorls of 0,26 mm in width that is expanded and thickened at its aperture. The dextral teleoconch is of lowly conical, almost planorbid shape with plane apical side, rounded umbilical side, and wide umbilicus. It measures about 1,7 mm in width, 0,6 mm in height, and consists of two whorls. The aperture is rounded and wider than high. The umbilicus is wide and shows all former whorls. A very similar Jurassic *Alexogyra magna* was described by GRÜNDEL (1998, Pl. 4, figs. 52-54, Pl. 5, fig. 55) with lowly trochospiral shell and almost 0,3 mm large protoconch that consists of 1,5 whorls.

Genus *Provalvata* BANDEL 1991

The genus is based on *P. helicoides* (de LORIO 1865) from the brackish water deposits of the Jurassic-Cretaceous transition of the Jura Mountains. The shell is of *Valvata*-like shape with round aperture and wide umbilicus. The protoconch grades indistinctly into the teleoconch but has a sinistral twist in its initial portion (BANDEL 1991, Pl. 3, figs. 8-15). The 5 whorls of

the shell form a low discoidal spire that is almost as high as wide (2 mm) and the protoconch measures almost 0,2 mm with its first, embryonic whorl.

Genus *Arieomphalus* BANDEL & RIEDEL 1994

The genus is based on *A. varicatus* (TAUSCH 1886) from the Santonian of Ajka in Hungary with a shell size of 2-3 mm and a planorbid, dextral conch with 3 to 4 whorls. The teleoconch has 7 to 8 varices, which are regularly arranged, and the whorls may be angulated or not. The protoconch consists of about one whorl that is 0,3 mm wide and sculptured very similarly to that of Recent *Valvata* (BANDEL & RIEDEL 1994, Pl. 14, figs. 1-3).

Remarks on the fossil species resembling *Palaeocarboninia*

Carboninia differs from *Bandellina* and *Doggerostra* by its higher shell, and *Palaeocarboninia jankei* could be placed between these based on the shell shape. *Bandellina* resembles the extant *Hyalogyra*, but has a protoconch with more whorls, and the increase in shell diameter of the teleoconch is less than in *Hyalogyra*. *B. cassiana* differs from *B. laevissima* by its larger larval shell (two whorls instead of one and three-quarters) that measures 0,27 mm in diameter, which is almost the same as found in the genotype (SCHRÖDER 1995). The extant *Hyalogyrina* is rather similar, but the increase in whorl diameter is larger, and the protoconch has fewer whorls. The Triassic genus *Alexogyra* could be included in the Hyalogyrinidae as suggested by BANDEL 1996. *Provalvata* with its small littoriniform to almost planorbid shell can be distinguished from Recent *Cornirostra* and fossil *Palaeocarboninia*, *Carboninia*, *Bandellina*, *Doggerostra*, and *Alexogyra* by the protoconch, which coils in the same axis in a sinistral way as the following dextral teleoconch, but has no larval shell. *Valvata*, in contrast, has a planispirally coiled protoconch (RIEDEL 1993). The earliest valvatid with protoconch known is represented by *Arieomphalus varicatus* and its planispiral protoconch is characteristic of the valvatids (RIEDEL 1993).

Comparison with living species

Family Valvatidae GRAY 1840

The family consists predominantly of members of the genus *Valvata* O. F. MÜLLER 1774 with characteristic planispiral embryonic shell that shows no sinistrality. According to WENZ (1938) valvatids have usually a small to very small thin shell that is lowly trochospiral to planorbid in shape with open umbilicus with few rounded whorls that may be smooth or bear spiral lirae

or more rarely spiral ribs. The aperture is round and thin and closed by a multispiral round operculum with central nucleus. The characteristic genus is *Valvata*.

