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About the Heterostropha (Gastropoda) from the Carboniferous and Permian

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With 79 figures

Contents

Abstract

Most species of Carboniferous and Permian gastropods of the subclass Heterostropha can be placed in the superfamily Streptacidoidea with more or less slender unsually small dextral teleoconchs and flatly coiled sinistral protoconchs. The family Streptacidae with the main genus *Streptacis* is interpreted to also hold the genus *Mapesella* n. gen. with flat protoconch and less rounded teleoconch whorls, and the Permian *Laxella* with whorls detached. In contrast to their smooth shell that of the Donaldinidae is ornamented with spiral ribs. Here in addition to *Donaldina* with slender shell with apical ramp in the teleoconch whorls and protoconch more or less flat on the apex of the teleoconch, the genera *Royalella* n. gen. with protoconch lifted from the top of the teleoconch forming a large angle with it, *Texasella* n.gen. with juvenile shell like *Royalella* and later whorls flattened and smooth, and *Yoospira* n. gen. with rounded whorls are added. A shorter shell characterizes *Heteroaclisina* n. gen. A different family is created with the Heterosubulitidae n. fam. that include the genus *Heterosubulites* n. gen. with fusiform smooth shell with flaring aperture. The family Stuoraxidae as known from the Triassic is recognized in a *Stuoraxis* with smooth planispiral shell from the Permian, originally called "*Straparollus minutus* PAN & ERWIN, 2002" and renamed as *Stuoraxis panhuazhangi* n. sp.. The following new species have been described: *Donaldina ohioensis* n. sp., *Donaldina texana* n. sp., *Donaldina media* n. sp., *Royalella minuta* n. sp., *Royalella streptaciformis* n. sp., *Texasella biformata* n. sp., *Yoospira knighti* n. sp., *Yoospira acuta* n.sp., *Yoospira morgantownenis* n. sp., and *Heteroaclisina putnamensis* n. sp. The evolutionary history of the Heterostropha across the Paleozoic-Mesozoic boundary does not document an extinction event, but it appears more appropriate to suggest

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a faunal revolution with several totally new groups appearing while the old ones continue. Streptacidoidea of Streptacidae and Donaldinidae as well as the archictectonicoids with *Stuoraxis* are found in the Triassic and their continuation into modern taxa can be documented. But in addition numerous new taxa of the Heterostropha arose during the Triassic that have no counterparts in the Paleozoic.

Zusammenfassung

Schnecken aus dem Karbon und Perm, die der Unterklasse Heterostropha zuzuordnen sind, können vornehmlich der Überfamilie Streptacidoidea zugeordnet werden. Die meisten ihrer Vertreter haben eine kleine, schlank turmförmige, rechtsgewundene Schale mit flach links-gewundenem Protoconch. Innerhalb der Familie Streptacidae mit *Streptacis* wird die neue Gattung *Mapesella* zugeordnet, deren Protoconch flach auf der Schalenspitze liegt und der Teleoconch etwas abgeflachte Windungen hat. Zudem gehört hierher die offen aufgewundene permische *Laxella*. Im Gegensatz zu den glatten Schalen der Streptacidae haben jene der Donaldinidae Spiralrippen. Bei *Donaldina* ist eine oben schräg abgeflachte Windung ausgebildet und der Protoconch liegt mehr oder weniger flach dem Apex auf. In der neuen Gattung *Royalella* ist der Protoconch schräg vom Teleoconch abgehoben, bei *Texanella* gleicht die Jugendschale jener von *Royalella* doch spätere Windungen sind glatt und abgeflacht, und bei *Yoospira* sind die Windungen gerundet. Bei der neuen Gattung *Heteroaclisina* nimmt die Schale rascher an Breite zu und hat weniger Windungen. Nicht den Strepacidoidea zuzuordnen ist die neue Gattung *Heterosubulites* mit subulitiformer Schale und breiter Mündung aus der neuen Familie Heterosubulitidae. Die triassische Familie Stuoraxidae lässt sich mit einer Art von *Stuoraxis* mit glatter planispiraler Schale auch aus dem Perm belegen und wurde als "*Straparollus minutus* PAN & ERWIN 2002" beschrieben, die hier in *Stuoraxis panhuazhangi* n. sp. umbenannt wird. Folgende neue Arten wurden beschrieben: *Donaldina ohioensis* n. sp., *Donaldina texana* n.sp., *Donaldina media* n. sp., *Royalella minuta* n. sp., *Royalella streptaciformis* n. sp., *Texasella biformata* n. sp., *Yoospira knighti* n. sp. *Yoospira acuta* n. sp., *Yoospira morgantownenis* n. sp.und *Heteroaclisina putnamensis* n. sp. Bei der Bewertung der Evolutionsgeschichte der Heterostropha über die Paläozoikum-Mesozoikum-Grenze hinweg wird das Modell bevorzugt, welches von einem Faunenumschwung verbunden mit einer Vervielfältigung im systematischen Bereich ausgeht und nicht von einer Faunenkrise. Die Streptacidoidea mit Streptacidae und Donaldinidae sowie Architectonicoidea wie *Stuoraxis* setzen sich in der Trias fort, es treten jedoch eine ganze Reihe neuer Taxa der Heterostropha hinzu, die im Paläozoikum keine Entsprechung haben.

I. Introduction

The subclass Heterostropha FISCHER, 1885 (=Heterobranchia GRAY, 1840) of the Gastropoda can be documented from Early Devonian (Emsian) time onward (FRÝDA & BLODGETT, 2001) and similar species lived at the Mid Devonian (BANDEL & HEIDELBERGER 2002). Both of these gastropods *Kuskokwimia* FRÝDA & BLODGETT, 2001 and *Palaeocarboninia* BANDEL & HEIDELBERGER, 2002 belong to a group that resembles in shape and can be connected with Mesozoic and Recent representatives of the *Valvata* relation (Valvatoidea). *Kuskokwimia* and *Palaeocarboninia* have a conical rounded shell with smooth surface, simple aperture and sinistral protoconch included in the apex of the dextral teleoconch. The protoconch as well as the teleoconch are coiled around a central axis that has the same orientation.

Carboniferous gastropods with sinistrally coiled heterostrophic protoconch but with the axis of coiling of the protoconch deviating from that of the teleoconch had been recognized among slender and turriform species (DONALD, 1898). They usually have a small shell with straight or curving pattern of growth lines, which resulted in their placement in one of the seemingly well established Paleozoic taxa, either among the Loxonematoidea or

the Murchisonioidea. Or they were interpreted to belong to the Pyramidelloidea which otherwise are known only from the Late Cretaceous onward and have a similarly deviating protoconch. DONALD (1898) noted the heterostrophic protoconch in the Early Carboniferous species, *Aclisina grantonensis* DONALD, 1898 from Scotland, which was later chosen as genotype to *Donaldina* KNIGHT, 1933. A similar case had been noted by MEEK (1872) in case of *Streptacis whitfieldi* from the Late Carboniferous of Illinois, USA. KNIGHT (1931) created the family Streptacididae to encompass Carboniferous species with a deviating protoconch as found among many species of the modern Pyramidellidae. Fortunately KNIGHT (1931) utilized the genus *Streptacis* for his family name and not *Aclisina*, which he also considered to represent a genus of that taxon. The genus *Aclisina* as it had been treated by the former author is problematic and contains species which are heterostrophic and others that are connected to a dextral protoconch, among the later probably the type species. But the status of its type species *A. striatula* is not safe (KNIGHT, 1941) in that regard, but probably it is not a member of the Heterostropha, BANDEL (2002) included it tentatively with the Orthonemidae. KNIGHT (1931) placed the Streptacididae in no specific larger taxon, but remarked that it may preliminarily be regarded as connected to ancient murchisonioid gas-tropods. Early Paleozoic species of murchisonioids are sometimes still considered as source to all kinds of later gastropod taxa (WAGNER, 2002).

KNIGHt et al. (1960) considered the Streptacididae to belong to the Pyramidelloidea, while KNIGHT (1931) had been more cautious. He had correctly noted that a very long time passed between the existence of the Streptacidae in the Carboniferous and Permian and that of the first undoubted Pyramidellidae at the end of the Mesozoic period. Therefore, KNIGHT's (1931) placement reflects more closely the course of evolution in nature than that of WENZ (1938) who had connected the Streptacididae with the Loxonematoidea, and thus a taxon based on the genus *Loxonema* which has since been documented to represent a peculiar member of the Archaeogastropoda belonging to the order Stylogastropoda (FRÝDA & BANDEL, 1997). Other Carboniferous genera that had been placed with loxonematids have since been recognized to represent Caenogastropoda (*Pseudozygopleura* relation BANDEL, 1991a, NÜTZEL, 1998), and Heterostropha (*Streptacis* relation KNIGHT, 1931; BANDEL, 1994a, 1995). ANDERSON et al. (1985) placed *Streptacis* in the Opisthobranchia, Pyramidelloidea as suggested by KNIGHT et al. (1960), but included in the genus also species with a non- sinistral protoconch, and here following the example of KNIGHT (1931) in this respect.

PONDER & LINDBERG (1997) speculated that sinistral gastropods living in the Early Paleozoic evolved into Heterobranchia (=Heterostropha) by developing a larger shell with higher spire. They suggested that sinistrally organized gastropod would get into trouble when they grew a larger shell. A larger and heavier shell would create difficulties in regard to the water entering the pallial cavity and also in discharging waste products. If these snails twisted their body backwards in reaction to the increased weight of their shell and its sinking down on the back the foot would come into a position next to the columella. This position was considered to have been inconvenient to the animal. But when the shell in further growth twists to the right the problem would be solved and opening to the mantle cavity would be situated opposite to the columella. PONDER & LINDBERG (1997) may have had in mind a model based on the Mimospirida (=Onychochilidae) of the Early Paleozoic representing a group of sometimes small sinistral gastropods and, in the Carboniferous, the Donaldinidae und Streptacidae which are gastropods with high spire and dextrally coiled shell connected to a sinistral protoconch. Even though small sinistral gastropods resembling Mimospirida have been recognized to Early Carboniferous and Mid-Devonian times (YOO,

1988, HEIDELBERGER & BANDEL, 1999), there are no transitions known to exist between these and the species that have sinistral early part and dextral later shell as in the Strepacidoidea. Also the placement of these sinistral species with the Mimospirida is in doubt (see below). If the model of PONDER & LINDBERG (1997) would be correct, most of the Heterostropha still solve this problem during their ontogeny usually at metamorphosis from free swimming veliger larva and planktic life to the life of a snail crawling by its foot on the bottom of the sea. The idea is nice but purely theoretical and it is also not in agreement with the fossil record, where the earliest known species of the Heterostropha are the small *Kuskokwimia* FRÝDA & BLODGETT, 2001 and *Palaeocarboninia* BANDEL & HEIDELBERGER, 2002, both with the sinistral early ontogenetic shell coiling around the same axis as the dextral teleoconch. HASZPRUNAR (1988) proposed a common ancestry to Heterobranchia (=Heterostropha) and Caenogastropoda and proposed to place such Heterostropha which are neither Opisthobranchia nor Pulmonata in the taxon Allogastropoda HASZPRUNAR, 1985. The known fossil record allows a relationship between members of the Heterostropha and Caenogastropoda only when their common ancestors have lived before the Devonian. Similarly first Opisthobranchia can be recognized not before the Triassic and earliest Pulmonata have been documented from the Jurassic. Information about gastropods of Silurian and Ordovician age is still vague and problematic. This becomes very evident when the model of gastropod evolution during that time proposed by WAGNER (2002) is consulted. In it the convergence of shell shape within different systematic lineages plays no role during the first 100 Million years of their evolution, as well as the shape and formation of the early ontogenetic shell. Apparently, in WAGNER's model, all gastropods of that time had the same type of ontogeny of which, lucky for the proposed model, almost nothing is known. It is therefore of no surprise that this new model of evolution in many ways resembles that proposed by KOKEN (1889).

All specimens utilized in this study from the MAPES collection are housed in the Ohio University Zoological Collection in Athens, Ohio, U.S.A., from the KNIGHT collection in the Smithonian Museum of Natural History in Washington, DC, USA.

II. Systematics

Subclass Heterostropha FISCHER, 1885

Description: Within the Heterostropha all those species that change from sinistral to dextral coiling during their ontogeny or have evolved from ancestors that had this development are included. Heterostropha hold the orders Allogastropoda and Euthyneura, the later with the suborders Opisthobranchia and Pulmonata.

Remarks: As far as we know up to date only representatives of the Allogastropoda lived during Paleozoic times. This contrasts to the ideas expressed by KOLLMANN & YOCHELSON (1976) who recognized Opisthobranchia from the Carboniferous and SOLEM & YOCHELSON (1979) who determined stylommatophoran pulmonates of different taxa to have existed during that time.

Heterostropha of Paleozoic times have been united under the term Opisthobranchia by KNIGHT et al. (1960). It was not until later that HASZPRUNAR (1985a,b) recognized the independence of the Allogastropoda and that it became evident that Opisthobranchia as well as Pulmonata need to be distinguished from them. KNIGHT et al. (1960) had noted the presence of a heterostrophic protoconch only in a few Paleozoic genera like *Donaldina* KNIGHT, 1933, *Streptacis* MEEK, 1872 and *Acteonina*. The last genus is not correctly named and *Acteonina* actually represents a Jurassic genus (SCHRÖDER, 1995, BANDEL, 1994b). Heterostrophic protoconchs in *Donaldina* and *Streptacis* have since been confirmed for Carboniferous species by HARPER (1977), ANDERSON et al. (1985), YOO (1988, 1994),

HERHOLZ (1990, 1992), BANDEL (1994a,b, 1997), NÜTZEL (1998), PAN & ERWIN (2002). The earliest occurrence of Opisthobranchia and Pulmonata in the fossil record has since moved into the Mesozoic and there is no longer an undisputed member of these, that can be united in the taxon Euthyneura before the Triassic (BANDEL, 1991a, 1994b) and they are well established in the Jurassic (GRÜNDEL, 1997a,b, 1998).

Order Allogastropoda HASZPRUNAR, 1985

Among the Carboniferous and Permian species of this order classified as Streptacidoidea, Architectonicoidea, and Heterosubulitoidea are included and the Valvatoidea should be expected since they existed already at Devonian times.

Superfamily Streptacidoidea KNIGHT, 1931

Description: According to BANDEL (1996) the Streptacidoidea (Strepacididae of KNIGHT et al., 1960) have high spired shells with sinistral protoconch, often rounded sinus in the outer lip high on the whorl and otherwise simple oval aperture. Their ornament consists of growth lines and/or spiral lirae. The protoconch is a discoidal (initially sinistral) whorl that caps the spire flatly or is deviated. The Streptacidoidea of the Late Paleozoic are considered to hold the families Streptacididae and Donaldinidae.

