Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda)

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with 70 figures, and 6 plates

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Abstract:

The Cirroidea are defined by their mode of coiling which is dextral in the initial whorls and sinistral and, less commonly, planispiral in the later whorls of the teleoconch. The superfamily consists of members with the characteristic embryonic shell of the subclass Archaeogastropoda and nacreous inner shell layers. Cirroidea appear with the Lower Devonian (Emsian) and are recognized until the Upper Cretaceous (Campanian). Two families are differentiated of which the Porcelliidae have a labral slit and the Cirridae are without such slit. Porcelliidae are further differentiated into two subfamilies, the Agnesiinae with sinistral teleoconch and the Porcelliinae with planispirally coiled shell. The very narrow slit and selenizone of Porcelliidae differentiates them from other slit bearing archaeogastropods. Cirridae appear in the Triassic and three subfamilies can be recognized. The central one connecting to the forms with labral slit in general shape of the shell are the Hesperocirrinae. Planispiral coiling characterizes the Cirrinae and minute rounded forms are included in the Cassianocirrinae. A new genus *Coloniacirrus* is defined and the three new species *Hesperocirrus ebbighauseni*, Hamusina maxwelli and *Hamusina kahrsi* are described.

Zusammenfassung:

Die Cirroidea werden nach der Einrollungsweise der Schale definiert, bei welcher eine anfangs rechtsgewundene Jugendschale in einen linksgewundenen und seltener auch planispiralen Teleoconch übergeht. Zudem handelt es sich um Archaeogastropoden mit typischer Embryonalschale und perlmutteriger Innenschicht, deren Geschichte vom unteren Devon bis in die obere Kreide verfolgbar ist. Zwei Familien, eine mit Mündungsschlitz, die Porcelliidae, und eine andere schlitzlos, die Cirridae, sind abgegrenzt. Die Porcelliidae lassen sich zudem in zwei Unterfamilien, Agnesiinae mit linksgewundener Schale und die Porcelliinae mit planspiraler Schale, untergliedern. Der sehr enge Schlitz grenzt dabei von ähnlichen Schlitzbandschnecken ab. Die Gattungen der Cirridae werden in drei verschiedene Unterfamilien aufgeteilt, von welchen die Hesperocirrinae die zentrale Einheit darstellen, deren Schalengestalt zu den geschlitzen Vorfahren vermittelt. Die Cirrinae zeigen den Trend zur planispiralen Einrollung und die Cassianocirrinae vereinigen winzige rundliche Formen. Die neue Gattung *Coloniacirrus* sowie die neuen Arten *Hesperocirrus ebbighauseni*, *Hamusina maxwelli* und *Hamusina kahrsi* werden vorgestellt.

1 Introduction

The shell of most gastropods is dextrally coiled. Sinistral shells occur here and there among dextral species, sometimes accidental as in *Helix* LINNAEUS, 1758 among the large stylommatophoran pulmonates of Europe or *Turbinella* LAMARCK, 1799 among the large neogastropods of the Indian Ocean. Rarely sinistral and dextral shells are found in about equal number within the same species as among some tropical species of the Achatinidae and Partulidae belonging to the stylommatophoran pulmonates. Some predominantly dextral genera have sinistral species as found for example in *Neptunea* RÖDING, 1798, *Volutopsius* MÖRCH, 1857 and *Busycon* RÖDING, 1798 among the Neogastropoda. Some families hold sinistral genera like *Blauneria* SHUTTLEWORTH, 1854 among the Ellobiidae H. & A. ADAMS, 1855 (Archaeopulmonata). There are also families with sinistral genera and species as the Triphoridae GRAY, 1847 among the Ctenoglossa, the Physidae among the Basommatophora. Superfamilies like the Clausilioidea of the stylommatophoran pulmonates are predominantly sinistral as well, and even large units like the Thecosomata BLAINVILLE, 1824 among the pteropods have a sinistrally coiled shell.

A change from one mode of coiling into the other is a regular feature observed in the subclass Heterostropha. Here most species with a planktotrophic larva bear a sinistrally coiled embryonic and larval shell and show a twist into the dextral coil, indicating either the time of metamorphosis, or a little later or somewhat earlier. But a change in the directional mode of coiling does not usually occur among the members of the other three subclasses of the gastropoda, the Archaeogastropoda, Neritomorpha and Caenogastropoda. An exception is represented by the sinistral ampullariid caenogastropod *Lanistes* MONTFORT, 1810 but here the

originally dextral embryonic shell is deformed into sinistral shape before it became mineralized (LEHMANN,1991).

Among fossil representatives of the Archaeogastropoda two large units are recognized, in which the early dextrally coiled shell changes into sinistral coiling during growth of the juvenile teleoconch. The first of these groups has mainly Paleozoic representatives with a narrow selenizone present in central position or low down in the whorl, characterized by genera like *Antitrochus*, *Hesperiella*, *Porcellia* and *Coloniacirrus*. The second group without slit occurs during Mesozoic times and is characterized by genera like *Hesperocirrus*, *Sororcula*, *Hamusina*, *Scaevola*, *Cirrus*, *Discocirrus*, *Cassianocirrus* and *Zardinicirrus*. It seems that neither of both groups have survived into the Recent fauna and members of the older, slit-bearing group have disappeared in the Triassic.

Placement of many of the members of the two groups in the taxonomic system had a confusing history related to the ignorance in regard to the morphology of the early whorls, the history of dealing scientifically with these shells during the process of describing and naming them, and the convergence of shell shapes encountered in different lineages of evolution. Studies of anatomy on members belonging into the group can not be carried out since it seems that no member survived until the end of the Cretaceous.

New data based on the morphology of the first part of the shell, the structural composition of the shell, and variation in the morphology of the shell allows to represent a new systematic approach to these sinistral gastropods. The study has been aided by a number of persons to whom I express my sincere thanks. Phil A. MAXWELL from southern New Zealand has provided me with a Lower Jurassic fauna from New Zealand kindly sent by Allen BEU from the Geological Survey of New Zealand in Lower Hutt. This fauna will be published in full detail later (BANDEL & MAXWELL in prep). George D. STANLEY Jr. (University of Montana) collected specimen in the Pucara Group of the Upper Triassic in Peru and I could study the HAAS collection from that section housed in the Museum of Natural History in New York thanks to Neil LANDMAN. R.M. LINSLEY from Colgate University (Hamilton, New York) made availabel to me a big collection of gastropods from the Gilmore City Limestone of Missisippian age from Iowa. Volker EBBIGHAUSEN enabled me to study his rich collection of Mid Devonian gastropods from the Paffrath syncline near Cologne and additional Mid Devonian material was made accessable to me by Winfried HAAS in the collection of the Paläontologisches Institut at the University of Bonn. Udo SCHEER from the Ruhrland Museum in Essen opened to me the collection of Upper Cretaceous gastropods from Kassenberg in Mülheim-Broich. At the Geologisch-Paläontologisches Institut in Hamburg Claudia TAEBEL, Hans-Jürgen LIERL and Andreas SCHARENBERG helped in preparation and photography of the studied specimen. The Deutsche Forschungsgemeinschaft (DFG) financially supported the study.

2 Taxonomic part

Superfamily Cirroidea COSSMANN, 1916

Diagnosis: The sinistral trochomorph archaeogastropods and their planispiral relatives have a nacreous inner shell layer. Their flattened protoconch consists of a dextral embryonic whorl surrounded by at first dextral than planispiral whorl of the teleoconch. Base is flat or rounded, pierced by an umbilicus or provided with olid columella. Aperture may be angular and rounded and provided with uninterupted outer lip or with labial slit. Ornament consists of axial ribs and spiral ribs in variable arrangement, is commonly tubercular where ribs cross. Growth striae run more or less obliquely backward over most of the whorl and turn to radial direction toward the columella. Holds the families Porcelliidae (Lower Devonian to Upper Triassic) and the Cirridae (Triassic to Upper Cretaceous).

2.1 Cirroidea with selenizone

Family Porcelliidae BROILI, 1924

Diagnosis: Porcelliidae represent the branch of the Cirroidea with a selenizone which is result of a narrow labial slit. Coiling of the conispiral to trochiform shell is sinistral, in some cases planispiral and here even slightly dextral. The labral slit generates a concave selenizone at approximately midheight or lower down to the edge of the base. Members of the subfamilies Agnesiinae and Porcelliinae are included in this family.

Subfamily Agnesiinae KNIGHT, 1956

Diagnosis: Trochospiral Porcelliidae with inward coiling protoconch and ornament of collabral and spiral elements. Genera are *Agnesia*, *Hesperiella*, *Antitrochus* and *Enantiostoma*.

Genus *Agnesia* DE KONINCK, 1883

Diagnosis: The subfamily diagnosis applies. The trochiform sinistral shell (17 mm in height and width in the type presented by KNIGHT, 1941) has a convex base that meets the flank in the selenizone. The base is evenly rounded and continues into the umbilicus. The apex has an immersed dextral protoconch that consists of rounded, smooth whorls (YOO, 1989) ornamented by collabral threads and folds. The rounded whorls of the teleoconch show growth lines inclined toward the selenizone which is narrow and bordered on each side by a fine rib and may bear a median carina. The genotype is represented by *Pleurotomaria acuta* PHILLIPS, 1836 from the Viséan of Belgium according to WENZ (1938,

Fig. 184) and *P. acuta* from the Lower Carboniferous of Yorkshire, England according to KNIGHT (1941).

Discussion: KNIGHT (1941) described the selenizone as being carinate as could be observed on the English holotype of *Agnesia* even though it is largely preserved as steinkern (KNIGHT 1941, Pl.38, Fig.2). WENZ (1938) described the selenizone as deep within a groove in the Belgian holotype. This indicates that each of these authors may have considered a different species of this genus as type, one found in England, the other from Belgium. A species with the apex preserved comes from the Lower Carboniferous of Australia (YOO 1989) and is here included into the general diagnosis of this genus. KOKEN (1889) had already reported that juvenile dextral whorls later grade into sinistral coiling in *Agnesia* from the Lower Carboniferous of Belgium.

Agnesia reticulata YOO, 1993 (YOO 1989, Pl. 8, Fig. 1 - 3) from the Lower Carboniferous of New South Wales has a clearly visible selenizone and is ornamented by obliquely intersecting linear ridges. The protoconch is coiled inward (dextrally) and the embryonic whorl lies in the concave apex. A sinistral teleoconch develops from the dextral juvenile shell.

Species *Agnesia costata* (GOLDFUSS, 1841)
Pl. 1 Fig. 1, 3

Description: The sinistral teleoconch with at least 4 whorls is 16 mm wide and 9 mm high. Whorls are rounded and the selenizone lies in a narrow shallow furrow on the median flank. Whorl flank is evenly rounded and continuous into the widely umbilicate base. Ornament consists of rounded axial ribs of the *Porcellia puzo* type which ends before reaching the suture and before touching the selenizone. There are about 17 ribs on the last whorl. Neither fine ornament below ribs, nor base, nor the initial whorl, nor the shape of the aperture are preserved in the specimen from the Middle Devonian of the Eifel (probably near Sötenich) that is part of the collection of the Paläontologisches Institut in Bonn.

Discussion: KOKEN (1889) suggested to place the sinistral trochospiral members of *Porcellia* described by SANDBERGER (1850-56) within the genus *Agnesia*. KOKEN (1889) also reported the presence of a planispiral form with high initial whorl (*Porcellia aberrans* KOKEN) in the Emsian limestones of Konieprus near Prag. The difference between *Agnesia* and *Porcellia* is gradational when *Porcellia costata* GOLDFUSS, 1841 is taken into account. It represents a lowly spired shell similar to that of the highspired *Hesperiella*. Thus the opinion of WENZ (1938) can be comprehended according to which *Hesperiella* is considered to belong into the same genus as *Agnesia*. In the Middle Devonian fauna of the Eifel and Paffrath synclines gradation of morphologies from turbiniform species of *Agnesia* to planispiral species of *Porcellia* on one side and high-spired species of *Hesperiella* on the other side are found.

Genus *Hesperiella* HOLZAPFEL, 1889

Diagnosis: The subfamily diagnosis of the Agnesiinae applies to this genus. The sinistral, high spired and pupiform shell has a short labral slit in the lower part of the outer lip that gives rise to a selenizone. Whorl flanks are rounded and angular toward the base. The initial whorl lies in a concavity of the apex of the teleoconch. Sutures are accompanied by the selenizone impressed in the lower whorl flank. Ornament consists of a series of widely spaced transverse costae above the selenizone and/or spiral lirae. Genotype is *Pleurotomaria contraria* DE KONINCK, 1843 of the Viséan of Belgium (KNIGHT, 1941 Pl.38, Fig.1).

Species *Hesperiella ebbighauseni* n. sp.
Pl. 1 Fig. 4,5,10,11

Diagnosis: The diagnosis of the genus applies. The selenizone lies at the edge between flank and base as is the case in *Antitrochus*. Sculpture consists of spiral ribs crossed by numerous axial ribs with granules on the points of crossing. The base is rounded and not umbilicate.

