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Advances in Conodont, Devonian and Carboniferous Research*

# Larval Shells and Shell Microstructures of exceptionally well-preserved Late Carboniferous Gastropods from the Buckhorn Asphalt Deposit (Oklahoma, USA)

With 8 Text-figures and 14 Plates

KLAUS BANDEL, ALEXANDER NÜTZEL & THOMAS E. YANCEY

## Abstracts

Gastropods from the mid-Pennsylvanian Buckhorn Asphalt Quarry in Oklahoma (U.S.A.) are very well preserved. Commonly, protoconchs and original shell microstructure are present and unaltered. Two pleurotomarioid gastropod species of the genera *Salterospira* and *Paragoniozona* are preserved with the early ontogenetic shell and with a nacreous shell structure. Two other nacreous archaeogastropods with a rotelliform shell lack a selenizone and are closely related to the Anomphalidae. They are tentatively assigned to the genus *Anomphalus*. A fifth tiny archaeogastropod lacks nacre and has exclusively crossed lamellar shell microstructure. It represents the oldest known archaeogastropod that lacks nacre. *Microdoma conicum* represents the trochomorph archaeogastropods; it has an inner nacreous layer, a crossed acicular layer, and an outermost thin calcitic layer. The protoconch of *Microdoma* is typical for archaeogastropods. The construction of the shell indicates that most archaeogastropods from Buckhorn Asphalt deposit have a nacreous inner layer, but one type has a crossed lamellar microstructure, like the modern Phasianellinae and Fissurelloidea, indicating the antiquity of this structural type within the Vetigastropoda (Archaeogastropoda). The Neritimorpha are present with the two neritopsid genera *Naticopsis* and *Trachydomia*. *Naticopsis* has a thick inner crossed lamellar layer and a thin prismatic outer calcitic layer. The families Goniasmidae, Orthonemidae, Pseudozygopleuridae, and Meekospiridae represent the Caenogastropoda. All reported species of these families have a crossed lamellar shell structure and a caenogastropod-type protoconch. There is now clear evidence that the Goniasmidae are Caenogastropoda, though they have a selenizone, a feature that is almost unknown in modern caenogastropods. Only a few modern caenogastropods have slit-like structures in their shell, e.g. the heteropod *Atlanta* and the worm snail *Siliquaria*. Both are distantly related to the slit-bearing Goniasmidae and it is unlikely that the slit is homologous in these groups. The fact that these ancient caenogastropods had a slit in the outer lip is most important for the reconstruction of the phylogeny of the Gastropoda. The Goniasmidae are present with the genera *Goniasma* (one species), *Stegocoelia* (three species), and *Cerithioides* (one species). The Orthonemidae are represented by the genera *Orthonema* and *Palaeostylus*. The genus *Orthonema* is present with a dextral species and the sinistral species *O. sinistrorsa*. Species of *Orthonema* have the same type of a heliciform larval shell that is present in the Goniasmidae. Therefore, the two families are probably closely related. *Palaeostylus* is present with a newly described species, *Palaeostylus batteni* n. sp. The Pseudozygopleuridae are present with a single species, *Pseudozygopleura peoriense*. The common species *Girtyspira minuta* belongs to the family Meekospiridae. The teleoconch has a faint spiral striation and a polished surface The protoconch/teleoconch transition indicates that its protoconch is paucispiral and ends with a faint, straight prosocline thread. The Heterostropha are present with the order Allogastropoda represented by two species of the genera *Donaldina* and *Pseudaclisina*, of which *Pseudoaclisina* is reported from North America for the first time.

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The exceptional preservation increases the number of shell characters considerably (protoconch, shell microstructure, micro-ornaments), even for seemingly well established taxa. The knowledge of these features greatly improves the systematics of several major groups of Late Palaeozoic gastropods and represents an important source of information for future phylogenetic analyses.