Remarks: Among the Streptacidoidea species may very well have evolved that are united in the Ebalidae BANDEL, 1994 (WARÉN, 1994) that existed from the Triassic, continued in the Jurassic (SCHRÖDER, 1995; GRÜNDEL, 1998; BANDEL et al., 2000), the Cretaceous (KIEL & BANDEL, 2001, Pl.1, fig.15-17) and still live in modern seas. The Cassianebalidae BANDEL, 1996 of the Triassic are similar as well. The Donaldinidae of Carboniferous to Triassic age may still survive in some recent species (BANDEL, 1991b, Pl.8, figs. 1, 5, 6; BANDEL, 1996, Fig.7). These resemble in shape of their shell closely the species from the Carboniferous and Triassic and differ from other modern gastropod groups anatomically. The Mathildoidea are quite apparent from the Triassic onward and usually have a highly ornamented shell differing from the smooth Cassianebalidae and Ebalidae as well as from the spirally ornamented Donaldinidae. The Pyramidelloidea commonly bear columellar folds and may have more pronounced ornament, besides appearing in the geological record not before Cretaceous time (SOHL, 1964; DOCKERY, 1993; BANDEL, 1996a, 1997; KIEL & BANDEL, 2001).

Family Streptacididae KNIGHT, 1931

Description: The shell is usually high-spired and slender with a sinus of the outer lip of the aperture that is reflected in the curving growth line pattern. The protoconch is sinistrally coiled and forms a low spire that may be attached with differing but species specific angles to the apex of the teleoconch. In species with a more yolk-rich ontogeny the number of protoconch whorls is smaller and heterostrophy not as well expressed. The teleoconch is ornamented by fine curving growth lines and is otherwise smooth or there may be very fine spiral lirae. Its whorls are more or less rounded, usually not high, sutures are impressed, and there is no open umbilicus. The sinus in the outer apertural lip usually lies below the suture and a lobe is present in its middle. The columellar lip is short and arched.

Differences: The closest group in shape of shell and size range appear to be the Ebalidae, in which species have a similar protoconch, smooth teleoconch but usually higher whorls. The genotype to *Ebala* measures 2,5 mm in height and shells found in this genus have 6-8 whorls. A Jurassic form with sinuous growth line pattern was coined *Falsoebala* by GRÜNDEL (1998, Pl.3) but otherwise is quite similar to *Ebala*.

Genus *Streptacis* MEEK, 1871

Description: The small shell is elongate and composed of many whorls which are smooth. Curving increments of growth are usually present with the sinus just below the suture and the lobe

near the lower middle of the apertural lip. The protoconch is sinistral and more or less detached from the teleoconch. Change over from sinistral to dextral coiling occurs in the transition from protoconch to teleoconch or in the very last part of the protoconch. The aperture is ovoid in shape. The type is *Streptacis whitfieldi* from the Late Carboniferous of the USA (KNIGHT, 1941, Pl.48, fig.4).

Streptacis whitfieldi MEEK, 1871

(figs. 1 - 5)

Description: According to KNIGHT (1931, Pl.2, Fig.1) 11 whorls were noted in an about 5,5 mm high shell with deep and oblique sutures and relatively high whorls. The aperture is almost oval and the base rounded. The protoconch is almost planispirally coiled and stands in an angle to the following whorls and the second whorl is free of the spire. KNIGHT (1941, Pl.48, fig.4) found about 9 whorls in an about 4,5 mm high shell from Danville, Illinois.

A specimen from the Salesville Formation, Missourian Series of the Pennsylvanian, from Mineral Wells, Texas, USA (MAPES coll.) (figs.1-3) has an about 0,25 mm wide protoconch that consists of more than 1,5 whorls and ends with a apertural constriction. This protoconch with less than 0,1 mm wide first whorl is a lowly coiled, planispiral but clearly sinistral shell that has its axis of coiling forming an angle of about 100° with the axis of the teleoconch. The transition from sinistral coiling to dextral coiling occurs in the change over from the protoconch to the teleoconch. Teleoconch whorls are as described by KNIGHT (1931) from his specimen from the Saint Louis outlier, Labette Shale Desmoinesian Series, Pennsylvanian of Missouri.

Differences: *Mapesella meeki* that had been treated as *Streptacis meeki* by KNIGHT (1931) has the protoconch planispirally and flat on the top of the teleoconch and it has less rounded whorls,

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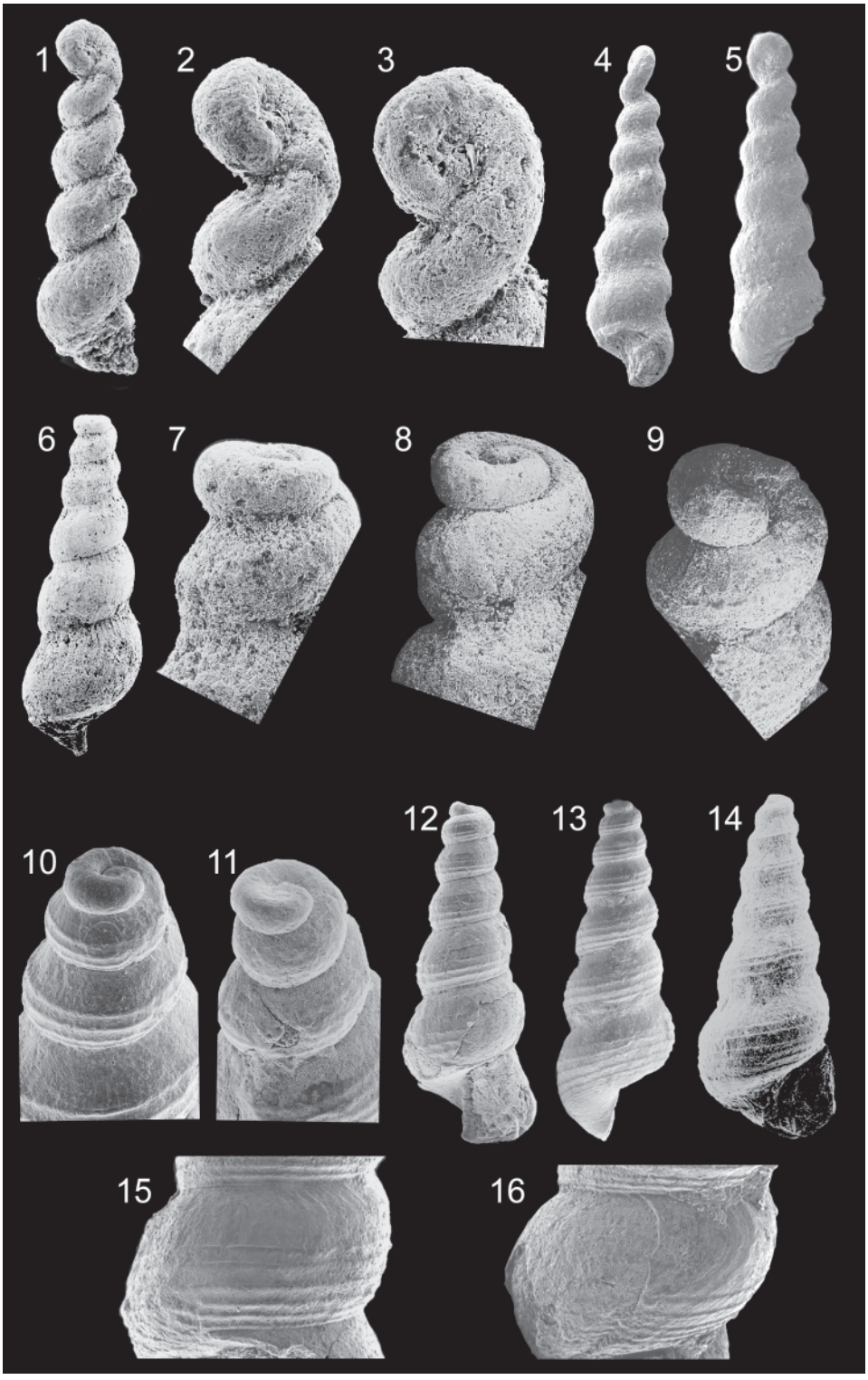
Fig.1: The shell of *Streptacis whitfieldi* MEEK 1871 is 1,1 mm high and from the Salesville Formation, Missourian Series of the Pennsylvanian, from Mineral Wells, Texas.
Fig. 2: The about 0,25 mm wide protoconch of *Streptacis whitfieldi* consists of more than 1,5 whorls and ends with a apertural constriction. Detail to fig.1.
Fig. 3: The detail to fig. 1 of *Streptacis whitfieldi* with the about 0,1 mm wide first whorl that is lowly coiled, planispiral but clearly sinistral shell.
Fig. 4: The shell of *Streptacis whitfieldi* is 1,2 mm high and its axis of coiling forms an angle of about 100° with the axis of the teleoconch. From East Mount Shale, Demoinesian Series of the Pennsylvanian, from Mineral Wells, Texas.
Fig. 5: The shell of *Streptacis whitfieldi* from East Mount Shale as in fig. 4 is about 1 mm long.
Fig. 6: The about 3 mm high shell of *Mapesella meeki* (KNIGHT, 1931) has rounded whorls and shallow sutures. Finis Shale, Graham Formation, Virgilian Series, Pennsylvanian, Jacksboro, Jack County, North Central Texas,
Fig. 7: The detail to fig. 6 with the protoconch of *Mapesella meeki* forming planispiral coil that is 0,3 mm wide.
Fig. 8: The detail to the shell in fig.6 of the protoconch of *Mapesella meeki* with the transition from sinistral spiral to the dextral one. The second whorl is 0,35 mm wide.
Fig. 9: The about 2 mm high portion of the shell of *Mapesella meeki* with the protoconch and the early teleoconch.
Fig.10: The protoconch of *Donaldina stevensana* (MEEK & WORTHEN, 1866) measures about 0,25 mm across. Its transition into the teleoconch is marked by the begin of spiral ribs and an apertural thickening. From Labette Shale, Pennsylvanian of Missouri.
Fig.11: The first whorl of *Donaldina stevensana* measures about 0,12 mm in diameter and its initial portion dips below apical surface. From Labette Shale, Pennsylvanian of Missouri.
Fig. 12: In *Donaldina stevensana* the shell appears straight sided and sutures are well expressed. The about 2 mm high shell is from the Labette Shale, Pennsylvanian of Missouri.
Fig. 13: In *Donaldina stevensana* whorls have a slightly flattened apical side and four to five spiral ribs with rounded grooves between them. The about 2 mm high shell is from the Labette Shale, Pennsylvanian of Missouri.
Fig. 14: The shell of *Donaldina stevensana* is about 2,5 mm high and from the Ames Shale from the top of the base of the Virgilian Series, Pennsylvanian of Morgantown, Ohio.
Fig. 15: The apertural sinus below the suture is well reflected in growth lines in the 0,6 mm high whorls of *Donaldina stevensana* from Labette Shale, Pennsylvanian of Missouri.
Fig. 16: Growth lines of *Donaldina stevensana* are sinuous reflecting a sinus in the apical portion of the outer lip and a low lobe in its lower part. The whorl is about 0,7 mm high. Location as in fig.15.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while *S. whitfieldi* has the protoconch forming an angle with the teleoconch and the whorls more rounded. ANDERSON et al. (1985, Fig.4, 10,11) described *Streptacis whitfieldi* from the Putnam Hill Shale, Desmoinesian Series with the protoconch broken away, but teleoconch well preserved. It closely resembles *Streptacis* sp. of the Early Carboniferous of Eastern Australia described by YOO (1994, Pl. 22, figs.4,5) and *Streptacis pravis* PAN & ERWIN, 2002 from the Late Permian of China (PAN & ERWIN, 2002, Fig.18, 1,2 (erroneously called *S. fragilis*) and 8, 9). In the Chinese specimen the protoconch is preserved and quite like that of *S. whitfieldi*, so that it would be quite difficult to distinguish this new Permian species from the Pennsylvanian one described by MEEK (1871) and KNIGHT (1931) from the USA.

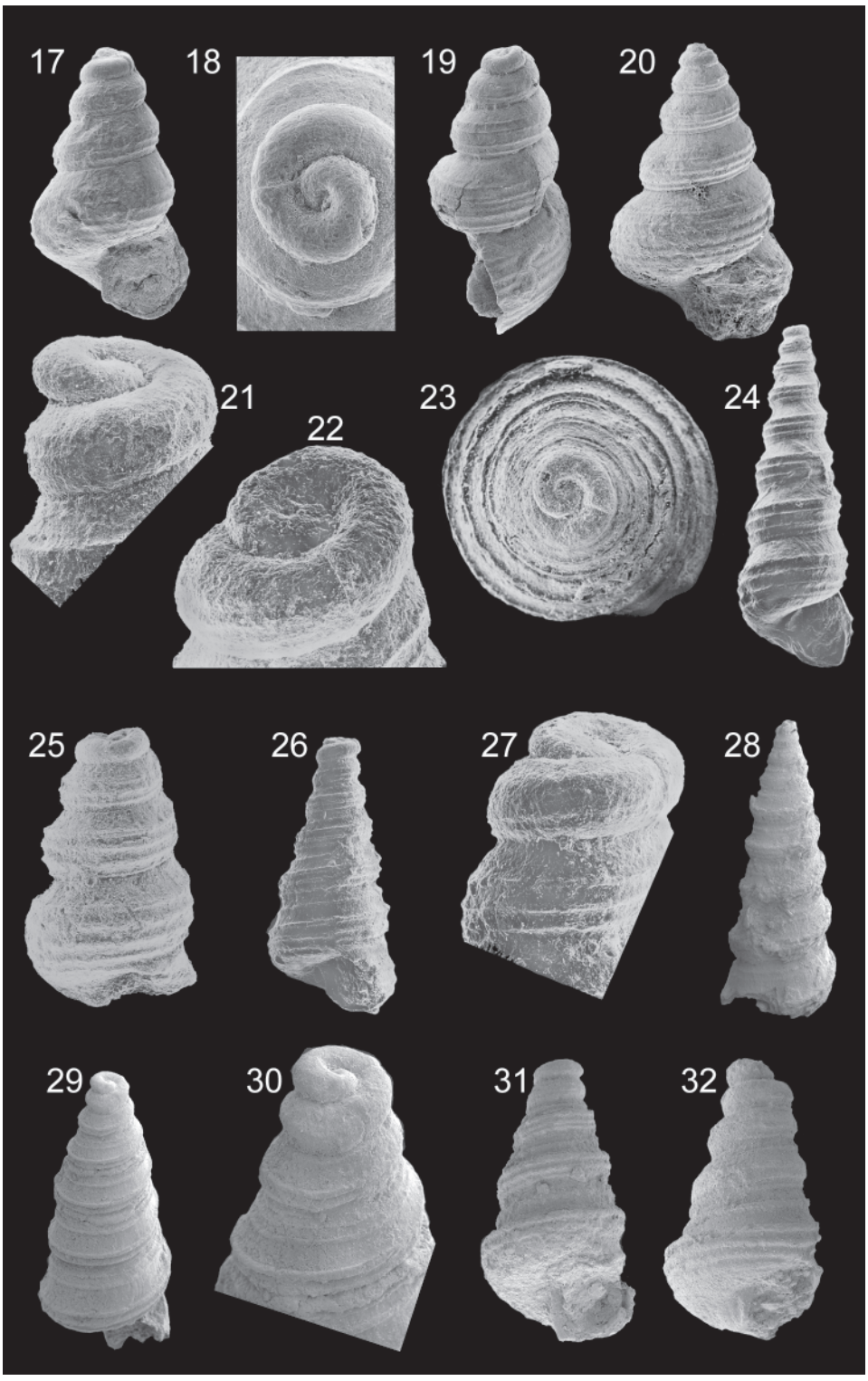
Genus *Mapesella* n. gen.