Differences: The shell is more slender than that of *Antitrochus nodulosus* and not umbilicate. Its sculpture differs from that of the Lower Carboniferous *Hesperiella* by consisting of spiral and axial elements while that of the genotype as well as from the species of Australia shows predominantely axial ribs.

Locus typicus: Unterthal, Quarry at MTB 4909 Kürten, R 83880, H 53390 near Cologne.

Stratum typicum: Unterer Plattenkalk, Givetium of the Paffrath syncline, Rheinisches Schiefergebirge.

Holotypus: The larger of the two specimen studied represents the holotype housed in the collection of the Museum of the Geologisch-Paläontologisches Institut, Hamburg with Nr. 2557.

Derivatio nominis: The two individuals were collected by Dr. Volker EBBIGHAUSEN and named in honor of this distinguished collector of Middle Devonian fossils.

Description: A shell with 7 whorls is about 6 mm high and 3 mm wide at the last whorl. Its apical angle amounts to about 30 degrees. The early shell amounting to the first whorl is dextrally coiled. Immediately after the first whorl the shell turns into the sinistral coil. Ornament of the teleoconch consists of 5 to 7 spirally arranged lirae crossed by about 40 axial lirae resulting in about 40 granules present on each spiral element. The aperture is as wide as high and of almost rounded, slightly quadrate shape with almost vertical orientation. The short labral slit lies close to the edge to the base, just above it. The selenizone is thus not covered by the following whorl but remains visible just above the suture. The base is flatly convex and evenly rounded provided

with the same ornament as covers the flanks.

Discussion: WENZ (1938) considered *Hesperiella* a synonym to *Agnesia* possibly based on the opinion of HOLZAPFEL (1895) who withdrew his earlier proposed genus *Hesperiella* because of opposition by KOKEN (1889). When HOLZAPFEL (1889) created the genus *Hesperiella* to encompass sinistral, slit-bearing, trochiform fossils from the Lower Carboniferous of Western Germany and Belgium he had described the flattened apex holding the embryonic whorl in a depresssion. Later KNIGHT (1941, Pl.38, Fig.1) encountered difficulties in tracing the selenizone clearly on the original of the type designated by himself (KNIGHT 1937) to be represented by *Pleurotomaria contraria* DE KONINCK, 1843 from the Lower Carboniferous of Belgium. Australian species of this genus described by YOO (1989, Pl.7, Figs.5 - 13) demonstrate a narrow selenizone within its groove. YOO (1988, 1989) described three species of Lower Carboniferous *Hesperiella* from New South Wales in Australia, of which one is slender, *H. robertsi* YOO, 1988 is of intermediate shape (YOO 1988, Figs 36 - 41), and the third is short. The protoconch coils inwards within the apex (YOO, 1988, Figs.39 - 41; 1989, Pl.7, Figs.5 - 13) and the selenizone is so close to the lower suture that it can be seen only in final whorl and is covered in earlier whorls.

The slender, small and delicate shell of *Hesperiella ebbighauseni* differs considerably from the lower and larger, more coarsely ornamented shell of *Agnesia costata*, so that from this point of view HOLZAPFEL's (1889) earlier view and proposed genus *Hesperiella* is quite acceptable and can easily be differentiated from *Agnesia*. The slit and selenizone of *H. ebbighauseni* resembles that of *Antitrochus* and *Porcellia*. The granular sculpture resembles that of *Hesperiella limata* HOLZAPFEL, 1889, while the shell is more slender.

Genus *Antitrochus* WHIDBORNE, 1891

Diagnosis: Diagnosis of the subfamily Agnesiinae applies to this genus. The shell is trochiform sinistrally coiled and sculptured by spiral lirae which are transsected by forewards inclined collabral growth lines. Fine granules are developed where lirae and lines cross. A narrow, deep slit at the basal periphery gives rise to a depressed selenizone forming the edge to the base. The genotype is *Antitrochus arietinus* WHIDBORNE, 1891 (= *Pleurotomaria elegans* ARCHIAC & VERNEUIL, 1842 = *Pleurotomaria nodulosa* SANDBERGER, 1842 = *Flemingia perversa* WHIDBORNE, 1892) from the Middle Devonian of Devonshire in England.

Species *Antitrochus nodulosus* (SANDBERGER, 1842)
Pl. 1, Fig. 2,6,7,8,9,12,13; Pl. 2, Fig. 1,2

Diagnosis: The diagnosis of the genus applies to this species. *Pleurotomaria nodulosa* according to SANDBERGER's (1842) original description is characterized by a sinistral shell with low conical shape and a narrow selenizone at the lower edge of each whorl. The umbilicus is narrow and nearly closed by the somewhat broadened inner lip of the aperture. Ornament consists of spiral tuberculate lirae crossed by inclined collabral growth lines.

Difference: The first whorls of *A. nodulosus* from the Givetium of Bergisches Land closely resembles those of Hesperocirrinae but in difference to these the teleoconch has a slit. The conical shape of the teleoconch differs from the pupiform shape of *Hesperiella*, to which *Antitrochus* is close regarding other features of the shell.

Description: Shells from the Givetium of Unterthal have grown to the size of 20 mm in height and 18 mm in width consisting of 6 sinistral whorls. The first whorl, in contrast, is dextrally coiled and forms a flatted apex of the shell in which the embryonic whorl is embedded in a concavity. The apex thus represents the widely open umbilicus of the first dextral whorl that consists of the embryonic shell and the begin of the juvenile teleoconch. Ornament of the teleoconch consists of spiral lirae transsected by inclined collabral growth lines forming small tubercules with each other. The base is flattened convex and ornamented in the same way as the flanks. The selenizone develops from a short labral slit and is flanked by two spiral lines and an additional one in its centre. Crescentic growth lunulae feature only the selenizone formed by almost fully grown individuals. The aperture is of rounded quadrangular outline.

Discussion: WHIDBORNE (1891) noted no slit and selenizone in his specimen from Devonshire which were restudied by KNIGHT (1941, Pl.53, Fig.1) as types to the genus *Antitrochus*. KNIGHT remarked that the exact shape of the apertural lip is still unknown. There can be little doubt that *Antitrochus arietinus* WHIDBORNE, 1891 actually represents a very similar, probably the same species as that described earlier by SANDBERGER (1842) as *Pleurotomaria nodulosa* from the Middle Devonian of Villmar in the southern Rheinische Schiefergebirge and in the same year by ARCHIAC & VERNEUIL (1842) from the same locality but with the different name *Pleurotomaria elegans*. KOKEN (1889, Fig. 3b) illustrated the apex and its dextral coiling. He noted that the selenizone may be very indistinct and can thus easily be missed in this species. SANDBERGERS's (1942) description can be applied to the numerous species found by Volker EBBIGHAUSEN near Cologne in Unterthal in the position of the Lower Plattenkalk of Givetian age. Since the slit in *Antitrochus* had not been considered the genus was thought to belong to the Gyronematinae KNIGHT, 1956 of the Holopeidae WENZ, 1938 in the Platyceratoidea HALL, 1859 by KNIGHT et al. (1960). Platyceratoidea with their name giving genus *Platyceras*

are based on a member of the Neritomorpha (BANDEL 1992). Within the Holopeidae, on the other hand, some genera like *Yunnania* represent true trochomorph archaeogastropods (BANDEL 1993). WENZ (1938) considered *Antitrochus* to belong to the Trochonematinae representing Trochomorpha of uncertain affinities (BANDEL 1993).

Genus *Enantiostoma* KOKEN, 1889

Diagnosis: The turbiniform sinistral shell has an open umbilicus and narrow selenizone in the periphery low on the flank of the rounded whorl. Ornament consists of sinuous collabral growth increments and spiral lirae. The type is *Pleurotomaria perversa* HÖRNES, 1856 from the Norian limestone of the Sandling (Hallstadt) in the northern Alpes (WENZ 1938, Fig.185, KNIGHT et al. 1960, Fig. 120,7).

Discussion: KOKEN (1896) described the sinistral, about 10 mm high and a little wider shell. He characterized the 2,5 initial whorls as planispirally coiled and axially ribbed. Within the third whorl the twist into the sinistral teleoconch occurs. Enantiostoma thus resembles *Antitrochus*, *Agnesia* and *Hesperiella*. WENZ (1938) considered *Enantiostoma* to be close to *Agnesia* which was accepted by KNIGHT et al. (1960).

Subfamily Porcelliinae BROILI, 1924

Diagnosis: The Porcelliinae have a pseudo-bilaterally symmetrical shell always with a dextrally trochospiral initial portion and a more or less planispirally coiled later teleoconch. The teleoconch is symmetrically, slightly dextrally or sinistrally coiled. The outer lip of the aperture bears a deep slit that produces a narrow, incised selenizone at or near mid-whorl. Apical depression may be as deep, deeper or a little shallower as the umbilicus. The embryonic whorl lies on a flattend apex, and the slit makes its appearence after 1 to 3 slit-less whorls of the teleoconch. The ornament consists of collabral ribs and lines that may be crossed by spiral lirae, axial nodes and arcuate ribs. Genera are *Porcellia* and *Coloniacirrus*.

Genus *Porcellia* LÉVEILLÉ, 1835

Diagnosis: Diagnosis of the subfamily Porcelliinae applies. Teleoconch may show a dextral or sinistral twist. The apertur is about as high as wide and its outer lip forms a median sinus with the narrow slit in its centre. Ornament consists of rounded axial folds arranged on the upper and lower shoulders onto which a fine network of transverse and revolving lirae is superimposed. Genotype is *Porcellia puzo* LÉVEILLÉ, 1835 from the Lower Carboniferous of northern France.

Species *Porcellia puzo* LÉVEILLÉ, 1835
Pl. 2, Fig. 3,4

Description: Generic diagnosis applies to the species. KNIGHT (1941) described it as dextral discoidal shell (up to 4 cm width) with trochiform early ontogenetic whorls and later whorls planispirally coiled with upper and lower whorl surfaces identically ornamented. The whorls are rounded and have symmetrically arranged folds on both shoulders that do not continue up to the slit. A fine network pattern formed by transverse and revolving lirae with sharp tubercules at crossing points cover surface and folds. The aperture is round, in juvenile whorls, slightly quadrangular with the deep narrow slit extending backward for about half a whorl. The narrow selenizone forms a cleft-like line on the median flank.

Specimens from the type locality Tournai in Belgium housed in the collection of the Institut für Paläontologie in Bonn demonstrate the dextral early teleoconch which consists of three rather lowly coiled, trochospiral and rounded whorls. They are a little more than 1 mm in width and lie in the concave apex of a shell that with 7 whorls measures almost 3 cm in width.

Discussion: HARPER (1977) described an unnamed species of *Porcellia* from the Lower Carboniferous (Mississippian) Gilmore Limestone from Humbolt in Iowa which resembles *P. puzo* in regard to the ornamental pattern. Here spiral threads are crossed by axial ribs forming a regularly beaded network. The whorl is less nodded than in *P. puzo* and its section is more angular. Trochospiral changes into planispiral coiling within the fourth whorl and the selenizone begins in the third whorl as could be noted on additional material from the same locality kindly provided by Bob LINSLEY. The slit is accompanied by a keel on its upper margin and occupies the outer portion of the upper flank of the last helical whorl. The embryonic whorl lies on a flat apex and is surrounded by a planispirally coiled first whorl of the teleoconch. Later a groove appears between suture and whorl and the selenizone occupies the periphery.

Species *Porcellia spinosa* GOLDFUSS, 1841
Pl. 2 Fig. 7,8,11,12; Pl. 3, Fig. 2,8

Description: The almost planispirally coiled, only slightly sinistral shell has three dextral initial whorls and later consists of 3 - 4 whorls, coiled planispirally, measuring about 2,5 cm in diameter and up to 1 cm in height at the aperture. The slit appears after the first whorl still on the dextral, juvenile teleoconch on the upper middle of the flank. On a shell with 1,5 mm width and within the fourth whorl the slit moves to the peripheral margin into a median position. Within the apex of the teleoconch the final whorl of the juvenile shell is seen with its umbilicus. The plane of the aperture is slightly inclined

demonstrating that the adult shell functioned as a sinistral shell. Ornament consists of rounded lateral folds appearing with begin of planispiral coiling. 23 folds can be counted on the last whorl and they disappear on the flanks. On the surface, including the folds, finer ribs are superimposed. These have the same width as the groove separating them. About 4 ribs can be counted between folds near to the suture, while about 8 are present at the margin since they branch or bifurcate on the flanks. In contrast to the folds ribs continue right up to the selenizone.

The studied specimen were collected by Volker EBBIGHAUSEN in Unterthal where they cooccur with the much more common *Porcellia cornuarietis*. A further specimen comes from the Eifel Syncline at Sötenich and is housed in the collection of the Institut of Palaeontology at Bonn.