Keywords: Mollusca, Gastropoda, Carboniferous, USA, Buckhorn Asphalt, Shell Structure, Nacre, Crossed Lammelae, Protoconch, Larval Shell, Systematics, Phylogeny

## Kurzfassung

[Larven-Gehäuse und Gehäuse-Mikrostrukturen von außergewöhnlich gut erhaltenen unterkarbonischen Gastropoden vom Buckhorn-Asphaltlager (Oklahoma, USA).] — Die Gastropoden des Buckhorn-Asphalts (Mittel-Pennsylvanian, Oklahoma, U.S.A.) sind außerordentlich gut erhalten. Protoconche und originale Schalen-Mikrostrukturen sind häufig noch vorhanden. Die beiden pleurotomarioiden Gattungen *Salterospira* und *Paragoniozona* werden durch jeweils eine Art vertreten, deren Protoconche erhalten sind und deren Schalenstruktur als Perlmutter vorliegt. Zwei weitere Archaeogastropoden mit Perlmutter stehen der Familie Anomphalidae nahe. Sie sind von rotelliformer Gestalt und tragen kein Schlitzband. Beide Arten werden unter Vorbehalt der Gattung *Anomphalus* zugeordnet. Einem weiteren Vertreter der Archaeogastropoda fehlt Perlmutter; stattdessen ist die Schale durch Kreuzlamellen-Struktur charakterisiert. Dies ist der älteste bekannte Archaeogastropode, dessen Schale nicht perlmutterig ist. Die Schale von *Microdoma conicum*, einem trochomorphen Archaeogastropoden, besteht aus einer inneren Permutter-Schicht, gefolgt von einer gekreuzt nadeligen Schicht und einer dünnen äußeren Kalzitschicht. Der Protoconch von *Microdoma* ist typisch für die Archaeogastropoden. Der Schalenaufbau zeigt, dass die meisten Archaeogastropoden des Buckhorn-Asphalts eine innere Schalenschicht aus Perlmutter besitzen. Lediglich eine Art weist Kreuzlamellen-Mikrostruktur auf, wie es auch bei den modernen Phasianellinae and Fissurelloidea der Fall ist. Dies zeigt, dass dieser Mikrostrukturtyp innerhalb der Vetigastropoda (Archaeogastropoda) alt ist. Die Neritimorpha sind mit den zwei neritopsiden Gattungen *Naticopsis* und *Trachydomia* vertreten. *Naticopsis* besitzt eine dicke innere Schalenschicht aus aragonitischer Kreuzlamelle und eine äußere dünne, prismatische Kalzitschicht. Die Familien Goniasmidae, Orthonemidae, Pseudozygopleuridae und Meekospiridae repräsentieren die Caenogastropoda. Die Schalen aller untersuchten Arten der Caenogastropoda weisen Kreuzlamelle als Mikrostrukturtyp und Caenogastropoden-typische Protoconche auf. Es gibt nun klare Hinweise, dass die Goniasmidae Caenogastropoden sind, obwohl sie ein Schlitzband tragen, ein Merkmal, dass von modernen Gastropoden so gut wie unbekannt ist. Nur wenige moderne Caenogastropoden zeigen schlitzartige Strukturen, z. B. der Heteropode *Atlanta* und die Wurmschnecke *Siliquaria*. Beide sind nicht nahe mit den Schlitz tragenden Goniasmidae verwandt, und es ist unwahrscheinlich, dass der Schlitz in diesen Gruppen homolog ist. Die Tatsache, dass diese altertümlichen Caenogastropoden einen Schlitz haben, ist für die Rekonstruktion der Stammesgeschichte der Gastropoda von größter Bedeutung. Die Goniasmidae kommen mit den Gattungen *Goniasma* (eine Art), *Stegocoelia* (drei Arten) und *Cerithioides* (eine Art) vor. Die Orthonemidae werden von den Gattungen *Orthonema* and *Palaeostylus* vertreten. Die Gattung *Orthonema* umfasst eine dextrale Art und eine sinistrale Art. Arten der Gattung *Orthonema* und der Familie Goniasmidae teilen eine gleichartige, heliciforme Larvalschale als Merkmal. Daher sind Orthonemidae und Goniasmidae vermutlich nahe verwandt. Die Gattung *Palaeostylus* ist mit der neuen Art, *Palaeostylus batteni* n. sp., vorhanden. Die Pseudozygopleuridae werden durch eine einzige Art, *Pseudozygopleura peoriense* vertreten. Die verbreitete Art *Girtyspira minuta* gehört der Familie Meekospiridae an. Ihr Teleoconch zeigt feine Spiralstreifung und eine polierte Schalenoberfläche. Der Übergang vom Protoconch zum Teleoconch zeigt, dass ihr Protoconch paucispiral ist und an einer feinen, gerade prosoclinen Naht endet. Die Heterostropha werden durch die Ordnung Allogastropoda vertreten, und zwar mit zwei Arten der Gattungen *Donaldina* und *Pseudaclisina*, von denen *Pseudoaclisina* erstmals aus Nordamerika nachgewiesen wird.