Diagnosis: The teleoconch and the protoconch coil around the same axis, but the first in dextral mode and the second initially in sinistral and later in planispiral mode. The protoconch is smooth and the teleoconch ornamented by fine collabral lines that reflect an apertural margin with shallow sinus on the upper and low lobe in the lower outer lip. The genotype is *Streptacis meeki* KNIGHT, 1931 from the Pennsylvanian (Late Carboniferous) Labette and Henrietta Shale of Missouri, USA.

Derivatio nominis: This little snail is called in honor of Royal MAPES, who collected it and knows the American Pennsylvanian and its fossil very well.

Differences: *Streptacis* differs from *Mapesella* by having a detached protoconch, higher whorls of the teleoconch, and less well developed growth line pattern.

Fig. 17: *Donaldina robusta* (STEVENS, 1858) with 1,3 mm high shell and of conical shape with the whorls rounded in such a way that the periphery lies a little below the middle of the sides. The shell is from the Labette Shale, Pennsylvanian of Missouri.
Fig. 18: Protoconch of *Donaldina robusta* from the Labette Shale of Missouri is set off from the teleoconch by a marginal thickening that occurs after a little more than 1,5 whorls and 0,2 mm width.
Fig. 19: The about 1,2 mm high shell of *Donaldina robusta* is from the Labette Shale, Pennsylvanian of Missouri with the smooth and rounded protoconch and spirally ornamented teleoconch.
Fig. 20: The about 2 mm high shell of *Donaldina robusta* is from the Labette Shale, Pennsylvanian of Missouri.
Fig. 21: The protoconch of *Donaldina ohioensis* is coiled around an axis that almost coincides with the columella of the teleoconch and consists of about 1,5 smooth whorls that form a lowly sinistral shell ending with a rounded apertural margin. Detail to fig. 24.
Fig. 22: The first whorl of the protoconch of *Donaldina robusta* measures about 0,1 mm in diameter and lies a little inclined on top of the teleoconch. Saint Louis outlier.
Fig. 23: Apical view of the almost 1 mm wide shell of *Donaldina ohioensis* n. sp. Detail to fig. 24.
Fig. 24: The 3 mm high slender turritelliform shell of *Donaldina ohioensis* n. sp is ornamented by four strong spiral ribs. Ames Shale, Early Virgilian Series of the Pennsylvanian of Near Morgantown, Ohio, holotype.
Fig. 25. A juvenile shell of *Donaldina media* of a little more than 1 mm in height from Washingtonville Shale, Ohio.
Fig. 26: The turritelliform shell of *Donaldina ohioensis* measures about 1,8 mm in height with angular whorls with a flattened apical flank and four strong ribs below it. Finis Shale Sacksboro.
Fig. 27: The protoconch of *Donaldina ohioensis* measures about 0,22 mm in diameter and detaches a little from the apex. Detail to fig. 26.
Fig. 28. The slender turritelliform shell of *Donaldina texana* has four strong spiral ribs and one or more ribs also on the apical shelf and between stronger ribs. The shell measures about 4 mm in length. Santa Anna Shale, Moran Formation, Wolfcampian, Early Permian, Stephans County, Texas.
Fig. 29: The juvenile shell of *Donaldina texana* representing the holotype is about 2,5 mm high. Locality as in Fig.28.
Fig. 30: The protoconch of *Donaldina texana* n.sp. The sinistral protoconch forms a planispiral apex of the shell and consists of smooth whorls. Detail to fig. 29.
Fig. 31: The juvenile shell of *Donaldina texana* is about 1,2 mm long and exposes the shape of the aperture.
Fig. 32: The juvenile shell of *Donaldina texana* is about 1 mm high. Together with Fig. 31 from the same locality as Fig.28.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Mapesella meeki (KNIGHT, 1931)

(figs. 6 - 8)

Description: According to KNIGHT (1931, Pl.2, Fig.2a,b) the high spired shell with 12 whorls is about 4,5 mm high. Whorls are rounded and sutures not deep. The protoconch lies on top of the teleoconch as planispiral coil. The specimen studied here from Labette Shale of Missouri and from Finis Shale, Graham Formation, Virgilian Series (Stephanian), Pennsylvanian, Jacksboro, Jack County, North Central Texas, consist of fewer whorls but shows the protoconch well that consists of about 1,5 whorls in planispiral coiling. The protoconch measures about 0,23 mm across, ends with a thickened apertural rim, and is formed by a sinistral but shallow coil. With begin of the teleoconch the whorl turns into a spirally coiled dextral shell (figs.7, 8). The whorls of the teleoconch have a sinuous growth line pattern reflecting a shallow sinus in the upper part and a low saddle in the lower portion of the apertural outer lip.

Differences: *Mapesella meeki* resembles *S. whitfieldi* in size and teleoconch shape but has less deep sutures and the protoconch lies flat on its apex. The axis if coiling of the protoconch does not deviate from the axis of coiling of the teleoconch. From Putnam Hill Shale, Desmoinesian Series, Pennsylvanian of Ohio *M. meeki* was described by ANDERSON et al., (1985, Fig.4,12-13). YOO (1994, Pl.22, Figs.4-5) described a *Streptacis* sp. which has a smooth and slender teleoconch with sinuous

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Fig. 33: The shell of *Donaldina media* n. sp. is about 1,5 mm high It has allometric growth of the juvenile teleoconch that increases in width of the growing whorls more rapidly during early growth than during later growth. Salesville Formation, Mineral Wells, Texas, as also figs. 34,35,36.

Fig. 34: Detail of fig 33 with the protoconch of *Donaldina media* that is coiled around the same axis as the teleoconch and consists of 1,5 smooth whorls that measure 0,22 mm in diameter.

Fig. 35: The about 1,8 mm high shell of *Donaldina media* with very regular ornament of the teleoconch whorls and represents the holotype.

Fig. 36: In the about 2 mm high shell of *Donaldina media* the apical angle decreases to almost 30° from about 50° in the first two whorls of the teleoconch.

Fig. 37: The juvenile shell of *Donaldina media* with about 1,5 mm high shell documents the wide spiral angle of the early teleoconch whorls. Cambridge Shale, Ohio.

Fig. 38: The detail to fig. 37 of *Donaldina media* with the smooth protoconch in the about 0,6 mm wide shell.

Fig. 39: *Royalella minuta* n. sp from Eastmount Shale Pennsylvanian, Mineral Wells, Texas, USA. The 0,9 mm high shell is the holotype.

Fig. 40: The same shell as in fig.42 of *Royalella minuta* n. sp is 0,6 mm high. From Salesville Formation, Missourian Series, Pennsylvanian, Mineral Wells, Texas, USA.

Fig. 41: The detail to fig. 40 of *Royalella minuta* with the protoconch that consists of 1,5 whorls with a diameter of about 0,2 mm.

Fig. 42: The 0,7 mm high shell of *Royalella minuta* with the axis of coiling the protoconch that forms an angle of about 50° with the columella of the teleoconch. Salesville Formation, Missourian Series, Pennsylvanian, Mineral Wells, Texas, USA

Fig. 43: The detail to fig. 42 of *Royalella minuta* with the protoconch ending in the apertural thickening.

Fig. 44: The about 1,2 mm high shell of *Royalella streptaciformis* n. sp. from East Mount Shale, Desmoinesian Series, Pennsylvanian, Mineral Wells, Texas, USA as are fig. 45,46,47.

Fig. 45: The very slender teleoconch of *Royalella streptaciformis* with rounded whorls and four spiral ribs visible on the whorls of the spire has a sinistrally coiled almost planispiral protoconch with coiling axis forming an angle of about 45° with the columella of the teleoconch. The about 2 mm high shell is the holotype.

Fig. 46: The protoconch of *Royalella streptaciformis* appears almost detached from the teleoconch. The protoconch consists of almost 1,5 whorls and is well detached from the teleoconch forming a large angle with it.

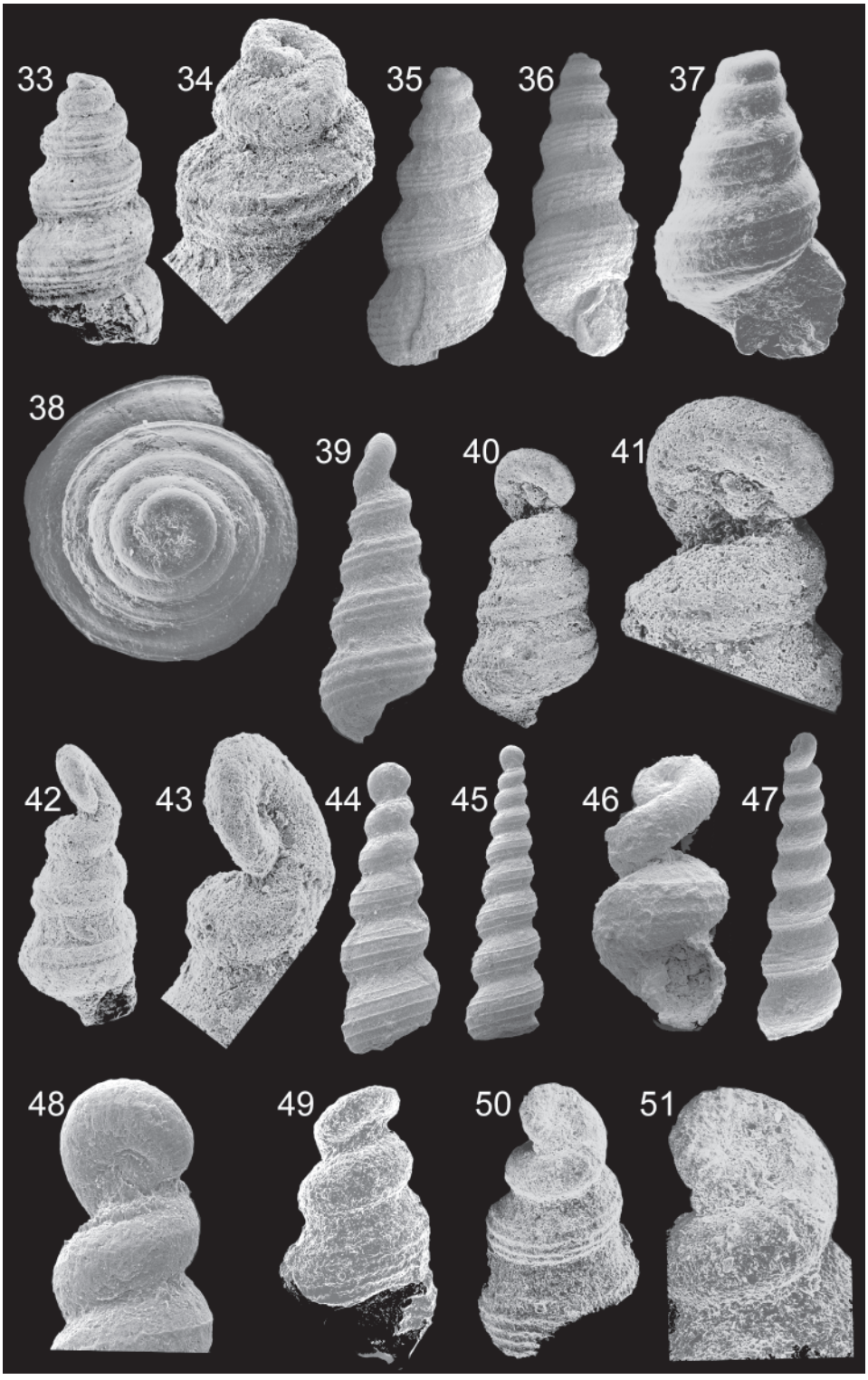
Fig. 47: The slender shell of *Royalella streptaciformis* with a height of about 1,5 mm and an apical angle of less than 20°.

Fig. 48: The detail to fig. 45 of *Royalella streptaciformis* with the about 0,2 mm wide protoconch and the begin of the teleoconch.

Fig. 49: Early whorls of a juvenile shell of 0,7 mm in height that may belong to *Texasella biformata* n.sp. from Ames Shale, Morgantown, Early Virgilian Series, Pennsylvanian, Ohio

Fig. 50: The same shell as in fig. 49 of *Texasella biformata* seen from the other side.

Fig. 51: The protoconch of fig 50 enlarged of *Texasella biformata* measures about 0,2 mm in diameter and consists of almost 1,5 smooth.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growth lines quite like those of *Mapesella meeki* from the Early Carboniferous of Eastern Australia, but its protoconch is detached from the teleoconch. From the Late Permian of South China *Streptacis fragilis* PAN & ERWIN, 2002 (perhaps the same as their *Streptacis pravis*) is very similar, while *Streptacis regularis* PAN & ERWIN, 2002 from the same area and time has similar growth line pattern on its teleoconch but its protoconch is more strongly detached (PAN & ERWIN, 2002, Fig.18, 1-5,10-11).