Differences: *Porcellia spinosa* is very similar to *Porcellia cornuarietis* in regard to the fine ornamental pattern but readily differentiated by its lesser sinistrality. Thus the apex is deeply concave, while it is almost plane in *P. cornuarietis*. The characteristic pattern of bifurcating ribs differs from that of the other species of *Porcellia*.

Species *Porcellia cornuarietis* SANDBERGER,1850
Pl. 2, Fig. 5,6,9,10,13; Pl. 3, Fig.3,4,5,6,7,9,11;
Pl. 4, Fig. 3

Description: The disc-like, clearly sinistral shell consists of almost planispiral whorls of the teleoconch which carries a trochospiral dextral juvenile shell. The flanks are ornamented by about 13 to 14 accurate folds per whorl which arise at the sutures, and continue across the flanks to the margin with backward turned ends and disappear on their approach to the selenizone. They become less prominent in the final whorl of the shell while they are the dominant feature in the third whorl. Onto them fine collabral ribs are superimposed in a very similar way as is developed in *Porcellia spinosa*. About 8 of them are counted near the suture and 12 near the margin in the last whorl. The apical portion of the shell is almost plane while the umbilical side is deeply concave. A shell with 5 whorls measures about 26 mm in diameter and 9 mm in height. On the later worls a fine spiral liration is also developed that is not seen on the earlier whorls.

Numerous individuals were collected by Volker EBBIGHAUSEN in the Quarry at Unterthal from the Givetian beds and studied. Four further individuals from the Eifel syncline at Sötenich from the collection of the Institut of Palaeontology in Bonn were also analysed.

Difference: The shell resembles that of *Porcellia puzo* but differs from it by the sinistral coiling of the teleoconch. It is very close in ornament, size and shape to *Porcellia spinosa* but in

contrast to the later has a more clearly sinistral teleoconch and thus a more flattened apex.

Discussion: The individuals described as *Porcellia cornuarietis* by KIRCHNER (1914) from the Sötenich syncline in the Eifel closely resembles *P. spinosa* and probably represents the same species. SANDBERGER (1850-56) characterized his species *P. cornu-arietis* as sinistral which is the case in the more common form found in Unterthal. KOKEN (1989) stated that *Porcellia striata* (= *Euomphalus striatus* GOLDFUSS) is the same species as *Pleurotomaria bifida* SANDBERGER from Geroldstein (Eifel) and represents an almost bilaterally symmetrical species, perhaps *P. spinosa* as described here. It could also represent *Coloniacirrus radiatus*. ROEMER (1842) noted in his description of *Porcellia calceola* from the Harz Mountains no slit, but otherwise this species closely resembles *Porcellia cornuarietis* and *P. spinosa*.

Genus *Coloniacirrus* n. gen.

Diagnosis: The planispiral slightly sinistral or dextral member of the Porcelliinae is flattened with acute margin and a low ornament consisting of fine sinuous collabral elements which may be crossed by spiral lines. The type is *Ammonites primordialis* SCHLOTHEIM from the Iberg-Limestone of the western Harz Mountains of Frasne age (Lower Upper Devonian).

Difference: *Coloniacirrus* differs from *Porcellia* by the low sinuous axial ribbing as well as the more flattenend shell shape, while the later has more rounded whorls and more nodular and prominent ornament.

Derivatio nominis: Named as member of the Cirroidea with occurrence near the city of Cologne, founded as Colonia Agrippina by the Romans.

Species *Coloniacirrus primordialis* (SCHLOTHEIM,1820)
Pl. 3 Fig. 1,10; Pl. 4, Fig. 8

Description: The discus-like shell is flattened with acute margin that bears the narrow furrow-like selenizone. The shell grows up to 60 mm and is then ornamented by numerous spiral lirae which are crossed by sinuous collabral lirae forming a regular reticulate pattern. The juvenile shell is covered by a dense pattern of arcuate axial ribs which curve back near the margin and disappear before reaching the selenizone. The aperture is slightly oval reflecting the sinistral coiling of the shell in its inclined outline.

Difference: The Middle Devonian *C. radiatus* closely resembles the Upper Devonian *C. primordialis* but has a less dense pattern of axial ribs. Ribs usually do not bifurcate at the margin as is normally the case in *C. radiatus*. A more sinistral touch of the

teleoconch is present in *C. primordialis* while *C. radiatus* is more dextrally coiled.

Discussion: The species was introduced as *Ammonites primordialis* by SCHLOTHEIM (1820, Pl. 9, Fig. 2), and transferred to *Bellerophon* by ROEMER (1842, Pl. 8, Fig. 16). KOKEN (1889, Fig. 7) stated and illustrated that the symmetrical teleoconch of *C. primordialis* bears a conical initial shell in its central apical depression. WHIDBORNE (1892) considered SCHLOTHEIM's figure of *Ammonites primordialis* as not sufficient to characterize the species. ROEMER's (1842) illustration is better even though he regards juvenile specimen of *C. primordialis* to belong to a different species called *Schizostoma carinatum*.

Species *Coloniacirrus radiatus* (GOLDFUSS, 1841)
Pl. 3, Fig. 12; Pl,. 4, Fig. 1,2,4,6

Description: The planorbid shell is concave on both sides and with 2,5 planispiral volution measures about 25 mm across and 8 mm in height. The dextral juvenile shell of trochospiral shape consists of about 3 rounded whorls. After these planispiral and slightly dextral coiling begins. Ornament consists of numerous regular ribs arcuated backward and becoming low and delicate near the flank where they bifurcate and finally end at the selenizone. The ornament is very similar on both sides, but the umbilicus represents a deeper concavity than the apical depression with the initial whorls in it.

Difference: *Coloniacirrus radiatus* is very close to *Porcellia angulata* CLARKE, 1884 from the Upper Devonian Iberg-limestone (CLARKE 1884, Pl. 5, Fig. 15), but has a denser pattern of axial ribs. From *C. primordialis C. radiatus* differs by an ornament of simple axial ribs, while the former has a pattern of axial and spiral lirae. From the Devonian of Russia EICHWALD (1860, Pl. 40, Fig. 26) described a similar form as *Euomphalus nanus* EICHWALD, 1860 which may also belong to this genus.

Discussion: A shell very close in shape to *Coloniacirrus radiatus* was figured and described by ARCHIAC & VERNEUIL (1842, Pl. 34, Fig. 3) as *Schizostoma radiata* from unknown locality in the Eifel, but characterized as sinistral. WHIDBORNE (1892) noted the coarser ornamental pattern of *C. radiatus* differing from the fine ornament of *C. primordialis*, also the more oval whorl diameter and the slower increase in whorl width in the former compared to the later. The specimen here considered to belong to *C. radiatus* comes from a Quarry at Unterthal in the Paffrath syncline to the east of Cologne from the Lower Plattenkalk of Givetian age and was collected by Volker EBBIGHAUSEN.

Discussion of Porcelliinae: KNIGHT (1941) studied the type to *Porcellia*, *P. puzo* and found 3 - 4 helicoidally coiled first whorls. BATTEN (1966, Pl. 5, Fig. 2 - 4) studied further individuals of *Porcellia* from the Lower Carboniferous of Belgium

and England and found their early whorls similar to those seen on *Mourlonia*. BATTEN (1966) thus suggested to place *Porcellia* with the family Eotomariidae, subfamily Eotomariinae and here the tribe Ptychomphalides WENZ, 1938. The Ptychomphalides have a selenizone constantly on the median portion of the whorl.

KOKEN (1889) considered Paleozoic *Porcellia* to belong to an own family which was named Porcelliidae BROILI, 1924. Into this unit KNIGHT et al. (1960) also added the Triassic *Kokenella* KITTL, 1891 and the Jurassic *Talantodiscus* FISCHER, 1885. KOKEN (1889) had not considered these as related to each other. This view was supported by BANDEL (1991) who considered the Triassic and Jurassic genera to represent relatives of lineages of slit bearing archaeogastropods not related to the Porcelliinae. The diagnosis of the Porcelliidae had representatives of the genus *Kokenella* as model, which is now changed in favour of KOKEN's (1889) original ideas.

Kokenella KITTL, 1891 from the Upper Triassic is characterized by a planispirally coiled shell with rounded whorls and lateral selenizone. *Kokenella costata* (MÜNSTER, 1841) is planispirally coiled with clearly dextral twist. The selenizone begins early in the teleoconch on the apical side and migrates onto the central flank (BANDEL 1988, 1991). It is much wider than that of the Porcellinae. The early whorls are nearly as planispiral as later whorls. This difference of *Kokenella* from *Porcellia* and *Coloniacirrus* had also been noted by KITTL (1891). He thus created the genus *Kokenella* separating the Triassic species from Paleozoic *Porcellia*. KOKEN (1889) had already suggested that Paleozoic *Porcellia* differs from Triassic "*Porcellia*" but had not drawn the taxonomic conclusions from his statement. The ornament of *Kokenella* consisting of a regular network of spiral and axial ribs of equal strength as well as the position and size of the selenizone connects *Kokenella* with pleurotomarians like *Dictyotomaria* KNIGHT, 1945 and *Zygites* KITTL, 1891 (BANDEL 1991).

Talantodiscus FISCHER, 1885 from the Middle Jurassic is a discoidal shell that demonstrates initial whorls protruding only slightly above the apical plane. Here the ornament consists of tubercules on the upper side near the periphery and sigmoidal transversal ribs on the base. *Talantodiscus* differs from *Kokenella* by the selenizone which remains in its position on the upper side of the whorl and does not migrate to the middle of the flank of the teleoconch. From *Porcellia* it differs by low early ontogenetic whorls and the much broader selenizone. BENFRIKA (1984) compared *Talantodiscus* to other Middle Jurassic Pleurotomariidae of Normandy (France) and reached the conclusion that it is related to them taxonomically connected by a number of species with intermediate shapes.

Thus the systematic position envisaged by KNIGHT et al. (1960) uniting the Triassic *Kokenella* and the Jurassic *Talantodiscus* with *Porcellia* in the family Porcelliidae is not supported. The three genera represent convergent planispirally coiled members of

independently evolved lineages of slit-bearing archaeogastropods. This interpretation comes close to ideas expressed by KOKEN (1889) and picked up by WENZ (1938) who had placed *Kokenella* and *Talantodiscus* with flat apices in the Pleurotomariinae while *Porcellia* was considered to belong into its own family the Porcelliidae.

2.2 Cirroidea without selenizone

Family Cirridae COSSMANN, 1916

Diagnosis: The diagnosis of the superfamily Cirroidea applies. The sinistral trochiform early teleoconch continues in conical or planispiral whorls ornamented by collabral ribs or lamellae crossed by spiral ribs. The embryonic whorl lies in a concavity formed by the dextral initial whorl of the teleoconch which only later changes into sinistral coiling mode and is ornamented by a dense pattern of axial ribs. Sutures are shallowly engraved or deeply channeled, depending on the position of the periphery and the overlap of following whorls onto former ones. This periphery may form a keel or a row of tubercules above the suture.

Discussion: Even though the family name is derived from the genus *Cirrus* SOWERBY, 1815 with the genotype *Cirrus nodosus* SOWERBY, 1815 from the Middle Jurassic (Bajocium) of France, its most characteristic species are found within the subfamily Hesperocirrinae. Less characteristic are the minute *Cassianocirrus* and *Zardinicirrus*. Recently HICKMAN & MCLEAN (1990) included the Cirridae with genera *Cirrus* and *Hamusina* among the Eucyclinae KOKEN, 1897 and placed them jointly with Amberleyidae WENZ, 1938 and Eucyclidae KOKEN, 1897 into the extinct tribe Eucyclini of that subfamily of the family Trochidae RAFINESQUE, 1815. HICKMAN & MCLEAN (1990) did not even mention the change of mode of coiling that distinguishes members of the Cirridae from members of modern and fossil Trochidae.

Subfamily Cirrinae COSSMANN, 1916

Diagnosis: The trochospiral sinistral early teleoconch of cirrid characters changes into a planispirally coiled shell during growth. Thus adult teleoconch is planispiral, slightly dextrally or slightly sinistrally coiled. Ornamentation consists of strong axial ribs that represent varices formed by interruptions in shell growth reflected in flaring and thickened apertural lips. The plane of the aperture in the adult shell is vertically oriented, parallel to the axis of coiling. The trochospiral spire projects above the apical surface in the fully grown individuals in *Cirrus* and it remains in or below the apical plane in *Discocirrus*.

Difference: Cirrinae differ from the other members of the family Cirridae by changing the style of coiling of teleoconch from

trochospiral to planispiral during growth of the shell. The sinistral early trochospiral whorl differentiates from the Discohelicidae SCHRÖDER, 1993 which have a planispirally coiled initial shell (SCHRÖDER 1992).