Genus *Valvata* O. F. Müller 1774

The type of the genus is *Valvata cristata* (O. F. MÜLLER 1774) from central Europe. The embryonic shell of *Valvata* was described by HADZISCHE et al. (1976) and RIEDEL (1993). *Valvata cristata* has a shell with a maximum diameter of about 4 mm and with all 4-5 whorls almost in one plane with flattened apical side and wide umbilicus on the base. The whorls meet only at their periphery and the aperture is circular. The closely related *Valvata piscinalis* O. F. MÜLLER 1774 that also lives in many ponds and lakes in Europe, has a trochospiral and moderately high shell with rounded whorls and narrow umbilicus. Shell size may be up to 5 mm high and 3-5 mm broad and the aperture occupies about 50 % of total shell height.

Remarks: In *Valvata* the gill has a characteristic shape and orientation in the pallial cavity (RATH 1988) with a characteristic pallial tentacle. Also the morphology of the sperm relates the group with the Allogastropoda (HEALY 1990, 1993). The taenioglossate radula of *Valvata* is an interesting character that appears to unite the species of this genus as well as most or all of its marine counterparts in the Cornirostridae with the caenogastropods, or is convergent to them regarding the radula. In this respect it is also interesting to remark that the radula of *Valvata* resembles a rather basic type found among Caenogastropoda with little modified radula (BANDEL 1984).

Family Cornirostridae PONDER 1990

The Valvatoidea based on the Valvatidae according to PONDER (1991) also include the marine Cornirostridae and the Orbitestellidae, which represent minute discoid gastropods. Marine members of the valvatoids have been described by PONDER (1990, 1991), WARÉN et al. (1993), FUKUDA & YAMASHITA (1997), BIELER et al. (1998).

Genus *Cornirostra* PONDER 1990

Here a small, smooth, depressed-trochiform shell with rounded whorls, a simple aperture and an open umbilicus is found. The genus is based on *Microdiscula pellucida* LASERON 1954 from the eastern coast of Australia (PONDER 1990).

BIELER et al. (1998, Figs. 1-4) described a species from southern Florida as *Cornirostra floridana* BIELER & MIKKELSEN 1998. It has an about 2 mm wide and high shell with a little more than three rounded and smooth whorls and apical angle of about 110°. The base is umbilicate and rounded as well. The aperture is simple continuous, rounded and oblique. The protoconch consists of 1,2 whorls and measures 0,18 mm in width. Its initial portion is sinistral and ornamented with a reticulate wrinkle pattern.

Genus *Tomura* PILSBRY & MCGINTY 1945

The 1,2 mm wide and 0,8 mm high shell has a relatively large aperture and small umbilicus that is accompanied by an edge. The genotype *Vitrinella bicaudata* PILSBRY & MCGINTY 1946 lives under stones in the intertidal area of southern Florida (ABBOTT 1974).

Tomura bicaudata has as characteristics a two-tailed foot (ABBOTT 1974) as is also found in *Cornirostra*, but differs from the latter by a smaller size and by having an edge around the umbilicus (PONDER 1990). BIELER et al. (1998, Figs. 14-17) noted the difference of their *Cornirostra floridana* in regard to *Tomura* as well. But since that time Mediterranean (WARÉN et al. 1997) and Japanese (FUKUDA & YAMASHITA 1997) species have been included in this genus and they do not all have the umbilical edge. WARÉN et al. (1993) placed the Mediterranean *Oxystele depressa* GRANATA 1877 into the genus *Tomura*. According to the shape of the foot it could belong here, but the shell has quite different shape and ornament, so that it should represent a different genus.

Remarks: A very similar difference in the umbilical shape as noted between *Cornirostra* and *Tomura* was used by GRÜNDEL (1998) to separate the genus *Doggerostr*a from the genus *Bandellina*, the first having a simple umbilicus and the second a ridged umbilicus.