Die ungewöhnlich gute Erhaltung der Gastropoden des Buckhorn-Asphalts erhöht die Anzahl bekannter Schalenmerkmale erheblich (Protoconch, Schalen Mikrostruktur, Mikro-Ornamente), und zwar auch für scheinbar wohl bekannte Taxa. Die Kenntnis dieser Merkmale verbessert die systematischer Zuordnung etlicher Großgruppen spätpaläozoischer Gastropoden und stellt eine wichtige Quelle für zukünftige phylogenetische Analysen dar.

Schlüsselwörter: Mollusca, Gastropoda, Karbon, USA, Buckhorn-Asphalt, Schalenstruktur, Perlmutter, Kreuzlamelle, Protoconche, Larvalschalen, Systematik, Phylogenie.

## Introduction

Sediments exposed in the Buckhorn Asphalt Quarry have produced some of the best-preserved gastropods known in Palaeozoic strata. Shells preserve original aragonitic mineralogy and shell microstructures as well as detailed shell micro-ornaments and even sometimes colour patterns. This provides additional data that can contribute to the understanding of phylogenetic relationships among familiar taxa. The main purpose of this study is thus not so much the tabulation and description of species of the Buckhorn gastropod fauna, but the documentation of shell characters that have been found in this unique material.

The described gastropod fauna is moderately diverse. Species identification and in some cases even generic assignments are uncertain because the exceptionally well-preserved, commonly minute specimens must be compared to taxa that are based on large and recrystallized specimens typical of Palaeozoic gastropods. In many specimens from the Buckhorn Asphalt deposit, only the early whorls are preserved and characters of the aperture, particularly those of the fully grown shell cannot be determined. In many cases, shells with characteristic micro-ornament, distinctive protoconch and shell microstructure cannot be compared with species described in the literature, because those features are normally not preserved. A close comparison is thus not possible in several cases. These difficulties concern mostly the alpha-taxonomy. However, the gastropod fauna of the Buckhorn Asphalt deposit is highly informative because it contains practically unaltered Palaeozoic shells that can be studied in such unusual detail that they can be compared to much younger and Recent forms.

The fauna studied herein is of mid Desmoinesian (Carboniferous) age. Desmoinesian gastropod faunas of the United States are comparatively well known and can be regarded as well studied compared to other time intervals. The Buckhorn gastropods are coeval with the fauna of the St. Louis Outlier that was described by KNIGHT (1930-1934). Gastropod faunas of the same age or close to it have been studied by various authors, e.g. HOARE (1980), HOARE & STURGEON (1978-1985), ANDERSON et al. (1985, 1990), HOARE et al. (1997), KUES & BATTEN (2001), and KUES (2002).

The biota of the Buckhorn Asphalt deposit of southern Oklahoma contains shells that are mineralogically and geochemically unaltered, preserving the condition at the time of death of the organisms. Shell material accumulating on the seafloor shortly after death of the organisms was sealed in oil which turned into asphalt, keeping the skeletal remains isolated from pore fluids and protecting them from diagenetic alteration. According to SQUIRES (1973, 1976), migration of this oil-asphalt material occurred during the Pennsylvanian. Partly mineralized skeletal material such as ligaments on bivalves is preserved for many species (YANCEY & HEANEY 2000). Even the organic matrix of shells such as sheaths around crystallites can be found (HEANEY & YANCEY 1993). The exceptional preservation of Buckhorn shell material allows accurate documentation of the protoconch, shell ontogeny, growth lines, minute shell ornamentation, and shell microstructure normally obscured in Palaeozoic fossils. It provides unaltered shell for documentation of major and minor element chemistry (CRICK & OTTENSMAN 1983) and stable isotope geochemistry (BRAND 1987; HEWITT et al. 1989). The non-cephalopod fauna contains a dominance of small shells, preserving shell down to sub-millimeter size range (the smallest described is a larval bivalve shell of 0.18 mm maximum dimension). Some of these are juveniles or larval shells of common Desmoinesian taxa, but many represent taxa that have not been previously described.