Genus *Cirrus* SOWERBY, 1816

Description: The diagnosis of the subfamily Cirrinae applies. The sinistral shell is of conical to subdiscoidal shape and is more or less umbilicate. The spire of the teleoconch succeeding the flat apex is acute and flanks are more or less concave. With reaching adult size trochospiral coiling grades into planispiral coiling. Ornamentation consists of collabral axial ribs which are inclined in conical whorls and straight in final whorls. Based on *Cirrus nodosus* SOWERBY, 1815 from the Middle Jurassic (Bajocium) of France.

Discussion: *Cirrus nodosus* SOWERBY, 1815 (1818) according to HUDLESTON (1886-96) and based on individuals of up to 3 cm width from the English Dogger has an adult shell that is about two times wider than high, sinistrally coiled and of subdiscoidal shape. The early teleoconch, in contrast, is conically coiled with an apical angle of about 30 degrees which later begins to expand into at last planispiral whorl. Ornaments consist of keels which accompany the edges of the flank and large, straight axial ribs that form tubercules with them. The aperture is angular at its outside and rounded within.

Genus *Discocirrus* AMMON, 1892

Description: DUBAR (1948, Pl. 9, Figs. 22 - 24) described the sinistral *Discocirrus armatus* DUBAR, 1948 from the Lias of Marocco as consisting of 6 whorls separated from each other by deep sutures. The shell measures about 3 cm in width, and the rounded aperture is 1,5 cm high. Ornament consists of straight prominent axial ribs as in *Cirrus* and the plane and vertically oriented aperture is quadrangular with rounded corners. Only the first whorls are trochospiral forming a convex apex which in the adult shell lies in a concavity (DUBAR 1948), similar as is the case in *Porcellia*. According to DUBAR (1948) *D. armatus* is close to the type of the genus *Porcellia tricarinata* GÜMBEL, 1861 from the Lower Jurassic.

Difference: *Cirrus* differs from *Discocirrus* by higher initial whorls that project from the apex, while they lie within the concavity of the apical depression in the later. *Discohelix* has a totally planispiral initial shell portion encompassing the embryonic shell and first whorls of the teleoconch (WENDT, 1968) but otherwise resembles *Cirrus* and *Discocirrus*.

Subfamily Hesperocirrinae HAAS, 1953

Diagnosis: Sinistral trochiform shells distinguished by the apex as is characteristic to Cirroidea and Cirridae with dextral embryonic shell and switch into sinistral coiling within the juvenile teleoconch. Flanks of whorls of the conical shell are straight or weakly to convexly rounded. Base is gently rounded or flat and connected to the flank by a more or less pronounced peripheral edge or keel. The periphery above the suture may be featured by a more or less pronounced keel that commonly bears nodules. There may be a narrow umbilicus or the columella is solid. Ornament consists of spiral lirae and spiral ribs crossed by oblique growth lines, lirae or ribs often forming tubercules when crossing each other. The aperture is quadrangular and may have rounded corners and in fully grown individuals may become rounded. The subfamily was initially intended by HAAS (1953) to hold only the genera *Hesperocirrus* and *Sororcula* from the Upper Triassic of Peru, but Jurassic and Cretaceous Cirridae considered to belong into the *Hamusina*-group of closely related genera have the same characteristics, but commonly a larger shell. Thus also species without open umbilicus are included here as well and the stratigraphic range is extended to the Upper Cretaceous.

Genus *Hesperocirrus* HAAS, 1953
Pl. 4, Fig. 5,7,11

Description: As stated by HAAS (1953) the species of the genus *Hesperocirrus* represents sinistral, trochiform shells of small to moderate size, distinguished by planispiral first whorls with numerous axial ribs in which the early ontogenetic shell is dextrally coiled. The sutures are shallow and accompanied by a dominant keel or a row of tubercules above and a minor keel or row below. The flat or gently rounded base is connected to an open umbilicus, which continues into a hollow columella. The aperture is angular with truncate base, sharp outer lip and inner one reflexed over the umbilicus. A fine revolving striation covers the whorl faces. The genus *Hesperocirrus* HAAS, 1953 is based on the genotype *Hesperocirrus robusteornatus* HAAS, 1953 from the Upper Triassic of Peru.

Difference: The early ontogenetic shell of *Hesperocirrus* from the Upper Triassic Pucara Group of Peru (HAAS 1953) resembles that of *Cassianocirrus contrarius* (MÜNSTER, 1841) and *Zardinicirrus sinistralis* BANDEL, 1993 from the almost contemporaneous St. Cassian Formation while they differ in regard to shell profile and sculpture of the postnuclear whorls (BANDEL 1993, in prep). From *Hamusina maxwelli* from the Jurassic of New Zealand *Hesperocirrus* differs by the absence of spiral striae on the juvenile shell and the presence of an open umbilicus.

Genus *Sororcula* HAAS, 1953

Description: The genus *Sororcula* HAAS, 1953 from the same stratigraphic position as *Hesperocirrus* differs in regard to its ornament of spiral rows of tubercules and more slender shell shape. The sinistral shell is slender-trochiform, and initial whorls are like those of *Hesperocirrus*. Later whorls are flat, and the umbilicus is narrow, the columella thus hollow. Sculpture consists of tubercules arranged in collabral rows of connected straight lines across sutures with a fine and dense revolving striation in the background. Specimen housed in the Museum of Natural History in New York (HAAS collection) demonstrate the dextral initial whorls at *Sororcula* as well as *Hesperocirrus* in several individuals (own observation).

Difference: The two species of *Sororcula* from the Peruvian Upper Triassic are very close in shape to *Hamusina maxwelli* from the Lower Jurassic of New Zealand and differ from it only by their open umbilicus.

Genus *Hamusina* GEMMELLARO, 1878

Diagnosis: The diagnosis of the Hesperocirrinae applies to the genus *Hamusina*. The high conical shell has no open umbilicus, and flattend whorl flanks have an angular peripheral carina as corner to the base which is almost flat or weakly rounded. The ornament consists of nodes and spiral threads connected to oblique growth lines. The aperture is angular to rounded. Genotype is *Turbo bertheloti* ORBIGNY, 1850 from the Upper Lias of France.

Difference: *Hamusina* differs from *Scaevola* by having flattenend and not rounded whorl flanks like the latter. *Hesperocirrus* and *Sororcula* have an open umbilicus and are generally smaller. Difference to *Aristerella* and *Shikamacirrus* consists only of a narrow umbilicus. *Sensuitrochus* differs by an ornament of spiral rows of tubercules and flattened flanks while *Auseria* has basically smooth whorls. In *Platyacra* the periphery lies almost in the middle of the whorl, while it is usually below that position in *Hamusina*.

Species *Hamusina maxwelli* n. sp.
Pl. 4, Fig. 9,10; Pl. 5, Fig 1,3,4,5

Diagnosis: The diagnosis of the genus *Hamusina* applies. The shell is of conical outline with collabral ribs inclined and continuous across the sutures. Ribs are transected by fine revolving striation. The base is flattened and the columella is massive. Outline of the aperture is subangular and its orientation is strongly oblique.

Difference: In comparison to the European members of *Hamusina*, the new species of New Zealand is very small. Ribs are inclined and

continuous across the sutures as is the case in *Sororcula costata* HAAS, 1953 from the Triassic of Peru, but the later has an open umbilicus.

Description: The embryonic shell of *H. novozelandica* is 0.15 mm wide and shows the characteristical archaeogastropod morphology with a lateral fold and apertural rim. The slender trochiform shell has an embryonic whorl embraced by a planispirally coiled, rounded first whorl of the teleoconch ornamented by a dense pattern of axial ribs. Dextral coiling changes into sinistral coiling in the second whorl of the teleoconch, and here sides of the whorls become flattened. Axial ribs decrease in number and are inclined toward the left base. They are continuous across the suture and across a ridge above the shallow suture. With more than 5 whorls the shell was probably fully grown and is only 3 mm high and 2,5 mm wide. The aperture is of subangular shape with the inner lip reflexed.

Derivatio nominis: Named in honor of the distinguished malacologist and paleontologist P. A. MAXWELL (New Zealand) who collected the material.

Stratum typicum and type locality: Kaiwara Valley in central southern New Zealand from Jurassic outcrops.

Holotypus and material: A number of individuals could be studied of which the one illustrated in Plate 4, Fig. 10 is the holotype deposited in the Geological Survey of New Zealand in Lower Hutt under number GS 9510A.

Species *Hamusina kahrsi* n. sp.
Pl. 5, Fig. 6,9; Pl. 6, Fig. 1-11

Diagnosis: The diagnosis of the genus *Hamusina* applies. The shell of *H. kahrsi* has grown to a size of about 5 cm consisting of about 9 whorls. The shell is higher than wide and has an apical angle of about 40 degrees. Whorls have a flattened to slightly concave or convex upper flank with a carina separating it from the convex base. The corner formed by the periphery is not covered by the following whorl but its position on the flank of whorls of the spire is somewhat variable within a single shell and among different individuals. A deep suture is usually present. Ornament consists of several (4 - 6) spiral ribs or rows of tubercules forming an intercalation of stronger and weaker elements. Tubercules of the spiral row on the periphery are the largest and consist of short gutter-like spines with concave side toward the aperture. The base is ornamented by acute spiral ribs separated from each other by rounded wider grooves. Spiral pattern of the ornament is transected by dense and foreward inclined growth lines which are raised into fine lamellae on the whorls flank and consist of simple lirae on the base. The shell has an outer calcitic layer and a thicker, inner, nacreous, aragonitic layer.

Difference: Variable position of the peripheral keel of *H. kahrsi* differs from that described from Jurassic species of this genus (HUDLESTON 1886-96, COSSMANN 1916) including the type of the genus *H. bertheloti*. Fine lamellar growth lines and gutter-like tubercules on the keel are characteristic to the species and differentiate from *Sensuitrochus* with regular tubercule rows and indistinct sutures and from *Shikamacirrus* with open umbilicus, both also of Cretaceous origin.

Derivatio nominis: *Hamusina kahrsi* is named in honor of E. KAHRS, the collector of the gastropod fauna from the Kassenberg in Mülheim-Broich.

Holotypus and material: The holotype is deposited with Nr. A1231/1 in the collection of the Ruhrlandmuseum at Essen and 22 further specimen housed in that collection with numbers A 840/1,2; A 1191/1,2; A 1231/2; A 1315/1,2,4,5,6,7,9,10; A 1328/1; A 1336/1,2,6,8; A 1357/1; A 1412/1,2,3.

Locus typicus and stratum typicum: The gastropods were extracted from cavity and fissure fillings in Carboniferous sandstone eroded by coastal currents at Cretaceous time and exposed in the quarry Kassenberg in Mülheim-Broich in Western Germany. These cavities were filled at Cenomanian times with red sandy limestones that contain the gastropod shells.

Description: The large shells of *Hamusina kahrsi* show quite a bit of variation in their shape and sculpture, while the apical angle remains quite constant. Most individuals are preserved with the outermost layer eroded or broken off and the outer surface of the inner shell layer exposed. Here the main features of the sculpture are still present, while they are not seen on the steinkern which is smooth. This sculpture on the outer side of the inner nacreous layer differs from the actual outer sculpture of the shell that had, during life, only been covered by an additional thin, organic, periostracal layer. The sculpture of the calcitic outer layer shows a delicate pattern of growth lamellae and tubercules where they cross the spiral ribs. Tubercules of the keel are actually short gutter-like spines. These ornamental features have changed on the surface of the layer below. Here growth lines are clearly visible but consist of smooth increments. Tubercules have a more rounded appearance with the gutter-like shape of those on the keel has totally disappeared. The finer spiral ribs with their tubercular pattern have disappeared as well or have become quite indistinct, so that ornament looks more regular and more evenly distributed. A smooth surface as is considered characteristic to the genus *Auseria* could thus have been derived from a *Hamusina* like ornament but with the outer shell layer not preserved.

The position of the periphery in whorls of individual shells varies in *Hamusina kahrsi*. While some keels lie almost in the middle part of a whorl, others have their place close to the suture or just above the suture. Those with the keel far up resemble shells of *Platyacra*, while others with the keel further down resemble

Shikamacirrus.

Discussion: The type of *Hamusina* is considered to represent the specimen figured by ORBIGNY (1850, Pl. 328, Fig. 7) of a rather large individual with 9 whorls seen in this illustration. The apex is not shown in detail. HUDLESTON (1886-96) noted the presence of a variety of *Cirrus leachi* in the Upper Lias of England and a close similarity of this form with what GEMMELLARO (1889) considered to belong into the genus *Scaevola* from the Lower Jurassic of Sicily. HUDLESTON (1886-96) also dicussed the confusion regarding the genus *Cirrus* from its origin by SOWERBY. He remarked that "SOWERBY had made a complete mess of his genus *Cirrus*." So here the solution of that mess attempted by HUDLESTON (1886-96) is being used to go on. The genus *Cirrus* is based on *Cirrus nodosus* as described and illustrated by HUDLESTON (1886-96) and also utilized by KNIGHT et al. (1960).

