Senckenbergiana lethaea	78	(1/2)	103 – 131	1 Abb., 5 Taf.	Frankfurt am Main, 10. 11. 1998

The systematic position of the Euomphalidae (Gastropoda)

With 1 Text-figure and 5 Plates

KLAUS BANDEL & JIŘÝ FRÝDA

Abstract

The core group of Euomphalidae with the genera *Euomphalus*, *Straparollus*, *Serpulospira*, *Phymatifer*, *Schizostoma*, *Nodeuomphalus* n. g. (Devonian to Permian) are characterized by a cyrtoconic, openly coiled, planispiral protoconch. This character distinguishes them from members of the four extant subclasses of the Gastropoda (Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostropha) and places the Euomphaloidea at a similarly high taxonomic level, the new subclass Euomphalomorpha. With *Euomphalopsis* the group may have made its first appearance in the Late Cambrian, and it is certainly present from the Mid Devonian to Late Permian and thus the range is about 300 million years in duration. Throughout the existence of the Euomphaloidea other gastropod units developed convergent shell forms which can be detected by the morphology of the protoconch and, in well preserved fossils, the mineralogical and structural composition of the shell. The new taxa Euomphalomorpha n. subclassis, *Nodeuomphalus* n. g., *N. paffrathianus* n. sp., and *"Planerotinus" scheeri* n. sp. are described.

Key words: Gastropoda, Euomphalidae, taxonomy, protoconch, Paleozoic.

Kurzfassung

[Die systematische Stellung der Euomphalidae (Gastropoda).] — Den Kernbereich der Familie Euomphalidae stellen die Gattungen *Euomphalus*, *Straparollus*, *Serpulospira*, *Phymatifer*, *Schizostoma* und *Nodeuomphalus* aus dem Zeitraum Devon bis Perm. Sie werden durch einen Protoconch gekennzeichnet, der mit einer eiförmigen Anfangskalotte ausgestattet ist, an die sich eine erste offene Windung anschließt. Dadurch verbleibt eine zentrale Öffnung im Inneren der ersten planspiraligen Windung sichtbar im Apex der Schale. Dieser Protoconch unterscheidet die neue Unterklasse Euomphalomorpha von den auch heute noch existenten Unterklassen der Gastropoda, den Archaeogastropoda, Neritimorpha, Heterostropha und Caenogastropoda. Mit *Euomphalopsis* war möglicherweise schon im späten Kambrium ein Vertreter der Euomphalomorpha present. Vertreter der Gruppe sind vom Mitteldevon bis zum späten Perm gesichert nachzuweisen. Schon seit dem Ordovizium treten innerhalb anderer Gastropoden-Taxa konvergente Arten auf, so daß nur bei einer Erhaltung des Protoconches, oder auch der Schalenstruktur, Euomphalomorpha gesichert erkannt werden können. Die neuen Taxa Euomphalomorpha n. subclassis, *Nodeuomphalus* n. g., *N. paffrathianus* n. sp., and *„Planerotinus" scheeri* n. sp. werden beschrieben.

Addresses of the authors: Prof. Dr. KLAUS BANDEL, Universität Hamburg, Geologisch-Paläontologisches Institut und Museum, Bundesstraße 55; D-20146 Hamburg, Germany. E-mail: bandel@geowiss.uni-hamburg.de – Dr. JIRÍ FRÝDA, Czech Geological Survey, Klárov 3/131; CS-11821 Praha 1, Czech Republic. E-mail: fryda@cgu.cz

Contents

A review of the systematic placement of the Euomphaloidea KONINCK 1881

KONINCK (1881) defined the taxon Euomphalidae to encompass Paleozoic gastropods with planispiral and low trochospiral shape in which whorls only touch or slightly overlap onto each other. He based his new taxon on Lower Carboniferous shells from Belgium, and noted that early whorls are commonly closed by septa, a keel is often present, and a shallow sinus is present at least on the upper, apical surface of the outer lip.

Later KOKEN (1889) connected the Paleozoic Euomphaloidea with slit-bearing Paleozoic gastropods. He observed a total convergence when euomphalid species and selenimorphs ("pleurotomarioideans") are traced back in time to the Ordovician. Here they meet in the genus *Raphistoma* which has the characters of both above-mentioned groups. He thus suggested that the Pleurotomarioidea and the Euomphaloidea arose from the same stock. KOKEN (1889) stated that euomphalids have a dextral protoconch and are thus coiled normally. Therefore *Euomphalus* and relations cannot be connected to *Solarium* (= *Architectonica* and relations) which has a sinistrally coiled protoconch in a dextrally coiled teleoconch. According to KOKEN (1889) the last straparollids lived in the late Permian "Zechstein" Sea. But KOKEN (1889) also connected the Paleozoic euomphalids with Mesozoic gastropods such as *Amphitomaria cassiana* (KOKEN 1889) and *Discohelix* DUNKER 1848, the shells of which are without a slit, and *Schizogonium* KOKEN 1897 having slit and spines. KOKEN related more distantly to the euomphalids Carboniferous genera like *Anomphalus* MEEK & WORTHEN 1867, *Omphalotrochus* MEEK 1864 and *Platyschisma* M'COY 1844, and he also noted connection to the Ordovician *Maclurites* LESUEUR 1818.

KITTL (1891) considered 16 species of the Upper Triassic fauna of the St. Cassian Formation of the Dolomites to belong to the Euomphalidae. He subdivided them into the genera *Euomphalus*, *Straparollus*, *Coelocentrus* ZITTEL 1882 and *Brochidium* KOKEN 1889. Some of these have later been transferred by BÖHM (1895) and KOKEN (1897) into the newly created genera *Woehrmannia* BÖHM 1895 and *Amphitomaria* KOKEN 1887. BANDEL (1988, 1993a) placed all so-called Euomphaloidea of the St. Cassian Formation into other groups with the exception of one species of *Serpulospira*.

COSSMANN (1915) divided the Euomphalidae into the planispirally coiled Euomphalinae and the trochospirally coiled Straparollinae. According to his model the evolution of the Euomphalidae proceeded in such way that species with loosely and openly coiled shells gave rise to species with more overlapping whorls. He thought that the *Euomphalus*-lineage holds Paleozoic *Euomphalus* and Triassic *Woehrmannia*, *Schizostoma* and *Amphitomaria*, Jurassic *Discohelix* as a relative of Triassic *Brochidium* and, among the modern relatives, *Pseudomalaxis* FISCHER 1885. The *Straparollus*-lineage supposedly contains amongst others Jurassic *Coelodiscus* and *Homalaxis* FISCHER 1885 (= *Omalaxis* DESHAYES 1830) from the Eocene.

KNIGHT (1934) supposed that Euomphalidae had a discoidal shell composed of two layers, of which the outer prismatic and

calcitic one contains traces of pigment and the inner is possibly nacreous. According to his observations, the nucleus is simple and dextral. He disagreed with the assumption of some authors that Euomphalidae were ancestral to Architectonicidae of modern times. He noted that KONINCK's (1881) illustrations of *Straparollus*, *Euomphalus*, *Schizostoma*, *Phymatifer* and *Phanerotinus* are notoriously inaccurate in detail, a view which cannot be supported by our own comparison of the original material and the illustrations. KNIGHT offered the suggestion that simple rounded nuclear whorls are characteristic of almost any nepionic gastropod, and thus, together with the erroneous interpretation of an inner nacreous layer of the shell, he disregarded the most important characters that the shell of euomphalids have to offer and that distinguish them from the other gastropods.

WENZ (1938) considered the Euomphaloidea to represent Archaeogastropoda. He thought that genera like *Euomphalus*, *Straparollus*, *Amphitomaria*, *Woehrmannia*, *Coelodiscus*, *Discohelix*, and *Brochidium* form the core of the family Euomphalidae. Their uniting factor is the flattened shell of discoidal and planispiral shape with a low protoconch and wide umbilicus. Whorls overlap only slightly and are of simple rounded shape with a more-or-less pronounced sinus at the upper peripheral margin of the aperture. In addition the Euomphalidae, WENZ (1938) included the Omphalocirridae, Platyacridae, Cirridae, Oriostomatidae, Poleumitidae and Macluritidae within the Euomphaloidea.

YOCHELSON (1956) interpreted the Euomphaloidea to have been derived from the Macluritoidea during Early Ordovician times. He thought that the group can be divided into three families: the Euomphalidae KONINCK 1881, the Helicotomidae WENZ 1938, and the Omphalotrochidae KNIGHT 1945. This scheme was also incorporated into the classification adopted by KNIGHT et al. (1960).

KNIGHT et al. (1960) thus interpreted the Euomphaloidea a little differently from WENZ (1938), and noted a calcitic outer layer and a non-nacreous inner layer composing the shell, in contrast to KNIGHT (1934) who had noted an inner nacreous layer in members of this group. KNIGHT et al. (1960) tried to keep only „archaeogastropods" in the group and sorted out all those species that had been recognized as Architectonicidae, and these were placed among the Mesogastropoda (and here in the Cerithioidea). KNIGHT et al. (1960) considered *Weeksia* STEPHENSON 1941 from the Upper Cretaceous of Tennessee (USA) as possibly the last representative of the group, as had been suggested by WENZ (1938) and SOHL (1960). The protoconch of *Weeksia* reveals, however, that this genus represents a member of the advanced Caenogastropoda (BANDEL 1988, 1993a).

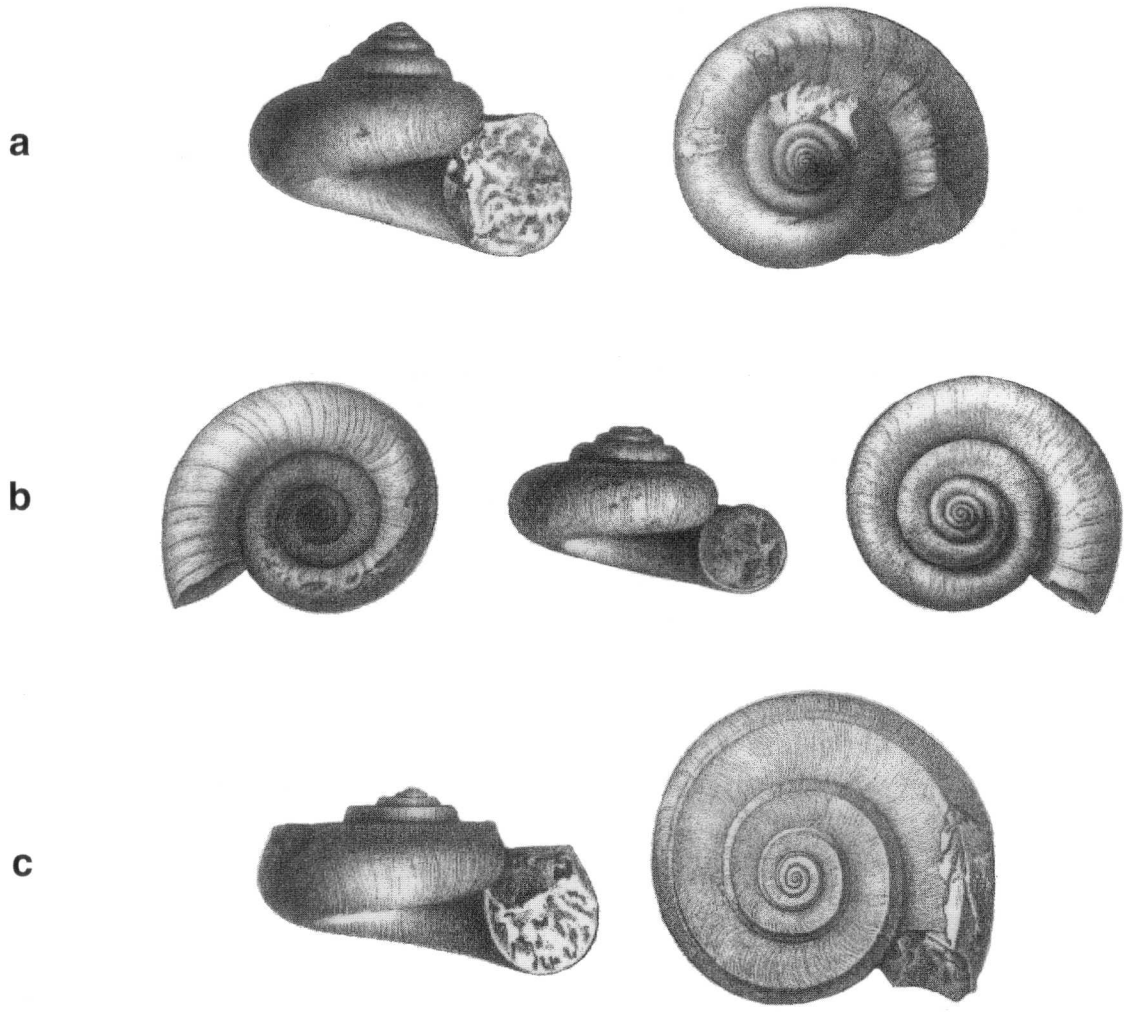
MCLEAN (1981) interpreted the deep sea, hot vent limpet *Neomphalus* MCLEAN 1981 as representing a living species of the Euomphaloidea. HONG-FU & YOCHELSON (1983) expressed the opinion that the history of the Euomphaloidea began in the Early Ordovician and that they evolved parallel to the Neritioidea and the Trochoidea as was suggested by MCLEAN (1981). HONG-FU & YOCHELSON (1983) also considered *Weeksia* to represent the youngest member of the Euomphaloidea but did not agree with MCLEAN's (1981) suggestions regarding the living *Neomphalus*. Based on fossil material from the Triassic of China, they reached the conclusion that Euomphaloidea had reached an acme in the Triassic as they had previously in the Carboniferous and the Permian.

LINSLEY & KIER (1984) proposed uniting the Onychochilacea (including Clisospiridae and Onychochilidae), Macluritacea, and (tentatively) the Euomphalacea into a new order Hyperstrophina of a new class Paragastropoda. DZIK (1982) and FRÝDA (1989, 1992) showed that the members of the superfamily Onychochiloidea have a sinistrally coiled shell with a sinistral and closely coiled protoconch. The protoconch of the Onychochiloidea shows quite different characters than occur in the Archaeogastropoda (FRÝDA 1995) and in the members of Euomphaloidea which have an planispirally and commonly openly coiled protoconch (see below). The proposed class Paragastropoda LINSLEY & KIER 1984 thus represents an artificial group uniting unrelated taxa.

LINSLEY (1978) described a new genus and species, *Hypomphalocirrus rugosus*, from the Middle Devonian of Michigan and placed it into his new family Omphalocirridae together with genus *Liomphalus* CHAPMAN 1916. According to LINSLEY (1978) his family Omphalocirridae is based on the genus *Omphalocirrus* RYCKHOLT 1860, but the same family (i.e. Omphalocirridae) had been established earlier by WENZ (1938) who thus has priority. LINSLEY (1978) found in all species of his Omphalocirridae a development of two morphotypes that he interpreted as the result of sexual dimorphism.

Most of "euomphaloidean" genera of Mesozoic and Caenozoic age are not related to the Paleozoic forms and not even to each other, as was demonstrated by BANDEL (1988, 1991, 1993a, 1996) and BANDEL & HEMLEBEN (1987). It has been demonstrated that among the Triassic species from the St. Cassian Formation forms that had been considered to belong to the Euomphaloidea represent a quite diverse collection. Some like *Amphitomaria* and relations are members of the Heterostropha, while others like *Woehrmannia* and relations represent nacreous archaeogastropods of the trochoidean type, and similar forms with planispiral shells like *Brochidium* are archaeogastropods. *Cortinella* has been separated from these because this genus has a neritimorph protoconch and thus it belongs to the subclass Neritimorpha (BANDEL 1993a, 1997). Only the one species from the Triassic attributed to the genus *Serpulospira* may actually belong to the old Paleozoic group of the Euomphaloidea (BANDEL 1993a) [but see below].

WEBERS et al. (1992) described a new species of *Euomphalopsis* ULRICH & BRIDGE 1931 from the Upper Cambrian of Antarctica and considered it to be morphologically close to *Straparollus* and thus to the core of the Euomphalidae as had been defined by KNIGHT et al. (1960). This open-coiled gastropod shell would thus represent the oldest member of the euomphaloids. WAGNER (1995), on the basis of analysis of the teleoconch characters, suggested that euomphaloideans may represent an independent gastropod branch. Even though we demonstrate here that this assumption is correct, the morphology of the teleoconch, however, cannot be used as a reliable character for determination of euomphaloideans because of the existence of strong morphological convergence with some members of all other higher taxa of gastropods (as demonstrated by BANDEL 1993a, 1997). The presence of similarly shaped Archaeogastropoda since the Ordovician is an established fact (see BANDEL & GELDMACHER 1996).



Text-fig. 1. KONINCK's (1881) illustrations of *Euomphalus* with *E. crotalostomus* M'COY (c), *Straparollus* with *S. ineptus* KONINCK (a), and *S. convolutus* KONINCK (b), *Schizostoma* with *S. catillus* MARTIN (d), and *Phymatifer* with *P. cornoniferus* KONINCK (e), and *P. pugilis* PHILLIPS (f). – Copied from KONINCK (1881), not in natural size.