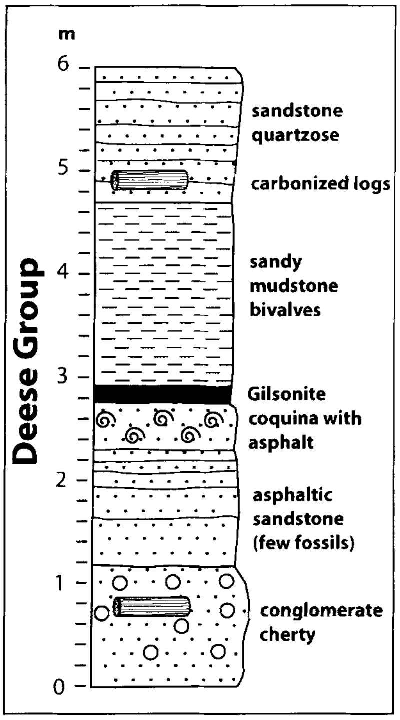

Text-fig. 1. Location of the Buckhorn Asphalt Quarry.

## Location, age, methods, repository

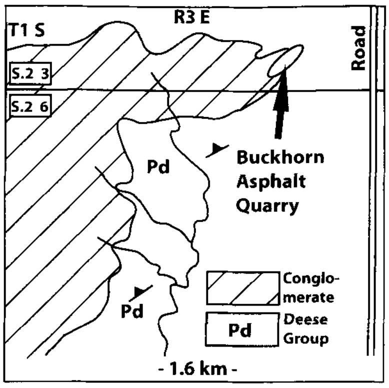
The material studied is from asphalt-impregnated sediments of the Boggy Formation within the Buckhorn Asphalt Quarry south of Sulphur, Murray County, Oklahoma (SE 1/4, sec. 23,-- T. 1S., R. 3E., Indian Baseline and Meridian) (Text-fig. 1, 2B). The Boggy Formation, of Late Carboniferous Desmoinesian Stage, is part of the Deese Group. The fauna studied herein is of mid Desmoinesian age which is equivalent with the Late Moscovian and the Westphalian C/D stage of Western Europe. Several hundred gastropods, most of them very small and fragile, were obtained from a sediment sample of about 10 cm maximum diameter. This sample was taken in June 1989 by Dr ETHAN GROSSMAN (Texas A & M University) and Mr ORSON MII (Taiwan Normal University). The sample contained numerous molluscs, especially cephalopod shell debris, bivalves, and gastropods. With several hundred specimens, gastropods are the most numerous group in this assemblage. The shells were obtained by dissolving the asphalt matrix with carbon tetrachloride in a Soxhlet-hydrocarbon extraction apparatus. The residue was sieved and picked. Well-preserved specimens studied here were mounted on stubs and examined with scanning electron microscopes. The illustrated and some additional specimens are housed in the Naturmuseum Senckenberg, Frankfurt am Main in Germany (SMF).

## Biotic assemblage and palaeoenvironment

A comprehensive and unequivocal interpretation of the palaeoenvironment of the Buckhorn Asphalt deposit is still lacking. Regional analysis by HEWITT et al. (1989) show that the Buckhorn area lay adjacent to structural highs on the Ardmore block, but near deep basinal waters of the Anadarko Basin and the deep oceanic basin between North America and Gondwana.



A



B

Text-fig. 2. – A. Generalized section and Geological situation of the deposits from the Buckhorn Asphalt Quarry. – B. Tectonic framework of the deposit within a fault zone near the Ouachita collision zone. Location of the Buckhorn Asphalt Quarry in contact with conglomerates of the Deese Group.