Genus *Laxella* PAN & ERWIN, 2002

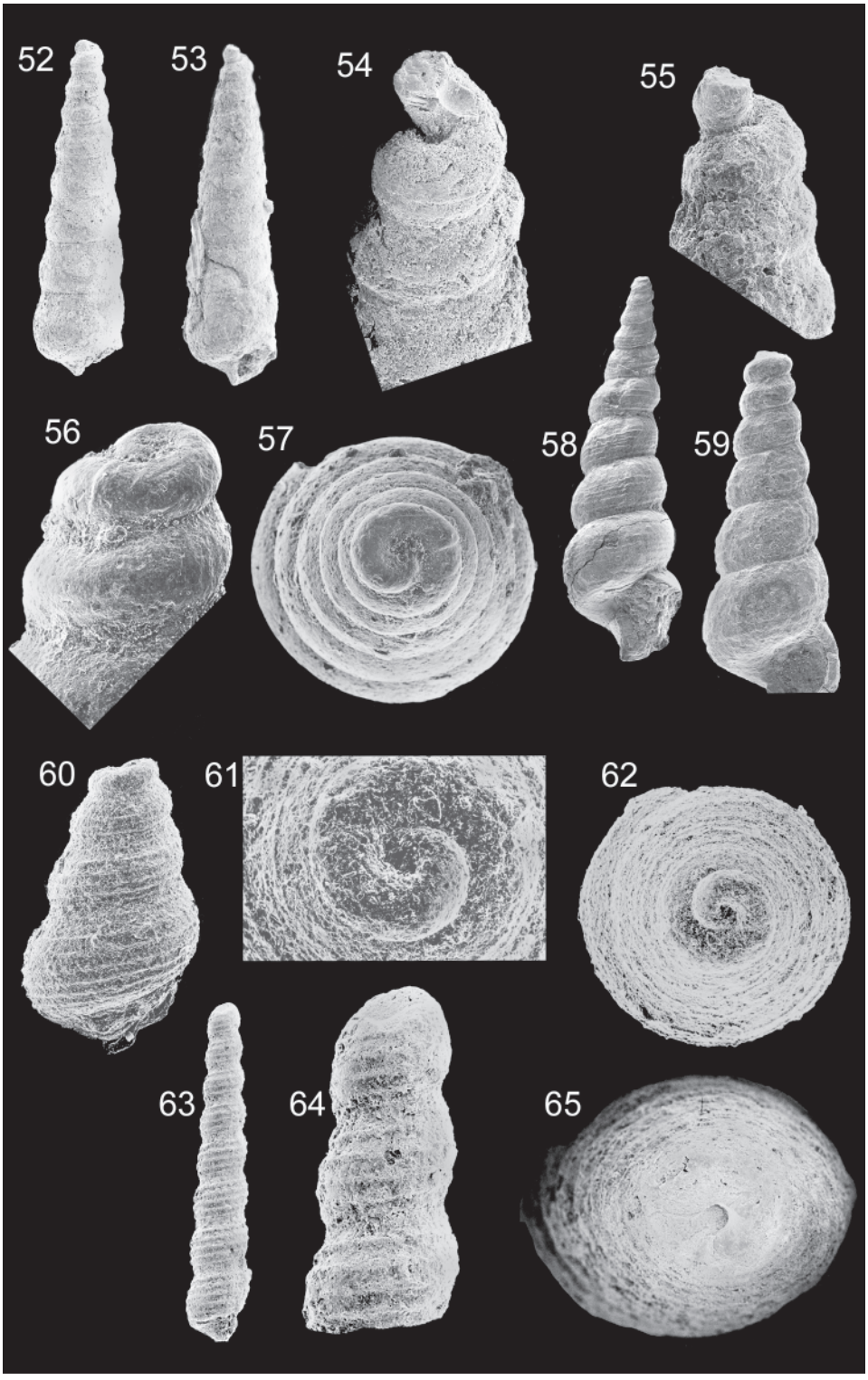
Description: The teleoconch of this genus forms an openly coiled screw while the protoconch is flatly sinistral. The type species is *Laxella micra* PAN & ERWIN, 2002 from the Late Permian of South China (PAN & ERWIN, 2002, Fig.18, 6-7).

Differences: *Laxella* resembles *Streptacis* in regard to the almost planispiral protoconch but differs from it by having an open cork screw-like shell.

Some species that had been placed in *Streptacis*, but do not belong here

KNIGHT (1931, Pl.2, figs.4,5) described *Streptacis scalpta* KNIGHT, 1931 and *Streptacis crenimarginis* KNIGHT, 1931 from the Pennsylvanian of Missouri which both represent high spired conical shells consisting of about 12 whorls and reaching a height of 12 mm. Their whorls are weakly convex and ornament consists of weak transverse costae, better developed in *S. scalpta* than in *S. crenimarginis*. In case of the first the protoconch was described as planispirally coiled. ANDERSON et al. (1985) again described *S. scalpta* from the Appalachian Basin and noted its smooth and dextral protoconch. So both of these species do not belong in the genus *Streptacis*, but can be seen in the relation of *Eoptychia* and *Platyconcha* representing Carboniferous species that can be placed among the caenogastropods (see BANDEL, 2002).

Fig. 52: The slender dextral conical teleoconch *Texasella biformata* is at first spirally ribbed and convex and later becomes smooth and has flattened sides. The 2,2 mm high shell is from Salesville Formation, Missourian Series, Pennsylvanian, of Mineral Wells in Texas, USA. Holotype.
Fig. 53: The about 2,3 mm high shell of *Texasella biformata* from Salesville Formation, Missourian Series, Pennsylvanian, of Mineral Wells in Texas, USA has the protoconch broken off as seen in fig.55.
Fig. 54: Detail to Fig. 53 of *Texasella biformata* with the protoconch partly broken off shows the shape of the rounded, smooth initial whorl.
Fig. 55: Different view of fig. 53 shows the transition from protoconch of *Texasella biformata* to its teleoconch with most of the protoconch broken off.
Fig. 56: The protoconch of *Yoospira knighti* n. sp. or a very similar species measures about 0,25 mm in diameter and ends in an apertural thickening. Together with fig. 57 from Cambridge Shale Missourian Series (Stephan), Pennsylvanian, near New Concord, Guernsey County, Ohio, USA, collected by Royal Mapes.
Fig. 57: Shell of *Yoospira knighti* seen in apical view with the smooth protoconch that consists of about 1,5 rounded whorls and in the second whorl the change into dextral coiling. The shell is 0,7 mm wide.
Fig. 58: The teleoconch with rounded whorls in the turriform shell of about 6 mm in height of *Yoospira knighti* n. sp is ornamented by spiral lirae that are acute and evenly distributed. from Labette Shale, Desmoinesian Series, Pennsylvanian, near Saint Louis, Missouri, USA., Holotype.
Fig. 59: The juvenile shell of about 2,5 mm in height of *Yoospira knighti* with smooth protoconch about 0.25 mm wide and teleoconch whorls rounded and spirally ornamented. Same locality as in fig.58.
Fig. 60: The 1,2 mm high shell of *Yoospira morgantownensis* n. sp (holotype) from Ames Shale, Morgantown, Early Virgilian Series, Pennsylvanian, Ohio and details in fig.61,62.
Fig. 61: The same shell as seen in fig. 60 of *Yoospira morgantownensis* with apical view and the smooth protoconch with 0,22 mm in diameter.
Fig. 62: The same shell as in Fig 60 of *Yoospira morgantownensis* is 0,7 mm wide in apical view.
Fig. 63: The slender shell of *Yoospira acuta* n. sp. from Salesville Formation Texas is almost 3 mm long. (Holotype).
Fig. 64: Five ribs are the ornament of the rounded whorls of *Yoospira acuta*. Detail to fig. 63.
Fig. 65: The transition to the protoconch is preserved in the top of the shell seen in fig. 63 of *Yoospira acuta* and with the umbilicus of the sinistral protoconch documents its position with the same axis of coiling as in the teleoconch.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Streptacis elegantissima (YOO, 1988) had originally been proposed as member of the genus *Loxonema* and later been changed into *Streptacis* by YOO (1994). But the protoconch is here dextrally coiled, so that this species does not belong in the Streptacidae. Therefore the new name *Austronema* is proposed by BANDEL (2002). *Streptacis gundyensis* YOO, 1994 with slender hydrobiform shell also represents no member of the Heterostropha and has therefore been included in the genus *Knightella* (see BANDEL, 2002).

Family Donaldinidae BANDEL, 1994

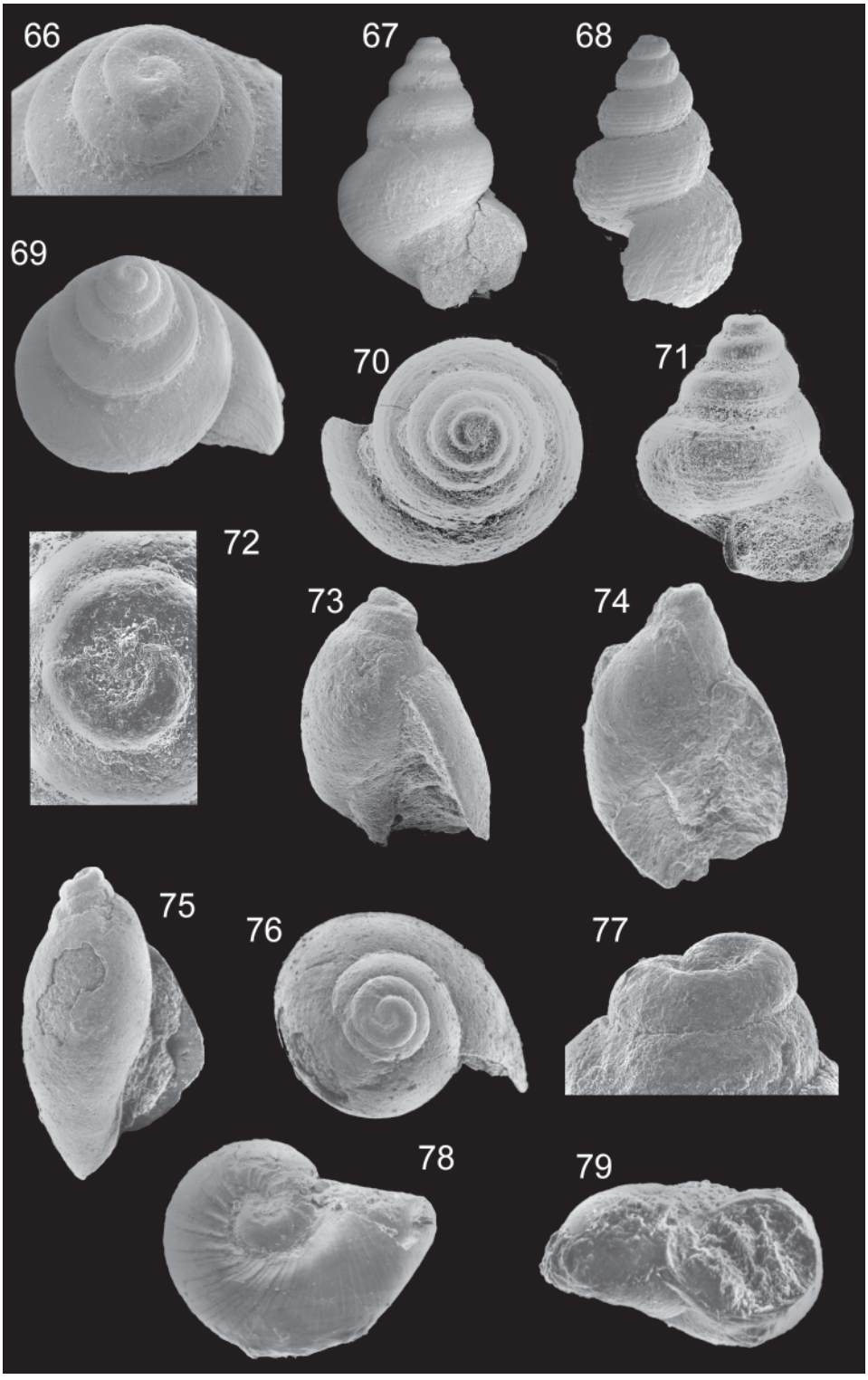
Description: Species of the Donaldinidae have the teleoconch ornamented by prominent spiral ribs. The protoconch is sinistrally coiled, commonly of nearly planispiral shape. The family is based on the genus *Donaldina* KNIGHT, 1933 (KNIGHT, 1941, Pl.48, fig.3).

Differences: Members of the Streptacidae, as well as of the Ebalidae, and Cassianebalidae of later occurrence are not ornamented by spiral ribs. The ornament of the Triassic to Recent Mathildidae includes also axial ribs and here many species and groups have a protoconch with ornament, with an apertural projection and with change in the mode of coiling occurring well within the larval shell. The Triassic Anoptychidae BANDEL, 1996 have a change of ornament in their teleoconch, but the juvenile teleoconch may resemble that of the Donaldinidae.

Genus *Donaldina* KNIGHT, 1933

Description: The shell has high spire and is ornamented with spiral threads confined generally to the lower part of the whorl. Growth lines are sinuous reflecting a depression on the outer lip below the suture. The protoconch is smooth throughout and within it the sinistral initial whorl changes into the dextral whorl. The genus is based on the Early Carboniferous *Donaldina grantonensis* (DONALD, 1898) from Scotland (KNIGHT, 1941, Pl.48, figs.3a-c).