The core group of Carboniferous genera

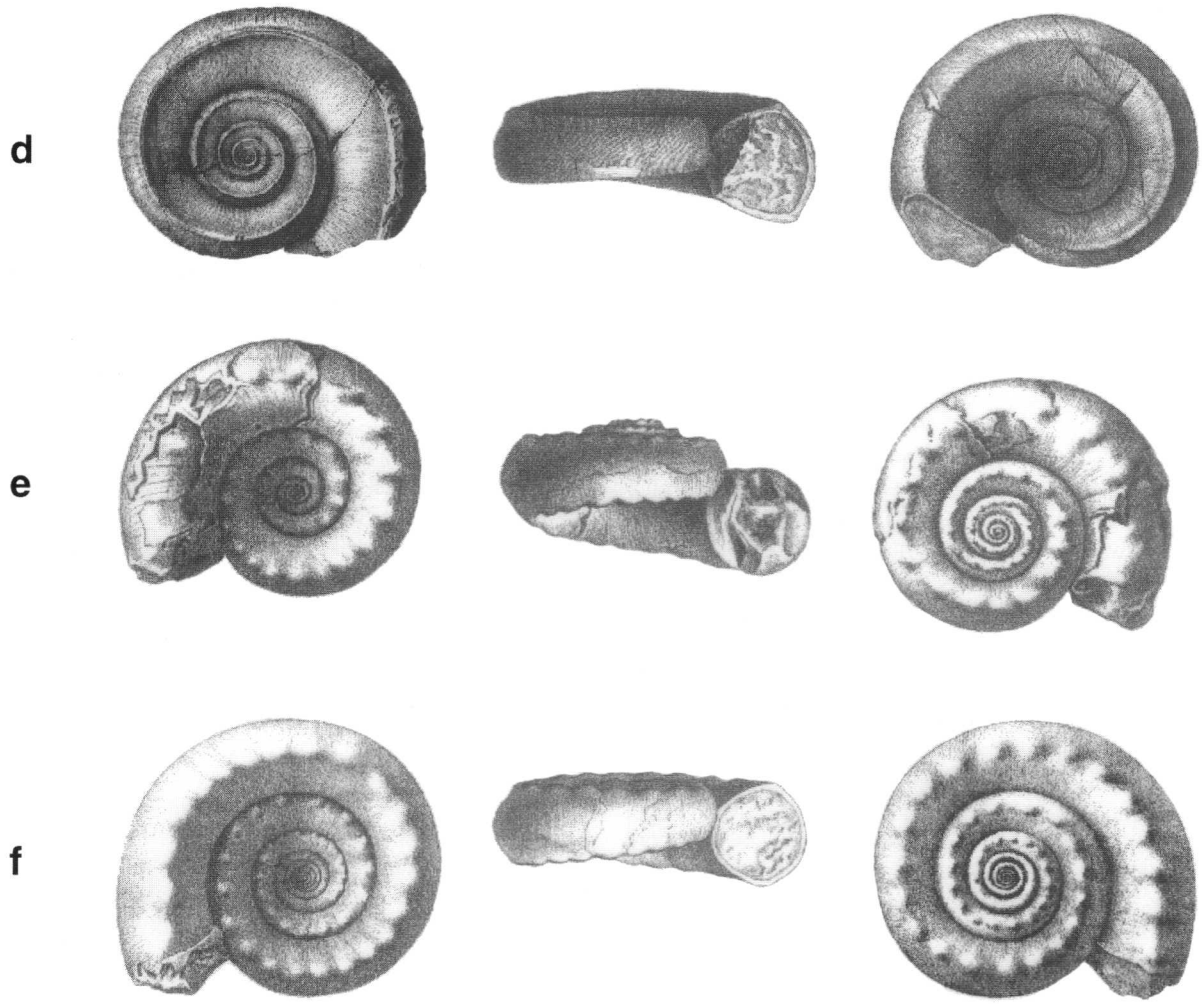
Superfamily Euomphaloidea KONINCK 1881

Emended diagnosis: The shell is initially planispirally to depressed discoidally coiled and the teleoconch may remain so or become trochospirally coiled. Whorls commonly do not overlap much onto each other or are detached from each other. The protoconch has an egg-shaped initial portion, of about 0.1 to 0.2 mm in width and height, that is succeeded by an openly coiled whorl that usually leaves a central gape before whorls touch. The shell consists of an outer calcitic layer and an inner aragonitic layer composed of needle-like biocrystallites oriented in spherulite sectors which are thus neither crossed lamellar nor nacreous in structure. The shell may or may not have a sinus in the upper part of the outer lip and may or may not have a recess in the lower outer lip. The umbilicus is always wide and open.

Remarks: The name of the superfamily Euomphaloidea was based on the genus *Euomphalus* by KONINCK (1881), for which MEEK & WORTHEN (1867) had chosen the species *E. pentangulatus* SOWERBY 1814 from the Early Carboniferous as type. According to WENZ (1938) the type originates from Belgium but according to KNIGHT (1934, 1941) and KNIGHT et al. (1960) it came from Ireland. Comparing the figures presented by both authors for both the types, from Belgium and from Ireland, we found them to be very close to each other and they may well represent the same species.

Family Euomphalidae KONINCK 1881

Diagnosis: The definition of the superfamily applies to the family. The protoconch is openly coiled and initially of



cyrtospiral shape, commonly leaving an open umbilical gape, and early teleoconch whorls are planispirally coiled and of rounded shape. The initial shell is comparatively large (larger than 0.1 mm in width of the initial cap) and shell structure of the teleoconch is unique in having a massive outer calcitic layer and an acicular inner aragonitic layer.

Genus ***Euomphalus*** SOWERBY 1814

Synonym: *Planotectus* YOCHELSON 1956.

Description: The type of *Euomphalus* (*E. pentangulatus* SOWERBY 1814) is quite a large shell of about 6 cm width and more than 2 cm height (KNIGHT 1941). The apical whorl is flattened commonly with an inward slope between the upper suture and the peripheral keel. The outer whorl face is strongly arched. The base shows rounded whorls and wide shallow umbilicus with all whorls of the shell visible. Growth lines and more-or-less faint spiral striae form an ornamental pattern (KONINCK 1881: pl. 15 figs. 1-7; KNIGHT 1934: pl. 20 figs. 3a-d; WENZ 1938: text-fig. 328; KNIGHT 1941: pl. 73 fig. 4).

Differences: *Straparollus* differs from *Euomphalus* in having rounded whorls without keel or angulation on the upper flank in late whorls of the teleoconch. *Serpulospira* differs by being loosely coiled with whorls not touching or marginally overlapping as in *Euomphalus*. *Schizostoma* has a keel on the base in addition to the upper keel, and *Phymatifer* bears a nodular sculpture in addition to the keel.

Remarks: According to KOKEN (1889) all Devonian euomphalids should be called *Straparollus* when young since they have several whorls of rounded shape in the early portion of their shell, and before other sculpture appears. These observations are confirmed here. The early whorls of *Euomphalus*, *Schizostoma* and *Phymatifer* show no keel or sinus. BATTEN (1966) described the initial whorls of the shell in

Euomphalus as rounded planispiral and embedded within the following whorls. This, however, can only be accepted in regard to the juvenile whorls of the shell, while the protoconch is cyrtoconic in its initial portion and usually has an opening present between it and the first succeeding whorl. The genus *Planotectus* YOCHELSON 1956 clearly represents an euomphalid. Specimens of this genus from the Natural History Museum in Washington (USA) have the characteristic openly coiled protoconch. This Permian genus and its type species *Planotectus cymbellatus* YOCHELSON 1956 is extremely close to the Carboniferous *Euomphalus* in general shape and can thus be considered to belong to this genus.

Studied species: *Euomphalus elegans* KONINCK 1881 from Namèche (Visean) from the KONINCK collection with 32 specimens (lots V 7/4, V 7/2 and V 7/3), very closely resembles the type of the genus (pl. 1 figs. 5-9). At 7 whorls the shell is more than 2 cm wide and 1 to 1.5 cm high and has three planispirally coiled rounded whorls before there is a low trochospiral coil connected to the beginning of formation of a peripheral angulation. One individual has a well-preserved protoconch, which begins with the bulbous and smooth initial portion succeeded by one whorl that leaves an open space in the center before it touches the back of the initial bulb. The first whorl measures about 0.6 mm in diameter. Only after the second whorl does the shell become planispiral, and in the third low trochospiral so that the apex lies in a depression. The base remains rounded and the umbilicus is wide and all whorls exposed. The initial whorl resembles that of the other euomphalids from the Visean in which this feature could be studied, such as like *Straparollus dionysii*, *Euomphalus pentagonalis* and *Straparollus aequalis*.

Euomphalus pentangonalis PHILLIPS 1836 from Visé, represented by 18 not fully grown shells (V 7/5) from the KONINCK collection, is about 1 cm high and as wide when having 6 whorls. In later whorls the shell becomes more planispirally coiled, with greater increase in width than in height, so that it resembles *E. pentangulatus*. When younger the shell closely resembles that of *Straparollus dionysii*, but begins coiling trochospirally after three whorls that are planispirally coiled (pl. 2 figs. 16-17). An angulation is formed only in the fifth whorl and this becomes prominent only on the last, more planispirally coiled whorls of the fully grown shell. It is only here that it aquires the shape of shell that with the whorl corners produces a pentagonal outline. The first whorl and even the beginning of the second whorl are openly coiled and it is only afterwards that whorls touch (pl. 1 fig. 4).

According to HARPER (1977) the juvenile shell of *Euomphalus springvalensis* WHITE 1876 from Early Visean age limestones of Gilmore City, Iowa (USA) has rounded, somewhat planispirally coiled juvenile whorls, while the adult shell has angular whorls and is fairly high. It reaches 3.6 cm in height and 4.0 cm in width and has flattened upper whorl surface, a blunt angulation, a flattened outer whorl surface and a flatly rounded base. Our own material from this locality (collected and provided by LINSLEY, Colgate Univ.) contained many juvenile shells that belong to two euomphalid species. The first one has two whorls that are planispirally coiled and from thereon the initiation of low trochospiral coiling, and may thus belong to *E. springvalensis*. The shells of the second one have three planispiral coils and perhaps they represent the initial whorls of *Serpulospira paradoxa* (WINCHELL 1863), which has also been described as common in this locality by HARPER (1977: pl. 2 figs. 9-13). Both shell types measure about 1 mm in diameter at two complete whorls and both have the central gape that is very similar to that of *E. reedsi* described below.

Euomphalus reedsi (KNIGHT 1934) with a shell consisting of about 5.5 whorls up to 12 mm wide and 3.5 mm high, represents a member of the *Euomphalus catilloides* (CONRAD 1842) group with an almost symmetrically coiled shell having gently concave apical and basal shell sides. According to KNIGHT (1934) this group of species is common in the Upper Carboniferous of the USA. In it *E. reedsi* is distinguished from the others by the rounded surface of the base of the whorls and protruding upper and outer edges of the inner whorls above the inner margin of the succeeding whorls (KNIGHT 1934: pl. 24). A specimen from the KNIGHT collection housed in the Smithsonian Institution in Washington/D.C., from the Labette Shale of the St. Louis/Pennsylvanian outlier, demonstrated the morphology of the protoconch rather well (pl. 2 figs. 21-24). The initial well-rounded whorl-cap measures between 0.15 and 0.2 mm in diameter and has a straight inner flank, and a rounded outer flank, and is thus of cyrtoconic shape. The diameter of the whorl remains about the same in the first coil at about 0.5-0.6 mm across and there is a distinct gape in its center. Whorls only touch after the first whorl is completed and remain loosely coiled but touching in the first two whorls. In their course the lower and upper corner develops an edge, which in the fourth whorl forms the characteristic sharp upper corner of the adult shell.

A very similar species from the Kendrick Shale Member of Breathitt Formation (Upper Westfalian B) from Kentucky has been preserved with original shell material. A polished, etched and gold-coated section viewed with the scanning electronic microscope demonstrated the ultrastructure of the shell. Etching brings out growth increments rather well but has also revealed the biocrystallites in their composition and arrangement. The outer layer of the shell is composed of calcitic material of massive structure (pl. 3 fig. 34). Below it, the inner layer is composed of aragonitic material arranged in needles (pl. 3 figs. 33-34). This type of structure may be called a spherulite sector or spherulitic prismatic structure and it may be found as a derivative or precursor to the characteristic molluscan biostructures, the nacre and the crossed lamellar structure (BANDEL 1975b, 1977, 1990). But here in *Euomphalus* a spherulite sector structure composed the whole inner layer, including callus layers that have been added to the shell interior later during ontogeny. There is no transition to more highly organized structures. Here, vertically oriented columnar sectors consisting of radially arranged needles may fuse to lenticular sheet-like sectors with similarly diverging needle orientation, and also of vertical arrangement. Needles of neighbouring sectors may transect each other marginally. A similar structure had been noted by BATTEN (1984).

The Mississippian (Early Carboniferous) limestone of Spergen Hill in Indiana holds three euomphalid species of which one could be attributed to the genus *Euomphalus* since an angulation appears on the apical whorl side within the third or fourth whorls (material consists of numerous shells from the Natural History Museum, Smithsonian Institution Nrs. 416810-E and 47982-2). The other two differ from each other by their mode of coiling, but develop no angulation and should therefore be included with the genus *Straparollus*. They differ from each other in that one species has a fairly regular increase in whorl width, so that a shell with 6 mm in diameter consists of five whorls, while in the other coiling is tighter and a shell with the

same diameter consists of six whorls. All three species, the one belonging to *Euomphalus* and the other two to *Straparollus* are alike regarding their initial shell portion. The protoconch has an initial egg-like part that measures about 0.15 mm in width and is succeeded by a first whorl that leaves a central opening before whorls touch in the second whorl. The first whorl of the shell measures about 0.35 mm across (pl. 2 fig. 25, pl. 3 fig. 26).

A species of *Euomphalus* from the German Zechstein (Hoerstgen, Nordrhein Westfalen, subsurface occurrence during excavation of coal mine exit) that resembles the Permian *Planotectus cymbellatus* of YOCHELSON's (1956) description has all the characters of the genus. Here the initial shell portion is almost 0.2 mm wide and high and of rounded shape with a bulbous side towards the central gape. It is succeeded by two planispiral and well-rounded whorls that come in contact with each other only after almost one whorl is completed. There is thus a large central cavity between the initial part of the protoconch and the following whorl. The apical edge that on later whorls forms a keel, inserts on the third whorl and the base remains well-rounded. The fully grown shell thus has a slightly concave, flattened apical portion and concave base with very wide umbilicus exposing all whorls in it (pl. 3 figs. 27-30).

Genus ***Schizostoma*** BRONN 1834

Synonym: *Amphiscapha* KNIGHT 1942.

Description: The type is *Schizostoma catillus* (MARTIN 1793) from the Lower Carboniferous of England as figured by KNIGHT (1941: pl. 73 figs. 3, 4) and also common in the Visean of Belgium (KONINCK 1881: pl. 17 figs. 1-3). The large discoidal shell has an apical whorl surface that is similar to that of *Euomphalus* bearing an elevated carina or keel, but in contrast to the latter there is an additional keel present on the base. The outer whorl face is regularly and smoothly arched.

Remarks: The genus *Amphiscapha* KNIGHT 1942 is described as having two keels, one on the upper and the other on the lower surface of each whorl. Its type is *Straparollus (Euomphalus) reedsi* KNIGHT 1934 from the Pennsylvanian Labette Shale of St. Louis, Missouri. Thus the whorl section is quadrangular, which differentiates *Amphiscapha* from *Euomphalus* which has no lower keel. There are, however, transitional species where a corner may be developed at the base. Differences between the genera are thus quite minute. The definition of *Amphiscapha* resembles that of *Schizostoma* so closely that the former may be considered a synonym of the latter. *Amphiscapha* simply represents North American species of *Schizostoma* of Late Carboniferous and Permian age. *Amphiscapha texana* YOCHELSON is clearly a 2.5 to 3 cm large euomphalid with the characteristically open protoconch (seen in the Smithsonian collection at Washington 1996). YOCHELSON (1956) compared *Amphiscapha* with *Amphitomaria cassiana* from the St. Cassian Formation. The latter has, however, been documented to represent a member of the Heterostropha (BANDEL 1988), with the characteristically sinistral protoconch of members of this subclass and also much smaller size of the initial shell and presence of a larval shell (BANDEL 1996: text-figs. 11a-d). This calls for caution in classifying *Amphiscapha* or *Schizostoma* from the Upper Paleozoic as long as the morphology of the protoconch remains unknown. But *A. texana* is clearly an euomphalid with the planispiral and large protoconch with a central gape. It is very close in shape to the type of *Amphiscapha, A. reedsi* (KNIGHT 1934). When an additional keel on the whorl flank is added the subgenus *Cyclioscapha* YOCHELSON 1956 is formed, but its correct place in the system remains unresolved.

Genus ***Straparollus*** MONTFORT 1810

Synonym: *Leptomphalus* YOCHELSON 1956.

Description: Characteristically 2-3 planispiral early whorls surround the protoconch before the shell may become trochospirally coiling or remain planispirally coiled. The type genus is *Straparollus dionysii* MONTFORT 1810.

Remarks: KNIGHT et al. (1960) considered *Euomphalus* to represent a subgenus of *Straparollus* because of the similarities that are present in their early ontogeny. The type of *Straparollus*, *S. dionysii*, also lived in the Early Carboniferous of Belgium and was illustrated for example by KONINCK (1881: pl. 14 figs. 16-18), WENZ (1938: text-fig. 336), KNIGHT (1941: pl. 73 fig. 1), BATTEN (1966: pl. 2 figs. 7, 8). According to KNIGHT (1941) the type comes from near to Namur, while WENZ (1938) figures the type species from Visé that represents KONINCK's original figure. Since *Euomphalus* and *Straparollus* are clearly differentiated by the morphology of their fully grown shell, the opinion of WENZ (1938) is supported, according to which both genera should be kept separated. The opinion of COSSMANN (1915), according to which both genera belong to different families can clearly be rejected since KONINCK (1881) had demonstrated the existence of species that are intermediate between *Euomphalus* and *Straparollus*. The data presented indicate that the types of both genera along with *Serpulospira*, *Phymatifer* and *Schizostoma* have the same type of protoconch and extremely similar early whorls.