Genus *Noerrevangia* WARÉN & SCHANDER 1993

The shell is like that of the type of *Tomura* with a wide umbilicus but its radula resembles that of *Hyalogyra* with more than 7 teeth in each row. The protoconch measures 0,27 mm in diameter and consists only of the embryonic whorl. The genus is based on *N. fragilis* WARÉN & SCHANDER 1993 from the northern Atlantic Ocean.

Remarks: It cannot be told from the description of WARÉN et al. (1993, Figs. 7-17) why they placed *Noerrevangia* with the Cornirostridae which have a basically taenioglossate radula and not with the Hyalogyrinidae with a radula having more than 7 teeth in each row as is the case in *Noerrevangia*.

Lecithotrophic early ontogenetic development and the resulting type of a simplified protoconch distinguish the shell of the type of this genus.

Family Hyalogyrinidae WARÉN & BOUCHET 1992

Genus *Hyalogyra* MARSHALL 1988

The extant *Hyalogyra* is more than 2 mm wide, and its protoconch has few whorls (LEWIS & MARSHALL 1996, Figs. 4 G, H). The shell is a little more depressed than that of *Hylogyrina* and *Xenoskenea*. The type species is *H. expansa* from the deep water near New Zealand living on sunken driftwood (MARSHALL 1988).

Genus *Hyalogyrina* MARSHALL 1988

The globular or depressed featureless shell has a sinistrally coiled protoconch. The genotype is *Hyalogyrina glabra* MARSHALL 1988 found off New Zealand on sunken driftwood. The extant *Hyalogyrina* with species like *H. grasslei* WARÉN & BOUCHET, 1993 lives near hydrothermal vents in the Guayamas Basin in about 2000 m depth (WARÉN & BOUCHET 1993).

WARÉN et al. (1997) described as new species *Hyalogyrina amphorae* WARÉN, CAROZZA & ROCCHINI 1997 from the deeper water of the western Mediterranean Sea. The holotype of this species, according to their illustrations, represents a member of the Heterostropha, while they also include in their species description individuals (WARÉN et al. 1997 Figs. 9, 15, 16), which are definitely members of other species and even belong to a different subclass of the Gastropoda, such as in Fig. 16 which shows the protoconch of an archaeogastropod.

Family Xylodisculiade WARÉN 1992

Genus *Xylodiscula* MARSHALL 1988

Xylodiscula with the type *X. vitraea* MARSHALL 1988 has a larval shell, while *X. librata* MARSHALL 1988 has direct development without larval shell. They are very similar to the larger *Hyalogyra*, but have more angular whorls and a more sinistral and tightly coiled protoconch. Members of the Xylodisculidae WARÉN 1992 also have a less rapid increase in whorl diameter of the smooth protoconch, and the teleoconch has an angular flank (MARSHALL 1988, Figs. 8 A-H). While MARSHALL (1988) considered *Xylodiscula* to represent a member of the Orbitestellidae, WARÉN & BOUCHET (1993) created an own family to include the genus.

Genus *Xenoskenea* WARÉN & GOFAS 1993

The small *Xenoskenea pellucida* (MONTEROSATO 1874) has a *Valvata*-like shell with rounded, simple whorls and maximum diameter of 2 mm. The protoconch consists of a little more than one whorl with the apex twisting inwards and a size of 0,25 mm in diameter (WARÉN et al. 1993, Figs. 26-30). An embryonic shell is not clearly distinguished from a larval shell so that there may be no free swimming larva or at least no plankton feeding larva. The teleoconch consists of 2,3 rounded whorls. The animal differs from *Cornirostra* by having a single end of the foot, a more lappet-like extension of the mantle instead of a pallial tentacle, and a radula with more than 20 teeth in each row. A very similar or the same species has been described as *Akritogyra conspicua* (MONTEROSATO) by WARÉN et al. (1997), which according to WARÉN (1992) was interpreted to represent an archaeogastropod.