A *Hamusina* preserved without the highly ornamented outer calcitic shell could be regarded as belonging to the genus *Auseria* FUCINI, 1895. Here the high conical shell is described as not umbilicate and provided with smooth whorls which are flat-sided to slightly convave and end in a sharp carinate edge to the flat or weakly concave base. The aperture is of quadrangular shape. The genotype is *Trochus* (*Auseria*) *pseudonustus* FUCINI, 1895 from the Lower Lias of Italy as illustrated by WENZ (1938, Fig. 367). *Auseria* thus differs from *Hamusina* only by the absence of an ornament of spiral lines and tubercules.

Hamusina kahrsi also demonstrates that another sinistral genus could possibly be considered just a variety of one of it individuals in general shape. This is *Platyacra* AMMON, 1882 with sinistral, highly turbinate shell with median carina that forms the periphery to the flattened base. But in contrast to *Hamusina*, the open umbilicus is accompanied by a carinate margin thus relating *Platyacra* to umbilicate genera of the *Hamusina*-group like *Aristerella* and *Shikamacirrus*. The early ontogenetic whorl of *Platyacra* is flattened with nucleus immersed in the first whorls of the teleoconch. Its genotype is represented by *Turbo impressus* SCHAFHÄUTL, 1863 from Rhaetian limestone of Bavaria illustrated by WENZ (1938, Fig. 359). According to KNIGHT et al (1960) the superfamily Amberleyioidea WENZ, 1938 holds forms with dextral or sinistral, trochiform or littoriniform shells that have round apertures and are sculptured by spiral and axial elements. Here the family Platyacridae WENZ, 1938 is included which supposedly also holds turbinate dextral or sinistral shells with apical truncation due to planispiral coiling of the early whorls.

The genus *Aristerella* DUBAR, 1948 is characterized by trochiform conical shell with slightly concave flanks and a narrow umbilicus. The periphery is acutely angular and the base is almost flat, slightly convex. Ornamentation consists of a nodose cord just above the suture and spiral threads covering the flanks as well as the base similar as present in some individuals of *Hamusina kahrsi*. The aperture is subquadrangular. The type *Amphitrochilia (Aristerella) undata* DUBAR, 1948 (DUBAR 1948, Pl. 10, Fig. 12) from the Lower Jurassic of Marocco was proposed (KNIGHT et al. (1960, Fig. 202,3). According to KASE (1984) it is closely related to *Shikamacirrus*. KASE (1984) distinguished it from the later by having isometrically expanded whorl sides, a weakly concave base and a different type of surface ornamentation, which are all features that may vary within a species as is seen in the case of *H. kahrsi*. DUBAR (1948) noted great similarity also to *Auseria*. The genus *Shikamacirrus* KASE, 1984 with its shell closely resembling that of *Sensuitrochus* differs from it by having an open umbilicus. KASE (1984) observed a planispiral protoconch in the type *Shikamacirrus nipponicus* KASE, 1984 from the Upper Aptian of Japan.

Genus *Sensuitrochus* QUINTERO & REVILLA, 1966

Description: The sinistral, conical trochiform shell has a solid columella and a rounded angular basal periphery. All other features like ornament consisting of spiral rows of tubercules, almost flat base covered with spiral sculpture and aperture of subquadrangular outline and wider than high are similar to *Shikamacirrus*. Type is *Sensuitrochus ferreri* from the Campanian of Northern Spain.

Species *Sensuitrochus ferreri* QUINTERO & REVILLA, 1966

Description: The shell is of conical shape with flattened flanks and indistinct suture. Ornament consists of spirally arranged rows of tubercules of which 7 can be counted on the flank of the about 7th whorl of the teleoconch. The base is flattened as well and forms a rounded corner with the flanks. It is ornamented by fine spiral lines up to the columella. There is no open umbilicus. The thick inner shell layer consists of nacre (HÄNSEL 1992). The species is found in the slumped mass of Campanian deposits at Torallola near Pobla de Segur in the southeren Pyrenees. It is part of a gastropod assemblage that lived in the environment of a pebble beach.

Difference: *Sensuitrochus* from the Campanian of northern Spain is very close to the genus *Shikamacirrus* from the Upper Aptian of Japan and can be differentiated mainly by absence of a narrow umbilicus. According to KASE (1984) the European *Trochus sp. sinistra* COSSMANN, 1904 differs from *S. nipponicus* by its lower conical shell outline and slightly concave base that is ornamented by axial ribs and spiral cords.

Genus *Scaevola* GEMMELLARO, 1879

Description: The diagnosis of Cirridae and Hesperocirrinae applies to the genus *Scaevola*. The turbiniform or conical shell with open umbilicus, rounded whorls and ornament of strong axial (collabral) ribs crossed by spiral threads has a base with only spiral threads. The shell is large (up to 5 cm high with about ten whorls). Sutures are deep since the whorls are rounded as well as the base and the edge between base and flank is rounded angular in the juvenile teleoconch and more rounded in the fully grown shells. The aperture is orbicular in late whorls.

The genotype according to HUDLESTON (1886-96) and KNIGHT et al. (1960) is represented by *Scaevola intermedia* (BUCKMAN, 1879) from the Lower Jurassic of Sicily.

Difference: The rounded whorl flanks differentiate *Scaevola* from the umbilicate *Aristerella* and *Skikamacirrus* as well as from the non-umbilicate *Hamusina*, *Auseria* and *Sensuitrochus*.

Discussion: The genus *Scaevola* is considered to represent a member of the Trochoidea subfamily Liotiinae ADAMS & ADAMS, 1854 by KNIGHT et al. (1960). According to WENZ (1938, Fig. 785) it occurs in the Jurassic of Europe with several species. KNIGHT et al. (1960) utilized D'ORBIGNY's (1850, Pl. 332, Fig. 9) figure of *Turbo calisto* D'ORBIGNY, 1850 to illustrate the type of *Spirocirrus* COSSMANN, 1916. HUDLESTON (1886-86, Pl. 25, Fig. 1) had a less complete specimen of this species with 5 cm height, similar to the French species. The rounded whorls closely resemble those of *Scaevola* from the Lower Jurassic of Sicily which is about 18 mm high and has one whorl less than *Turbo calisto* of D'ORBIGNY (1850). Thus the later is very close to the former in size but with more rounded whorls. Thus *Spirocirrus* can be regarded a synonym to *Scaevola*. HUDLESTON (1886-96) placed *Scaevola* in the *Cirrus calisto* relation but close to the *Cirrus leachi* group, which also has representatives similar to *Hamusina*. HUDLESTON (1886-96) demonstrated that individuals of *Scaevola leachi* (SOWERBY, 1818) from the Dogger of England are quite variable in shape, ornament and width of the umbilicus representing about as much variation as is seen among individuals of *Hamusina kahrsi* in the Cenomanian of Germany.

Subfamily Cassianocirrinae n. subfam.

Diagnosis: Very small Cirridae with rounded whorls, round aperture and low trochospiral teleoconch.

Difference: Cassianocirrinae differ from Cirrinae by having rounded whorls and trochospiral shape of the teleoconch and from Hesperocirrinae by small size and rounded whorl diameter in the whole shell.

Genus *Cassianocirrus* BANDEL, 1993

Description: The trochoform sinistral shell has a dextral smooth embryonic whorl, a planspirally coiled juvenile whorl with axial ribs. The postembryonic whorl is rounded and loosely coiled. Later trochospiral whorls overlap more onto each other but are also of rounded shape. The inclined aperture is round with thickened margin. The genotype is *Euomphalus contrarius* MÜNSTER, 1841 from the Upper Triassic St. Cassian Formation of the Dolomites (Italian Alpes).

Difference: *Cassinocirrus* differs from *Zardinicirrus* by a continuous sculpture of axial ribs and from *Hesperocirrus* and *Sororcula* by the rounded shape of the whorls of the teleoconch. Its small size differentiates it from the Jurassic Cirridae.

Species *Cassianocirrus contrarius* (MÜNSTER, 1841)
Pl. 5, Fig. 7,8

Description: The shell is only 5 mm wide and 3,5 mm high and regularly sculptured by axial ribs that increase in width with whorl dimension. The embryonic shell is immersed within the apex and transforms from the low dextral coil into the sinistral coil after only one whorl of the teleoconch is completed. The sinistral teleoconch consists of only one-threequarts whorls forming a narrow and deep umbilicus. The thickened apertural margin forms an angle of about 45 degrees with the axis of coiling.

Genus *Zardinicirrus* BANDEL, 1993

Description: The naticoid sinistral shell begins with two planspirally coiled whorls. The embryonic shell has the characteristic lateral folds of the Archaeogastopoda and is succeeded by the planispiral shell sculptured with numerous axial ribs. The following sinistral shell begins in the third whorl and is sculptured only by growth lines. The genotype is *Zardinicirrus sinistralis* from the St. Cassian Formation of the Italian Dolomites.

Difference: *Zardinicirrus* differs from *Cassiancirrus* by its axial sculpture present only on the first juvenile whorl of the teleoconch and the smooth sinistral later whorls of the teleoconch are unknown from other Cirridae.

Species *Zardinicirrus sinistralis* BANDEL, 1993
Pl. 5, Fig. 2,10

Description: The small shell of about 2,1 mm width and 1,5 mm height with four whorls has an embryonic shell of 0,12 mm in diameter. The planispirally coiled juvenile teleoconch is covered

by about 24 sharp ribs. It continues in sinistral coiling of one and a half whorls with rounded aperture that has almost the hight of the whole shell (1,5 mm).

Discussion: The genus *Drepanoconcha* ZILCH, 1949 is based on the genotype *Drepania pulchra* DE GREGORIO, 1930 from the Lower Jurassic of Sicily. The small sinistral elevated shell has a flat apex with early whorls planispirally coiled and later whorls convex with narrow collabral riblets. It may represent a relative to the tiny *Zardinicirrus*.

3 Summary and Discussion

Members of the Devonian genus *Antitrochus* have the characteristic protoconch of *Hamusina* or *Hesperocirrus* as found in the Middle Jurassic of Europe and New Zealand and the Upper Triassic of Peru. HAAS (1953) had noted this similarity between *Sororcula/Hesperocirrus* on one hand and *Antitrochus* on the other hand, but interpreted it due to convergence.

In the modern superfamily Seguenzioidea of the Vetigastropoda (Archaeogastropoda), that is closely associated with the Trochoidea (BANDEL 1979), species with and without labral slit are found (MARSHAL 1983, 1988; QUINN 1983, 1987). The begin of formation of a labral slit in the ontogeny of slit-bearing Archaeogastropoda is not connected to their metamorphosis to bottom life. Usually the phase following embryonic development as crawling benthic snail is without slit. In some species several whorls may be produced without a slit (BANDEL 1982, 1991). The slit forms early or late during juvenile stages and it is thus not difficult to imagin the transformation of a species with slit to one without a slit. The opposite probably occurred in the Seguenziidae, even though a potential representative of this group (*Laubella*) living in the Triassic had a slit (BANDEL 1991). The first case is used in the interpretation of the Cirroidea. Here slit bearing forms are the older Porcelliidae, and the slit was lost in their transition to the Cirridae. Transitional forms may have been quite small as is the case in the species from St. Cassian Formation belonging to the genera *Zardinicirrus* and *Cassiancirrus*.

Key to the genera of the Cirroidea:

1. Shell with selenizone (Porcelliidae) 3
2. Shell without labial slit (Cirridae) 9
3. Teleoconch trochspirally coiled (Agnesiinae) 5
4. Teleoconch planispirally coiled (Porcelliinae) 8
5. Selenizone on basal periphery 7

6. Selenizone in central position on flank
   Agnesia of low trochospiral shape, Paleozoic
   Enantiostoma Triassic

7. *Antitrochus* trochiform spiral rows of tubercules
Hesperiella rounded trochiform with axial ribs

8. *Porcellia* rounded with strong axial folds
Coloniacirrus flattened with low arcuate ribs

9. Trochiform shell shape 11

10. Planispiral teleoconch (Cirrinae)
Cirrus initial whorls high
Discocirrus initial whorls low

11. Rounded whorls, minute (Cassianocirrinae)
Cassianocirrus axially ornamented
Zardinicirrus late teleoconch smooth

12. Conical shell shape (Hesperocirrinae) 13
13. Open umbilicus 15
14. Solid columella 16

15. *Hesperocirrus* Triassic with tuberculated keels
Sororcula Triassic with slender shell
Scaevola Jurassic with rounded whorls
Shikamacirrus Cretaceous with tuberculate ribs
Aristerella Jurassic with tuberculate keel
Platyacra turbinate with median carina

16. *Hamusina* with nodular ribs
Sensuitrochus Cretaceous with tuberculate ribs
Auseria Jurassic with tuberculate keel

The following taxonomic arrangement is suggested:

The superfamily Cirroidea is contained in the class Gastropoda and its subclass Archaeogastropoda with the order Vetigastropoda. In it the Porcelliidae represent those genera that have a labial slit like the high-trochospiral *Hesperiella*, the trochiform *Antitrochus*, the low turbiniform *Agnesia* (Agnesiinae), the highly sculptured planispiral *Porcellia* with rounded whorls and discus-like *Coloniacirrus* with compessed whorls (Porcelliinae). The *Agnesia* branch is continuous into the Upper Triassic with *Enantiostoma*. At the same time (Triassic) the slit-less family Cirridae makes its appearance which in regard to the general shell shape is very similar to its Paleozoic slit bearing relatives and ancestors. Here conical trochiform genera like *Hesperocirrus*, *Sororcula*, *Hamusina*, *Auseria*, *Platyacra*, *Aristerella*, *Shikamacirrus* and *Sensuitrochus* and turbiniform *Scaevola* are united among the Hesperocirrinae. The planispirally coiled *Cirrus* and *Discocirrus* are united in the Cirrinae and the small Triassic *Cassianocirrus* and *Zardinicirrus* form the Cassianocirrinae.