As had been suggested by KOKEN (1889), YOCHELSON (1956) proposed a relationship among Paleozoic Gastropoda ranging from trochospiral species with round whorl diameter to planispiral species with angular diameter and keels. *Straparollus* was considered to have occupied a median position with a mid to low trochospiral shell with whorls of almost round cross-section, and a shallow sinus on the upper part of the outer lip. But this latter feature is not present in the genotype as originally proposed by KONINCK (1881). *Leptomphalus* YOCHELSON 1956 contains species with lowly coiled whorls similar to *Straparollus*. It can be considered synonymous with *Straparollus* as defined by KONINCK (1881), who had also included planispiral species in this genus. Species of *Leptomphalus* can thus be placed within the genus *Straparollus*.

The species named *Straparollus australis* MAXWELL 1961 and *Straparollus brevis* YOO 1988 with a low spiral shell, and *Straparollus davidi* DUN & BENSON 1920 by YOO (1988, 1994) have short and smooth protoconchs included in a planispiral first whorl. They thus belong to another group of gastropods with trochospiral protoconch without central gape, and probably belong to the Archaeogastropoda. YOO (1994: pl. 3 figs. 6-8) documented that the protoconch may be succeeded by 5 to 6 whorls with a sharp demarcation to the following 2.5 whorls. Such changes in teleoconch morphology can be encountered among several genera of Recent and fossil Trochoidea (HICKMAN & MCLEAN 1990; BANDEL 1993a).

Studied species: *Straparollus dionysii* from Visé in Belgium demonstrates a protoconch with an open coil (pl. 1 fig. 4). In a specimen from lot V 7/3 from the KONINCK collection of the Natural History Museum in Brussels that probably belongs to this species, the initial whorl begins with a rounded cyrtoconic portion succeeded by one open coil in which the whorl remains totally detached in the centre of the next planispiral coil. The studied specimen is very close to illustrations of *Straparollus dionysii* by KONINCK (1881) and thus a representative of the characteristic euomphalid in the core of the group as suggested by KNIGHT et al. (1960: text-fig. 108, 4a,b) (pl. 1 figs. 11-14). *S. dionysii* has a first whorl of 0.5 to 0.7 mm in diameter but openly coiled with the initial portion wider than 0.1 mm (pl. 1 fig. 15). In contrast to *Euomphalus reedsi*, there is not only a gape in the center of the initial whorl but the whole initial whorl may be openly coiled. *Straparollus dionysii* from Visé (of the lot V 5/3 from the collection KONINCK in Brussels holding 11 specimen) have the largest individual measuring about 3 cm in width and 2 cm in height consisting of 7.5 whorls (pl. 1 figs. 11-15). Fully grown individuals have four planispiral whorls with the initial portion forming a shallow concavity in the apex. Only later in ontogeny the shell begins with the trochospiral coil resembling the shell KNIGHT (1934: pl. 20 fig. 1) illustrated as such.

Straparollus aequalis SOWERBY 1812 from Visé, studied in two lots from the KONINCK collection, has the largest specimen (pl. 2 figs. 18, 19) consisting of 6.5 whorls and 4 cm in width with a planispirally coiled shell (lot V 5/2). There are 19 further but smaller individuals in the sample and there is another lot (V 5/1) with 16 individuals, all of which exhibit the same type of regular dextral coiling with a flattened apex that is broadly concave due to a increase in whorl diameter with growth and a wide and deep umbilical side with all whorls clearly visible in the umbilicus. The initial shell is openly coiled and has the same character as noted in *Straparollus dionysii*. The initial portion of the first whorl is not well preserved, but the first whorl is detached from the succeeding whorls and further whorls barely touch, with the suture remaining very deep throughout growth. *S. aequalis* is clearly different from *S. dionysii* in remaining planispirally coiled throughout while only the first three whorls are planispiral in the latter.

Straparollus pileopsideus PHILLIPS 1841 from Visé of the KONINCK collection (V 5/4) with 12 specimens has a shell that with 10 mm in diameter is about 4 mm high and consists of almost 6 whorls. Its shape is intermediate between *S. aequalis* and *S. dionysii* with almost five whorls planispirally coiled before coiling forms a dextral low trochospire. The apex is weakly concave, while the umbilicus is deep and wide. The first whorl measures about 0.4 mm in diameter, is largely detached from the second whorl that measures less than 1 mm in diameter and has a central gape with the egg-like initial part suspended freely in it (pl.1 fig. 2).

Straparollus laevigatus LEVEILLÉ 1835 from the Tournaisian of Le Hon, with four individuals from the KONINCK collection (lot T 1/12), is very similar to *S. aequalis* in having planispiral coiling with a flattened slightly concave apex and wide umbilicus. Here the initial whorl has an even wider inner gape, and the shell measures 6 mm in width with four whorls. The first whorl begins with a cyrtoconic initial part but immediately afterwards whorls touch so that only an inner gape remains open (pl. 1 fig. 1).

Straparollus fallax KONINCK 1843 from Visé (of the KONINCK collection lot 8/1) has a rounded conical shell with tighter coiling in later whorls but also demonstrates central gape and planispiral coiling of the initial whorls (pl. 1 fig. 10). A shell with about 7 whorls is about 2.2 cm high and 2.4 cm wide with very narrow umbilicus and rounded base. The first three whorls are rounded measuring about 2.5 mm across. From thereon the shell becomes trochospirally coiled and whorls overlap and aquire weakly convex flanks. While the umbilicus is very wide at first, it becomes narrower with growth. Growth lines commonly are prominent and slightly sinuous forming a wide lobe at the basal corner.

Genus ***Phymatifer*** KONINCK 1881

Description: The shell resembles that of *Euomphalus* but carries nodes on the angular margins of the apical and umbilical sides. The flank between both is well-rounded.

The genus is based on the species *Euomphalus pugilis* PHILLIPS 1836 from the Lower Carboniferous of England (KNIGHT 1941: pl. 73 fig. 6) also well represented in the Lower Carboniferous of Belgium (KONINCK 1881: pl. 15 figs. 13-16). Preservation and general shape of the shell from Visean localities in Belgium are similar to species of *Euomphalus* and *Straparollus* from the same locality. It is therefore assumed that shell composition was similar. The characteristic protoconch of the Euomphalidae has not yet been confirmed on a species of the genus *Phymatifer*, but it probably belongs here.

Difference: Size and general shell shape of *Phymatifer* is that of *Euomphalus* and *Schizostoma* but the keels on both apical and umbilical sides of the shell carry nodes.

Genus ***Serpulospira*** COSSMANN 1915

Description: The juvenile shell is trochospirally or planispirally coiled with whorls in contact with each other, while the protoconch shows open coiling with gap in the nucleus. Later whorls of the teleoconch detach from each other and form an open spiral. Ornament consists of growth lines reflecting a simple shape of the apertural lips. The type species is the Devonian *Serpularia centrifuga* ROEMER 1843 which according to KNIGHT (1941: 316, pl. 71 fig. 4) came from the Upper Devonian (Iberg Limestone, Adorfium) of Bad Grund in the Harz Mountains.

Differences: The open spiral shell with detached whorls differentiates *Serpulospira* from other genera like *Euomphalus* and *Straparollus*. The circular shape of the aperture differentiates it from genera like *Euomphalus*, *Schizostoma* and *Phymatifer*. Juvenile shells cannot be differentiated from those of other euomphalids.

Remarks: *Serpulospira centrifuga* should be from the Upper Devonian and closely resembles the specimen from the Middle Devonian Paffrath Syncline as shown below. WENZ (1938: text-fig. 340) figures the Carboniferous *Serpulospira serpula* (KONINCK 1843) from Belgium to illustrate the genus *Serpulospira* as well as ?*Phanerotinus*, relying on KONINCK (1881, 1883) who used the genus *Phanerotinus* to describe shells from the Lower Carboniferous of Belgium that look like

Serpulospira from the Middle Devonian. KONINCK (1883) recognized the type genus of *Phanerotinus* SOWERBY 1844, *Euomphalus cristatus* PHILLIPS 1836, from the Visean of Belgium, even though it did not carry the leaflike expansions of the holotype from England as illustrated by KNIGHT (1941: pl. 70 figs. 1, 2). This was probably a bad choice and as a consequence KONINCK (1883) used the genus name *Phanerotinus* to describe several species from Visé and Tournai. Of these *Serpulospira serpula* may actually include *S. vermilia* (GOLDFUSS 1844) and *S. intermedia* (KONINCK 1883) if the species is allowed to include some variation in its mode of open coiling. All these species or forms from Tournai have a ridge on the apical whorl side which clearly distinguishes them from Devonian *Serpulospira* and the Australian *S. scalariformis* YOO 1988. The species described by KONINCK from Visé apparently have no or a less developed apical fold on their whorls.

Serpulospira scalariformis YOO 1988 represents a characteristic member of the genus *Serpulospira*. It represents a minute shell that is openly coiled and carries a bulbous protoconch with smooth, curved outline (YOO 1994: pl. 2 figs. 8-10; pl. 3 figs. 1-5). The protoconch forms an open half coil with thickened end and smooth surface. It thus represents the characteristic protoconch of the Euomphalomorpha. DZIK (1994: text-fig. 35C) described some small gastropods from the Famennian of the Holy Cross Mountains in Poland, among them one open coiled shell consisting of little more than one whorl which he attributed to *Serpulospira crassitesta* (TIETZE 1870). The initial shell portion is quite like that of the Euomphalomorpha in having a rounded bulbous shape and a strong twist into the succeeding whorl which is of completely detached coiling. The dimension of the initial part with more than 0.1 mm and the diameter of the first whorl having a size of more than 0.5 mm as well as totally planispiral coiling, indicates that it is an euomphalid protoconch, but it does not need to be a member of the genus *Serpulospira* as suggested by DZIK (1994). It could also represent the protoconch of another euomphalid genus, as such protoconchs are for example also found in species of *Euomphalus* and *Straparollus*.

Middle Devonian Euomphaloidea from the Paffrath Syncline

Genus ***Straparollus*** MONTFORT 1810

Type species: The genus *Straparollus* MONTFORT 1810 is based on *Straparollus dionysii* from the Lower Carboniferous of Belgium.

Discussion: *Straparollus (Straparollus)* MONTFORT 1810 brought together dextrally coiled shells with rounded whorl profile and without any kind of angulations. KAYSER (1889) established the new subgenus *Philoxene* for shells of the same morphology as found in *Straparollus (Straparollus)* but with shell fragments attached to their outer shell surface. He chose *Euomphalus laevis* ARCHIAC & VERNEUIL 1842 from the Middle Devonian of Germany as the type species. This opinion was accepted by KNIGHT (1941) and KNIGHT et al. (1960). LINSLEY & YOCHELSON (1973), after studying some Middle and Upper Devonian straparollids, expressed the opinion that „the habit of attaching foreign matter to the shell is not an adequate criterion for differentiation of Paleozoic gastropods at any taxonomic level" (p. 19). However, contrary to their expressed opinion they used the regularity and the position of the attachment scars as characters to distinguish species (f.e. p. 9). LINSLEY & YOCHELSON (1973) studied only three individuals of the type species. We can present data based on more than 70 complete shells of the type species of *Straparollus (Philoxene)* KAYSER 1889 from the type locality. They indicate that LINSLEY & YOCHELSON's opinion about the validity of attachment scars in generic placement can not be supported regarding the subgenus *Straparollus (Philoxene)*.

Straparollus laevis (ARCHIAC & VERNEUIL 1842)

Pl. 4 figs. 37-43

1842 *Euomphalus laevis*, ARCHIAC & VERNEUIL: 363, pl. 33 fig. 8.
1844 *Euomphalus laevis*, GOLDFUSS: 88, pl. 191 fig. 8.
1853 *Euomphalus laevis*, SANDBERGER: 213-214, pl. 25 fig. 6.
1853 *Euomphalus laevis* var. *turritus*, SANDBERGER: 213-214, pl. 25 fig. 7.
1889 *Philoxene laevis*, KAYSER: 292, pl. 8 fig. 5.
1913 *Euomphalus laevis*, PACKELMANN: 223.
1915 *Euomphalus (Philoxene) laevis*, KIRCHNER: 214.

Description: Shells are moderately sized, subdiscoidal, dextrally coiled and have a wide umbilicus. The rounded whorl profile is without any distinct angulation and sutures are deep. The young part of the shell is nearly planispirally coiled. During subsequent shell growth the whorls move downward thus forming a low, dextral shell. The apex of the shell is flat or slightly concave at its centre. The whorls are attached to each other below whorl periphery of the preceding whorl in adult forms. The width of the deep umbilicus amounts to about one third of total shell width. The apertural margin is circular in its profile and the aperture is distinctly radial. The shell ornamentation consists only of irregularly spaced, fine growth lines.

Discussion: From more than 70 complete shells of *Straparollus laevis* from the Paffrath area, and thus including the type locality of this species, we found specimens with and without attached foreign matter on their outer shell surface. Both varieties of individuals have a shell of the same shape and thus we considered them to belong to the same species. This observation supports LINSLEY & YOCHELSON's (1973) opinion on the invalidity of the subgenus *Straparollus (Philoxene)*. The foreign matter consists of fragments of molluscan shell or of crinoids and is attached on the shell periphery sometimes in a very regular way but often also irregularly. LINSLEY & YOCHELSON's (1973: 9) observation that the attachment scars are evenly spaced in *Straparollus laevis* from Europe and contrast with the way in which attachment scars are arranged in North American species is most probably only a result of the rather limited amount of material studied by those workers.

Protoconch: The specimens of *Straparollus laevis* (ARCHIAC & VERNEUIL 1842) from the locality Sötenich in the Eifel

have the typical protoconch of the *Euomphalus*-type (HEIDELBERGER, in prep.).

Stratigraphic position: Mid Devonian limestones of Givetian age.

Material: More than 70 complete shells from the Unterthal, and 5 complete shells from the Schladethal, Unterer Plattenkalk, Bergisches Land, Germany (collection EBBIGHAUSEN).

Genus *Serpulospira* COSSMANN 1915

Type species: The genus *Serpulospira* is based on *Serpularia centrifuga* ROEMER 1843 from the Devonian of Germany.

Discussion: ROEMER (1843) considered the type species *Serpulospira centrifuga* to be a worm tube and placed it into genus *Serpularia*. Later KONINCK (1843) described the species *Euomphalus serpula* for Carboniferous and Devonian shells with open-coiled whorls, later considered by KONINCK (1883) to belong in the genus *Phanerotinus* KONINCK (1883). ARCHIAC & VERNEUIL (1842) recognized this species of KONINCK from the Middle Devonian of Germany (p. 363, pl. 33 fig. 9). COSSMANN (1915: 144) based his new genus *Serpulospira* on ROEMER's species from Germany. KNIGHT (1941) designated a badly preserved specimen from the Grund locality (Germany) to be the holotype of the type species of *Serpulospira*.

Thus, species level taxonomy of *Serpulospira* is rather complex because many Devonian species were described and at least some of them are synonyms. Two Lower Devonian species, *S. (S.) soluta* (SPITZ 1907) and *S. (S.) lituites* (SPITZ 1907) are known from Emsian limestones of the Carnic Alps (Austria) (JHAVERI 1969). WHIDBORNE (1892) described *S. (S.) centrifuga*, and his new *S. (S.) munda* (both placed in *Phanerotinus*) from the Middle Devonian of England. Many further species of *Serpulospira* were described from the Eifelian and Givetian of North America (see LINSLEY 1968; LINSLEY & YOCHELSON 1973; BLODGETT & JOHNSON 1992). The latter authors established a new subgenus *Straparollus (Eleutherospira)* uniting in it both dextral and sinistral shells that are very high-spired. It differs from *Straparollus* sensu strictu by having a higher spire, but there are transitional individuals, so that the new subgenus is somewhat doubtful.

Serpulospira serpula (KONINCK in ARCHIAC & VERNEUIL 1842)

Pl. 4 figs. 44-48

Description: The shell has a moderate size, and consists of a planispirally coiled juvenile shell that changes into a slightly sinistral or dextral, openly coiled adult shell during ontogeny. The younger part of the spire is nearly planispiral and sutures are deep. The later teleoconch has disjunct coiling of the rounded whorls without angulations. The aperture is vertical and of circular outline. The diameter of the adult whorl comprises about 20% of the total shell width. Ornament consists only of irregularly spaced, fine growth lines.

Discussion: The species name *Euomphalus serpula* is the first published and figured name for this species from the Devonian of the Paffrath area. KONINCK (1843) used this name for Carboniferous and Devonian species with openly coiled shells. ROEMER's (1843) name *Serpularia centrifuga* that is considered to have priority over KONINCK's name (see LINSLEY & YOCHELSON 1973) was actually published later than that of ARCHIAC & VERNEUIL (1842). As noted by BLODGETT & JOHNSON (1992), ROEMER's species came from the Frasnian Iberg Limestone of the Harz Mountain and is thus younger than the Middle Devonian species figured by ARCHIAC & VERNEUIL (1842) with the name *Euomphalus serpula* KONINCK. WHIDBORNE (1892: 261) noted that *Euomphalus serpula* KONINCK in figure 9 a, b in ARCHIAC & VERNEUIL (1842) represents a synonym of his *Phanerotinus mundus* (= *Serpulospira*). KARCZEWSKI (1989) noted *Serpulospira centrifuga* also from the Early Givetian of Poland. Here we use the earliest available name for individuals from the Paffrath area.