The sediments in the Buckhorn quarry are heterogeneous and comprise conglomerates, shales, and coquinas with abundant cephalopods (Text-fig. 2B). The Buckhorn Asphalt biota is preserved in mixed terrigenous and calcareous sediment. Based upon the presence of plant remains and scour channels in some of the beds exposed at the Buckhorn Quarry site, SQUIRES (1973) suggested that the asphalt-impregnated sediments were deposited in a near shore marine environment under moderately turbulent conditions. CRICK & OTTENSMAN (1983) postulated a depositional setting below fair-weather wave base, in a depositional environment characterized by episodic disturbances. The occurrence of abundant shell fragments, common wood fragments, some bitumen clasts and common mudstone clasts in shell-bearing sediments suggests significant transport before deposition. Shallow water organisms like large, probably herbivorous naticopsid snails were seemingly transported into deeper water environments. Many gastropods and bivalves in the Buckhorn Asphalt deposit have outer shell surfaces scarred with microborings characteristic of the upper photic zone microboring assemblage of BUDD & PERKINS (1980); tiny tubules penetrating the shell, similar to borings produced by cyanobacteria. These provide an indication of the environment in which the animals lived before transport and deposition. Probably most of the gastropods described herein were shallow water organisms. Finally, the sediments of the Buckhorn Asphalt deposit accumulated in moderately deep water conditions adjacent to a small land mass near deep marine waters of an open ocean basin. The cephalopod-rich coquinas may represent more or less autochthonous material.

Part of the Buckhorn biota consists of a biotic assemblage infrequently preserved in Palaeozoic strata - an assemblage characterized by the occurrence of common orthocone cephalopods and 'edentulous' bivalves. Assemblages that are similarly rich in cephalopods and such bivalves are known in the Silurian and Devonian cephalopod limestones of Bohemia and at many other sites along the margins of the Proto-Tethys Sea (KRÍZ 1979), in the Late Devonian Naples fauna of New York described by CLARKE (1904) and in the Early Carboniferous Culm facies of Europe (AMLER 1998). However, these deposits differ from the Buckhorn Asphalt deposit in other respects.

## Gastropod Systematics

The higher systematics of the Gastropoda has been the object of far reaching changes during the last fifteen years. HASZRPUNAR (1988), PONDER & WARÉN (1988), and PONDER & LINDBERG (1997) modified the traditional classification of THIELE (1929-1935), WENZ (1938-44), WENZ & ZILCH (1959-1960), and KNIGHT et al. (1960a, b). Most of these changes are based on new data on the anatomy of gastropods and the application of the principles of phylogenetic systematics. However, the gastropod treatises of WENZ (1938-44), WENZ & ZILCH (1959-1960), and KNIGHT et al. (1960 a, b) are still the last attempts to cover all gastropod genera. From the palaeontological point-of-view, it is reasonable to recognize four subclasses of the class Gastropoda: Archaeogastropoda (including Vetigastropoda and Docoglossa), Neritimorpha, Caenogastropoda and Heterostropha. This system reflects evidence not only from anatomical features but can also be inferred from shell morphology, especially from protoconch morphology. It is thus applicable for palaeontology if preservation is sufficient and it takes the fossil record into consideration, which is largely ignored by neontologists. According to BANDEL (1982), the Archaeogastropoda have a protoconch of less than one whorl that is never planktotrophic. This protoconch shows a particular deformation pattern because, unlike all other gastropods, it first forms an unmineralized bilaterally symmetrical cap that is subsequently spirally deformed, and finally mineralized. All other gastropods grow spirally from the beginning. The Neritimorpha can have planktotrophic larval development and may produce a characteristic involute larval shell (ROBERTSON 1971; BANDEL 1982). Even the Caenogastropoda can have planktotrophic larval development but if so, they produce orthostrophic larval shells with several well defined whorls that commonly have elaborate ornaments. Even non-planktotrophic caenogastropods have always more than one protoconch whorl. The Heterostropha have a sinistral protoconch and a dextral teleoconch i.e., a reversal of coiling during ontogeny. In some Heterostropha this reversal takes place within the larval stage and thus within the protoconch (BANDEL 1995). A few Heterostropha have a dextral protoconch and a sinistral teleoconch.

While all these protoconch types occur in Recent gastropods, a fifth type of gastropod protoconch is restricted to several Palaeozoic gastropod groups. It is characterised by an openly coiled initial whorl (e.g. DZIK 1994; FRÝDA & BANDEL 1997; FRÝDA & MANDA 1997; BANDEL & FRÝDA 1998; NÜT-

ZEL 1998; NÜTZEL et al. 2000; NÜTZEL & MAPES 2001). But this type is not present in the gastropod material studied here.