Fig. 66: The detail to fig. 69 of *Heteroaclisina putnamensis* n. sp. with the almost planorboid, sinistral protoconch ending in a apertural thickening.
Fig. 67: The shell of *Heteroaclisina putnamensis* from Cambridge Shale, Pennsylvanian, Ohio is 2,1 mm high.
Fig. 68: The sutures of *Heteroaclisina putnamensis* without sediment glued to them are deep. The 1,2 mm high shell is from Cambridge Shale, Ohio.
Fig. 69: *Heteroaclisina putnamensis* seen from the upper side (detail in fig. 66) is 1,1 mm wide and from Cambridge Shale, Ohio.
Fig. 70: The shell of *Heteroaclisina putnamensis* is about 1 mm wide, from the Putnam Hill Shale, Keller Mine, Desmoinesian Series, Pennsylvanian, Ohio, USA.
Fig. 71: The shell of *Heteroaclisina putnamensis* is about 1 mm high and spiral lirae feature the well rounded whorls and the rounded base that has a narrow open umbilicus. Putnam Hill Formation of Keller Mine in Ohio, from Cambridge Limestone from near New Concord in Ohio. Holotype.
Fig. 72: The protoconch of *Heteroaclisina putnamensis* coils sinistrally around the axis that is oriented like the columella of the teleoconch and measures almost 0,2 mm in diameter.
Fig. 73: The shell of *Heterosubulites blatta* (KNIGHT, 1931) has a wide aperture with flaring outer lip and almost straight margin forming a wide notched siphon. All individuals of this species are from the Saint Louis outlier, Pennsylvanian of Missouri.
Fig. 74: Apertural view of *Heterosubulites blatta* with about 1,2 mm high shell and the anterior, wide aperture.
Fig. 75: The shell of *Heterosubulites blatta* seen from the side 1,7 mm high, from Henrietta Shale, Saint Louis outlier.
Fig. 76: The apical view of the shell of *Heterosubulites blatta* in fig. 75 shows 4 whorls of which about 1,5 are sinistral to planispiral. The shell is about 1,2 mm wide.
Fig. 77: The embryonic whorl of *Heterosubulites blatta* measures a bit more than 0,12 mm in diameter and twists with its apex below the planispiral second whorl, is thus sinistrally coiled. The sinistral first whorl grades into the dextral shell within the second whorl and is clearly dextral after 1,5 whorls are completed. Detail to fig.75.
Fig. 78: The protoconch of a juvenile illustrated by HERHOLZ (1992) resembles closely that of *Stuoraxis*. It is from the Westfalian (A-B) of the Late Carboniferous of the Ruhr Area, Germany and measures about 0,3 mm across.
Fig. 79: The side view of the specimen in fig. 78 documents the twist from sinistral to dextral coiling in the transition from the protoconch to the teleoconch in the *Stuoraxis*- like juvenile shell.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Differences: *Donaldina* differs from *Neodonaldina* by the presence of a subsutural ramp, which is not developed in the teleoconch of the later. *Donaldina* resembles *Heteroaclisina* regarding ornamentation but has a more slender shell. *Yoospira* differs by having rounded whorls and spiral lirae distributed all over. BATTEN (1966, Figs.11-22) described a number of species that he attributed to belong to the genus *Donaldina* from the Early Carboniferous of Belgium and England, of which the protoconch remained unknown. They may represent Heterostropha of the *Donaldina - Yoospira* type or belong to the caenogastropods of the *Aclisina* and *Stegocoelia* relation.

Donaldina stevensana (MEEK & WORTHEN, 1866)

(figs. 10 - 16)

Description: According to KNIGHT (1931, Pl.1, fig.1a-g) the shell is high (7 mm high and 12 mm wide) and sub-cylindrical with many whorls (about 12) that have rounded sides. He called this species *Aclisina stevensana*. The shell appears straight sided and sutures are well expressed. Each whorl has a slightly flattened apical side and on its periphery and lower in the first whorl of the teleoconch four, later, in the fourth whorl five and later up to seven spiral ribs with wide rounded grooves between them. The base is rounded and has finer spiral lirae which become covered by the following whorl. The aperture is elongate rounded with a sinus below the deep suture. Growth lines are, thus, sinuous reflecting a sinus in the apical portion of the outer lip and a low lobe in its lower part.

New observations on shells from the KNIGHT collection (Smithsonian Institute) indicate that the protoconch consists of almost 1.5 whorls of which the first one is sinistral grading into planispiral and within the second the planispiral coil changes into the dextral teleoconch. The first whorl measures about 0,12 mm in diameter and its initial portion dips below apical surface. The protoconch measures about 0,25 mm across and is a little wider than high. Its transition into the teleoconch is well visible due to the onset of spiral ribs with the begin of the teleoconch and the presence of an apertural thickening at the end of the protoconch. This species is from Labette Shale, Pennsylvanian of Missouri. KUES & BATTEN (2001, Fig.18,4-8) found this species also in the Pennsylvanian of New Mexico, and it is also is very common in the Ames Shale from the top of the base of the Virgilian Series, Pennsylvanian of Morgantown, Ohio.

Differences: *Donaldina robusta* occurring together with *D. stevensana* has a larger apical angle and more spiral ribs that may be stronger and provided with little irregular crests. According to KNIGHT (1931) *Aclisina* (=*Donaldina*) *swallowiana* GEINITZ, 1866 is close in shell shape and size but has coarser ribs as ornament, but he did not describe this species.

Donaldina robusta (STEVENS, 1858)

(figs. 17 - 18)

Description: According to KNIGHT (1931, Pl.1, fig.2a-f) who called this species *Aclisina robusta* the shell has a high spire, measures about 8 mm in height,3,5 mm in width and consists of 12 whorls. It is of conical shape with the whorls rounded in such a way that the periphery lies a little below the middle of the sides.

Additional material from the Labette Shale of Missouri documented that the protoconch is here very well set off from the teleoconch by a marginal thickening that occurs after a little more than 1,5 whorls. The first whorl clearly dips below apical surface and in the last half whorl the plane shell begins to twist into the dextral spire. The first whorl of the protoconch lies a little inclined on top of the teleoconch, and spiral ornament of the teleoconch appears after the first half whorl of teleoconch is smooth and rounded. The first whorl measures about 0,1 mm across and the protoconch is less than 0,2 mm wide and wider than high. The number of ribs on the teleoconch whorls slowly increases with whorl growth and ribs become a little nodded. The aperture is rounded. Growth lines are sinuous reflecting a sinus in the apical portion of the outer lip and a low lobe in its lower part.

KUES & BATTEN (2001, figs.18, 9-12) found this species also in the Pennsylvanian Flechado Formation of New Mexico.

Differences: *Donaldina stevensana* has a flatter and larger protoconch, a more rapid begin of teleoconch ornament and a narrower shell than present in *D. robusta*. *Donaldina filosa* YOO, 1988 from the Early Carboniferous of New South Wales, Australia described by YOO (1988, Figs.104-109), YOO (1994, Pl.22, figs.12-14) is slender and has rounded whorls with sinuous collabral growth increments and 5-6 spiral cords in the lower portion of each whorl. The protoconch consists of 1.5 smooth whorls which are attached flatly on top of the teleoconch with submerged first whorl. The rounded whorls of the teleoconch distinguish from both *Donaldina* species from the Labette Shale of Missouri. BANDEL et al (2002) described a *Donaldina* from the Buckhorn Asphalt of the Pennsylvanian of Oklahoma that closely resembles *Donaldina stevensana.* Here the embryonic whorl is so well preserved that its very delicate ornament consisting of a fine groove and ridge pattern is still present.

Donaldina ohioensis n. sp.

(figs. 21, 23, 24, 26, 27)

Diagnosis: The slender turritelliform shell is ornamented by four strong spiral ribs of which the lower one comes to lie in or just below the suture. Growth lines are sinuous, and the sinistral protoconch forms a planispiral apex of the shell with smooth whorls.

Derivatio nominis et locus typicus: This *Donaldina* is named according to its occurrence in Ohio. The stratum is Ames Shale, Early Virgilian Series of the Pennsylvanian of near Morgantown, Ohio, Appalachian Basin, USA.

Holotype: The specimen in fig. 24 represents the type.

Description: The turritelliform shell may consist of 8 whorls of the teleoconch and measures about 4 mm in height with an apical angle of about 20°. The protoconch is coiled around an axis that almost coincides with the columella of the teleoconch and consists of about 1,5 smooth whorls that form a lowly sinistral almost planispiral shell ending with a rounded and pronounced apertural margin. Its diameter is about 0,22 mm and it detaches a little from the apex. The whorls of the teleoconch are a little angular with a flattened apical flank and strong ribs below it. These count four with the lower one disappearing in the suture. The aperture is simple, about as wide as high and somewhat angular with columellar lip almost straight.

Differences: *Donaldina texana* is similar regarding shape and general style of ornament, but whorls are more angular and the number of ribs in later teleoconch is more irregular in that Permian species, that may well have evolved from the Pennsylvanian *Donaldina ohioensis*. *Donaldina stevensana* has similar shell shape but the ornament of spiral ribs is more delicate, and the apical plane on the whorls of the teleoconch are not as pronounced as is the case in *D. ohioensis*.

Donaldina texana n. sp.

(figs. 28 - 32)

Diagnosis: The slender turritelliform shell is much like that of *D. ohioensis* but in addition to four strong spiral ribs there are one or more ribs also on the apical shelf and between stronger ribs. The sinistral protoconch forms a planispiral apex of the shell and consists of smooth whorls.

Derivatio nominis et locus typicus: Many individuals (about 150) were studied from Santa Anna Shale, Moran Formation, Wolfcampian, Early Permian, Stephans County, Texas, and the species is named according to its place of occurrence in Texas, collected by Royal MAPES.

Holotype: The individual illustrated in fig. 29 represents the holotype.

Description: The turritelliform shell consist of about 8 whorls of the teleoconch and measures about 4 mm in height with an apical angle of about 20°. The protoconch is coiled around an axis that coincides with the columella of the teleoconch. It consists of about 1,5 smooth whorls that form a

lowly sinistral almost planispiral shell ending with a rounded and pronounced apertural margin. Protoconch diameter is about 0,2 mm. The whorls of the teleoconch are angular with a broad, flattened to concave apical flank and the rib below it commonly forming the peripheral edge or even a keel. The ribs below count three and may be variable in strength. Among individuals quite same variety exists within later whorls and spiral ribs also appear on the apical flank. Among individuals of this species variations are common regarding spacing and number of spiral ribs in the whorls of the adult shell. The aperture is simple, about as wide as high and somewhat angular with columellar lip almost straight.

Differences: *Donaldina texana* closely resembles *D. ohioensis* differing from it by the more irregular ornament and the more angular whorl outline with the first strong rib usually forming a keel and being larger than the other ribs. *Donaldina heshanensis* PAN & ERWIN, 2002 from the Late Permian of China has an inclined and detached protoconch but regarding its teleoconch whorls closely resembles *D. ohioensis* and *D. texana*.

Donaldina media n. sp.

(figs. 33 - 38)

Diagnosis: The shell intermediates between *Donaldina robusta* and *D. ohioensis* in shape with well flattened shoulder and below it 4-5 spiral ribs of about equal size. It differs from these two by having allometric growth of the juvenile teleoconch that increases in width of the growing whorls more rapidly during early growth than during later growth. The protoconch is coiled around the same axis as the teleoconch and consists of 1,5 smooth whorls.

Derivatio nominis and locus typicus: This *Donaldina* comes is in the middle (Latin medius) between the two other species of *Donaldina* with plane apical shoulder and is named accordingly. *D. media* comes from the Salesville Formation, Missourian Series, Pennsylvanian (Late Carboniferous), Mineral Wells, Texas, USA.

Holotype: The individual illustrated in fig. 35 represents the holotype.

Description: The apical angle decreases to almost 30° from about 50° in the first two whorls of the teleoconch. The protoconch consists of 1,5 whorls which are sinistrally coiled but almost planispiral. The end of the protoconch is marked by a thickened, round apertural margin. The protoconch measures about 0,22 mm in diameter and coils around an axis that lies in continuation of the columella of the teleoconch. In the first whorl of the teleoconch the apical shoulder is still rounded, while it is flattened from the second whorl onwards. There are about 6 whorls of the teleoconch in a shell of 3 mm in height. The ornament consists of rather regularly spaced fine spiral ribs of which four to five are seen on the whorl sides below the corner of the slightly convex to plane apical flattening. The base is rounded and there may be a very narrow umbilical slit. The aperture is simple, about as high as wide with almost straight inner lip and rounded outer lip. Individuals of this species or very closely related forms are also from Cambridge Shale, Ohio (MAPES, coll.)

Differences: In shape *D. media* resembles most closely *D. robusta* but differs from it by decreasing apical angle during growth of the teleoconch (allometric growth), by having a flatter apical side of the whorls, and more pronounced corner at the whorl. In that regard it resembles *D. ohioensis* which is more slender and usually has one spiral rib less on the whorls of the spire.

Genus *Royalella* n. gen.

Diagnosis: The very slender minute shell consists of more than 8 rounded whorls and measures less than 3 mm in height. Ornament is by spiral ribs or lirae, and the coiling axis of the sinistral, almost planispiral protoconch forms a large (usually more than 40°) angle with the columella of the teleoconch. The protoconch is almost detached from the teleoconch. The type to the genus is *Royalella minuta*.

Derivatio nominis: This genus is called in honour of Royal MAPES, who collected this species and most of the material on which this study is based.

Differences: The Triassic *Cassianebala* BANDEL, 1996 resembles *Royalella* in regard to the detached appearance of the protoconch regarding the teleoconch. But the protoconch is ornamented and teleoconch smooth in *Cassianebala* while the opposite is the case in *Royalella*. The spirally ornamented teleoconch also distinguishes from *Streptacis*. *Donaldina heshanensis* and *Donaldina eleganta* described by PAN & ERWIN (2002) from the Late Permian of China belong to *Royalella*.

Royalella minuta n. sp

(figs. 29 - 43)

Diagnosis: The minute slender shell with 8 whorls measures about 2 mm in height. The axis of coiling the protoconch forms an angle of about 50° with the columella of the teleoconch. The whorls have a flattened inclined upper shoulder of the teleoconch, are wider than high, and are ornamented by three sharp lirae of which only two remain visible on the spire. The protoconch is sinistral and planispirally coiled with transition to the teleoconch sharply marked.

Derivatio nominis and locus typicus: Minutus in Latin means tiny. So this is the tiny one of the two small species of *Royalella* described here. *Royalella minuta* comes from East Mount Shale and from Salesville Formation, Missourian Series, Pennsylvanian, Mineral Wells, Texas, USA, collected by Royal MAPES.

Holotype: The individual illustrated in fig. 39 represents the holotype.

Description: The shell is very slender with apical angle about or less than 20°. There are about 10 whorls of the teleoconch which compose the slender shell with very regular and slow increase in whorl diameter. The protoconch consists of 1,5 smooth whorls with a diameter of about 0,2 mm. The change from protoconch to teleoconch is indicated by change in direction of coiling, as well as onset of the ornament consisting of three spiral ribs of which one lies on the rounded base and is covered by the following whorl. The whorls of the teleoconch are flattened in their upper portion with the second rib forming the periphery that lies low on the whorl. The base is rounded, and the aperture is simple, about as wide as high.

Differences: See *R. streptaciformis.*

Royalella streptaciformis n. sp.

(figs. 44 - 48)

Diagnosis: The very slender teleoconch with rounded whorls and four spiral ribs visible on the whorls of the spire has a sinistrally coiled almost planispiral protoconch with coiling axis forming an angle of about 45° with the columella of the teleoconch. The protoconch appears almost detached from the teleoconch..

Derivatio nominis and locus typicus: This *Royalella* with its detached protoconch and slender minute shell resembles *Streptacis*. The shells were collected by Royal MAPES from East Mount Shale, Desmoinesian Series (Westfal), Pennsylvanian, Mineral Wells, Texas, USA

Holotype: The specimen illustrated in fig. 45 represents the holotype.