Protoconch: The specimens of *Serpulospira serpula* from the Sötenich locality in the Eifel Mountains, contained in the collection of D. HEIDELBERGER, has the characteristic openly coiled, planispiral protoconch of the *Euomphalus*-type (HEIDELBERGER, in prep.).

Remarks: The studied material, from Middle Devonian limestones of Givetian age, contains two morphotypes of the species *Serpulospira serpula*. One resembles *Euomphalus serpula* (ARCHIAC & VERNEUIL 1842: 363, pl. 33 figs. 9, 9a and ROEMER 1876: pl. 32 fig. 10). Here the adult shells have disjunct whorls that are coiled closely to the plane perpendicular to the shell axis (pl. 4 fig. 48). Some shells have distinct sinistral coiling of the openly coiled adult whorls. From these we studied 5 complete shells from the Schladethal, Bergisches Land, Germany (collection EBBIGHAUSEN). The second morphotype (of ARCHIAC & VERNEUIL 1842: 363, pl. 33 fig. 9b) has sinistral coiling of the younger whorls and dextrally coiled later whorls forming an openly coiled trochiform shell (pl. 4 figs. 44-47). These have been studied with 10 complete shells from the Schladethal, Unterer Plattenkalk (collection EBBIGHAUSEN).

The second morphotype of *Serpulospira serpula* has a lower spired shell than present in the extremely high-spired *Straparollus (Eleutherospira)* BLODGETT & JOHNSON 1992 from the North-American Devonian. BLODGETT & JOHNSON (1992) included both sinistrally and dextrally coiled shells in their subgenus.

None of the shells described here had a concavity (sinus) developed on the upper part of the whorl as is characteristic of *Serpulospira centrifuga* (ROEMER 1843). This feature of the type species of the genus *Serpulospira* is also absent in *Serpulospira diversiformis* LINSLEY 1968 from the Middle Devonian of North America. According to LINSLEY (1968), the missing sinus as well as smaller shell size distinguishes *S. diversiformis* from *S. centrifuga*. *Serpulospira serpula* of the first morphotype resembles *S. diversiformis* and *S. swickae* BLODGETT & JOHNSON 1992, but both latter species appear to have at first a dextrally coiled shell. We, therefore, think that all morphotypes are just varieties of one and the same species.

Genus *Nodeuomphalus* n. g.

Type species: *Euomphalus labadyei* ARCHIAC & VERNEUIL 1842.

Etymology: The name is combination of the generic name *Euomphalus* and word node.

Diagnosis: This euomphalid gastropod has a whorl profile with a sharp angulation at the upper whorl face and the base of the whorl is ornamented by a spiral row of distinct nodes. Specimens of the type species, *Nodeuomphalus labadyei* from Sötenich in the Eifel Mountains have the typical openly coiled, planispiral and large protoconch of the *Euomphalus*-type (HEIDELBERGER, in prep.).

Discussion: The genus *Nodeuomphalus* is distinguished from all other euomphalid genera by the presence of a spiral row of nodules ornamenting the periumbilical angulation of its shell base. In addition to this character the new genus differs from *Straparollus, Philoxene*, and *Serpulospira* in the shape of the whorl profile. While all these latter genera have a rounded whorl profile *Nodeuomphalus* is angular in cross-section. *Serpulospira* and *Straparollus (Eleutherospira)* can be also distinguished from *Nodeuomphalus* by openly coiled adult whorls. *Straparollus (Amphiscapha)* KNIGHT 1942 (= *Schizostoma*) is distinguished from *Nodeuomphalus* by its sinistrally coiled shell. *Euomphalus* and *Straparollus (Leptomphalus)* YOCHELSON 1956 (= *Straparollus*) have a similar whorl profile to *Nodeuomphalus* but differ in an obtuse angulation on the upper whorl surface and lack of a spiral row of nodes on the shell base. The genus *Cylicioscapha* YOCHELSON 1956, which had originally been considered a subgenus of *Amphiscapha,* is distinguished from *Nodeuomphalus* by the presence of an irregularly noded angulation on both upper and lower whorl sides. The genus *Phymatifer*, based upon a nodose straparollid which has been considered to represent a subjective synonym of *Euomphalus* (see KNIGHT et al. 1960), has nodes on both upper and lower whorl surfaces in contrast to *Nodeuomphalus* with such a keel only on the base. The two species described here show no transitional shell shapes.

Composition: In addition to the type species *Nodeuomphalus labadyei*, *Euomphalus basinodosus* (KIRCHNER 1915) and *Nodeuomphalus paffrathianus* n. sp. from the Middle Devonian of Germany, and *Straparollus (Euomphalus) nodibasis* (GORDON & YOCHELSON 1987) from the Carboniferous of North America are placed in the genus *Nodeuomphalus*.

Nodeuomphalus labadyei (ARCHIAC & VERNEUIL 1842)

Pl. 5 figs. 49-53

1842 *Euomphalus labadyei*, ARCHIAC & VERNEUIL: 362-363, pl. 33 fig. 6.
1844 *Euomphalus labadyei*, GOLDFUSS: 83, pl. 189 fig. 12.
1876 *Euomphalus labadyei*, ROEMER: pl. 29 fig. 8.
1895 *Euomphalus labadyei,* HOLZAPFEL: 396.
1896 *Euomphalus labadyei,* KOKEN: 510.
1913 *Euomphalus labadyei,* PAECKELMANN: 223.
1915 *Euomphalus labadyei,* KIRCHNER: 217.
1922 *Euomphalus labadyei,* PAECKELMANN: 36.

Diagnosis: A species of *Nodeuomphalus* with a subdiscoidal, depressed spire; the sharp upper angulation at the last whorl always forms the topmost part of the spire.

Description: The moderately sized shell is discoidal and dextrally coiled with wide umbilicus. The whorl profile is subpentagonal with two distinct angulations of which the upper one is protruding and very sharp. The whorl profile between the suture and the upper angulation is flat or slightly concave. Below it the whorl side is rounded down to the obtuse basal angulation. The width of the aperture equals one third of the total shell diameter. Ornament consists of fine growth lines and the spiral row of 15-25 rounded nodes which surround the wide umbilicus and are radially elongate, continuing from the lower obtuse angulation into umbilical wall of the whorl.

Stratigraphic position: Middle Devonian limestones of Givetian age.

Material: 6 complete specimens from the Bücheler Schichten, Herrenstrunden, Bergisches Land, Germany (collection EBBIGHAUSEN).

Nodeuomphalus paffrathianus n. sp.

Pl. 5 figs. 54-59

Holotype: Senckenberg Museum, catalogue number SMF XII 3428 figured here pl. 5 figs. 57-59.

Etymology: *paffrathianus* – according to its type locality Paffrath near Cologne.

Diagnosis: A species of *Nodeuomphalus* having a slightly elevated spire with a flat or slightly depressed initial part.

Description: The moderately sized, slightly elevated and dextrally coiled shell has a wide umbilicus that occupies about one third of the total shell diameter. The subcircular whorl profile displays a flat sutural ramp perpendicular to the shell axis that is abaxially bordered by a sharp spiral angulation. Below it the whorls are continuously curved into the rounded shell base. The aperture has a shallow but distinct sinus in place of the upper angulation. Ornament consists of growth lines which are more distinct on the upper ramp and on the spiral row of rounded and radially elongated nodes around the umbilicus. The number of nodes increases during ontogeny to about 25 in one whorl and they are continuous into the umbilical wall.

Discussion: *Nodeuomphalus paffrathianus* is distinguished from the type species *N. labadyei* in having a slightly elevated spire. *N. labadyei* has a subdiscoidal, depressed spire in which the sharp upper angulation on the last whorl always forms the topmost part of the spire, while the spire protrudes in *N. paffrathianus*. The shape of the young, flat shell of *N. paffrathianus* resembles that of the adult shell of *N. labadyei* suggesting that a close relationship exists between the species. KIRCHNER (1915) described *Euomphalus basinodosus* from the Middle Devonian of the Eifel, that resembles *N. paffrathianus* and is thus transferred into the new genus *Nodeuomphalus*. *N. basinodosus* is closer to *N. paffrathianus* in also having a protruding spire and can be distinguished from it by having a higher spire and an obtuse angulation at the periphery.

Material: 20 complete specimens from the Bücheler Schichten, Herrenstrunden, Bergisches Land, Germany (collection EBBIGHAUSEN).

Stratigraphic position: Mid Devonian limestones of Givetian age.

Other potential members of the Euomphaloidea

A number of species from older Paleozoic strata resemble the Euomphalomorpha of the Carboniferous and Permian but their protoconch is unknown. They are thus problematic in their higher taxonomic placement. We thus present a short survey of those genera that may in the future be included in the Euomphaloidea as soon as their protoconchs are known.

The genus *Monitorella* ROHR 1994 is based on the 4 cm large *M. auricula* from the Middle Ordovician of Nevada described by ROHR (1994: text-fig. 4, 9-25). The subhemisperical shell has a flat base (if seen as dextral), slightly tangential aperture, a deep apical cavity surrounded by an angular crest and a rounded lower outer edge. The operculum is plate-like and has a projecting muscle process. If seen as a sinistral shell the umbilicus forms a conical groove.

ROHR (1980) noted from the Ordovician some species that closely resemble *Euomphalus*, and he placed them into the genus *Helicotoma* SALTER 1859 because of its greater age. According to ROHR (1988) *Helicotoma* is common in the Lower and Middle Ordovician of North America, Europe and Asia. It is characterised by a discoidal, phaneromphalous shell with a flattened upper surface, a carina at the angular whorl shoulder, and cords at mid whorl and adjacent to the umbilical suture. From the Middle Ordovician of Nevada ROHR (1994) described two further species with the same general characteristics, one of which *Helicotoma gubanovi* ROHR 1994 bears a pseudoselenizone just below the carina forming the edge of the flattened apical part of the shell. The protoconch is unknown. Other species were placed by ROHR (1980) within the genus *Boucotspira* ROHR 1980, including species which very closely resemble *Euomphalus pentangulatus* in the shape of their shell. Another genus that could well represent closely related species to the Devonian and Carboniferous *Euomphalus* is *Ophiletina* ULRICH & SCOFIELD 1897. Species have discoidal, nearly planispiral shells that carry a midwhorl horizontal flange and are common in the Ordovician (ROHR 1988).

In the genus *Sinutropis* PERNER 1903 are grouped discoidal, deeply phaneromphalous shells with rounded subhexagonal or subpentagonal whorl profile and a U-shaped sinus at the upper outer surface. Early whorls are depressed, and sutures are deeply impressed. The whorl face is broadly convex between sutures. Ornament consists of fine, closely spaced revolving lines. Growth lines curve backwards from suture to sinus at shoulder, then forward along the outer edge of the whorl. Ordovician species of *Sinutropis* described by ROHR (1988) look like the Silurian (Ludlow) species described by PERNER (1903) from Bohemia.

Members of the genus *Pachystrophia* PERNER 1903 look similar to *Lesueurilla* KOKEN but are not sinistrally coiled. The shell is discoidal, phaneromphalous with rounded whorls, loosely coiled with fine spiral ornamentation (ROHR 1988). According to ROHR (1994) the Middle Ordovician *Helicotoma tennesseensis* ULRICH & SCOFIELD 1897 resembles *Lesueurilla isabellaensis* CULLISON 1944 but the latter species is more flattened in shell shape. The protoconch is not known in either *Pachystrophia* or *Leseurella*.

Members of the genus *Lytospira* KOKEN 1896 are described as discoidal and also openly coiled as is the case in *Serpulospira*, but with whorl profile subtriangular with a rounded angulation at the crest of the whorl (ROHR 1988 from the Upper Ordovician of Alaska). The rate of expansion is slow and in many species foreign objects are attached to the outside of the shell. According to LINSLEY & YOCHELSON (1973) *Lytospira* is the oldest reported carrier shell genus. KOKEN (1896, 1925) and YOCHELSON (1963) described carrier shells from Norway and ROHR (1994) from the Ordovician of Nevada.

The genus *Ecculiomphalus* PORTLOCK 1843 is also characterized as a discoidal, uncoiled shell which is lenticular in cross section and has an acute midwhorl angulation. The apertural lip is sinuous above and below in addition to a V-shaped sinus at midwhorl. The type has a crest at the upper angulation of the whorl which is not present in the Upper Ordovician species described by ROHR (1988).

The genus *Walcottoma* ROHR 1994 is based on the c. 2.5 cm large *Walcottoma frydai* ROHR 1994 from the Middle Ordovician of Nevada. The low spired, gradate phaneromphalous shell has an inwardly inclined ramp bordered by a carina at the upper-outer edge. A V-shaped sinus is found in the aperture at the carina and a strong spiral cord characterises the midwhorl with a second present just above midwhorl. Weaker spiral cords are found below midwhorl and on the base. According to ROHR (1994) *Walcottoma* is closely related to *Helicotoma* from which it differs by its single strong spiral cord at midwhorl while the latter has weaker spiral ornament and a lower spire. *Polhemia taneyensis* CULLISON 1944 is similar in shell profile and ornamentation, but the upper whorl surface extends above the whorl shoulder. The shell resembles *Trochonema*, but the trochonematoids have no deep sinus high on the whorl.

The genus *Polhemia* CULLISON 1944 from the Ordovician is similar to *Trochonema* in general shell shape but has a groove at the upper suture (KNIGHT et al. 1960), and to the genus *Barnesella* BRIDGE & CLOUD 1947 the shell of which is loosely coiled but with whorls in contact, discoidal with flat base and a triangular profile with the apertural notch at a sharp crest. The width of the whorl doubles per volution. *Barnesella* differs from *Lecanospira* BUTTS 1926 in a greater rate of whorl extension (ROHR 1994). The general shape of the shell with flattened apical region and keeled umbilical part resembles a sinistral *Euomphalus*. In the case of his species *B. measuresae* ROHR 1994 from the Middle Ordovician of Nevada, ROHR (1994: text-figs. 6, 11-19) reconstructed it as dextral with concave apex. KOBAYASHI (1959) described a very similar shell as *Lesueurilla zonata* from the Arenigian of Malaya which has a more rounded outer edge.

The genus *Malayaspira* KOBAYASHI 1958 has a discoidal loosely coiled shell which has a slightly convex base and is widely umbilicate of hyperstrophic shape. The cross-section is rounded-square with angulations present at upper-inner, upper-outer and lower-outer edges and a weaker angulation at upper-inner edge. The growth lines are strongly developed on the base of the shell, and they are V-shaped at the crest of the whorl. *M. hintzei* ROHR 1994 measures 4.5 cm across and looks like a sinistral *Euomphalus* with three keel-like spiral ribs on the upper surface and strong growth lines around the concave apex. ROHR (1994) created the genus *Rossospira* ROHR 1994 based on the Middle Ordovician *R. harrisae* ROHR 1994 from Nevada that measures 4 cm and looks like an openly coiled *Malayaspira*. Its spire is sunken and the base flat, the shell openly coiled, discoidal with rounded, four sided whorl profile. A V-shaped sinus characterises the carina and a frill is present at the lower-outer edge.

Problematic taxa that resemble the Euomphalomorpha

Genus ***Rhenomphalus*** n. g.

Type species: *Nautilus germanus* PHILLIPS 1841.

Etymology: A combination of the generic name *Euomphalus* and word Rhenus (Latin for the River Rhine).

Diagnosis: The very flat, discoidal, almost symmetrically but dextrally coiled shell has a subpentagonal whorl profile with its flat areas being perpendicular to the shell axis on both upper and lower whorl surfaces. Ornament consists of spiral cords on upper and lower sides of the whorl.

Discussion: *Rhenomphalus* n. g. differs from all euomphalids as well as all other known Paleozoic gastropod genera by its shell shape and its whorl profile. The very flat, discoidal, almost symmetrically but dextrally coiled shell has a subpentagonal whorl profile with the flattened top and base perpendicular to the shell axis. *Straparollus*, *Philoxene*, *Eleutherospira* BLODGETT & JOHNSON 1992, and *Serpulospira* have rounded whorl profiles without any angulation. *Serpulospira* and *Eleutherospira* can also be distinguished from *Rhenomphalus* by its opened coiling in adult whorls. *Amphiscapha*, *Euomphalus* and *Straparollus (Leptomphalus)* may be distinguished from *Rhenomphalus* by their different whorl profile. *Amphiscapha* is also sinistrally coiled. In general shell shape *Rhenomphalus* resembles the Triassic genus *Zardinihelix* BANDEL 1988 from which it may be distinguished by the different type of shell ornamentation which has no spiral ribs. BANDEL (1988, 1993a) demonstrated that *Zardinihelix* from protoconch morphology and shell structure belongs within the Vetigastropoda of the subclass Archaeogastropoda, while the taxonomic place of *Rhenomphalus* remains unresolved since protoconch and shell structure are still unknown.

Composition: *Rhenomphalus germanus* (PHILLIPS 1841) from the Middle Devonian of Germany and England.

Rhenomphalus germanus (PHILLIPS 1841)

Pl. 5 figs. 60-63

	1841	*Nautilus germanus* PHILLIPS: 118, pl. 48 fig. 226.
?	1853	*Euomphalus decussatus*, SANDBERGER: 210, pl. 25 fig. 3.
	1854	*Nautilus germanus*, MORRIS: 308.
	1888	*Nautilus germanus*, ETHERIDGE: 168.
	1889	*Euomphalus germanus*, WHIDBORNE: 30.
	1889	*Euomphalus decussatus*, WHIDBORNE: 30.
	1892	*Euomphalus germanus*, WHIDBORNE: 256-257, pl. 25 figs. 4, ? 5.

Diagnosis: Tentative monotypy, see that of genus.