## Systematic descriptions

### Subclass Archaeogastropoda THIELE 1925

The archaeogastropod protoconch consists only of the embryonic shell and has no larval shell (BANDEL 1982). The protoconch usually consists of less than one whorl that has become mineralized after it had been deformed (see above). Thus, protoconch characters are highly diagnostic for this subclass of the Gastropoda (BANDEL 1982, 1991a, 1993a).
Nacreous shell structure among the Gastropoda is found exclusively amongst archaeogastropods of the order Vetigastropoda (BØGGILD 1930; BANDEL 1990). Of the six archaeogastropod species present in the Buckhorn Asphalt deposit, five have a nacreous shell. One of the five has a shell composed of crossed lamellar microstructure, similar to the microstructure of the Docoglossa (= Patellogastropoda), some slit-bearing Vetigastropoda (Scissurelloidea and Fissurelloidea), and the trochomorphs Phasianellinae and Skeneidae (HICKMAN & MCLEAN 1990; BANDEL & GELDMACHER 1996).

### Order Vetigastropoda SALVINI-PLAWEN 1980
### Superfamily Pleurotomarioidea SWAINSON 1840

### Genus *Salterospira* BATTEN 1966

Type species: *Salterospira tabulata* BATTEN 1966, Early Carboniferous, England.

### *Salterospira*? sp.

Pl. 1 figs 1-8

Description: The shell is turbiniform with a flatly coiled apex of about two whorls and a depressed first whorl. It is small; the largest investigated specimen consists of 3.2 whorls with 0.9 mm height and 1.1 mm width. The aperture is not preserved but growth lines indicate that it was circular and simple. The whorls are almost circular in transverse section and approximately as high as wide (up to 0.4 mm). Sutures are impressed and the base is distinctly phaneromphalous. A slit becomes distinct after the second whorl, producing a selenizone located a short distance below the upper suture. The first 1.0 – 1.5 teleoconch whorls are smooth, with the exception of nearly orthocline growth lines. Numerous (up to 15) revolving threads start gradually after second whorl. On the third teleoconch whorl numerous distinct axial threads appear that may become angulated at revolving threads.

The protoconch consists of 0.8 smooth whorls (archaeogastropod-type). It is clearly demarcated from the teleoconch by a collabral impression that has a projecting labrum in the middle of the whorl. The protoconch measures 0.18 mm in width and the first whorl is 0.21 mm wide. It lies in an apical plane formed by the first two whorls.

The shell is composed of aragonite with an inner nacreous layer and an outer layer of dissected crossed-acicular structure or intersected-crossed platy structure. In addition, there seems to be a thin outermost layer without clear structure.

Remarks: Protoconch features, nacreous shell and selenizone place this species in the order Vetigastropoda (Archaeogastropoda). Notable features are the phaneromphalous base, spiral teleoconch ribbing, the undulating growth line pattern, and the selenizone located just below the upper suture. The generic assignment of this species is not certain. The depressed, planispiral form of the juvenile resembles the juvenile whorls of the two Early Carboniferous species of *Salterospira* from England which were reported by BATTEN (1966). However, the mature teleoconch whorls of BATTEN's species have an almost vertical whorl face while the whorls of the present specimens are round and convex. Moreover, the selenizone of BATTEN's species lies low on the whorl while the present specimens have it near the upper suture.

Material: Eight specimens, SMF XII/10-3500 (Pl. 1 figs 1, 4, 5, 8), SMF XII/10-3501 (Pl. 1 figs 2, 3, 6, 7), six specimens SMF XII/10-3502.

### Genus *Paragoniozona* NELSON 1947

Type species: *Paragoniozona nodolirata* NELSON 1947, Early Pennsylvanian, Vinton Canyon, Franklin Mountains, Texas, U.S.A.

### *Paragoniozona nodolirata* NELSON 1947

Pl. 1 figs 9-10, Pl. 2 figs 11-16

Description: The small subturbinate shells that were studied here represent apices of a larger pleurotomarioid species. The largest studied specimen comprises 3.5 whorls and is approximately 1.4 mm high and wide. The whorls are convex, almost circular in transverse section with impressed sutures. The base on the early whorls is narrowly phaneromphalous. The body whorl is ornamented with up to eight distinct revolving cords. The growth lines are weakly prosocyrt to prosocline in the early teleoconch whorls. In later whorls, growth lines have a distinct sinus slightly above the periphery. Growth lines may become angulated when meeting with the revolving cords.