Description: The slender shell consists of more than 10 whorls with a height of about 2 mm and an apical angle of less than 20°. The protoconch consists of almost 1,5 whorls and is well detached from the teleoconch forming a large angle with it. The initial whorl is distinctly sinistrally coiled, and transition from planispiral to dextral coiling occurs at the contact between protoconch and teleoconch which is also marked by an apertural rim. The teleoconch whorls are rounded, wider than high and have a slow increase in diameter. Of the five spiral ribs that ornament each whorl the basal one becomes covered by the succeeding whorl. Spiral ribs may be low or more strongly expressed and are separated from each other by broad interspaces. Growth lines indicate that the outer lip of the aperture has an apical sinus. The aperture otherwise is simple with almost straight columellar lip and equal width and height.

Differences: *Royalella streptaciformis* closely resembles *R. minuta* regarding general shell shape and the almost detached position of their protoconch on the top of the teleoconch. They differ from each other in case of *R. minuta* having flattened whorl flanks and fewer more pronounced spiral ribs than *R. streptaciformis* with rounded whorls and four to five less pronounced spiral ribs. *Donaldina eleganta* PAN & ERWIN, 2002 closely resembles *Royalella streptaciformis* but has smooth early whorls of the teleoconch. *Donaldina heshanensis* PAN & ERWIN, 2002 has more pronounced spiral ribs. Both of these species from the Late Permian of China described by PAN & ERWIN (2002, Fig.15, 6-8 and Fig.17, 3-10) represent members of the new genus *Royalella*.

Genus *Texasella* n. gen.

Diagnosis: The slender dextral conical teleoconch is at first spirally ribbed and convex and later becomes smooth and has flattened sides. The sinistral protoconch is smooth, almost planispirally coiled and its axis of coiling deviates from the axis of coiling of the teleoconch. Shells are small, fully grown about 3 mm high consisting of about 12 whorls. The genus is based on *Texasella biformata* from Salesville Formation, Missourian Series, Pennsylvanian, of Mineral Wells in Texas, USA.

Derivatio nominis: This small shell comes from the Carboniferous of Texas and is named accordingly.

Differences: The change in ornament of the teleoconch distinguishes *Texasella* from *Donaldina*, and also the strongly deviating protoconch of the first differs from that of the second.

Texasella biformata n. sp.

(figs. 49 - 55)

Diagnosis: As for the genus.

Derivatio nominis: The shell has two types of ornament, spiral in the early whorls of the teleoconch and smooth flattened whorls later on. Latin for two shapes-"biformatus"

Locus typicus: *Texasella biformata* is from Salesville Formation of Mineral Wells in Texas, USA, collected by Royal MAPES.

Holotype: The individual illustrated in fig.52 represents the holotype.

Description: The axis of coiling of the protoconch forms an angle of about 60° with the columellar axis of the teleoconch. The protoconch measures a little more than 0,2 mm in diameter, consists of almost 1,5 smooth, rounded whorls in almost planispiral but distinctly sinistral coiling, and its end with a thickened margin. With onset of the teleoconch dextral coiling begins. The first five whorls of the teleoconch are ornamented by two strong spiral ribs and their sides are rounded. On later whorls the ribs disappear, and sides become more weakly convex. The aperture is about as wide as high with rounded outer lip, almost straight inner and columellar lip, and a little flattened base. A shell with 11 whorls of the teleoconch measures about 3 mm in height. Juvenile shells belonging here are from Ames Shale, near Morgantown, Ohio.

Differences: *Royalella heshanensis* (PAN & ERWIN, 2002) from the Permian of China regarding its protoconch and first teleoconch whorls closely resemble *Texasella* and differs by having three instead of two spiral ribs and by not changing the whorls of the teleoconch in shape during growth of later whorls (PAN & ERWIN,2002, Fig.17,3-10).

Genus *Yoospira* n. gen.

Diagnosis: The shell regarding protoconch and teleoconchs shape is like that of a slender *Donaldina* but has a spiral lination as ornament of the teleoconch like *Neodonaldina*. The spirally ribbed teleoconch is of turritelliform shape with rounded whorls. The flatly coiled smooth protoconch with distinctly sinistral first whorl changes into the dextral coil within its last portion. Its axis of coiling deviates only little from that of the teleoconch. The genotype is *Donaldina minutissima* YOO, 1994 from the Tournaisian (Early Carboniferous) of near Gundy in New South Wales, Australia.

Derivatio nominis: A small spiral shell that is named in honour of E.K. YOO from Sydney, Australia.

Differences: In contrast to *Donaldina* the ornament of the post-juvenile teleoconch whorls of *Yoospira* covers the whole side of each well rounded whorl. There is no smooth apical shoulder. The change from sinistral to dextral coiling occurs within the protoconch right next to the onset of the teleoconch. *Yoospira minutissima* (YOO, 1994) described by YOO (1994, Pl. 21, figs.1-6) differs from *Donaldina filosa* YOO, 1988 mainly by having a more strongly deviating protoconch and by having spiral ribs all over the whorl sides (YOO, 1994, Pl.22, figs.12-14). The Triassic *Neodonaldina* has a similar protoconch change in coiling directions but, in addition, a larval projection of the outer lip. The protoconch of *Yoospira*, in contrast, ends with straight apertural margin. *Pseudoaclisina* YOO, 1994 from the Early Carboniferous of Australia has a very similar teleoconch but differs by having a simple and smooth lowly coiled dextral protoconch. The same appears to be the case in *Palaeoalvania* YOO, 1994 where the protoconch also appears to be not clearly sinistral (YOO 1994 Pl.20, figs.11,12). ,

Yoospira knighti n. sp.

(figs. 56 - 59)

Diagnosis: The teleoconch with rounded whorls in a turriform shell is ornamented by spiral lirae that are acute and evenly distributed. Five of these lirae are present on the first teleoconch whorl and they increase in number in succeeding whorls. The protoconch is smooth and consists of rounded whorls of which the first is sinistral and within the final portion of the second whorl the coiling changes into dextral.

Derivatio nominis and locus typicus: Named for J. Brooks KNIGHT who so ably described many of the gastropods from the Carboniferous of the USA. The type is from Labette Shale, Desmoinesian Series (Westfalian), Pennsylvanian, near Saint Louis, Missouri, USA.

Holotype: The individual illustrated in fig. 58 represents the holotype.

Description: The high-spired shell has distinctly convex whorl profile. Its sutures are impressed and whorls are rounded. The base is rounded and not umbilicate. Teleoconch ornamentation consists of 5 to 6 fine spiral threads that are more or less evenly spaced and crossed by sinuous growth lines. More such spiral lirae may sometimes be intercalated. The protoconch is smooth, consists of 1,5 whorls, and has a diameter of about 0.25 mm. The initial whorl is distinctly sinistrally coiled and within the second whorl the whorl becomes planispiral and turns into dextral direction. The begin of the teleoconch is clearly indicated by the onset of the spiral ribs of the teleoconch and protoconch margin is simple and smooth. A shell with 9 whorls of the teleoconch may be up to 4 mm high. Its apical angle is about 20° and whorl growth is isometric. The same or a very similar species is from Cambridge Shale Missourian Series (Stephan), Pennsylvanian, near New Concord, Guernsey County, Ohio, USA, collected by Royal MAPES.

Differences: *Yoospira knighti* differs from *Donaldina stevensana* that occurs in the same fauna by having more rounded whorls more spiral lirae as ornament and a lower apical angle of about 20° instead of about 25°. *Yoospira minutissima* from the Early Carboniferous of eastern Australia (YOO, 1994, Pl. 21, figs.1-6) has a small shell with more than 10 whorls an measures only 2.6 mm in height. *Y. minutissima* is more slender and a little smaller than *Y. knighti*. *Yoospira minutissima* resembles the Triassic representatives of the family Neodonaldinidae BANDEL, 1996 which have a ”tofanellid” protoconch with a strong larval hook at the transition to the teleoconch.

Yoospira acuta n. sp.

(figs. 63 - 65)

Diagnosis: The high whorls form a slender acicular shell that with 9 whorls is about 2 mm high and forms a spiral angle of about 10°. Spiral ribs are well developed and 5 of them are present on each whorl of the teleoconch.

Derivatio nominis and locus typicus: This *Yoospira* is slender, pointed in shape (acuta). It comes from Salesville Formation of the Pennsylvanian of Mineral Wells in Texas (MAPES, coll.). The holotype is the figured speciemen (fig. 63).

Description: The acicular shell as in the diagnosis is provided with a smooth protococh that is onyl preserved in fragments. But its umbilicus lies on top of the columella of the teleococh, so that it is sinistrally coiled and measures about 0,18 mm in diameter. Whorls of the teleococh are as wide as high and the aperture is simple and rounded.

Differences: Among the three species of *Yoospira* here described *Y. acatua* is the most slender one and has the most prominent spiral ribs.

Yoospira morgantownensis n. sp.

(figs. 60 - 62)

Diagnosis: The rounded whorls with acute spiral ribs n the juvenile shell with 5 whorls form a spiral angle of about 30°. The protoconch lies flat on the teleoconch and both coiled around the same axis.

Derivatio nominis and locus typicus: This *Yoospira* is from near Mogantown, Ohio and is named accordingly. It comes from the Ames Shale, Early Virgilian Series, Pennsylvanian of Ohio (MAPES coll.). The illustrated specmen is the holotype.

Description: The protoconch lies flatly on top of the teleoconch. Its first whorl is a little inclined with relatively strong sinistral twist. It ends after almost 1,5 whorls and 0,22 mm in diameter. A marginal thickening as well as succeeding spiral ornament of the first whorl of the teleoconch clearly documents its end. Whorls of the teleoconch are rounded and wider than high.

Differences: *Yoospira morgantownensis* is the least pointed one of the species of *Yoospira* described here. Its ornament is more distinctly developed than is the case in *Yoospira knighti.*

Genus *Heteroaclisina* n. gen.

Diagnosis: Like *Yoospira* in shell ornament and protoconch but the teleoconch has turbiniform shape and is relatively short with a more rapid increase in whorl diameter. With 6 whorls the shell is about 2 mm high and half as wide. The genotype is *Heteroaclisina putnamensis* n. sp from Putnam Hill, Ohio State, USA.

Derivatio nominis: The name is a combination of heterostrophic (Hetero-) and teleoconch shape as in *Aclisina*, which probably represents a caenogastropod (BANDEL, 2002).

Remarks: The genus *Aclisina* KONINCK, 1881 has a *Littorina* – like shell shape with the whorl side ornamented by spiral threads. According to KNIGHT et al. (1960, fig.191,4) the outer lip of *Aclisina* has a slit, which is not really present but may represent a more or less well developed subsutural sinus.

Differences: *Pseudoaclisina* is more slender than *Heteroaclisiona* and *Palaeoalvania* more hydrobiform, but all three are rather similar regarding the spiral ornament of the teleoconch. In contrast to *Heteroaclisina* both *Pseudoaclisina* and *Palaeoalvania* as well as *Aclisina* have a dextral protoconch and do not represent members of the Heterostropha (BANDEL, 2002).

Heteroaclisina putnamensis n. sp.

(figs. 66 - 72)

Diagnosis: As for the genus.

Derivatio nominis and locus typicus: This *Heteroaclisina* comes from the Putnam Hill Shale and is named accordingly. It place of origin is Keller Mine, of Desmoinesian Series, Pennsylvanian, Ohio, USA, collected by Royal MAPES.

Holotype: The individual illustrated in fig. 71 represents the holotype.

Description: Spiral lirae feature the well rounded whorls and the rounded base that has a narrow open umbilicus. The protoconch lies on top of the littoriniform teleoconch and coils sinistrally around the axis that is oriented like the columella. The smooth protoconch with it whorls rounded and almost planispirally coiled measures almost 0,2 mm in diameter. Teleoconch whorls are ornamented by up to 15 fine spiral lirae with flat interspaces between them and about 6 of these remain visible on the whorls of the spire, while the others become covered by the succeeding whorl. The aperture is rounded with simple thin outer lip, and its orientation is almost vertical. The shell consists of about 6 whorls, is about 2 mm high, and 1 mm wide. Specimen were studied from the Putnam Hill Formation of Keller Mine in Ohio, from Cambridge Limestone from near New Concord in Ohio, and from Ames Shale, Morgantown, Pennsylvanian, Ohio (all MAPES coll.).

Differences: Members of the Valvatoidea are usually smooth, but may have similar shell shape (BANDEL & HEIDELBERGER, 2002). Among the Donaldinidae *Heteroaclisina* is the genus with the relatively shortest shell and fewest whorls.

Carboniferous species that resemble Donaldinidae but probably do not represent allogastropods (Heterostropha)

The genera *Aclisina, Kimina, Palaeoalvania, Palaeoaclisina, Sinistriconcha* which were placed with the heterostrophic groups probably do not belong to the Heterostropha. The genus *Kimina* YOO, 1994 with smooth small shell of a *Hydrobia*- like shape and a flat protoconch was considered by YOO (1994) to represent a member of the Heterogastropoda (a taxon that included some Allogastropoda and Ctenoglossa) with deviated protoconch. *Kimina* is based on *K. globosa* YOO, 1994 from the Late Tournaisian of eastern Australia (YOO, 1994, Pl.20, figs.1-7). Its protoconch is not sinistral and not really deviating. YOO (1994) suggested a relation with the recent *Rissoella*, but the time gap between these small species from the Early Carboniferous to recent *Rissoella* is very large, thus there remains quite some doubt about the suggested relation. The other species *K. australis* YOO, 1994, and *K. minor* YOO, 1994 are very similar but have slightly different shape of the teleoconch (YOO, 1994, Pl.17, figs.1-5, Pl.19, figs.1-7). FRÝDA & BANDEL (1997, Pl.1, fig.4-6) have since described very similar shells from the Early Devonian of Bohemia as *Kimina yooi* including them among the morphogroup *Eucochlis* of the Trochomorpha NAEF, 1911 that includes Paleozoic gastropods with shell shapes indicating a possible relation to the Trochoidea (see BANDEL & GELDMACHER, 1996).

Similarily the genus *Palaeoalvania* YOO, 1994 based on *Aclisina talenti* YOO, 1994 from the Early Carboniferous of Australia with hydrobiform small (2 mm) shell with many whorls which are ornamented by spiral cords has a smooth protoconch that is not really deviated as had been suggested by YOO (1994, Pl.20, figs.8-13). BANDEL et al. (2002) suggested to place a species with rounded base, ornament consisting of 4 spiral lirae, and protoconch of one smooth planispiral whorl in this genus. Here the protoconch is demarcated from the teleoconch by a faint suture and measures 0.21 mm to 0.22 mm in diameter. It remains to be shown by more complete specimen whether this Late Carboniferous species from the USA is really related to the Early Carboniferous *Palaeoalvania* and to which group of gastropods they may belong.