Description: The shell is very flat, discoidal, almost symmetrical but dextrally coiled with wide and shallow umbilicus and concave apex. The whorl profile is subpentagonal, with apical and basal flat areas perpendicular to the shell axis and their width amounting to more than one half of the total apertural width. The lateral side of the whorl is symmetrically and gently arched and sutures are very shallow. The orientation of the aperture is radial and its width measures about a quarter of the total shell width. The upper and lower whorl sides of the shell are ornamented by four spiral cords the outermost of which forms the corner. These regularly spaced spiral ribs are crossed by fine radial threads. The lateral side of the whorl is smooth with only very fine spiral lines (pl. 5 fig. 62). Several less prominent spiral cords of decreasing width occur on the adaxially inclined area of the whorl profile. Ornament of the umbilical area consists of two weak spiral cords.

Discussion: *Rhenomphalus germanus* was described by PHILLIPS (1841) as *Nautilus* from the Devonian sediments of England. Later, WHIDBORNE (1892) noted that *Euomphalus decussatus* SANDBERGER 1853 represents a junior synonym of *Euomphalus germanus*. WHIDBORNE (1892: 257) studied PHILLIPS's type and specimens labelled by Mr. E. B. TAWNEY with the designation *Euomphalus decussatus* SANDBERGER in the Woodwardian Museum and thus not SANDBERGER's original type material. However, the specimen figured by SANDBERGER (1853: pl. 25 fig. 3) as *Euomphalus decussatus* appears to represent a different specimen than that figured by WHIDBORNE (1892: pl. 25 fig. 4) as *Euomphalus germanus*. In addition, both specimens figured by WHIDBORNE (1892: pl. 25 figs. 4, 5) show some differences (e.g. absence and presence of ornamentation of the lateral side of the whorl). All this indicates the necessity to revise the type material of *Euomphalus germanus* and *Euomphalus decussatus*.

The species *Euomphalus rota* SANDBERGER (1853: pl. 25 fig. 3) from the Middle Devonian *Stringocephalus* Limestone of Villmar (Germany) shows the same general shape of the shell and the whorl profile as *Rhenomphalus germanus*. This species probably belongs to *Rhenomphalus* and the type material is being revised by HEIDELBERGER (in prep.).

Genus ***Phanerotinus*** SOWERBY 1844

Type species: *Euomphalus cristatus* PHILLIPS 1836.

Description: All but the early whorls of the shell are openly coiled and there are large, leaf-shaped, grooved extensions which protrude horizontally from the upper of the outer whorl face. The type is *Euomphalus cristatus* PHILLIPS 1836 from the Early Carboniferous of England.

Remarks: KONINCK (1883) mixed the genera *Straparollus* and *Phanerotinus* by considering that *Phanerotinus cristatus* without the leaf-like spines would look like an euomphalid with loosely coiled whorls, which shows no sinus or a slit in its aperture. *Phanerotinus*, however, is a very characteristic shell illustrated by KNIGHT (1941 and KNIGHT et al. 1960) and its place within the system of the Gastropoda is still dubious (MORRIS & CLEEVELY 1981).

"Phanerotinus" scheeri n. sp.

Pl. 3 figs. 31-32

Holotype: The single shell available represents the holotype, number A 1271, Ruhrlandmuseum, Essen.

Type locality: Cenomanian rocky shore deposits of the Kassenberg, near Mühlheim, Ruhr.

Etymology: Named after UDO SCHEER, Custodian of the Ruhrlandmuseum, Essen.

Diagnosis: The openly coiled shell of 2 cm in diameter has 7 long gutter-like spines on its last planispiral whorl attached so they point to the sides. Ornament consists of growth lines and fine spiral lirae.

Description: The early whorls are not preserved but may well have not been openly coiled and would amount to no more than 5 mm. The preserved whorl measure 1.5 cm in diameter without the spines and consists of a rounded tube-like spiral with prominent growth lines and fine spiral lirae as ornament. The aperture is rounded and periodically expands into a long spine, seven of which are arranged on the last whorl with non-spinous areas in the spaces between individual spines. The last spine present is a little longer than 10 mm and 3 mm wide at its base, acutely triangular and pointed. The frontal spine portion is straight, formed like a narrow gutter with margins close to each other and closed at their base after the spine has left the apertural position. Spines in section are u-shaped. The last spine also shows some rounded ribs crossing the growth lines. Ornament of the spines otherwise is by growth lines that continue with those of the shell near the spine. The location of a spine indicates an interruption of shell growth documented by some thickening of the apertural margin.

Difference: *Phanerotinus cristatus* has more scale-like triangular spines that continue from one to the next following spine, while spines in *"Phanerotinus" scheeri* are more acicular and interrupted by rounded whorl margins. The open coiling distin-guishes it from modern *Guildfordia* GRAY 1850 and Triassic *Coelocentrus* ZITTEL 1882, both of which have similarly shaped spines but a closed trochospirally coiled shell.

Remarks: The spiny species from Kassenberg is morphologically closely related to this Carboniferous type of the genus *Phanerotinus* (KNIGHT et al. 1960: fig. 109, 6). It also resembles the Triassic genus *Coelocentrus* ZITTEL 1882 with 4 species described by BANDEL (1993a). Here the shell margin also extends periodically into gutter-like extensions but the shell is clearly dextrally trochospirally coiled and whorls remain attached to each other. *Coelocentrus* like *Phanerotinus* had periods of apertural growth with spine-extensions and periods without. BANDEL (1993a) demonstrated that *Coelocentrus* is a member of the Archaeogastropoda with the characteristic protoconch of this subclass, as well as with inner nacreous shell structure that is also characteristic of many members of this. *Coelocentrus polyphemus* (LAUBE 1868), representing the largest species of the group from the St. Cassian Formation measures up to 15 mm in diameter, is thus also smaller than *"Phanerotinus" scheeri* besides being closely coiled and low trochospiral. *Coelocentrus pichleri* (LAUBE 1869) has a similar arrangement of spines and also a fine spiral liration as ornament. Each whorl carries 8 to 14 spines that have grown in a similar manner as noted in the modern genus *Guildfordia* from the Pacific Ocean (BANDEL & HEMLEBEN 1975). WENZ (1938) considered the genus *Coelocentrus* to be restricted to the Triassic species but also suggested that *Omphalocirrus goldfussi* from the Devonian and *Echinocirrus armatus* (KONINCK 1843) from the Carboniferous represent older relatives uniting the three genera in the family Omphalocirridae of the Euomphaloidea. *Phanerotinus* also has its place in the *Euomphalus* relation in KNIGHT et al. (1960: fig. 106, 6), but *Omphalocirrus* was placed closer to *Maclurites* LESUEUR 1818 and *Echinocirrus* RYCKHOLT 1860 near to the slit-bearing *Luciella* KONINCK 1883. This latter placement is quite wrong since *Echinocirrus* has no slit, and the others are also quite erroneous especially since KNIGHT et al. placed the genus *Coelocentrus* as synonymous with *Omphalocirrus*. The place of *"Phanerotinus" scheeri* in the systematics of the Gastropoda is still quite open, as is the place of *"Phanerotinus" cristatus*. Both species have a similar teleoconch, but may very well represent convergent shells that belong to different gastropod units.

Genus ***Serpulospira*** COSSMANN 1915

Type species: *Serpulospira centrifuga* (ROEMER 1843).

"Serpulospira" pustulosa (KOKEN 1889)

Pl. 3 figs. 35-36

Description: The 6 mm wide and up to 2 mm high shell described by BANDEL (1993a: pl. fig. 8) consists of a last whorl that is detached and openly coiled. A similar shell was illustrated by ZARDINI (1978: pl. 1 fig. 21). Ornament consists of lamellar growth lines and fine spiral lirae that produce a wavy pattern with the collabral elements. The shell has oval cross-section and is slightly dextrally coiled. The aperture is of somewhat oval outline, a little wider than high and rounded less evenly on the base than in the upper portion. KITTL (1891) reported that earlier whorls touch each other but that the nucleus may have been open, and the whole shell is almost planispiral with a dextral coiling mode. Two shells from the St. Cassian Formation (from marls exposed near Rifugio Dibona on the road to Falzarego Pass from Cortina d'Ampezzo) have similar sculpture of collabral axial ribs of the adult shell and are coiled (pl. 3 fig. 35). One of these has the initial whorl preserved (pl. 3 fig. 36) and which measures only about 0.06 mm in width and appears to be twisted into sinistral direction initially. The later wavy pattern of the collabral axial folds of the teleoconch is not developed in the first four whorls.

Remarks: WENZ (1938: text-fig. 340) illustrated a *Serpulospira serpula* from the original drawing of KONINCK that resembles *Serpulospira pustulosa* from the Upper Triassic in regard to pattern of ornament and general shell shape (BANDEL 1993a). However, a fragment of *"Serpulospira" pustulosa* from the Late Triassic St. Cassian Formation of the Alpe di Specie locality demonstrated a composition of aragonitic crossed lamellar structure throughout, which does not fit with the Euomphalomorpha. The protoconch observed on the younger shell portions from the Dibona locality in the same formation demonstrate features like smaller size and slight sinistral twist of the initial shell portion that also do not fit with Euomphalomorpha. It is not certain that the juvenile shells really represent the initial part of the more fully grown and openly coiled shell portions, but structure of the latter and shape of the former indicate that they represent one or two problematic species that are not related to *Euomphalus* and *Serpulospira*.

KOKEN (1889) had placed this Triassic species in the genus *Brochidium* KOKEN 1889, but this genus has a type that is clearly an archaeogastropod with calcitic outer shell layer (BANDEL 1993a). ZARDINI (1978) considered *"S." pustulosa* to be close to the genus *Pseudotubina* KOKEN 1896 which is also a problematic taxon.

Genus ***Omphalocirrus*** RYCKHOLT 1860

The type is *Euomphalus goldfussi* ARCHIAC & VERNEUIL 1842 from the Givetian limestone of the Eifel Mountains (according to WENZ 1938: 201, text-fig. 356) while KNIGHT (1941: pl. 68 fig. 4) places its type locality at Paffrath, near Cologne.

Omphalocirrus goldfussi (ARCHIAC & VERNEUIL 1842)

According to KNIGHT (1941) the < 6 cm wide shell is planispirally coiled and widely umbilicate and its lower whorl has gutter-like spines arranged in a row if the shell is considered dextral. Ornament consists of transverse striae and the first four whorls have no spines. The whorls are rounded as is the aperture.

Remarks: WENZ (1938: text-fig. 356) considered *Omphalocirrus* to have a sinistral shell with the spines in this case pointing upwards and the base flattened. Even though *Coelocentrus* represents a Triassic spine-bearing, slit-less archaeogastropod (BANDEL 1993a) with dextral shell and spines pointing upwards, KNIGHT et al. (1960) considered it to represent a synonym of *Omphalocirrus*. This is even less comprehensible if one takes into account that KNIGHT et al. (1960) placed *Omphalocirrus* in the family Macluritidae FISCHER 1885 with sinistral shells. They thus abolished the Family Omphalocirridae WENZ 1938 in which WENZ (1938) had united the genera *Omphalocirrus*, *Echinocirrus* RYCKHOLT 1860 from the Carboniferous, and *Coelocentrus* ZITTEL 1882 from Triassic with planispirally coiled shell shape and the presence of hollow spines. The systematic reshuffle by KNIGHT et al. (1960) is quite problematic since *Maclurites* and relations are still not well known, and the genera placed in the Macluritidae such as *Lecanospira* BUTTS 1926, *Macluritella* KIRK 1927, *Maclurites* and *Palliseria* WILSON 1924 have no spines. KNIGHT et al. (1960) considered *Omphalocirrus* a sinistrally coiled shell, following WENZ (1938) in this respect, but placed it with the Macluritidae because of supposedly sinistral coiling. *Echinocirrus* in contrast was interpreted as belonging to the Luciellidae KNIGHT 1956 of the Pleurotomarioidea, which is erroneous since there is no selenizone known in *Echinocirrus*, while it is broad and clearly visible below the marginal frill in *Luciella* KONINCK 1883. Thus, it is well documented that *Coelocentrus* does not belong to the Euomphaloidea, while the same can not as yet be stated for *Omphalocirrus* and *Echinocirrus*.

Convergent species unrelated to the Euomphalomorpha

Among the Triassic species of the St. Cassian Formation, *Amphitomaria* KOKEN 1897 as well as *Woehrmannia* BÖHM 1895 and *Brochidium* KOKEN 1889 had usually been considered to represent close relatives to *Euomphalus* and *Straparollus* (WENZ 1938; KNIGHT et al. 1960) until BANDEL (1988) demonstrated conclusively that they belong to taxonomic units that are still living. The first is a member of the Architectonicoidea and can be related to the modern genus *Pseudomalaxis* FISCHER 1885 (BANDEL 1988, 1996). Later, the Family Amphitomariidae BANDEL 1996 was erected to include planispirally coiled architectonicoids with a sinistral protoconch and one or two angular keels on the flank of the teleoconch. Besides *Amphitomaria* it holds *Neamphitomaria* BANDEL 1988 from the Cretaceous and the Tertiary. *Woehrmannia* with two species was demonstrated to represent a trochoidean archaeogastropod with nacreous shell and the characteristic protoconch. The latter feature is also present in *Brochidium*, which has an unusual calcitic outer shell layer and may thus not be a relative to any modern member of the Trochoidea, but it is certainly a member of the Archaeogastropoda (BANDEL 1993a: pl. 2 figs. 8-9, pl. 3 figs. 4, 10). A minor complication surrounding the genus *Brochidium* was resolved by separating from it a new genus *Cortinella* BANDEL 1988. It has since been possible to trace the taxonomic place of *Cortinella* by its characteristic protoconch to be among the Neritimorpha and (here) to belong to its own larger taxon, the Cortinelloidea (BANDEL, in press). A relationship of the predominantly Jurassic genus *Discohelix* DUNKER 1848 to *Euomphalus*, as assumed by KNIGHT et al. (1960), does not exist. *Discohelix* belongs to the Archaeogastropoda, and here to the Trochoidea (BANDEL 1988; SCHRÖDER 1995) or to the Cirroidea COSSMANN 1915, which represents an extinct group of nacreous Archaeogastropoda (BANDEL 1993b; FRÝDA 1997).

Among modern species with planispiral shells resembling Paleozoic Euomphalomorpha, the protoconch usually unfailingly reveals their difference to the latter by being smaller and not openly coiled. Small planispiral gastropods of the genera *Eudaronia* COTTON 1945, *Adeuomphalus* SEGUENZA 1876 and *Palazzia* WARÉN 1991 represent questionable Archaeogastropoda, probably representing representatives of the Skeneidae according to WARÉN (1991). Species of *Palazzia* are confusingly similar to *Ammonicera* VAYSSIERE 1893, but the species of *Ammonicera* always have a strongly sculptured protoconch with spiral ridges and ribs and an indistinctly hyperstrophic initial whorl (SLEURS 1985). The latter are Heterostropha, of which since Triassic times there are numerous species and genera resembling small euomphalids (BANDEL 1996).

Cretaceous and Early Tertiary gastropods such as *Weeksia* STEPHENSON 1941 or *Omalaxis* DESHAYES 1830 have been commonly placed in the Euomphaloidea, but they are actually representatives of the Caenogastropoda with a characteristic dextrally coiled protoconch (BANDEL 1993c). STEPHENSON (1941) transferred the species *Pseudomalaxis amplificata* WADE 1926 to the Euomphalidae and erected the genus *Weeksia* for it, noting the naticoidal dextral protoconch instead of the flat protoconch that is seen in *Pseudomalaxis* FISCHER 1895. This way the characteristic species of the Late Cretaceous Ripley Formation changed generic names, but STEPHENSON (1941) was not aware of the taxonomic implications of his actions. He had

placed both genera in the Euomphalidae which he considered a family of the Rhipidoglossa (= Archaeogastropoda). Actually, *Pseudomalaxis* belongs to the subclass Heterostropha, and *Weeksia* to the subclass Caenogastropoda and Euomphalidae not to the subclass Archaeogastropoda. So there are 4 subclasses included in this mix-up, clearly indicating the confusion that may arise from the shell convergence that is so commonly found among gastropods.

Taxonomic conclusions

The cyrtoconic and planispiral openly coiled protoconch was found in the following genera that form the core group of the superfamily Euomphaloidea KONINCK 1881: *Euomphalus, Straparollus, Serpulospira, Phymatifer, Schizostoma,* and *Nodeuomphalus.* This unusual protoconch character suggests that euomphaloidean gastropods form a natural group and distinguishes them from any other gastropod subclass.

Subclass Euomphalomorpha nov.

Diagnosis: A subclass of the Gastropoda in which the protoconch is openly coiled and carries a bulbous initial obliquely egg-shaped portion that has a smooth, curved outline. The protoconch forms an open half coil with thickened end and smooth surface. This characteristic protoconch of the Euomphalomorpha distinguishes it as its own subclass of the Gastropoda. Most probably the shell structure of an outer calcitic layer and an inner aragonitic layer composed of acicular needles in spherulitic sector arrangement is also characteristic of the members of this subclass, but is rarely preserved in the altered fossil shells.

Differences: Archaeogastropoda have a protoconch that has been pulled into a spiral shell with lateral folds and not an openly coiled cyrtoconic shell as present in the Euomphalidae. Usually in the Euomphalidae the initial portion is much smaller and protoconch teleoconch distinction is clear after less than one protoconch whorl (BANDEL 1982). Neritimorpha with planktotrophic early ontogeny have a much narrower initial shell portion (less than 0.1 mm in width) which usually is tightly coiled, and among most modern species the interior whorls of the trochospiral shell have been dissolved (BANDEL 1992). Only in the Neritopsidae do the inner walls remain, but here the shell is of globular trochospiral coiling. Caenogastropoda have a dextrally and Heterostropha a sinistrally coiled larval shell without umbilical gape and smaller initial diameters when they have planktotrophic larvae (BANDEL 1975a, 1982 and here lit.). In the case of lecithotrophic development the protoconchs are trochospiral without umbilical gape.