Cirroidea are here considered a superfamily of the Vetigastropoda with nacreous inner shell layer and the characteristic protoconch

of the Archaeogastropoda. To our present knowledge the superfamily made its appearance in the Lower Devonian (Emsian) coming from the same stock as Trochoidea and Pleurotomarioidea. They rapidly diversified into species with shell shape ranging from high trochispiral to planispiral and all provided with a narrow labral slit. During the Triassic time members of the Porcelliidae with labral slit transformed into Cirridae without such a slit. Both groups can be connected to each other by species with a small body size that retained the character of juvenile Porcelliidae. With begin of Jurassic time these small forms gave rise to larger ones and diversified into groups of different shell shape from high trochospiral to planispiral interconnected by intermediate forms. Low spire forms of the Cirridae, and here in the Cirrinae-branch, may have given rise to the Discohelicidae with planispiral apex. In the Upper Cretaceous (Campanian) the history of the Cirroidea ends.
It is quite possible that the Cirroidea represent a totally fossil group of the Archaeogastropoda that has no living representatives.

Cirroidea with their characteristic change in direction of coiling in the teleoconch have developed parallel to and independent from other larger groups of the Vetigastropoda like the Pleurotomarioidea, the Trochoidea and the Fissurelloidea since at least Devonian time. Their ecological place has been on hard substrates in the shallow, well agitated, warm sea. They are found connected to an abundance of sessil colonial animals. Thus they could have been living by grazing on algae like many of the Trochoidea or by feeding on animals like sponges, coelenterates, bryozoans or tunicates like many Pleurotomarioidea or utilized plants and animals as food as found among the Fissurelloidea.

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Plate 1

Fig. 1: Lateral view of *Agnesia costata* from the Mid-Devonian of the Eifel. Shell diameter 16 mm.

Fig. 2: Apical view of 9 mm high shell of *Antitrochus nodulosus* from the Givetian of Unterthal near Cologne.

Fig. 3: Apical view of 16 mm wide shell of *Agnesia costata*, same as Fig. 1.

Fig. 4: Apical view of the 6 mm high holotype of *Hesperiella ebbighauseni* from the Givetian of Unterthal in the Paffrath syncline near Cologne.

Fig. 5: Lateral view of 4 mm high shell of *Hesperiella ebbighauseni* from the same locality as holotype (Fig. 4).

Fig. 6: *Antitrochus nodulosus* with peripheral selenizone well developed in 16 mm high shell from the Givetian of Unterthal.

Fig. 7: Apertural view of *Antitrochus nodulosus* with 9 mm high shell from the Givetian of Unterthal.

Fig. 8: Apical view of *Antitrochus nodulosus* with dextral first whorl in a 4 mm wide shell. Locality Unterthal near Cologne, Givetian time.

Fig. 9: Apertural view of *Antitrochus nodulosus* from Unterthal near Cologne, Givetium; 1 mm high shell.

Fig. 10: Apex of the 3.2 mm wide holotype of *Hesperiella ebbighauseni* with dextral first whorl in sinistral teleoconch.

Fig. 11: Apical view of 2.9 mm wide shell of *Hesperiella ebbighauseni*. Detail to Fig. 5.

Fig. 12: 21 mm high shell of *Antitrochus nodulosus* from Unterthal near Cologne, Givetum.

Fig. 13: Apical view of 4 mm wide *Antitrochus nodulosus* from Unterthal near Cologne, Givetium.

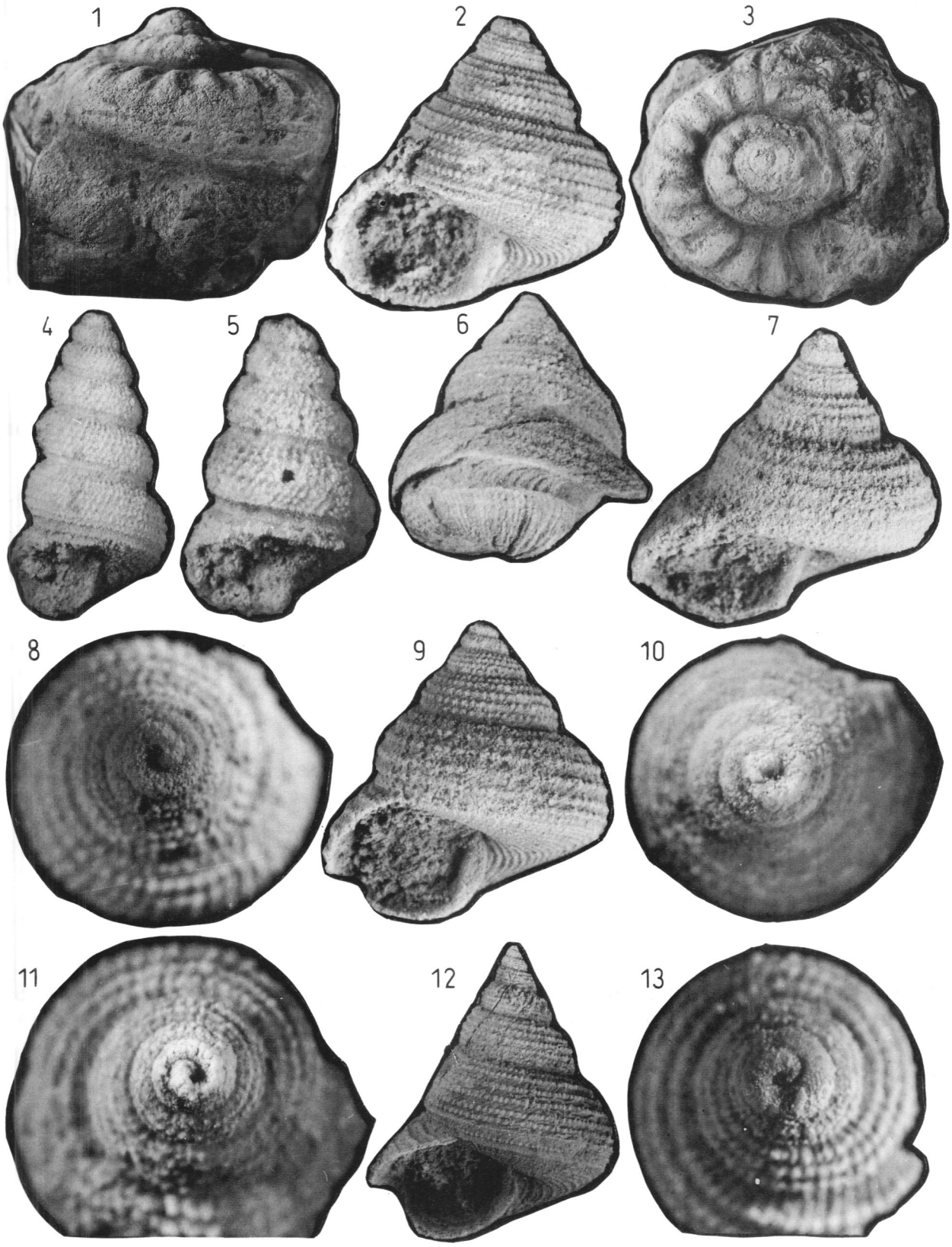
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Plate 2

Fig. 1: Last whorl of 7 mm height of *Antitrochus nodulosus* (detail to Fig. 2) with slit and selenizone in peripheral edge.

Fig. 2: *Antitrochus nodulosus* from the Givetian of Unterthal in lateral view of 17 mm high and 16 mm wide shell.

Fig. 3: Lateral view of *Porcellia puzo* from the Lower Carboniferous of Tournai in Belgium. Shell diameter is 20 mm.

Fig. 4: Apical view of *Porcellia puzo* from the Lower Carboniferous of Tournai in Belgium. Maximum shell diameter is 25 mm.

Fig. 5: *Porcellia cornuarietis* with 8 mm high aperture from the Givetian of Unterthal near Cologne.

Fig. 6: *Porcellia cornuarietis* with 5 mm high aperture from Girzenberg near Sötenich in the Eifel.

Fig. 7: *Porcellia spinosa* with 12 mm wide shell from Mid-Devonian strata of Girzenberg near Sötenich in the Eifel.

Fig. 8: *Porcellia spinosa* with 20 mm wide shell from the Givetian of Unterthal near Cologne.

Fig. 9: Lateral view of 2 mm high shell of *Porcellia cornuarietis* from Girzenberg near Sötenich (same shell as shown in Pl. 3, Fig. 6).

Fig. 10: The umbilicus of the initial whorl lies in the apex of the teleoconch in a 10 mm wide *Porcellia cornuarietis* from the Givetian of Unterthal near Cologne.

Fig. 11: Apical view of a fully grown shell (24 mm wide) of *Porcellia spinosa* from Girzenberg near Sötenich in the Eifel.

Fig. 12: A 14 mm wide apical view of *Porcellia spinosa* from the Mid-Devonian Girzenberg near Sötenich in the Eifel.

Fig. 13: Fully grown, about 26 mm wide an 10 mm high shell of *Porcellia cornuarietis* from the Givetian of Unterthal near Cologne.

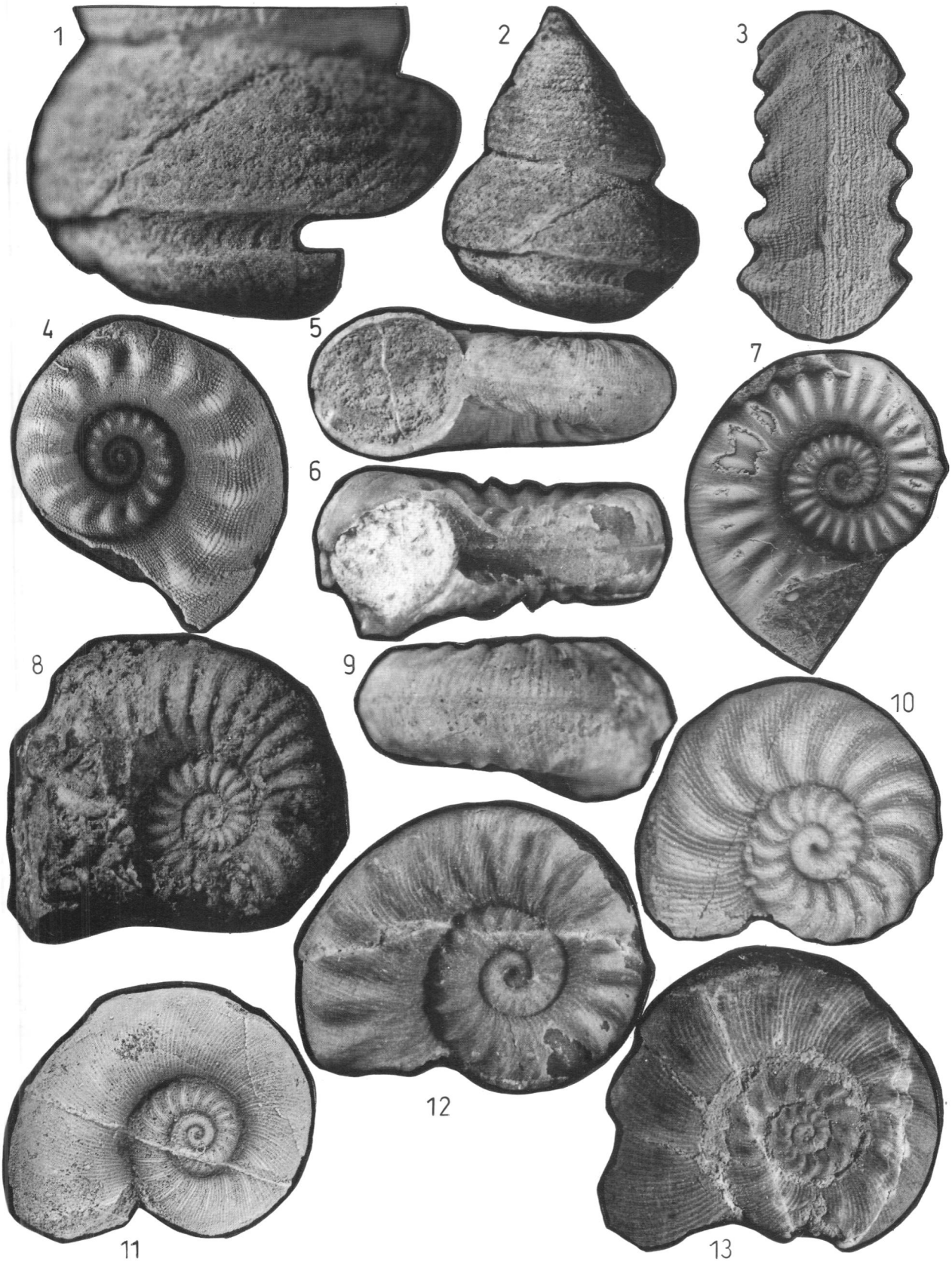
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Plate 3

Fig. 1: Interior whorls *Coloniacirrus primordialis* from the Iberg near Bad Grund (Harz Mountain) of Adorfian age (visible shell about 3 mm wide).