Pseudoaclisina YOO, 1994 based on *Aclisina turgida* had been suggested by YOO (1988) to represent a murchisoniid but YOO (1994) changed his view and suggested that it represents a member of the Heterogastropoda instead. Since YOO (1994) presented no reason for his transformation from *Aclisina* to *Pseudoaclisina*, the later genus could be regarded as invalid. *Pseudoaclisina turgida* has no heterostrophic protoconch (YOO, 1994, Pl.21, fig.11), and is a small shell with the spire having rounded whorls and deeply incised sutures. The protoconch consists of only one smooth whorl. Another species from the same locality, *Pseudaclisina microspirulata,* has a slender, pupiform shell with high spire and ornament of many fine spiral ribs the teleoconch while the protoconch consists of 1,5 lowly coiled whorls with no clear sinistral coiling mode apparent from the illustrations. Both species are from the Tournaisian of eastern Australia (YOO (1994, Pl. 21, Figs. 7-10). In a juvenile shell that resembles *Pseudoaclisina microspirulata* but comes from the Late Carboniferous of Oklahoma, USA the base is rounded and not umbilicate and the aperture is rounded as well. It was

suggested to represent a *Pseudoaclisina* sp. by BANDEL et al. (2002, Pl.14, figs.138-140) since is has a protoconch that could be interpreted as heterostrophic but formed during a lecithotrophic ontogeny. A more likely place for the Late Carboniferous species from Oklahoma would be the genus *Donaldina* and here a relation with *Donaldina stevensana*.

Family Heterosubulitidae n. fam.

Diagnosis: The fusiform shell is small and has an aperture that is anteriorly widened and a protoconch with sinistral initial whorl. The transition from protoconch to teleoconch is indistinct. The family is based on the genus *Heterosubulites*.

Genus *Heterosubulites* n. gen.

Diagnosis: The small fusiform shell has a small spire and a large body whorl with flaring apertural margin. The smooth protoconch has a sinistral initial whorl and coiling changes into dextral within the second whorl. Transition from protoconch to teleoconch is indistinct. The aperture is anteriorly widened. The genotype is *Ceraunocochlis blatta* KNIGHT, 1931 from the Henrietta Shale, Late Carboniferous, Missouri, USA (KNIGHT 1931, Pl.21, fig. 2a-d).

Derivatio nominis and locus typicus: The species *Ceraunocochlis blatta* had been interpreted to represent a subulitid gastropod by KNIGHT (1931), and it is here shown to have a sinistral protoconch. The genus name is thus a combination of heterostrophic (Hetero-) and *Subulites* representing the base genus to the subulitids. The locality is from the Labette Shale, Desmoinesian Series (Westfalian), Pennsylvanian, of the Saint Louis outlier, Missouri.

Heterosubulites blatta (KNIGHT, 1931)

(figs. 73 - 77)

Description: The number of whorls is almost four in a 1,7 mm high shell that is about 1,2 mm wide. The spire is short and rounded with flattened top and the body whorl large, lymnaeiform. The aperture is wide and the outer lip flares and ends in front with an almost straight margin forming a wide notched siphon. The inner lip forms a callus on the former shell and in its continuation toward the anterior shell end its columellar portion is twisted up.

The embryonic whorl measures a bit more than 0,12 mm in diameter and twists with its apex below the planispiral second whorl, is thus sinistrally coiled. The protoconch is not differentiated from the teleoconch by growth lines, but this may be due to preservation since protoconch and teleoconch are smooth. The protoconch could consist of 1,7 to 2 whorls and has a diameter of about 0,35 mm. The sinistral first whorl grades into the dextral shell within the second whorl and is clearly dextral after 1,5 whorls are completed.

Superfamily Architectonicoidea GRAY, 1850

Description: The shell consists of a sinistrally coiled almost planispiral protoconch with thickened rim of the rounded aperture is succeeded by a planispiral and discoidal to lowly conical dextral teleoconch. The larval part of the protoconch may be smooth or have collabral ribs, the teleoconch is ornamented by spiral ribs or smooth, rarely also with axial elements. The superfamily has as central taxon the modern Architectonicidae, but includes also the Triassic Stuoraxidae.

Remarks: Architectonicidae and Mathildidae have been noted to be quite distinct from each other by the Triassic (BANDEL 1988, 1991a, 1995). Their continuation in the fossil record is documented in the Jurassic (GRÜNDEL, 1976, 1997a,1998; SCHRÖDER ,1995; BANDEL et al., 2000). The anatomy of the Mathildidae and Architectonicidae is similar to each other when compared to other groups of Allogastropoda as was noted by HASZPRUNAR (1985,1988). Protoconchs of architectonicids that lived during the Triassic usually remained in a size range around and below 0,3 mm and they increased in size range to up to around 0,5 mm with the Cretaceous (SOHL, 1964; DOCKERY, 1993 ; KIEL & BANDEL,

2001). A protoconch resembling that of the architectonicids from the Late Carboniferous of Western Germany was described by HERHOLZ (1990,1992). It measures about 0,3 mm across and consists of about two whorls (figs. 78, 79), which are very similar to those documented by PAN & ERWIN in their *"Straparollus minutus"*.

Family Stuoraxidae BANDEL, 1996

Description: The teleoconch is minute (up to 1 mm), has rounded whorls and is almost planispirally coiled. The protoconch is of the planktotrophic type as is found commonly among members of the architectonicids (ref. see BANDEL et al., 1997). The embryonic shell as well as the early larval shell are sinistrally coiled, and in the larval shell coiling becomes planispiral before the point of transition into the teleoconch is reached. The larval shell is ornamented by collabral folds. A characteristic genus is *Stuoraxis* with genotype from the Late Triassic of the Italian Alps.

Genus *Stuoraxis* BANDEL, 1996

Description: The small shell (about 1 mm) consists of rounded whorls that overlap only slightly onto each other forming a shallow dextral coil with a wide umbilicus. Ornament of the teleoconch consists only of fine growth lines. The aperture is almost round, of simple outline and vertically oriented. The protoconch with about two whorls is of lowly conical shape and measures about 0,3 mm in diameter. The sinistral embryonic whorl of about 0,1 mm in diameter is succeeded by the larval shell that twists into the planispiral coil within the second whorl. The larval portion of the protoconch is ornamented by transversal folds and its apertural rim is thickened. The genus is based on *Stuoraxis lehmanni* BANDEL, 1996 from the Stuores Alm above St. Cassian, Late Triassic, Dolomites, Italy (BANDEL, 1996, Figs. 12a,b,c,d, Figs.13e,f,g,h).

Differences: Among the heterostrophic species of the St. Cassian Formation *Stuoraxis* and *Alexogyra* BANDEL, 1996 are the only almost planispiral species with round whorl diameter and without sculpture of the teleoconch whorls. They are distinguished from each other by the axial ornament of the protoconch in *Stuoraxis* that is not present in *Alexogyra*. Smooth planispiral shells are also noted in the archaeogastopod *Triadoskenea ampezzana* BANDEL 1993 from the St. Cassian Formation, but here the protoconch has the characteristics of an archaeogastropod (BANDEL, 1993, Pl.4, fig.5-7), consisting of less than one whorl with the characteristic lateral folds. From the mid Jurassic of northern Germany and Poland GRÜNDEL (1998, Pl.4, figs.47-51) described *Stuoraxis parvula* GRÜNDEL, 1998 with the characteristic protoconch but only about 1,5 whorls and with the apertural varix. It resembles *Stuoraxis lehmanni* and differs by having an ornamented embryonic whorl and slightly tighter coiling of the teleoconch.

Stuoraxis panhuazhangi n. sp.

Description: According to PAN & ERWIN (2002, Fig.10.6-11) the shell consists of more than three whorls of which the first two represent the protoconch. The smooth embryonic whorl is sinistrally coiled and the larval shell is ornamented by fine collabral threads in the first half of its whorl, while its later part is smooth ending with an apertural rim. The protoconch measures about 0,35 mm in diameter. The teleoconch whorls are rounded in shape and smooth with plane apical and basal sides. With about 1,3 teleoconch whorls it measures about 1 mm in width but are only about 0,3 mm high. The location of occurrence according to PAN & ERWIN (2002) is from Late Permian Heshan Formation of near the city of Heshan, Guangxi Province in South China.

Derivatio nominis: This species was described by PAN & ERWIN (2002) as *Straparollus minutus* which represents a species name that had already been utilized for another quite different gastropod by KONINCK (1842-1851, 1883) from the Viséan of Belgium. Aside from the preoccupied species name the genus *Straparollus* MONTFORT, 1810 belongs to the Euomphaloidea which were documented to be characterized by quite different protoconchs (YOO, 1988, BANDEL & FRÝDA, 1998) with large initial whorls that are uncoiled in their begin. The Chinese Late Permian "*Straparollus minutus*"

with typical architectonicoid protoconch, thus, needs another name, which is suggested here to honour the discovery of a beautifully preserved Permian gastropod fauna by PAN HUA-ZHANG, (Nanjing).

Remarks: PAN & ERWIN (2002) erroneously described the teleoconch of their *Straparollus minutus* as "surface of mature shell ornamented with prominent collabral costae separated by wide and depressed interspaces …" since the individuals illustrated by them (Fig.10, 6-11) are quite smooth in the portion of the shell that is part of the teleoconch. A protoconch of very similar ornament and shape as that present in *Stuoraxis panhuazhangi* had been illustrated and described by HERHOLZ (1992, Figs.1,2) from the Late Carboniferous (Westfal) of the Ruhr Area in Germany, (figured here in figs.78, 79).

Superfamily Valvatoidea GRAY, 1840

Description: The shell is trochiform to discoidal, variously ornamented with a heterostrophic protoconch with sinistral coiling around the same axis as the dextral teleoconch. The aperture is simple. Included are the fresh water Valvatidae GRAY, 1840 and their fossil counterpart the Provalvatidae BANDEL, 1991, as well as the marine Cornirostridae PONDER, 1990.

Remarks: From the Carboniferous and Permian species with valvatiform shells that have a recognizable sinistral protoconch have not been described up to date. BANDEL & HEIDELBERGER (2002) included the Mid-Devonian *Palaeocarboninia jankei* BANDEL & HEIDELBERGER, 2002 in the Valvatoidea. *Palaeocarboninia* has a sinistral protoconch that consists of embryonic and larval shell and is coiled along the same axis as the dextral teleoconch as is the case in the living *Cornirostra* PONDER 1990 from the shallow sea of Australia. *Palaeocarboninia* BANDEL & HEIDELBERGER (2001) with valvatiform, smooth teleoconch of 1 mm in height and 0,9 mm in width, that is dextrally coiled along the same axis as the sinistrally coiled smooth protoconch of 0,2 mm in diameter. The protoconch consists of an embryonic and a larval shell forming about 1,5 whorls. The diameter of the first protoconch whorls is less than 0,1 mm. The 4,5 convexly rounded smooth whorls are sculptured only by indistinct growth lines. The aperture is only slightly wider than high with evenly rounded outer lip.

The shell is very similar to *Carboninia* BANDEL, 1996 from the Triassic St. Cassian Formation and has only a less elevated spire and a deeper impressed embryonic whorl. *Bandellina* SCHRÖDER, 1995 from the Cretaceous of Poland has a much more depressed shell.

Palaeocarboninia is from the Givetian, late Mid Devonian of the Eifel in Germany. Still a bit older is *Kuskokwimia moorei* FRÝDA & BLODGETT, 2001 from the Emsian (late Early Devonian) of west-central Alaska. Here the sinistral protoconch is very small and embedded in the rounded apex of the shell that resembles more that of *Strobeus* as known from the Early and Late Carboniferous of the USA (HARPER, 1977; BANDEL, 2002) than *Cornirostra* or *Valvata*. The sinistral protoconch is here only about 0,1 mm wide.

Comparison with some minute sinistral species with an unknown affiliation

Small shells with sinistral trochiform shape with rounded whorls and small protoconch are, for example, found in the genus *Sinistriconcha* HEIDELBERGER & BANDEL, 1999. According to HEIDELBERGER & BANDEL (1999, Figs.44-46) the conical shell is sinistrally coiled with simple protoconch, smooth rounded whorls and vertical aperture. The genotype is *Sinistriconcha lierli* HEIDELBERGER & BANDEL, 1999 from the middle Devonian of Sötenich (Eifel), Germany. It consists of 4,5 whorls, measures almost 1 mm in height and 0,85 mm in width. The protoconch is simple and rounded and the first whorl measures about 0,1 mm in diameter.

Sinistriconcha minutissima (YOO, 1988)

Description: According to YOO (1988, 1994) the species differs from *Onychochilus physa* LINDSTRÖM, 1884 (the type to the genus *Onychochilus*) in being much smaller in size and in lacking ornamentation. The shell is minute (about 0,8 mm high and 0, 55 mm wide) sinistral, pupiform with 4 smooth convex whorls. The protoconch is rounded and smooth and the first whorl measures about

0,15 mm across (YOO, 1988, fig.14). The base is rounded and there is an open umbilicus (YOO, 1988, figs,12,13). The aperture is rounded with simple straight outer lip and with weak inclination in regard to the axis of coiling. *S. minutissima* lived in the Early Carboniferous of New South Wales, Australia.

Differences: The Early Carboniferous *Sinistriconcha minutissima* differs from the Mid Devonian *S. lierli* by having a more rounded pupoid shape. Because of its small size BANDEL (1997) suggested that is may represent a larval shell, but the Devonian species of *Sinistriconcha* can not be interpreted that way (HEIDELBERGER & BANDEL, 1999). These small gastropods most probably represent small sized species with benthic life and of still quite unresolved relation to other gastropods. The shells of species of the Onychochilidae and Clisospirinae usually have a strongly inclined apertural plane, a large conical protoconch of about 0,5 mm in diameter and, commonly, collabral ribs as ornament of the teleoconch. *Sinistriconcha* has an almost vertical apertural plane, a small rounded protoconch and smooth teleoconch.