More difficult is the distinction of gastropods which cannot be clearly placed within one of these units. These have usually lived prior to the Carboniferous and are recognized to represent independent taxa by FRÝDA & BANDEL (1997) based on gastropods extracted from Early Devonian rocks of the Prague Basin. DZIK (1994) illustrated quite a number of small gastropods from the Ordovician of the Holy Cross Mountains in Poland and the Silurian of the Carnic Alps in Austria. They are not perfectly spirally coiled and thus may have a gape in the apex of the initial shell portion. They are distinguished from the protoconchs of Euomphalomorpha by two features. The first is that they are trochospirally coiled and not planispirally, as is the case in Euomphalomorpha, and secondly their initial shell portion is smaller and less bulbous than found in all Euomphalomorpha studied so far. Those of these ancient gastropods living prior to the Carboniferous that resemble Caenogastropoda and Heterostropha when fully grown have been placed in the Peruneloidea FRÝDA & BANDEL 1997. Their potential relatives that lived in the Carboniferous, with few exceptions, no longer had an openly coiled protoconch (BANDEL 1997; NÜTZEL 1997). An exception is found among the *Platyceras*-relations that had the characteristic fishhook-like protoconchs from Ordovician time (BOCKELIE & YOCHELSON 1979; DZIK 1994) and which still occurred in the Late Carboniferous (KNIGHT 1934; BANDEL 1997).

Remarks: The oldest member of the group of Gastropoda representing the Euomphalomorpha may be the genus *Euomphalopsis* ULRICH & BRIDGE 1931 from the Upper Cambrian of Antarctica and North America (WEBERS et al. 1992). The Antarctic *Euomphalopsis splettstoesseri* WEBERS, POJETA & YOCHELSON 1992 is openly coiled, with young stages of the teleoconch in contact and protoconch large and potentially cyrtoconically coiled (but poorly preserved). It resembles *Straparollus* and *Serpulospira* but has a more rapid increase in shell diameter during growth. The asymmetrical shell is slightly sinistrally coiled. The type of the genus *Euomphalopsis, E. involuta* ULRICH & BRIDGE 1931 from the Lower Ordovician of Missouri, USA expands less rapidly in shell diameter during growth and is thus closer to *Straparollus*. The nucleus of *Euomphalopsis* is unknown (KNIGHT 1941: pl. 72 fig. 4).

The Gastropoda can be classified into four subclasses, the Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostropha. All these differ from each other in the morphology and formation of their protoconchs (BANDEL 1982). The Euomphaloidea with genera like *Euomphalus*, *Serpulospira*, *Straparollus*, *Schizostoma*, *Phymatifer* and *Nodeuomphalus* cannot be fitted in one of these groups. If Late Cambrian *Euomphalopsis* is a representative of the Euomphaloidea, which is still doubtful, this group of gastropods is as old as the other four. If Late Triassic *„Serpulospira" pustulosa* and Upper Cretaceous *Phanerotinus scheeri* represent members of the Euomphaloidea, which is still equally unproved, the group would have existed far into the Mesozoic times. A range of Ordovician to Permian for the Euomphaloidea can be reliably assumed. The calcitic outer shell layer connected to an inner aragonitic crossed lamellar layer brings the Euomphaloidea close to the Neritimorpha, but morphology of the shell, especially of the protoconch sets them apart. It is quite possible that Euomphaloidea represent an independent subclass of the Gastropoda of equal level to the four established ones, and in this case should be called the Euomphalomorpha.

References

ARCHIAC [E. J. A. D. DE S.] & VERNEUIL, E. [P. P. DE] (1842): On the fossils of the older deposits in the Rhenish Provinces. – Transactions of the geological Society of London, (2) **6** (2): 303-410, London (R. & J. E. Taylor); pls. 25-38, Paris (Bourgogne & Martinet).

BANDEL, K. (1975): Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). – Abhandlungen, mathematisch-naturwissenschaftliche Klasse, Akademie der Wissenschaften und der Literatur, Mainz, **1975** (1): 1-133; 16 text-figs., 21 pls.; Mainz. – [1975a]

BANDEL, K. (1975): Entwicklung der Schale im Lebenslauf zweier Gastropodenarten; *Buccinum undatum* und *Xancus angulatus* (Prosobranchier, Neogastropoda). – Biomineralisation, **8**: 67-91; 7 text-figs., 8 pls.; Mainz. – [1975b]

BANDEL, K. (1977): Übergänge von der Perlmutter-Schicht zu prismatischen Schichttypen bei Mollusken. – Biomineralisation, **9**: 28-47; 2 text-figs., 5 pls.; Mainz.

BANDEL, K. (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – Facies, **7**: 1-197; 109 text-figs., 6 tabs., 22 pls.; Erlangen.

BANDEL, K. (1988): Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **67**: 1-33, 6 text-figs., 7 pls.; Hamburg.

BANDEL, K. (1990): Shell structure of the Gastropoda excluding the Archaeogastropoda. – In: J. G. CARTER [Ed.], Skeletal Biomineralization: Patterns Processes and Evolutionary Trends, **1**: 117-134, 25 text-figs.; New York (Van Nostrand Reinolds).

BANDEL, K. (1991): Schlitzbandschnecken mit perlmutteriger Schale aus den triassischen St. Cassian-Schichten der Dolomiten. – Annalen des Naturhistorisches Museums in Wien, (A) **92**: 1-53; 10 text-figs., 17 pls.; Wien.

BANDEL, K. (1992): Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritomorpha (Gastropoda). – Paläontologische Zeitschrift, **66** (3/4): 231-240, 3 text-figs.; Stuttgart.

BANDEL, K. (1993): Trochomorpha aus der triassischen St. Cassian Formation (Gastropoda, Dolomiten). – Annalen des Naturhistorischen Museums in Wien, **95**: 1-99, 16 pls.; Wien. – [1993a]

BANDEL, K. (1993): Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda). – Freiberger Forschungshefte, (Paläontologie) **C 405**: 41-81, 6 pls.; Leipzig. – [1993b]

BANDEL, K. (1993): Caenogastropoda during the Mesozoic times. – Scripta Geologica, Spec. Issue, **2**: 7-56, 15 pls.; Leiden. – [1993c]

BANDEL, K. (1996): Some heterostrophic gastropods from Triassic St. Cassian Formation with a discussion on the classification of the Allogastropoda. – Paläontologische Zeitschrift, **70** (3/4): 325-365, 18 text-figs.; Stuttgart.

BANDEL, K. (1997): Higher classification and pattern of evolution of the Gastropoda. A synthesis of biological and paleontological data. – Courier Forschungsinstitut Senckenberg, **201**: 57-81, 1 tab., 3 pls.; Frankfurt a. M.

BANDEL, K. (in press): The new neritimorph family Cortinellidae (Gastropoda, Mollusca). – Neues Jahrbuch für Geologie und Paläontologie; Stuttgart.

BANDEL, K. & GELDMACHER, W. (1996): The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda. – Freiberger Forschungshefte, **C 464**: 1-71, 15 pls.; Freiberg.

BANDEL, K. & HEMLEBEN, C. (1975): Anorganisches Kristallwachstum bei lebenden Mollusken. – Paläontologische Zeitschrift, **49**: 298-320, 38 text-figs.; Stuttgart.

BANDEL, K. & HEMLEBEN, C. (1987): Jurassic heteropods and their modern counterparts (Planktonic Gastropoda, Mollusca). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **174**: 1-22, 34 text-figs.; Stuttgart.

BATTEN, R. L. (1966): The lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset (Parts I and II). – Palaeontographical Society Monographs [for 1965], **119**: 53-109, 5 pls.; London.

BATTEN, R. L. (1984): The calcitic wall in the Paleozoic families Euomphalidae and Platyceratidae (Archaeogastropoda). – Journal of Paleontology, **58** (5): 1186-1192, 2 text-figs.; Tulsa/Okla.

BLODGETT, R. B. & JOHNSON, J. G. (1992): Early Middle Devonian (Eifelian) gastropods of central Nevada. – Palaeontographica, (A) **222**: 83-139, 3 text-figs., 2 tabs., 19 pls.; Stuttgart.

BOCKELIE, T. G. & YOCHELSON, E. L. (1979): Variation in a species of 'worm' from the Ordovician of Spitsbergen. – Skrifter om Norsk polarinstitutt, **167**: 225-237; Oslo.

BÖHM, J. (1895): Die Gastropoden des Marmolatakalkes. – Palaeontographica, **42**: 211-308, pls. 9-15; Stuttgart.

COSSMANN, M. (1915): Essais de paléoconchologie comparée 13. – 345 p.; Paris (Presses Universitaires de France).

DZIK, J. (1982): Larval development and relationships of Mimospira; a presumably hyperstrophic Ordovician gastropod. – Geologiska Foereningens i Stockholm Foerhandlingar, **104** (3): 231-239; Stockholm.

DZIK, J. (1994): Evolution of 'small shelly fossils' assemblages of the Early Paleozoic. – Acta palaeontologica polonica, **39** (3): 247-313, 37 text-figs.; Warszawa.

ETHERIDGE, R. (1890): Description of Upper Silurian fossils from the Lilydale limestone upper Yarra district, Victoria. – Records of the Australian Museum, **1**: 60-68, pls. 8-9; Sydney.

FRÝDA, J. (1989): A new species of *Mimospira* (Clisospiridae, Gastropoda) from the Late Ordovician of Bohemia. – Věstník Ustředního ústavu geologického, **64** (4): 237-241, 2 text-figs., 2 pls.; Praha.

FRÝDA, J. (1992): Mode of life of a new onychochilid mollusc from the Lower Devonian of Bohemia. – Journal of Paleontology, **66** (2): 200-205, 2 text-figs., 2 pls.; Tulsa/Okla.

FRÝDA, J. (1995): Shell ontogeny of some Lower Paleozoic gastropods and its significance for higher taxonomy. – In: A. GUERRA, E. ROLAN & F. ROCHA, Twelfth International Malacological Congress: 305-306; Vigo.

FRÝDA, J. (1997): Oldest representatives of the superfamily Cirroidea (Vetigastropoda) with notes on their early phylogeny. – Journal of Paleontology, **71** (5): 839-847, 4 text-figs.; Tulsa/Okla.

FRÝDA, J. & BANDEL, K. (1997): New Early Devonian gastropods from the *Plectonotus (Boucotonotus) - Palaeozygopleura* Community in the Prague Basin (Bohemia). – Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, **80**: 1-57, 11 pls.; Hamburg.

GORDON, M. & YOCHELSON, E. L. (1987): Late Mississippian Gastropods of the Chainman Shale, west-central Utah. – Professional Papers, U. S. Geological Survey, **1368**: 1-112, 9 pls.; Washington/D.C.

HARPER, J. A. (1977): Gastropods of the Gilmore City Limestone (Lower Mississippian) of Northcentral Iowa. – Dissertation. – [Unpubl.]

HEIDELBERGER, D. (in prep): Mitteldevonische (Givetium) Gastropoda (Mollusca) aus dem Rheinischen Schiefergebirge. – Dissertation an der Universität Hamburg; Hamburg.

HICKMAN, C. S. & MCLEAN, J. H. (1990): Systematic revision and suprageneric classification of trochacean gastropods. – Natural History Museum of Los Angeles County, Science Series, **35**: 1-169; Los Angeles.

HOLZAPFEL, E. (1895): Das Obere Mitteldevon (Schichten mit *Stringocephalus Burtini* und *Maeneceras terebratum*) im Rheinischen Gebirge. – Abhandlungen der Königlich Preussischen Geologischen Landesanstalt, N. F., **16**, text: 460 p., 14 text-figs., atlas: 19 pls.; Berlin.

HONG-FU, Y. & YOCHELSON, E. L. (1983): Middle Triassic Gastropoda

from Qingyan, Ghizhou Province, China: 3–Euomphalacea and Loxonematacea. – Journal of Paleontology, **57** (5): 1098-1127, 5 text-figs., 16 tabs.; Tulsa/Okla.

JHAVERI, R. B. (1969): Unterdevonische Gastropoden aus den Karnischen Alpen. – Palaeontographica, (A) **133** (4-6): 146-176, 5 text-figs., 1 tab., pls. 19-23; Stuttgart.

KARCZEWSKI, L. (1989): Slimaki a malze dewonskie z gor Swietokrzyskich. – Biuletyn panstwowego Instytutu geologicznego, **363**: 97-133, 5 pls.; Warszawa.

KAYSER, F. H. E. (1889): Über einige neue oder wenig bekannte Versteinerungen des rheinischen Devon. – Zeitschrift der Deutschen geologischen Gesellschaft, **41**: 288-296, pls. 13-14; Berlin.

KIRCHNER, H. S. (1915): Mitteldevonische Gastropoden von Sötenich in der Eifel. – Verhandlungen des Naturhistorischen Vereins der preussischen Rheinlande und Westfalens, **2**: 189-261, 2 text-figs., 2 pls.; Bonn.

KITTL, E. (1891): Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. Teil I. – Annalen des k. k. naturhistorischen Hofmuseums, **6**: 166-262, pls. 1-9; Wien.

KNIGHT, J. B. (1934): The gastropods of the St. Louis, Missouri, Pennsylvanian Outlier: VII. The Euomphalidae and Platyceratidae. – Journal of Paleontology, **8** (2): 139-166, pls. 20-26; Menasha/Wisc.

KNIGHT, J. B. (1941): Paleozoic gastropod genotypes. – Special Papers of the geological Society of America, **32**: 1-510, 32 text-figs, 96 pls.; Washington/D.C.

KNIGHT, J. B. (1945): Some new Genera of Paleozoic Gastropoda. – Journal of Paleontology, **19** (6): 573-587, pls. 79-80; Tulsa/Okla.

KNIGHT, J. B. (1956): New families of Gastropoda. – Washington Acad. Sci. J., **46** (2): 41-42; Washington/D.C.

KNIGHT, J. B., COX, L. R., KEEN, A. M., SMITH, A. G., BATTEN, R. L., YOCHELSON, E. L., LUDBROOK, N. H., ROBERTSON, R., YONGE, C. M. & MOORE, R. C. (1960): Mollusca – General features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda – General features Archaeogastropoda and some (mainly Paleozoic) Caenogastropoda and Opisthobranchia. – In: R. C. MOORE [Ed.], Treatise on invertebrate Paleontology, Part I Mollusca 1: I1-I351, text-figs. 1-216; Lawrence/Kan. (Geol. Soc. Amer., Univ. Kansas Press).

KOBAYASHI, T. (1959): On some Ordovician fossils from northern Malaya and her adjacence. – Journal of the Faculty of Science, University of Tokyo, Section 2, Geology, Mineralogy, Geography, Geophysics, **11** (4): 387-407, pls. 24-27; Tokyo (Maruzen Co.).

KOKEN, E. (1889): Über die Entwicklung der Gastropoden vom Cambrium bis zur Trias. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Suppl. **6**: 305-484, pls. 10-14; Stuttgart.

KOKEN, E. (1896): Die Leifossilien, ein Handbuch für den Unterricht und das Bestimmen von Versteinerungen. – 848 p.; Leipzig.

KOKEN, E. (1897): Die Gastropoden der Trias um Hallstatt. – Abhandlungen der k. k. geologischen Reichsanstalt, **17**:1-112, 23 pls.; Wien.

KOKEN, E. (1925): Die Gastropoden des Baltischen Untersilur. – In: J. PERNER [Ed.], Mémoires de l'Académie des sciences de Russie, Classe Physico-Mathématique, (8) **37** (1): 1-326, pls. 1-41; Saint Pétersbourg.

KONINCK, L. DE (1843): Description des animaux fossiles qui se trouvent dans le terrain carbonifère de la Belgique. – IV + 716 p., pls. A-H, 1-60; Liège.

KONINCK, L. G. DE (1881): Faune du calcaire carbonifère de la Belgique. Troisième partie: Gastéropodes. – Annales du Musée royal d'Histoire naturelle de Belgique, Série paléontologique, **6**: 1-170, 24 pls.; Bruxelles.

KONINCK, L. G. DE (1883): Faune du calcaire carbonifère de la Belgique 4. partie, Gastéropodes (suite et fin). – Annales du Musée royal d'Histoire naturelle de Belgique, Série paléontologique, **8**: 1-240, pls. 22-54; Bruxelles.

LINSLEY, R. M. (1968): Gastropods of the middle Devonian Anderdon limestone. – Bulletins of American Paleontology, **54** (244): 333-465, 14 pls.; Ithaca.

LINSLEY, R. M. (1978): The Omphalocirridae; a new family of Palaeozoic Gastropoda which exhibits sexual dimorphism. – Memoirs of the National Museum of Victoria, **39**: 33-54, pls. 2-10; Melbourne.

LINSLEY, R. M. & KIER, W. M. (1984): The paragastropoda: a proposal for a new class of Paleozoic Mollusca. – Malacologia, **25**: 241-254; Ann Arbor/Mich.

LINSLEY, R. M. & YOCHELSON, E. L. (1973): Devonian carrier shells (Euomphalidae) from North America and Germany. – Professional Papers, U. S. Geological Survey, **824**: 1-26, 3 text-figs., 6 pls.; Washington/D.C.