The protoconch is orthostrophic, of archaeogastropod-type and consists of about 0.8 whorls that appear to be smooth, but if well preserved, exhibit a very fine meshwork ornament. Protoconch diameter is 0.26 mm - 0.27 mm; the diameter of the first whorl, 0.30 mm to 0.31 mm, is rather large. The transition to the teleoconch is indistinct and the apical portion well rounded.

The shell is aragonitic, with an outer dissected crossed-acicular layer, a thick inner nacreous layer, and an innermost glaze.

Remarks: Although the apical specimens illustrated here resemble mature specimens of genera like *Shansiella* or *Rhabdotocochlis*, they belong to *Paragoniozona nodolirata* because we have compared our material with larger individuals of this species. In *Paragoniozona nodolirata*, the placement of the selenizone near the lower suture as well as the rounded edge of the base develop only in later whorls.

Material: Three specimens, SMF XII/10-3503 - SMF XII/10-3505.

## Order Trochomorpha NAEF 1911

According to BANDEL & GELDMACHER (1996), Trochomorpha holds all extant species of the Trochoidea as defined by HICKMAN & MCLEAN (1990) and the fossil species of Archaeogastropoda without slit and selenizone.

## Family Anomphalidae WENZ 1938

### Genus *Anomphalus* MEEK & WORTHEN 1867

Type species: *Anomphalus rotulus* MEEK & WORTHEN 1867 from the Middle Pennsylvanian, U. S. A.

Remarks: Two rotelliform, small, umbilicated archaeogastropods without slit are present in our material. KNIGHT et al. (1960a) noted that despite its name, *Anomphalus* contains a wide variety of umbilical characters, from heavily cryptomphalous to phaneromphalous, and that the Anomphalidae are probably nacreous. The species described here, clearly have a thick inner nacreous layer and confirm the deduction of a nacreouslayer being present. Both species that we assign to *Anomphalus* have a fine striation of spiral asymmetric ridges. Fine striation has not been reported from *Anomphalus* or from any other anomphalid. However, it is likely that very fine ornament is destroyed by recrystallization and therefore could have been present in specimens from other formations but was not preserved.

### *Anomphalus* sp. 1

Pl. 2 figs 17-20, Pl. 3 fig. 21

Description: The shell is rotelliform and small. The largest specimen consists of 3.5 whorls and is 0.9 mm high and 1.4 mm wide. The whorls are flatly convex and oval in outline. The sutures are flat. The base is narrowly phaneromphalous. The aperture is fractured but according to growth line pattern it was simple with a straight outer lip. The ornament of the teleoconch whorls consists of numerous fine spiral asymmetric ridges, which are frequently displaced at junctions with the prosocline growth lines. The spiral ornament starts almost immediately after the protoconch.

The protoconch consists of less than one whorl and is of archaeogastropod-type; it is smooth and has a diameter of 0.15 mm, the first whorl measures 0.18 mm to 0.19 mm.

The shell is aragonitic, with a thin outer layer of intersected crossed-platy structure, underlain by a prismatic layer, a dissected crossed-acicular layer and a thick inner nacreous layer, which is covered by a prismatic inner glaze.

Remarks: The present species belongs to the Vetigastropoda and within them to a group with aragonitic shell and nacreous microstructure. In living archaeogastropods with similar shell structure, the inner glaze forms quite a way behind the aperture, demonstrating that one of the studied fossil specimens represents the apex of a larger shell. Thus, the generic assignment of this species is treated with some caution. It seems that the shell was not slit-bearing. The rotelliform shell shape indicates that this species is related to *Anomphalus*. On the other hand, there are species in which the slit starts to develop on the third teleoconch whorl or even later. The slit of *Borestus costatus* YOO 1988 from the Early Carboniferous of Australia starts on the third teleoconch whorl. In the Triassic nacreous species *Lancedellia costata* (ZARDINI 1978), the slit appears after the fifth whorl (BANDEL 1991a).

Material: Two specimens, SMF XII/10-3506 - SMF XII/10-3507.

### *Anomphalus* sp. 2

Pl. 3 figs 22-28

Description: The low-spired, nearly rotelliform shell is known from two specimens only; the larger specimen consists of 3.2 whorls. It is 0.8 mm high and 1.1 mm wide. The whorls are flatly convex and of oval outline. The sutures are flat. The base is phaneromphalous. The aperture is fractured. The growth lines are prosocline and curve strongly backward at the suture. Therefore, the upper part of the outer lip projects strongly. The ornament of the teleoconch whorls consists of numerous fine asymmetric ridges that start gradually after the second whorl.