Fig. 2: The dextral inital whorls of *Porcellia spinosa* from the Givetian of Unterthal near Cologne are seen in the apex of the teleoconch (visible shell about 3 mm wide).

Fig. 3: Apical view of *Porcellia cornuarietis* with 20 mm wide shell from the Givetian of Unterthal near Cologne.

Fig. 4: Lateral view of *Porcellia cornuarietis* with 3,5 mm wide shell with narrow selenizone from Unterthal (Givetium).

Fig. 5: Umbilical view of same individual of *Porcellia cornuarietis* as shown in Fig. 3.

Fig. 6: The apical view of the teleoconch of *Porcellia cornuarietis* from Girzenberg near Sötenich (Middle Devonian) with 5,5 mm wide shell demonstrates the umbilicus of the early dextral whorls.

Fig. 7: Apical view of a 14 mm wide shell of *Porcellia cornuarietis* from the Givetian of Unterthal near Cologne.

Fig. 8: The 14 mm wide shell of *Porcellia spinosa* seen from the umbilical side with the dextral initial whorls as in Fig. 2 from Girzenberg near Sötenich in the Eifel.

Fig. 9: Lateral view of *Porcellia cornuarietis* from the Givetian of Unterthal demonstrates the long, narrow slit and selenizone in a 20 mm wide shell.

Fig. 10: Apertural view of *Coloniacirrus primordialis* with slightly sinistral shell of 10 mm width and with 3 mm high aperture from the Adorfian of the Iberg near Bad Grund (Harz Mountains).

Fig. 11: The juvenile teleoconch of *Porcellia cornuarietis* with slightly sinistral mode of coiling surrounds the dextral initial whorls in a 3 mm wide shell from the Girzenberg near Sötenich. (View of same shell Plate 4, Fig. 3).

Fig. 12: Apertural view of *Coloniacirrus radiatus* as shown in Figs. 4 and 6 on Plate 4 from Unterthal (Givetium), 19 mm shell diameter.

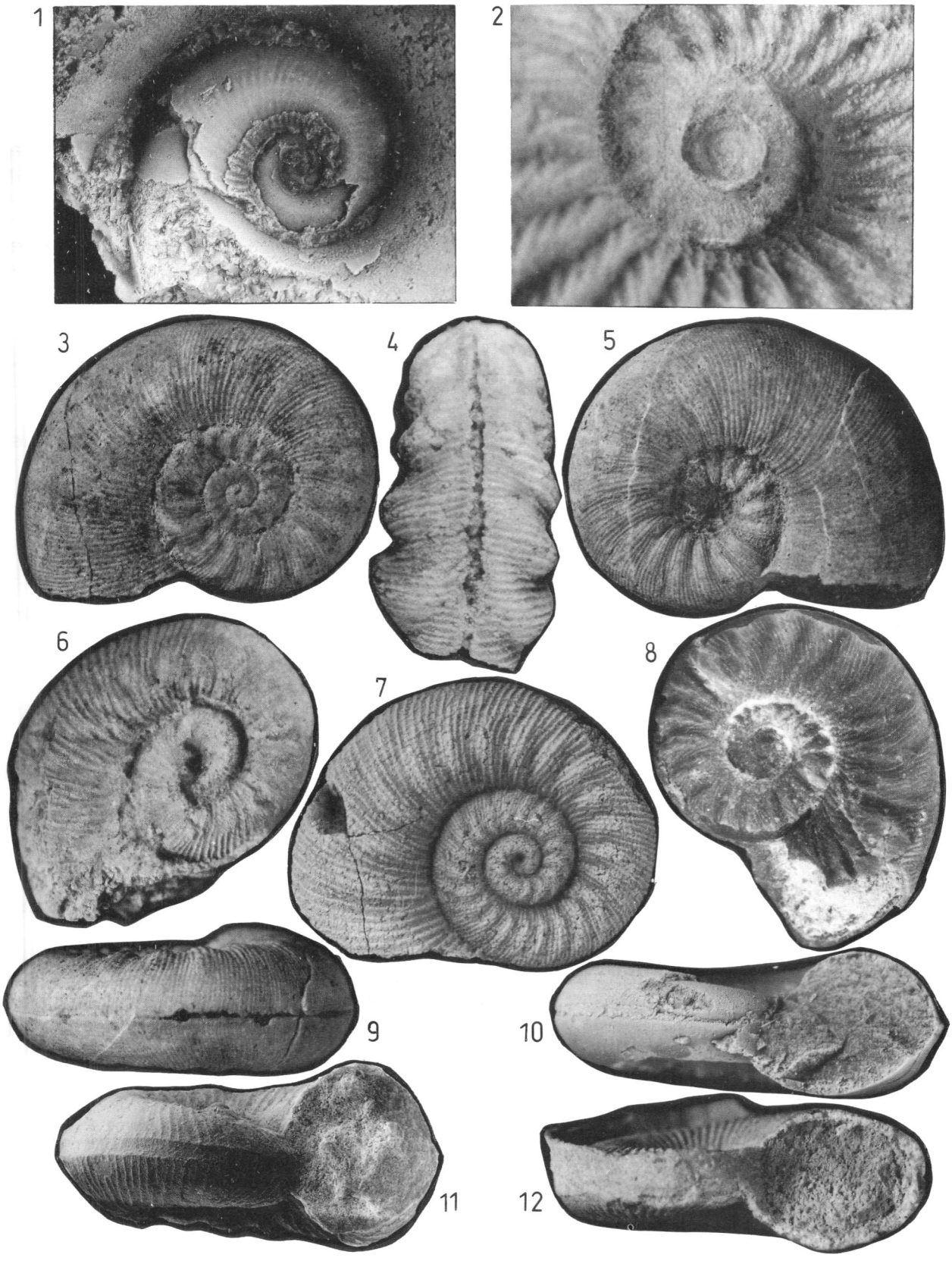
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Plate 4

Fig. 1: The 10 mm wide shell of *Coloniacirrus primordialis* from the Adorfian Iberg near Bad Grund (Harz Mountains) is slightly sinistrally coiled (Pl. 3, Fig. 10).

Fig. 2: Lateral view of *Coloniacirrus radiatus* of 19 mm wide shell shown also in Figs. 4 and 6 demonstrates the narrow concave selenizone. From Unterthal, Givetium.

Fig. 3: View onto the dextral initial shell found in the umbilicus of the teleoconch of *Porcellia cornuarietis* from Girzenberg near Sötenich in the Eifel. Same individual as shown in Plate 3, Fig. 11 with about 3 mm wide shell.

Fig. 4: Apical view of *Coloniacirrus radiatus* from the Givetian near Cologne. Same individual as in Fig. 2.

Fig. 5: Apertural view of *Hesperocirrus robusteornatus* from the Upper Triassic Pucara Group of Peru. Shell about 3 mm high.

Fig. 6: Umibilical view with dextral early whorls in their centre of same individual as in Fig. 2 and 4 with 19 mm wide shell from the Paffrath syncline.

Fig. 7: Lateral view of same individual of *Hesperocirrus robusteornatus* as is figured in Fig. 5.

Fig. 8: View onto the 40 mm wide shell of *Coloniacirrus primordialis* from Iberg (Adorfian stage of Upper Devonian, Harz Mountain).

Fig. 9: Lateral view of a 1,5 mm high shell of *Hamusina maxwelli* from the Kaiwara Valley of southern New Zealand with planispiral early teleoconch (Lower Jurassic).

Fig. 10: Lateral view of the holotype of *Hamusina maxwelli* from the Lower Jurassic of Kaiwara Valley in southern New Zealand with an about 2 mm high shell.

Fig. 11: Apical view of *Hesperocirrus robusteornatus* as illustrated in Fig. 5 and 7, demonstrating the planispirally early teleoconch succeeding the dextral embryonic shell and followed by the sinistral late teleoconch.

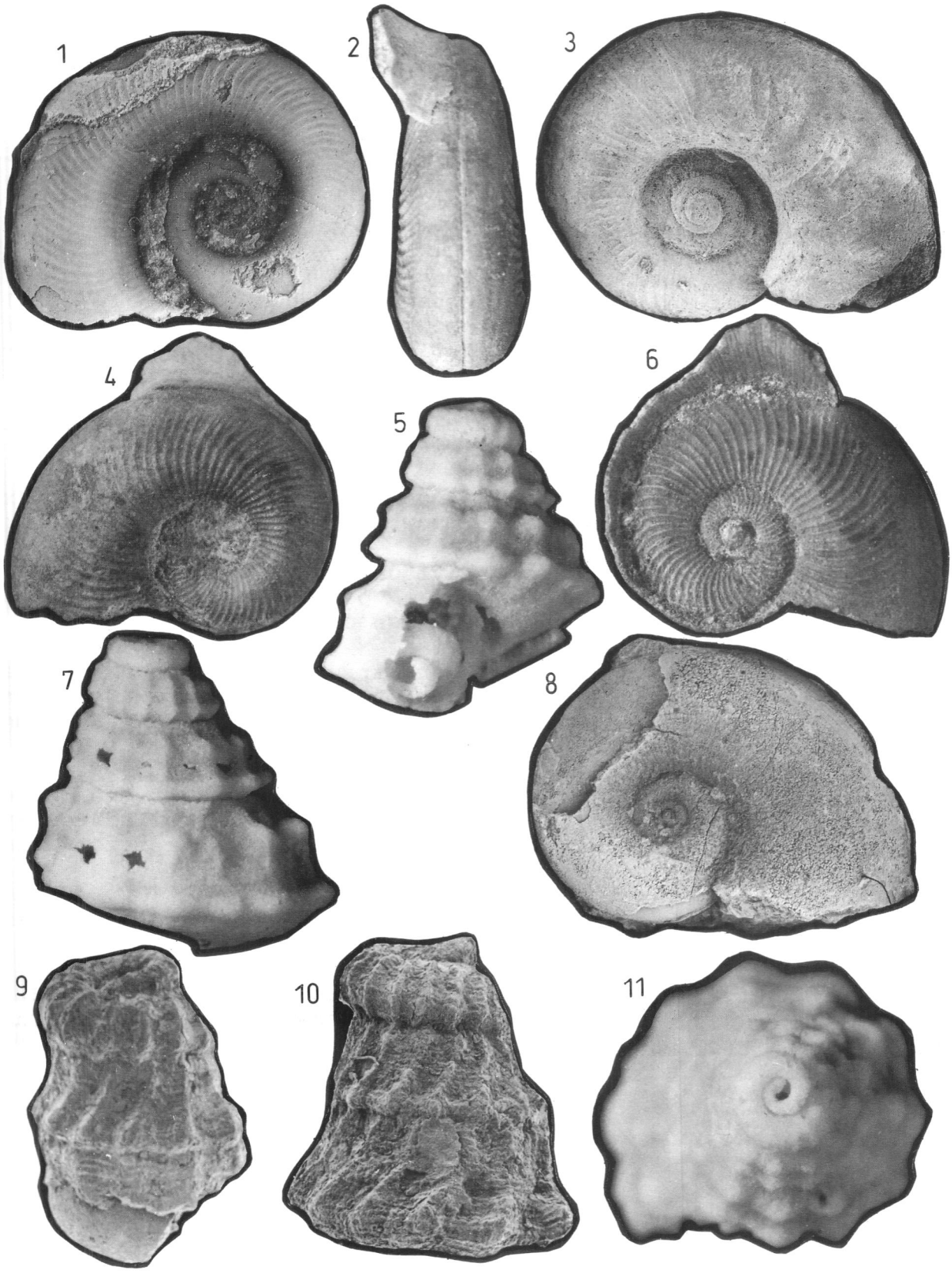
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Plate 5

Fig. 1: Embryonic shell and first axially ornamented teleoconch of *Hamusina maxwelli*. Detail to Fig. 3. The first whorl measures about 0,35 mm across (embryonic shell).