MCLEAN, J. H. (1981): The Galapagos Rift Limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic Mesozoic radiation. – Malacologia, **21**: 291-336, 18 text-figs.; Ann Arbor/Mich.

MEEK, F. B. & WORTHEN, A. H. (1867): Contributions to the palaeontology of Illinois and other Western States. – Proceedings of the Academy of Natural Sciences of Philadelphia, 1866: 251-275, pls. 14-32; Philadelphia.

MORRIS, N. J. & CLEEVELY, R. J. (1981): *Phanerotinus cristatus* (PHILLIPS) and the nature of euomphalacean gastropods. – Bulletin of the British Museum of Natural History (Geology), **35**: 195-212, 12 text-figs.; London.

NÜTZEL, A. (1997): Über die Stammesgeschichte der Ptenoglossa (Gastropoda). – Berliner Geowissenschaftliche Abhandlungen, (E) **26**: 1-229, 35 pls.; Berlin.

PAECKELMANN, W. (1913): Das Oberdevon des Bergischen Landes. – Abhandlungen der Königlich Preußischen Geologischen Landesanstalt, N. F., **70**: 1-356, 4 text-figs., pls. 2-7, 1 map; Berlin.

PAECKELMANN, W. (1922): Der mitteldevonische Massenkalk des Bergischen Landes. – Abhandlungen der Preußisch Geologischen Landesanstalt, N. F., **91**: 1-112, 2 text-figs., 1 pl., Berlin.

PERNER, J. (1903): Gastéropodes. – In: J. BARRANDE, Système silurien du centre de la Bohême. IV. – **1**: 1-164, 3 text-figs., 89 pls.; Prague.

PHILLIPS, J. (1841): Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset. – XII + 231 p., 60 pls.; London (Longman, Brown, Green & Longmans).

ROEMER, F. A. (1843): Die Versteinerungen des Harzgebirges. – XX + 40 p., 12 pls.; Hannover.

ROEMER, F. A. (1876): Lethaea palaeozoica. Atlas; Hannover.

ROHR, D. M. (1980): Ordovician-Devonian Gastropoda from the Klamath Mountains, California. – Palaeontographica, (A) **171** (4-6): 141-199, 2 text-figs., 1 tab., 11 pls.; Stuttgart.

ROHR, D. M. (1988): Upper Ordovician gastropods from the Seward Peninsula, Alaska. – Journal of Paleontology, **62** (4): 551-566, 6 text-figs.; Tulsa/Okla.

ROHR, D. M. (1994): Ordovician (Whiterockian) gastropods of Nevada: Bellerophontoidea, Macluritoidea, and Euomphaloidea. – Journal of Paleontology, **68** (3): 473-486, 8 text-figs.; Tulsa/Okla.

SALTER, S. W. (1859): Figures and descriptions of Canadian organic remains, Decade I. – Geological Survey of Canada, 47 p., pls. 1-10; Montreal.

SANDBERGER, G. & SANDBERGER, F. (1850-1856): Die Versteinerungen des Rheinischen Schichtensystems in Nassau. – Lfg. 1-9: XV + 564 p., 1 encl., 1 map. Atlas: 41 pls.; Wiesbaden (Kreidel & Niedner).

SCHRÖDER, M. (1995): Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. – Palaeontographica, (A) **238** (1-4): 1-95, 14 text-figs., 1 tab., 15 pls.; Stuttgart.

SOHL, N. F. (1960): Archaeogastropoda, Mesogastropoda and Stratigraphy of the Ripley Owl Creek, and Prairie Bluff Formation. – Professional Papers, U.S. Geological Survey, **331A**: 1-151, text-figs. 1-11, pls. 3-18; Resten.

SOWERBY, J. (1812): The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and

depths in the earth. Vol. I. – 234 p., 102 pls.; London.

STEPHENSON, L. W. (1941): The larger invertebrate fossils of the Navarro Group of Texas. – The University of Texas Publication, **4101**: 642 p., 13 text-figs., 95 pls.; Austin.

THEIN, M. L. & NITECKI, M. H. (1974): Chesterian (Upper Mississippian) Gastropoda of the Illinois basin. – Fieldiana, Geology, **34**: 238 p., 103 text-figs.; Chicago.

WAGNER, P. J. (1995): Stratigraphic tests of cladistic hypotheses. – Paleobiology, **21**: 153-178, 14 text-figs.; Chicago.

WARÉN, A. (1991): New and little known "skeneimorph" gastropods from the Mediterranean Sea and the Atlantic Ocean. – Bolletino Malacologico, **27**: 149-247, 47 text-figs.; Milano.

WEBERS, G. F., POJETA, J. jr. & YOCHELSON, E. L. (1992): Cambrian Mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctica. – Memoirs, Geological Society of America, **170**: 181-248, 19 pls.; Boulder/Colo.

WENZ, W. (1938-44): Gastropoda, Teil I. – In: O. H. SCHINDEWOLF [Ed.], Handbuch der Paläozoologie, **1-7**: 1-1639; Berlin.

WHIDBORNE, G. F. (1891): A monograph of the Devonian fauna of the south of England. Part III. The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. – Palaeontographical Society, [Monographs.]: 155-250, pls. 14-20; London

WHIDBORNE, G. F. (1892): A monograph of the Devonian fauna of the south of England. Part IV. The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. – Palaeontographical Society, [Monographs.]: 251-344, pls. 25-31; London.

YOCHELSON, E. L. (1956): Euomphalacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea, [Part] 1 Permian Gastropoda of the southwestern United States. – Bulletin of the American Museum of Natural History, **110**: 173-275, 24 pls.; New York.

YOCHELSON, E. L. (1963): The Middle Ordovician of the Oslo Region, Norway. 15, Monoplacophora and Gastropoda. – Norsk Geologisk Tidsskrift, **43**: 113-213, 8 pls.; Oslo.

YOO, E. K. (1988): Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. – Records of the Australian Museum, **40**: 233-264, 164 text-figs.; Sydney.

YOO, E. K. (1994): Early Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. – Records of the Australian Museum, **46**: 63-120, 23 pls.; Sydney.

ZARDINI, R. (1978): Fossili Cassiani (Trias Mediosuperiore) Atlanti dei Gasteropodi della Formazione di S. Cassiano Raccolti della Formazione di S. Cassiano raccolti nella regione Dolomitica attorna a Cortina d'Ampezzo. – 58 p.; Cortina d'Ampezzo.

ZITTEL, K. A. (1881-1885): Handbuch der Palaeontologie 2. Mollusca und Arthropoda. – 900 p., 719 text-figs.; München, Leipzig.

Manuskript zum Druck eingereicht (submitted) am 15.10.1997, überarbeitet (revised) bis 23.03.1998, angenommen (accepted) am 25.03.1998.

Plate 1

Fig. 1. *Straparollus laevigatus* LEVEILLÉ 1835. – Tournaisian of Le Hon. – KONINCK collection (lot T 1/12) – a juvenile shell of 5.2 mm diameter which has the central apical gape and the cyrtoconic initial shell shape well developed.

Fig. 2. *Straparollus pileopsideus* PHILLIPS 1841. – Visé, Belgium. – KONINCK collection (lot V 5/4) – the first three whorls have a diameter of 2.5 mm with a central apical gape and rounded initial shell portion.

Fig. 3. *Straparollus dionysii* MONTFORT 1810. – Visé, Belgium. – KONINCK collection (lot V 7/3) – the first two whorls measuring 1.5 mm across demonstrate the bulbous initial shell portion and open coiling.

Fig. 4. *Euomphalus pentangonalis* PHILLIPS 1836. – Visé, Belgium. – KONINCK collection (lot V 7/5) – the first whorl and the beginning of the second whorl openly coiled. The first 2.5 whorls measure 2.2 mm in diameter.

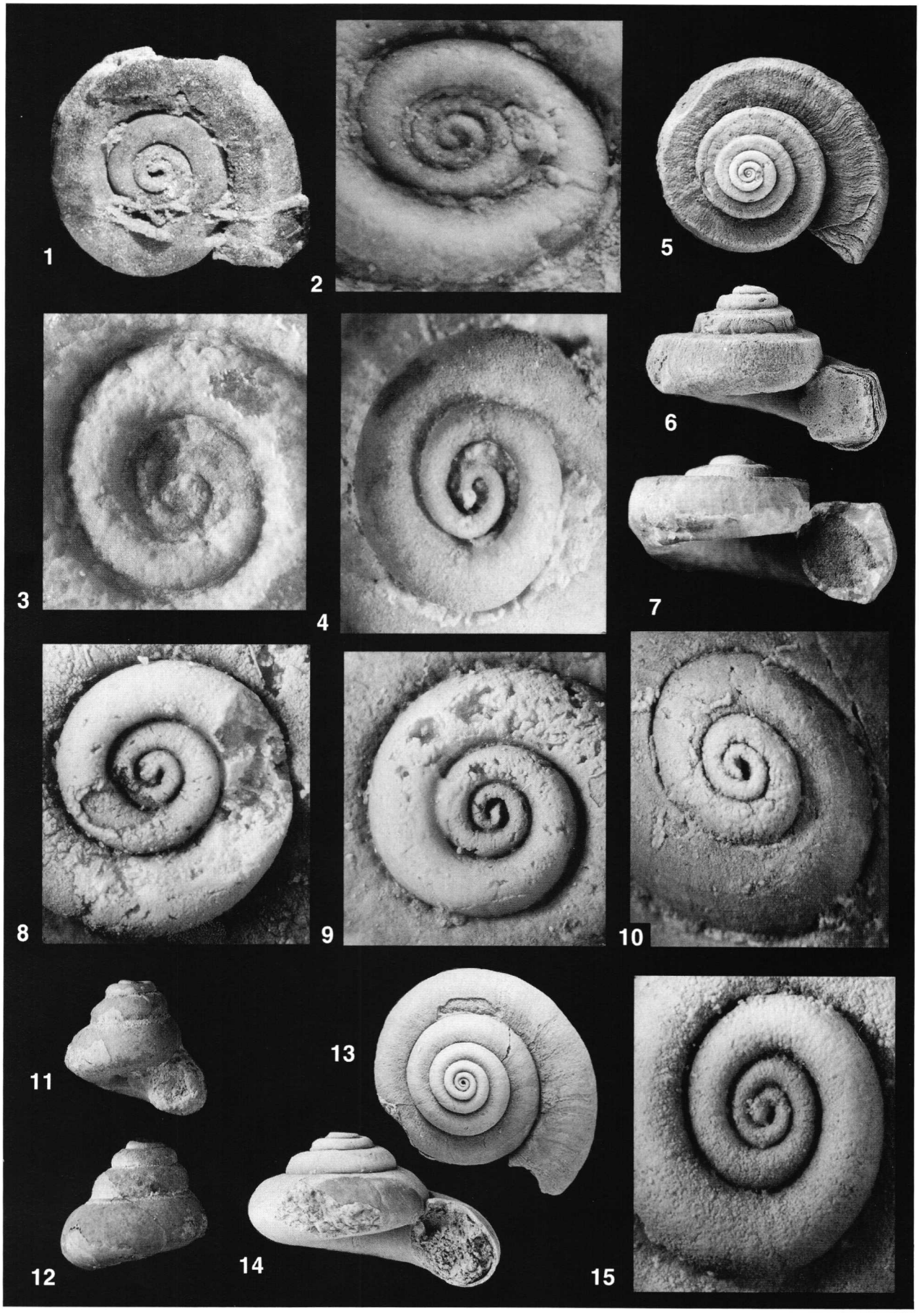
Figs. 5-9. *Euomphalus elegans* KONINCK 1881. – Namèche (Visean). – KONINCK collection.

5. The shell in apical view measures 24 mm in width (lot V 7/4).
6. The same shell as in fig. 5 seen in apertural view.
7. Apertural view of smaller shell with 16 mm width (lot V 7/4).
8. The first three whorls have a diameter of about 3 mm and show the rounded initial part and the central opening of the apex. (lot V 7/3).
9. As in fig. 8 but different individual.

Fig. 10. *Straparollus fallax* KONINCK 1843. – Visé, Belgium. – KONINCK collection (lot 8/1) – has tighter coiling but also demonstrates the central gape and planispiral coiling of the initial whorls, the first three measuring about 2.5 mm across.

Figs. 11-15. *Straparollus dionysii* MONTFORT 1810. – Visé, Belgium. – KONINCK collection (lot V 5/3).

11-12. The juvenile shell of 11 mm in height is trochospirally coiled and seen in apertural and adapertural position.
13-14. The 28 mm wide and 19 mm high shell demonstrates a broadening of shell shape with later growth.
15. The initial shell portion is flatly coiled with the first three whorls measuring about 2.5 mmin diameter and has a narrow central gape.



K. BANDEL & J. FRÝDA: The systematic position of the Euomphalidae (Gastropoda)

Plate 2

Figs. 16-17. *Euomphalus pentangonalis* PHILLIPS 1836. – Visé, Belgium. – KONINCK collection (lot V 7/5).

16. The juvenile shell seen from the apertural side is 11 mm high.
17. Same as in fig.16 but seen from the apical side and of 11 mm in shell width. The initial whorl is openly coiled.

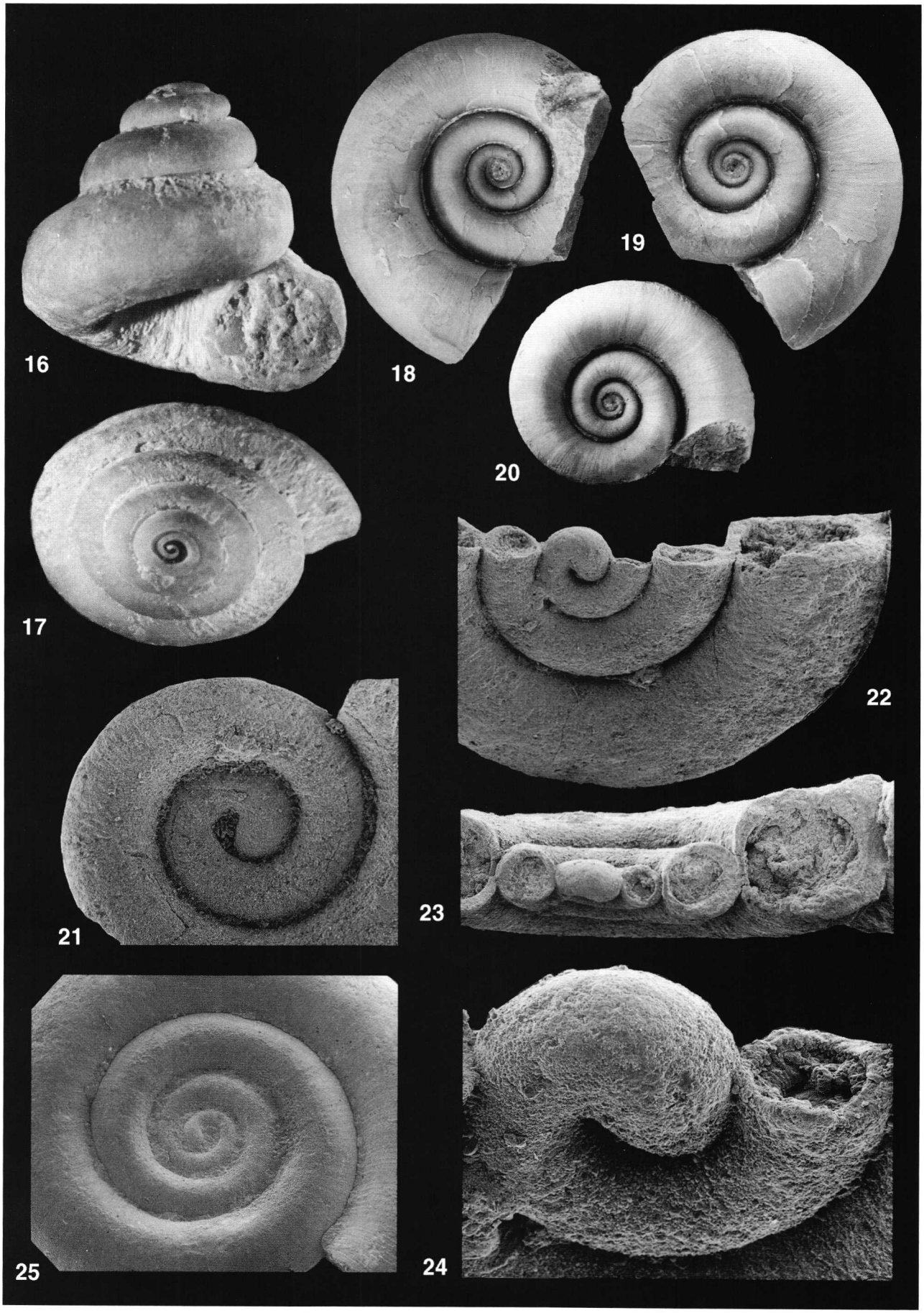
Figs. 18-20. *Straparollus aequalis* SOWERBY 1812. – Visé, Belgium. – KONINCK collection (lot V 5/2) – is planispirally coiled throughout ontogeny.

18-19. The 46 mm diameter shell is almost alike seen in apical (19) and umbilical (18) view.
20. The 13 mm wide shell in apical view with initial apical gape and regularly rounded whorl shape.

Figs. 21-24. *Euomphalus reedsi* (KNIGHT 1934). – Late Carboniferous of the USA. – KNIGHT collection, Smithsonian Institution, Washington/D.C. from the Pennsylvanian Labette Shale of the St. Louis outlier.

21. A shell with almost 1 mm in maximum diameter horizontally is seen in umbilical view, demonstrating the initial apical gape and the rounded intitial shell.
22-24. The same shell seen in different perspectives with about 2 mm visible shell diameter (22, 23) and about 0.6 mm wide first whorl (24).