Family Pyramidellidae GRAY 1840

Genus *Pseudoskenella* PONDER 1973

Pseudoskenella depressa was described by PONDER (1973) as pyramidellid living on the tentacles of the serpulid worm *Galeolaria* and with simple pyramidellid head and outside outlook. They possess an operculum, and the shell is like that of *Tomura*, helicoidal in shape with heterostrophic protoconch forming a little more than one whorl. In contrast to the flat "pyramidellid" *Cyclostremella* the shell is smooth.

Family Amphibolidae GRAY 1840

Archaepulmonata MORTON 1955

The globose, dextral shell of these archaepulmonates belonging to the Amphibolidae GRAY 1840 with low spire and convex whorls is usually provided with an umbilicus and an operculum. The protoconch is sinistral and twists into the dextral teleoconch at metamorphosis from larval to benthic life (HARBECK 1996, Pl. 5 and 6). *Amphibola* and *Salinator* live in the tidal zone of Australia and East Asia. Among the Archaepulmonata, the Amphibolidae appear to be primitive because of keeping the operculum after metamorphosis and also retaining the osphradium in full size (FARNIE 1924, PILKINGTON & PILKINGTON 1984, LITTLE et al. 1985). *Amphibola* SCHUMACHER, 1817 is not so similar since its shell has a cornered periphery

and bears low spiral ribs on its posterior flattened whorl sides. There is also an apertural slit forming almost a selenizone in adult shell.

Genus *Salinator* HEDLEY 1900

Salinator has a smooth, lowly coiled to moderately high shell with rounded whorls that is about as wide as high to higher than wide. The protoconch in the three species of *Salinator* that were analysed, is similar in shape. It consists of a sinistral embryonic whorl that is to a large part covered by the larval whorl. Metamorphosis to benthic life occurs with about two whorls completed and following teleoconch whorls are dextrally coiled. The width of the embryonic shell is about 0,1 to 0,12 mm, that of the whole protoconch about 0,3 - 0,4 mm. The protoconch umbilicus is very narrow and points upwards from the apex of the teleoconch, so that the axes of coiling are about the same.

Concluding remarks

Among modern species with heterostrophic protoconch and *Valvata*-like shape there are representatives of quite different taxa. Besides *Valvata* of the fresh water Valvatidae the related marine Cornirostridae have a similar shell, clearly distinguished by the sinistral protoconch with smaller embryonic portion. But other gastropod groups such as those placed in the Hyalogyrinidae and Xenodisculidae have shells that can easily be mistaken for those of the Cornirostridae, and in case of lecithotrophic development even with representatives of other gastropod groups such as the Archaeogastropoda and Caenogastropoda with a nonsinistral protoconch. Among the Heterostropha also members of the Pyramidellidae may be of similar shape as is the case in *Pseudoskenella* and even those of the Archaeopulmonata may be similar such as of the genus *Salinator*. This convergence in shell shape among rather different branches of the richly diversified Heterostropha (= Heterobranchia) is not so amazing if the antiquity of the group with such a shell is taken into consideration. No incontestable direct lineage from the Devonian *Palaeocarboninia* to all Recent heterostrophic genera can be drawn explaining the different aspects of this highly diverse group. During evolution of the Gastropoda many faunal turnovers have occurred since Devonian times and large natural groupings such as the Latrogastropoda (Neogastropoda and Neomesogastropoda of the sea), or the Stylommatophora (pulmonate landsnails) holding many thousands of species can not even be traced beyond the base of the Cretaceous and, thus, not half the time back as the valvatiform Heterostropha, of which *Palaeocarboninia* is the oldest known representative having lived about 380 million years ago.

Acknowledgement

We thank EBERHARD JANKE (Elsdorf) for providing us with micromorph gastropods, K. HEIDELBERGER for preparation, B.-P. LÜTTE for stratigraphical excursion and further informations, T. URBAN (Hamburg) and M. RUPPEL (Frankfurt/M) for SEM photographs.

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Received: January 30, 2001.

Revised manuscript accepted by the Tübingen editors: July 1, 2001.

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