Fig. 2: Embryonic shell and early teleoconch of *Zardinicirrus sinistralis* from the Upper Triassic St. Cassian Formation of the Dolomites (Italian Alps). Detail to Fig. 10. The embryonic shell (first whorl) measures about 0,17 mm across.

Fig. 3. Apical view of *Hamusina maxwelli* from the Jurassic of southern New Zealand demonstrates the embryonic shell (Fig. 1) in a depression of the early teleoconch and the late begin of sinistral coiling. The planispiral early teleoconch-whorl measures almost 1 mm across.

Fig. 4: Lateral view of *Hamusina maxwelli* with 1,3 mm high shell from Kaiwara Valley in southern New Zealand.

Fig. 5: The detail of Fig. 4 of *Hamusina maxwelli* shows the apex of the shell from the Jurassic of New Zealand. Width 1,1 mm.

Fig. 6: Lateral view of an individual of *Hamusina kahrsi* (A 1231/2) of 19 mm height that has a peripheral keel, as is characteristic to *Platyacra*. Cenomanian of Mülheim/Broich.

Fig. 7: Apertural view of *Cassianocirrus contrarius* from the Upper Triassic St. Cassian Formation of the Alps (Northern Italy, Cortina d` Ampezzo). The shell is 5 mm wide and 3,5 mm high.

Fig. 8: Apical view of *Cassianocirrus contrarius* of the same individual as shown in Fig. 7 with planispirally coiled early teleoconch, bearing the embryonic shell in a depression and twisting into sinistral coiling in the following whorl.

Fig. 9: Basal view of *Hamusina kahrsi* of the same individual as figured Plate 6, Fig. 5. Width 26 mm.

Fig. 10: Apical view of *Zardinicirrus sinistralis* from the St. Cassion Formation, Dolomites, southern Alps of 2,1 mm width. Detail of initial whorls in Fig. 2.

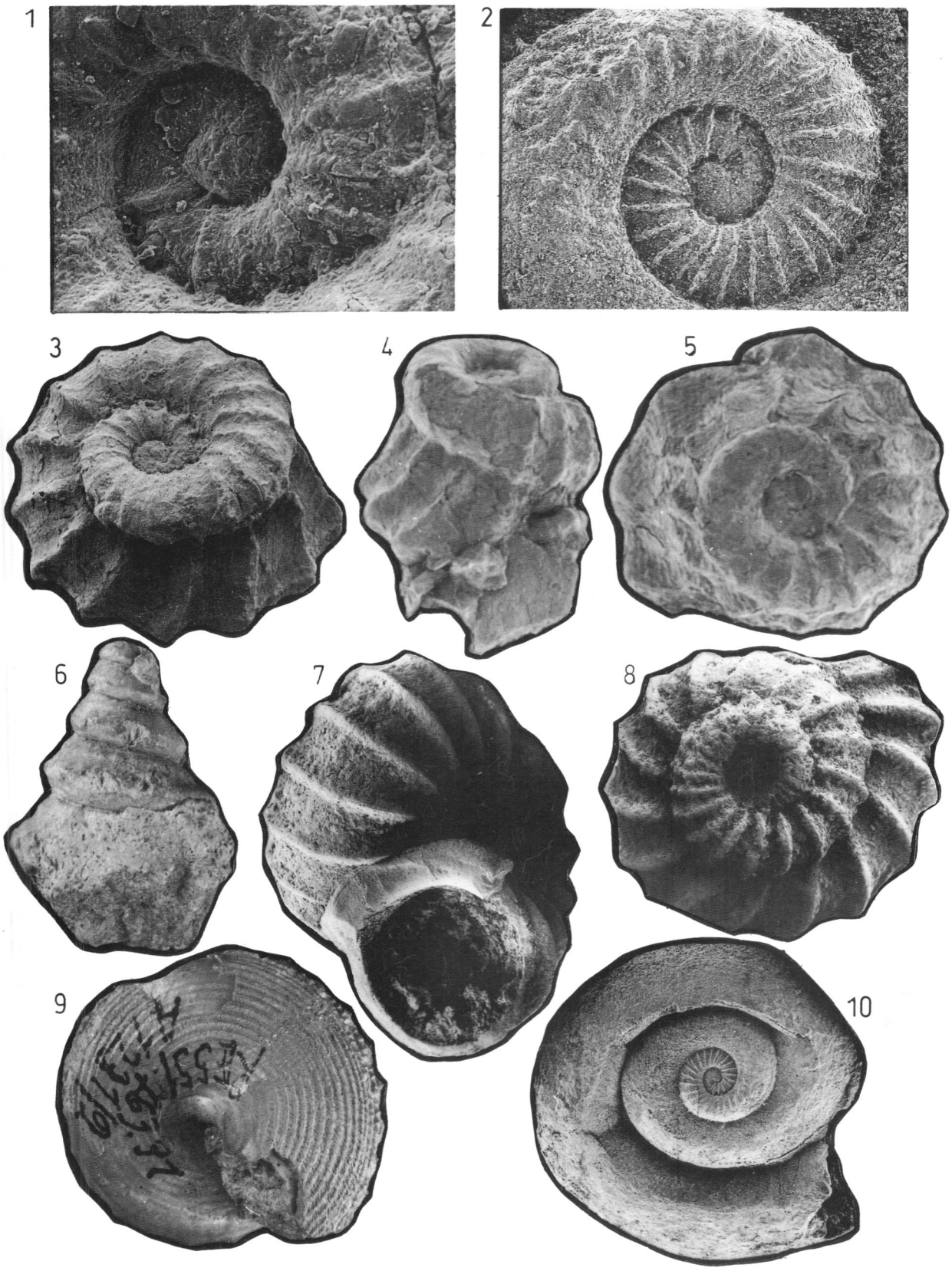
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Plate 6

All figures are of *Hamusina kahrsi* from the Cenomanian of the Kassenberg at Mülheim/Broich.

Fig. 1: Lateral view of holotype with sculpture of the outer shell layer preserved (left) and inner layer exposed at right. 21 mm high shell also shown in Fig. 11.

Fig. 2: The outer shell layer of this 21 mm wide shell has been broken off and nacreous layer shows rounder ornamented features and growth line pattern (A 1191/1).

Fig. 3: Lateral view of holotype, see Figs. 1 and 11.

Fig. 4: The 36 mm high shell shows a more median peripheral keel in younger whorl of the teleoconch and a more basal keel in the last whorl (A 1421/3).

Fig. 5: Apertural view of 25 mm high shell (Nr. A 1291/2). Here whorls are almost flat and keel lies just above suture.

Fig. 6: The 25 mm high shell has almost straight flanks and the keel is almost covered by succeeding whorl. (Nr. A 1357/1).

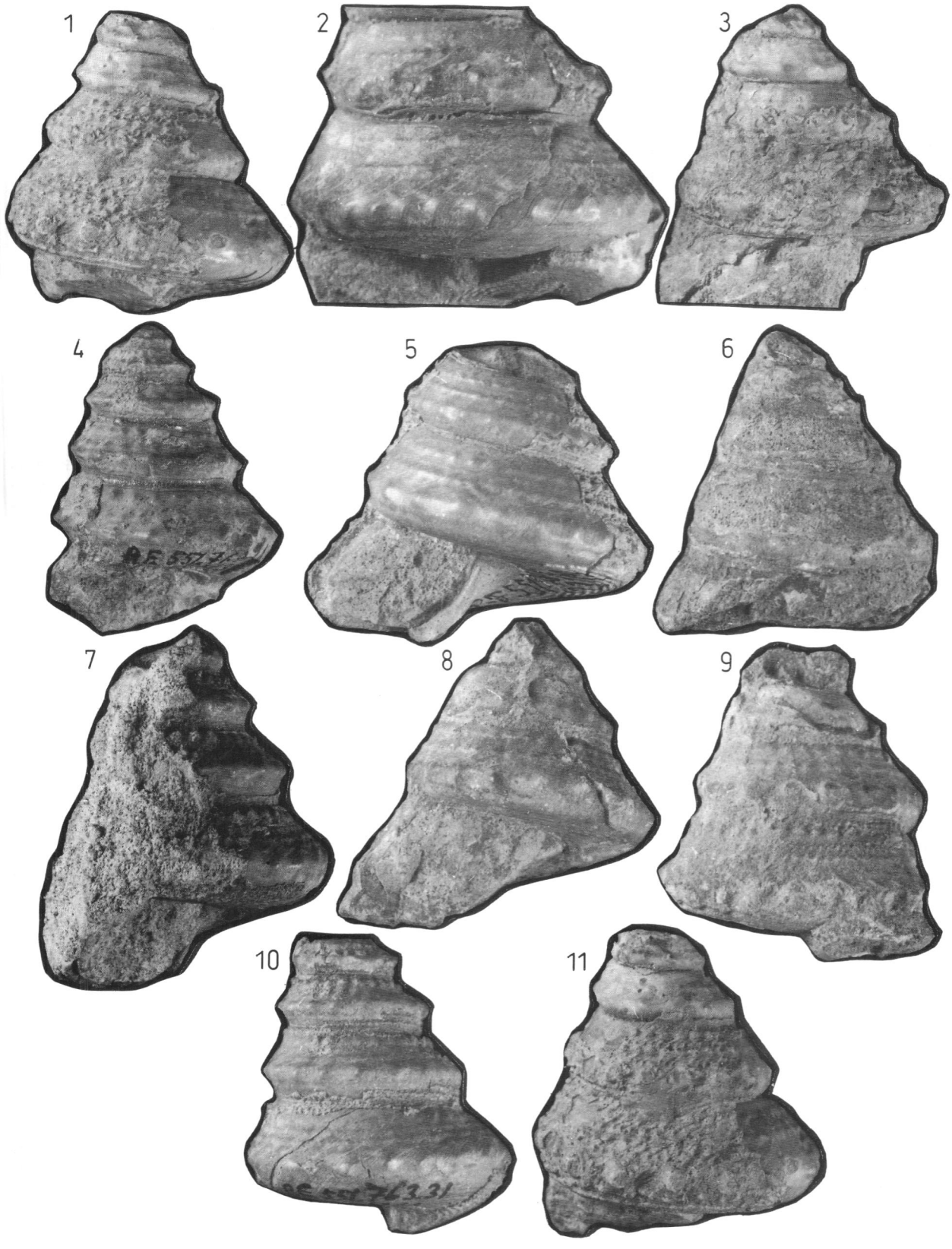
Fig. 7: Lateral view of 36 mm high specimen. (No. A 1412/1).

Fig. 8: Lateral view of 21 mm high and 22 mm wide shell with angular aperture (A 1336/6).

Fig. 9: Lateral view of individual shown in Fig. 8 with original ornament well preserved.

Fig. 10: Lateral view of about 36 mm high and 25 mm wide shell with ornament of the surface of the nacreous layer preserved (A 1412/1).

Fig. 11: Lateral view of holotype (A 1336/1) of 26 mm height and 21 mm width demonstrating well the outer, calcitic layer with ornament.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Palökologie und Paläobiogeographie "mariner" Kalkalgen im kontinental-lakustrischen Niederhäslich-Kalk des intramontanen Döhlen-Beckens (Unterrotliegend, Assel, Elbe-Zone)

Palaeoecology and Palaeobiogeography of "marine" calcareous algae from the continental-lacustrine Niederhaslich limestone of the intermontane Döhlen basin (Lower Rotliegend, Asselian, Elbe zone)

UTE GEBHARDT, Hamburg & JÖRG SCHNEIDER, Freiberg

mit 7 Bildern und 3 Tafeln

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Schlüsselworte: Unterperm, Unterrotliegend, lakustrine Karbonate, marine Kalkalgen, Taxonomie, Palökologie, Paläoklimatologie, Paläobiogeographie

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Abstract
Zusammenfassung
1 Einleitung
2 Systematik
2.1 Algae incertae sedis
2.2 Chlorophyta
2.3 Phylloide Algen
3 Geologische Situation und Environment
4 Zur Palökologie der Algenflora und Vertebratenfauna des Niederhäslich-Sees
5 Klimasituation, Paläowindrichtungen, Paläobiogeographie

Abstract

A flora of "marine" calcareous algae with *Eolithoporella*, *Heteroporella*, *Macroporella*, cf. *Clavaporella*, cf. *Anthracoporella*, ?*Epimastopora*, and *Nuia* (see SCHNEIDER & GEBHARDT 1990) as well as *Succodium*, *Saxonia* n.gen., *Girvanella*, and phylloid algae (this paper) has been discovered in certainly lacustrine limestones of the intermontane Döhlen Basin (Lower Permian, Asselian, Elbe lineament). In dependence of depth, turbulence and their position to the chemocline 5 associations of algae can be distinguished. The coexistence of a rich amphibian fauna and marine algae is