Fig. 25. *Euomphalus* sp. – Spergen Hill, Mississippian of Indiana, USA. – 1.7 mm diameter for the first three whorls has a central gape in the apex as well as a wider initial portion of the shell.



K. BANDEL & J. FRÝDA: The systematic position of the Euomphalidae (Gastropoda)

Plate 3

Fig. 26. *Euomphalus* sp.– Spergen Hill, Mississippian of Indiana, USA. – 3.7 mm diameter in the juvenile shell has the same rounded whorls as found in *Straparollus* sp. from the same locality. Smithsonian collection, Washington/D.C. Nr. 47982-2.

Figs. 27-30. *Euomphalus* sp. – German Zechstein (Coal mine at Hoerstgen, Nordrhein-Westfalen) with well developed initial open coiling.

27. The half-grown shell measures 3 mm in diameter and shows the initial openly coiled part, succeeded by an evenly rounded whorl portion, followed by the formation of an apical keel.
28. Umbilical view of a 2.3 mm large shell of which details are shown in figs. 29 and 30.
29. The first whorl has an diameter of about 0.7 mm and is openly coiled.
30. The initial bulb measures a little more than 0.15 mm in diameter and is well differentiated from the succeeding protoconch.

Figs. 31-32. *"Phanerotinus" scheeri* n. sp. – Cenomanian rocky shore deposits of the Kassenberg near Mühlheim, Ruhr. It represents the type species with specimen Nr. A 1271 from the Ruhrland Museum, Essen.

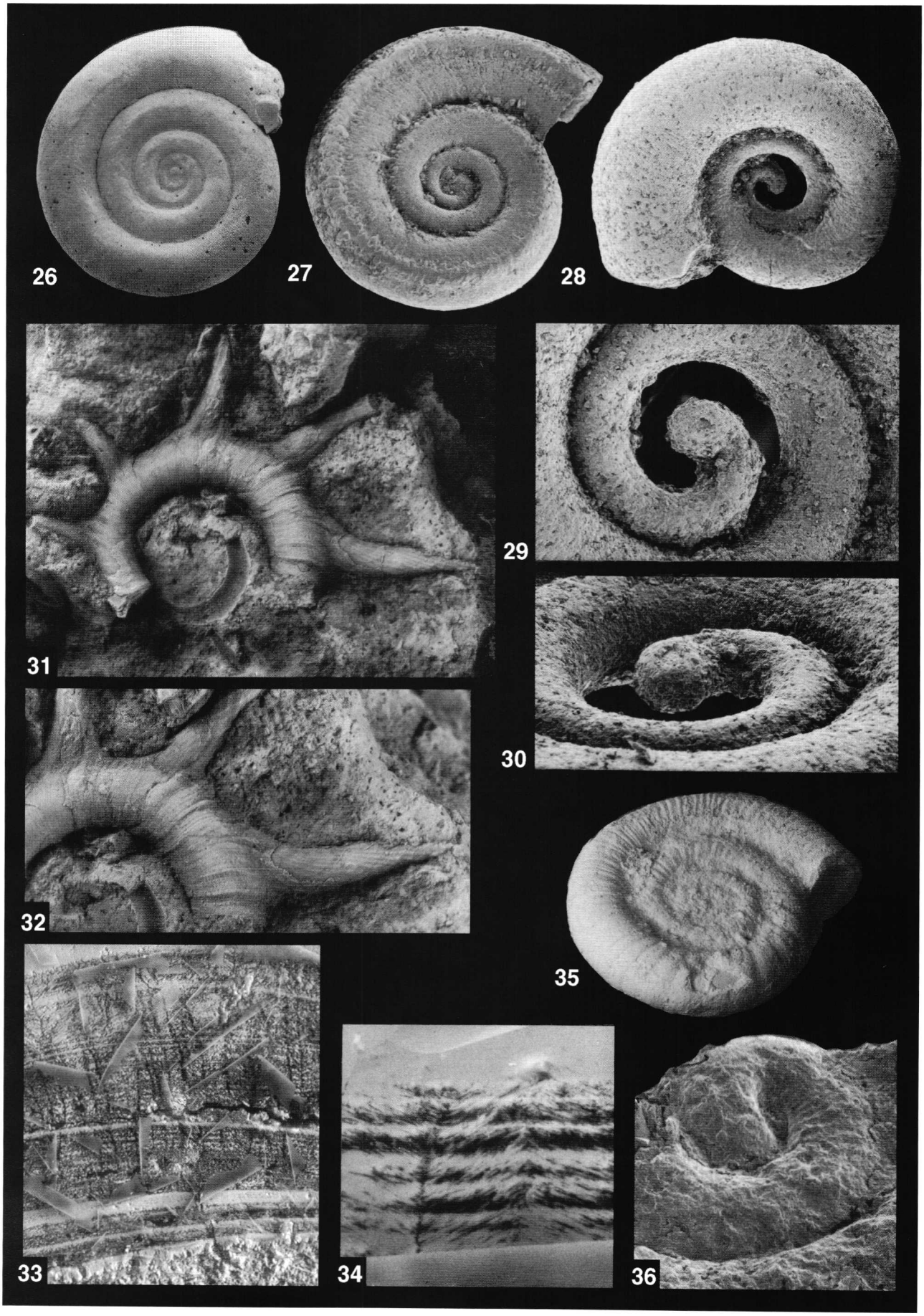
31. The openly coiled late shell portion with spines measures 34 mm in maximum diameter.
32. Detail of fig. 31 with the 10 mm long spine and its ornament of growth lines and undulating ribs.

Figs. 33-34. The shell of *Euomphalus* sp. – Kendrick Shale Member of Breathitt Formation (Upper Westfalian B) from Kentucky in polished and etched section demonstrates an outer massive calcitic layer (upper part of illustration) and inner aragonitic layer composed of needles arranged in spherulitic sectors of about 50 microns width.

33. Artefacts formed due to coating cross the structure of spherulitic sectors and etched out growth increments parallel to inner shell surface. The base of the picture represents about 0.3 mm.
34. The enlargement of the onset of a spherulitic sector below the massive calcitic outer layer demonstrates roof-like arrangement of needles and growth increments. The sector is about 50 micron wide.

Figs. 35-36. *"Serpulospira" pustulosa* (KOKEN 1889). – St. Cassian Formation near Rifugio Dibona on the road to Falzarego Pass from Cortina d'Ampezzo – coiled juvenile shell (35) and initial whorl preserved (36).

35. The juvenile shell measures 1.3 mm in diameter.
36. The initial shell measures only about 0.06 mm in width and appears to be twisted in a sinistral direction initially. The first whorl measures 0.17 mm across.



K. BANDEL & J. FRÝDA: The systematic position of the Euomphalidae (Gastropoda)

Plate 4

Figs. 37-40. *Straparollus laevis* (ARCHIAC & VERNEUIL 1842). – Middle Devonian limestones of Givetian age, Unterer Plattenkalk, Unterthal, Bergisches Land, Germany (collection EBBIGHAUSEN); 19 mm wide shell.

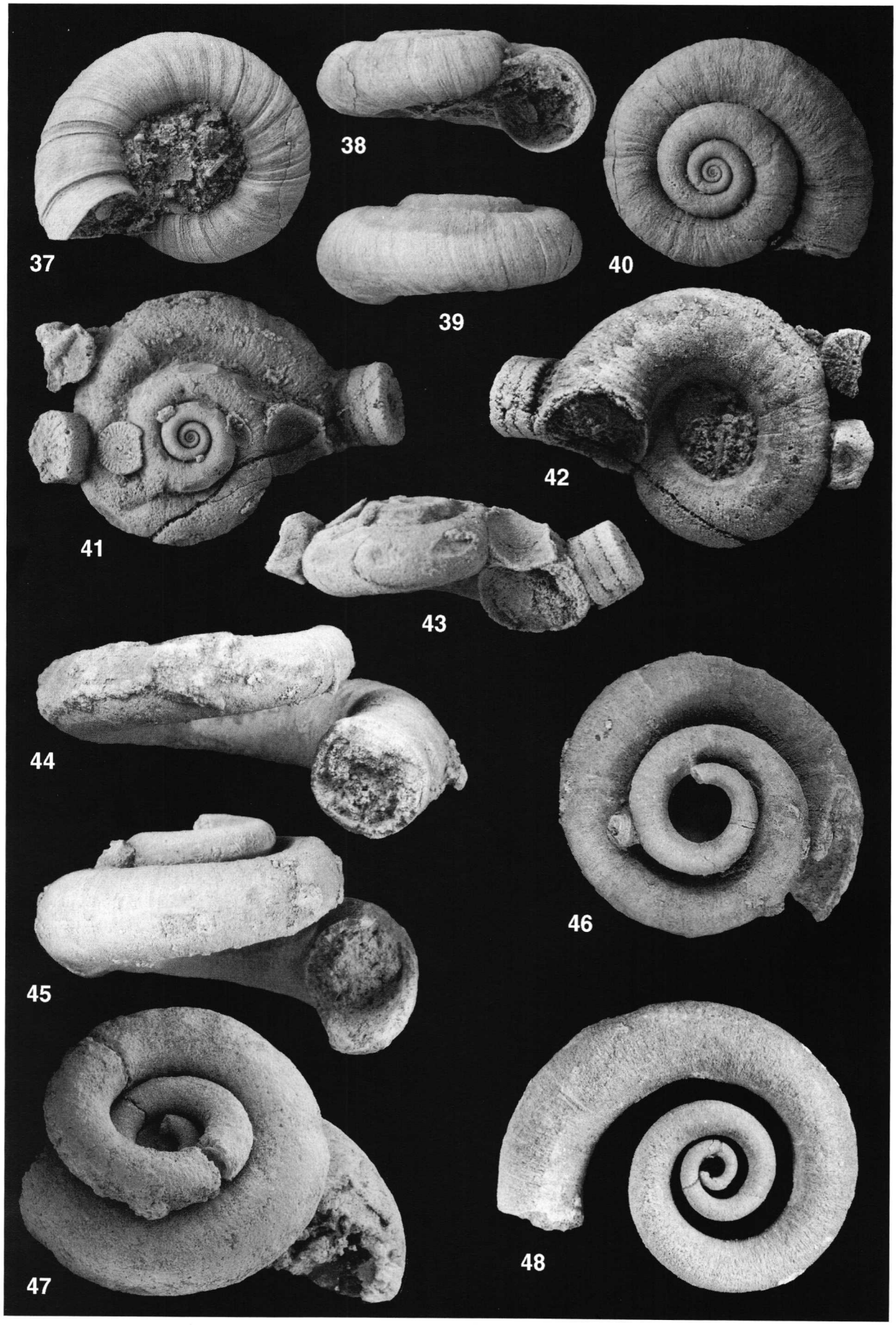
37. The umbilical view with distinct growth lines.
38. The apertural view with circular aperture.
39. Lateral view.
40. Apical view.

Figs. 41-43. *Straparollus laevis* (ARCHIAC & VERNEUIL 1842). – Middle Devonian limestones of Givetian age, Unterer Plattenkalk, Unterthal, Bergisches Land, Germany (collection EBBIGHAUSEN). The shell has attached foreign matter on its periphery consisting of fragment of molluscan shell and of crinoids [= *Straparollus (Philoxene)*]. The shell is 18 mm wide.

41. Apical view.
42. Umbilical view.
43. Lateral view.

Figs. 44-48. *Serpulospira serpula* (KONINCK in ARCHIAC & VERNEUIL 1842). – Middle Devonian limestones of Givetian age, Unterer Plattenkalk, Schladethal, Bergisches Land, Germany (collection EBBIGHAUSEN).

44. The 50 mm wide shell of morphotype A is openly and dextrally coiled.
45. The lateral of shell belonging to the morphotype A has a width of 47 mm.
46. The apical view of the same shell as in fig. 45.
47. The early shell of morphotype A with sinistral coiling in the young shell and dextral coiling in the later shell. The shell is 6 mm wide.
48. The axial view of the shell of morphotype B with disjunct whorls that are coiled closely to the plane and perpendicular to the shell axis. The shell is 24 mm wide.



K. BANDEL & J. FRÝDA: The systematic position of the Euomphalidae (Gastropoda)

Plate 5

Figs. 49-53. *Nodeuomphalus labadei* (ARCHIAC & VERNEUIL 1842). – Middle Devonian limestones of Givetian age, Bücheler Schichten, Herrenstrunden, Bergisches Land, Germany (collection EBBIGHAUSEN). The shell is 17 mm wide.

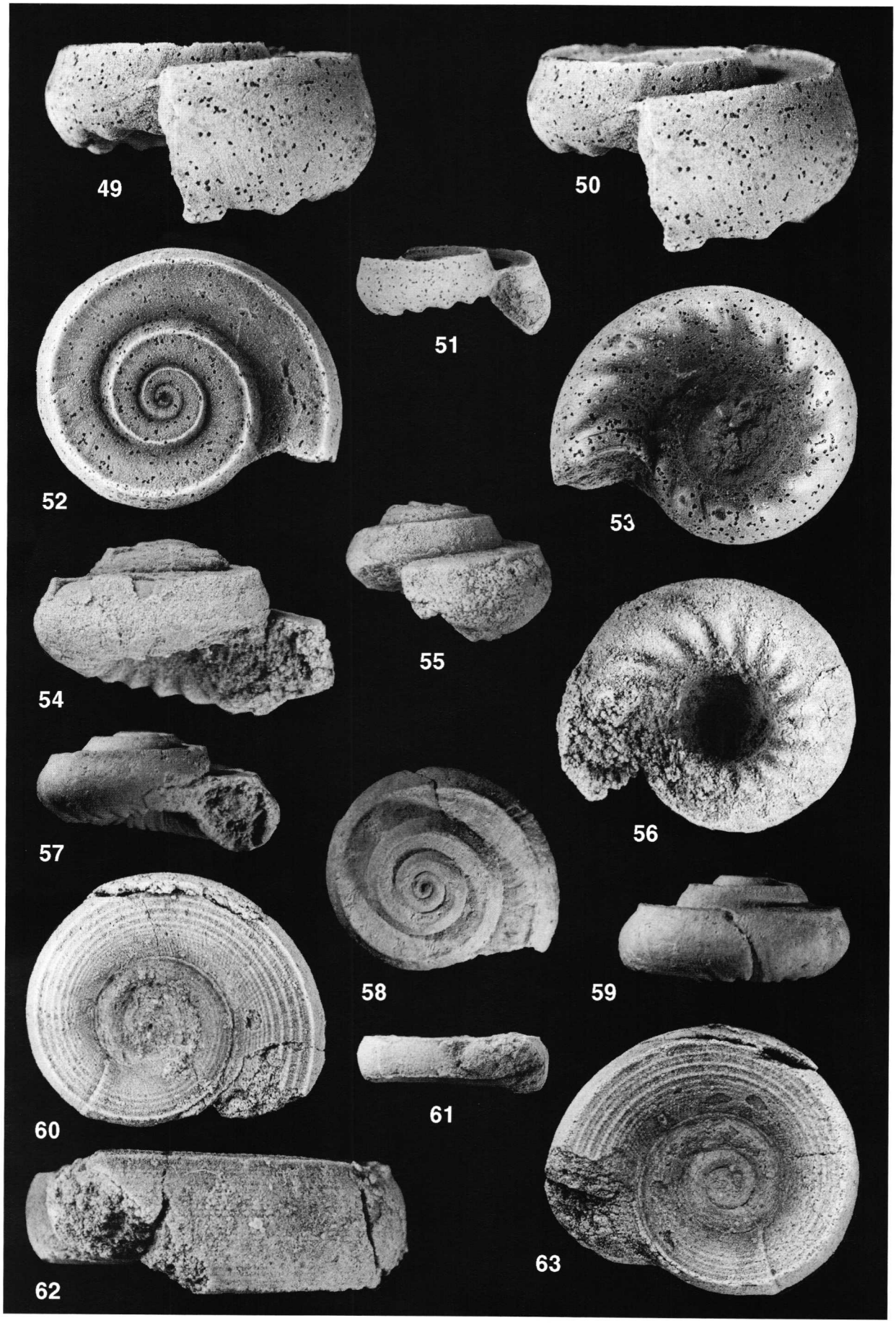
49. Lateral view.
50. Oblique view.
51. Apertural view.
52. Apical view with a sharp upper angulation.
53. Umbilical view with a spiral row of distinct nodes.

Figs. 54-59. *Nodeuomphalus paffrathianus* n. sp. – Middle Devonian limestones of Givetian age, Bücheler Schichten, Herrenstrunden, Bergisches Land, Germany (collection EBBIGHAUSEN).

54. Apertural view of the 18 mm wide shell (paratype A) showing the whorl profile and a spiral row of distinct nodes on the shell base.
55. The same shell as in fig. 54 seen in lateral view.
56. Basal view of paratype A showing a spiral row of distinct nodes (same shell as fig. 54).
57. Apertural view of the h o l o t y p e (SMF XII 3428) with 17 mm wide shell.
58. Apical view of the same shell (fig. 57) showing a sharp upper angulation.
59. Lateral view of the h o l o t y p e (fig. 57).

Figs. 60-63. *Rhenomphalus germanus* (PHILLIPS 1841). – Middle Devonian limestones of Givetian age, Unterer Plattenkalk, Unterthal, Bergisches Land, Germany (collection EBBIGHAUSEN). The 20 mm wide shell is shown in different orientations.

60. Apical view with a typical ornament.
61. Apertural view.
62. Lateral view showing fine spiral lines of the ornament.
63. Umbilical side with ornament similar to that of the apical shell side.


49
50
51
52
53
54
55
56
57
58
59
60
61
62
63