Remarks: The order Mimospirina DZIK, 1983 with genera like *Mimospira* KOKEN & PERNER, 1925 (KNIGHT, 1941, Pl.91, fig.1), *Onychochilus* LINDSTRÖM 1884 (KNIGHT, 1941, Pl.90, fig.3) and *Clisospira* BILLINGS, 1865 (KNIGHT, 1941, Pl.91, fig.2) consists of turbiniform species with collabral ornament indicating a strongly oblique aperture, and in case with well described shell they all have a rather large protoconch measuring about 0,5 mm (WÄNGBERG-ERIKSSON, 1979, DZIK, 1983, BANDEL, 1997; FRÝDA, 1989, 1992, 1999, FRÝDA & ROHR, 1999). In KNIGHT et al. (1960) the Onychochilidae KOKEN, 1925 and the Clisospiridae MILLER, 1889 were treated as separate units. In this regard they followed WENZ (1938) who differentiated the Clisospiridae with *Clisospira* and *Mimospira* with conical shell and strongly inclined apertural plane, from the Onychochilinae with the genus *Onychochilus* with more rounded whorls. While the former was considered as a questionable member of the Trochonematoidea ZITTEL 1895, the later was interpreted to represent a sinistral group of the Subulitoidea. KNIGHT et al. (1960) preferred to arrange differently with *Onychochilus* as member of the Macluritoidea FISCHER, 1885 and *Mimospira* and *Clisospira* representing doubtful archaeogastropods. DZIK (1983) connected those sinistral forms which KNIGHT (1941) had collected in his plates 90 and 91 within the taxon Mimospirina, united by a smooth large conical protoconch. LINSLEY & KIER (1984) excluded these sinistral fossils from the Gastropoda, creating the taxon Paragastropoda.

About Streptacidae and Donaldinidae and their possible modern counterparts

The following Carboniferous and Permian genera can be recognized to belong to the Heterostropha:

Family Streptacidae;

Streptacis with smooth shell and deviating protoconch,

Mapesella with sinuous growth lines on teleoconch and flat protoconch with same coiling axis,

Laxella with smooth uncoiled shell.

Family Donaldinidae;

Donaldina slender shell with apical ramp and spiral ornament, protoconch more or less flat onapex,

Royalella small shell like *Donaldina* with protoconch lifted from the top,

Texasella early teleoconch like *Donaldina* or *Royaella* and later whorls flattened and smooth,

Yoospira high spire without apical ramp and with spiral ornament on rounded whorls,

Heteroaclisina turbiniform shell without apical ramp.

Family Heterosubulitidae;

Heterosubulites with fusiform smooth shell and flaring aperture.

Family Stuoraxidae;

Stuoraxis with smooth planispiral shell.

Streptacidae can be interpreted to continue in the Ebalidae. This later family Ebalidae BANDEL, 1994 (=Ebalidae WARÉN, 1994) consists of species with sinistral protoconch and transition into the dextral teleoconch at contact between protoconch and teleoconch. The family is based on the genus *Ebala* LEACH ,1847 with the modern genotype *Ebala nitidissima* (MONTAGU) that lives in the Mediterranean Sea and the Northern Atlantic Ocean (FRETTER et al., 1986, figs.439,440). Within the Pyramidellidae there are similar species but they are usually larger in size and bear more sculpture.

According to WARÉN (1994) Ebalidae also differ from the Pyramidellidae by having a complicated jaw apparatus. The genus *Ebala* contains species with small (1-3 mm), slender, cone shaped shell with about 8 whorls that have a convex profile and deep marked oblique sutures. The protoconch of *E. nitidissima* consists of two nearly planorboid whorls. *Ebala*'s head bears two triangular tentacles which are heavily ciliated. There are two eyes and anterior to the tentacle lies a short mentum. *E. nitidissima* lives in 5-50 m depth. Its spawn was described by THORSON (1946). It consist of a mass of 5-8 0.1 mm large eggs in a gelatinous mass, from which veligers hatch after about 6 days with a 0,12 mm large shell.

Ebala differs from *Streptacis* by having relatively higher whorls of the teleoconch while the protoconch is similar and also almost planispiral changing into the dextral teleoconch with strong twist of the axis of coiling. Also protoconch dimension and shape are quite similar. The Triassic *Ebala cassiana* BANDEL, 1996 is very similar in size and shape as is also the Jurassic *Ebala liassica* SCHRÖDER, 1995 (SCHRÖDER, 1995, Pl.10, figs.18-21) from the Early Jurassic of northern Germany, and the Late Cretaceous *Ebala* sp. from Jordan (BANDEL et al., 1999).

The Ebalidae as well as the Streptacidae differ from the Triassic Cassianebalidae BANDEL, 1996 based on *Cassianebala speciensis* BANDEL, 1996 from the St. Cassian Formation, Late Triassic of the Italian Alps by having no folds on their larval shell and by a more elongated aperture of the teleoconch that ends in a narrow posterior end. Cassianebalidae have a similar teleoconch which may have many whorls that are ornamented with growth lines that reflect a slightly sinuous outline of the apertural lip, and fine spiral lirae. Here the sinistral almost flatly coiled protoconch is wider than the first whorl of the teleoconch and is ornamented by radiating ribs.

The genus *Loxebala* BANDEL, 1996 has a teleoconch like that of *Cassianebala* but its protoconch coils sinistrally around the same axis as the dextral teleoconch. In its genotype *Loxebala vallandroensis* BANDEL, 1996 from the St. Cassian Formation the transition from protoconch to teleoconch is connected to a pattern of axial folds on the larval shell (BANDEL, 1996, Figs. 2a,b,c,d). In the way in which the protoconch is connected to the teleoconchs the Cassianebalidae resemble those species of the Streptacidae of the genus *Streptacis* which have the coiling axis of the protoconch forming a high angle with the teleoconch, while it lies flatly on the top of the teleoconch in *Loxebala* as well as in *Mapesella*.

Streptacidae and Ebalidae may belong to one monophyletic line of descendents of Allogastropoda that lived in the Early Carboniferous sea and are still living in Recent Oceans. They would, thus, have survivd for about 350 Million years, comparable to the Ctenoglossa, as was documented by NÜTZEL (1998). But in the later case many more species

are involved with a much greater variety of shapes than is noted in the *Streptacis-Ebala* relation. The Streptacidae of the Carboniferous closely resemble the Donaldinidae and there appear to be transitions between them, while from the Triassic on members of both families are quite distinct from each other, as far as we can say, with the rather limited knowledge of the species belonging to this group of usually minute Heterostropha up to now.

With exception of the Heterosubulitdae the other genera of Heterostropha discussed above can be recognized also in relatedspeces or genera from the Triassic St Cassian Formation of the Italian Alps (BANDEL 1994b, 1995, 1996). In case of the Donaldinidae, for example, *Donaldina zardinii* BANDEL, 1996 has a sinistral protoconch with about 0,25 mm in diameter that deviates with its axis of coiling from that of the teleoconch. Ornament of the teleoconch consists of small subsutural ramp with one spiral lira and at least 3 spiral ribs on the flanks. Whorl profile is rounded below and flattened above (BANDEL, 1996, Fig.4). Also the members of the family Neodonaldidae based on *Neodonaldina* BANDEL, 1996 consists of species with small, slender and high-spired shell that has rounded whorls sculptured with spiral costae. Here the protoconch consists of a sinistral embryonic and larval shell coiling around the same axis as the teleoconch (BANDEL, 1996 Figs. 5a-d, fig. 6a-g). The larval shell measures 0.2 mm in height and width but in contrast to that of the Donaldinidae has a hook-like basal projection on its aperture.

Representatives of the Donaldinidae with characteristic shell shape and size may very well still be living in the shallow water of the tropical Indo-Pacific and can well be differentiated from the much more modern Pyramidellidae (BANDEL, 1991b). KOLLMANN & YOCHELSON (1976) expressed doubt about the place of the *Streptacis* relation within the Pyramidellidae, since this later group can not be found in most of the Mesozoic faunas. This has been confirmed (BANDEL 1994b; SCHRÖDER 1995; GRÜNDEL 1997a,b,1998). Modern species that look very similar to the Carboniferous *Donaldina* are found in the genus *Murchisonella* MÖRCH, 1875 with its genotype *Murchisonia* (*Murchisonella*) *spectrum* MÖRCH, 1875 that lives in the Caribbean Sea. Shells of similar species were found near Cebu in the Philippines (BANDEL, 1991a; fig.7a,b) and collected from shallow coral reefs at Lizard Island in the great Barrier reef of Australia.

BANDEL (1996) noted a characteristic mantle edge in *Murchisonella* from the Barrier reef in Australia. *Murchisonella* has two prominent ciliated pallial tentacles that are stretched out from the margin of the mantle using the sinus that lies below the suture in the outer lip of the aperture of the shell. The cilia of the frontal pallial tentacle are continuous with a ciliated band present in the pallial cavity that extends to is apical end at about three quarters of the body whorl. The head is also of characteristic shape with small simple eyes close to each other in the back and triangular flattened tentacles extending to the sides covered by cilia. Between the tentacles two ciliated lobes cover the mouth which opens in the center below them and they search about when the animal is active aided by sense cilia on their frontal end. Also the propodium is densely ciliated. Motion of the foot is continuous and rapid while the shell is dragged behind and periodically pulled forward in short jerks by contraction off the retractor muscle. The foot carries a large transparent operculum that is able to seal the aperture tightly. This organization of the head and the mantle edge is quite different from that seen in pyramidellids in general and also those that were collected from the same location of the shallow sea near Lizard Island and studied alongside.

The basic design of the protoconch of many modern Heterostropha (=Heterobranchia) has not changed since the Late Paleozoic. If one compares the larval shells from the Red Sea illustrated by BANDEL et al. (1997, Pl.24, fig. f-k) with those of the Late Paleozoic

Streptacidoidea and Stuoraxidae their similarity to each other is evident. Even when the comparison between Permian and Triassic Heterostropha shows strong differences, these are not due to extinction, but due to the new appearance of quite a number of new groups.

When the groups known from the Triassic are characterized, the following Allogastropoda can be recognized. Besides Streptacidoidea the new high spired Mathildoidea DALL, 1889 with Mathildidae DALL, 1889, Anoptychiidae BANDEL, 1994, Tofanellidae BANDEL, 1994, Trachoecidae BANDEL, 1994 and Ampezzanildidae Bandel, 1994 have developed and differentiated see also ZARDINI, 1978, 1980, 1985). GRÜNDEL (1997a, 1998) was able to recognize most of these also from Jurassic faunas, as had been suggested in the study of SCHRÖDER (1995) in part. BANDEL, GRÜNDEL & MAXWELL (2000) found many of these also from the Jurassic of New Zealand, and current studies indicate their presence in the mid-Jurassic of Madagascar as well.

The lowly coiled Architectonicoidea GRAY, 1850 are richly diverse in the Triassic and most of the forms recognized there can also be traced into the Jurassic GRÜNDEL (1998). Some representatives of the Architectonicidae GRAY, 1850, Cassianaxidae BANDEL, 1996, Amphitomariidae BANDEL, 1996, Stuoraxidae BANDEL, 1996, Hyalogyrinidae WARÉN & BOUCHET, 1993, Xylodisculidae WARÉN, 1992, Anomalorbidae BANDEL, 1991, Omalogyridae G.O. SARS, 1878 and Glacidorbidae PONDER, 1986 have been recognized. The amazing record of *Stuoraxis* from the Permian of China confirms the, at that time somewhat insecure, obervation of HERHOLZ (1990, 1992) who had recognized a larval shell as found among architectonicids in the Westphalian (Late Carboniferous) of Western Germany.

Among the marine Valvatoidea GRAY, 1840 of the family Cornirostridae PONDER, 1990 new records have been made among modern species from the Caribbean Sea (BIELER et al., 1998) so that this group can now be traced in the sea as well as with the Provalvatidae BANDEL, 1991 and Valvatidae GRAY, 1840 in fresh water. GRÜNDEL (1997) noted a Jurassic species for Triassic *Carboninia* BANDEL, 1996 and *Bandelina* SCHRÖDER, 1995. With the oldest representative in the Devonian this group still needs a record between that time and the Triassic. Ignorance of this group is probably due to the simplicity of shell shape and minuteness of its species. Since most representatives are only about 2 mm in size or even smaller.

The Opisthobranchia appear first with the Cylindrobullinidae WENZ, 1947 as was noted by (KOKEN, 1889) and they have no Paleozoic counterparts as can also be extracted from the study of NÜTZEL et al. (2000). What has been considered to represent Carboniferous opisthobranchs (KOLLMANN & YOCHELSON, 1976) are non heterostrophic gastropods with amazing convergent shell shape (see BANDEL, 2002). The very rapid spreading of species of the genera like *Actaeonina* was documented from the Triassic (see BANDEL, 1994b) and their transformation into different cephalaspidean opisthobranchs occurred during the Jurassic (see SCHRÖDER, 1995 and GRÜNDEL, 1997b).

Pulmonata can not be recognized in the Triassic with any certainty while basommatophoran pulmonates appear well recognizable in the Jurassic, and stylommatophoran ones in the transition from Jurassic to Cretaceous (BANDEL, 1997). KIEL & BANDEL (2001) recognized the oldest safe ellobiid archaeopulmonate only from the Campanian (Late Cretaceous) of Spain. It was suggested that the Ellobiidae H. & A. ADAMS 1855 could be represented by the Misurinellidae based on *Misurinella* BANDEL, 1994 from the Late Triassic since it closely resembles modern *Blauneria* SHUTTELWORTH, 1874 in shell shape (HARBECK, 1996) but the Late Cretaceous *Haszprunariella* KIEL & BANDEL, 2001 appears closer and probably represents a member of the Allogastropoda.

So what happened after the Permian Triassic transition regarding the Heterostropha among the gastropods?

PAN & ERWIN (2002) discussed the so called extinction pattern during the late Permian and especially the transition to the Triassic. They suggested that extinction became concentrated in the final million years of the Permian. But was there really extinction? When the fauna of the Early Carboniferous to the end of Permian is taken as a whole it looks as if there was a steady evolution of species within pretty much the same groups in the two large families the Streptacidae and Donaldinidae, and others were rare belonging to groups that can be related to the Architectonicoidea and Valvatoidea. Members of the two families of the Streptacidoidea still appear to be present in the Late Triassic. So nothing can be stated regarding extinction that could not be explained by the rather large time gap between the Late Permian South- Chinese fauna and the Late Triassic North Italian fauna. But quite obviously a lot of different Heterostropha on top of the Streptacidoidea had evolved since (see BANDEL, 1994, 1996), among them quite credible early Opisthobranchs, as had already been noted by LAUBE (1868), KITTL (1894) and KOKEN (1889). So when it comes to the question, extinction or faunal revolution, in case of the Heterostropha among the gastropods the second option appears to be the more realistic one.

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