The protoconch consists of less than one whorl and is of archaeogastropod-type; it is smooth and has a diameter of 0.15 mm; the first whorl measures 0.18 mm to 0.19 mm.

The shell is aragonitic and has a microstructure similar to *Anomphalus* sp. 1. It has a thin outer layer of intersected crossed-platy structure, underlain by a dissected crossed-acicular layer and a thick inner nacreous layer that is covered by a prismatic inner glaze. As in *Anomphalus* sp. 1, the inner glaze has formed quite a way behind the aperture.

Remarks: The present specimens could represent a small species or apices of larger shells. The spiral asymmetric ridges on this species start much later and the spire is more protruding than in *Anomphalus* sp. 1. The most remarkable feature of the present species is the strongly backward curving growth lines that have a sharp deflection at the periphery, which is in the attachment line of the subsequent whorl, exactly at the suture. Therefore, the deflection is covered by the following whorl. As a result, this structure is only visible on the last whorl. There is a corresponding projecting upper portion of the outer lip. This growth line pattern is not present in *Anomphalus* sp. 1. The archaeogastropod species described next has the same growth line pattern, but it does not have a nacreous shell microstructure, and it is more high-spired.

Material: Two specimens, SMF XII/10-3508 - SMF XII/10-3509.

## Family uncertain

### Trochomorph archaeogastropod with crossed lamellar structure

Pl. 4 figs 29-38, Pl. 5 fig. 39

Description: The shell is small and of turbiniform shape; the largest studied specimen consists of 4.2 whorls, is 1.4 mm high and 1.3 mm wide. The whorls are convex and almost circular in transverse section. The aperture is simple and almost circular. The base is narrowly phaneromphalous. Some shells are smooth except for growth lines and spiral furrows on the base. However, other specimens have numerous fine spiral grooves on the whorl face of the teleoconch whorls. The growth lines are strongly deflected at about the whorl periphery. The base of the final whorl shows several spiral grooves and a shallow sinus.

The protoconch is of archaeogastropod-type and consists of 0.8 whorls with a smooth surface. It has a diameter of 0.14 mm to 0.16 mm; the first whorl measures 0.16 mm to 0.18 mm. The composition of the shell is exclusively aragonitic and it has crossed-lamellar microstructure.

Remarks: This tiny archaeogastropod resembles the nacreous *Anomphalus* sp. 2 described above in size, smooth shell surface with fine spiral ornamentation and a pronounced peripheral deflection of the outer lip. But the present shell is obviously not nacreous and it is more high-spired. Furthermore, the spiral ornament of *Anomphalus* sp. 2 starts almost immediately after the protoconch, in contrast to the present non-nacreous species where it is restricted to late teleoconch whorls. The illustrated specimens show breakage and shell repair. Some specimens have mature apertures indicating that they represent fully grown individuals of a small species.

This archaeogastropod is distinguished from other small turbiniform archaeogastropods by its non-nacreous shell, which is unusual among trochomorph archaeogastropods (BØGGILD 1930; BANDEL 1990, 1993a). Crossed lamellar structure is characteristic only for the Tricoliinae and Phasianellidae. These two groups have been traditionally placed with the Turbinidae (Trochoidea) due to their calcified operculum (HICKMAN & MCLEAN 1990). But recent observations on their anatomy show deviations from the general trochoidean pattern, placing them apart (HASZPRUNAR pers. comm.). In the phylogenetic analysis of HICKMAN & MCLEAN (1990), the Phasianellinae/Tricoliinae/Gabrieloninae form a derived group within the Turbinidae that is characterized by loss of nacre. Therefore, these authors considered the loss of nacre as a derived state within the trochoids. According to HICKMAN & MCLEAN (1990), Fissurelloidea and Skeneidae have lost nacre independently from the subfamilies mentioned previously. Even the Skeneidae CLARK 1851 contain a diverse, insufficiently known group of usually small to minute archaeogastropods that commonly lack a nacreous shell. The Late Triassic *Triadoskenea* BANDEL 1993 is a planispiral, small, smooth archaeogastropod with a shell exclusively composed of crossed lamellar structure (BANDEL & GELDMACHER 1996). The present tiny archaeogastropod could be a precursor or a close relative of a precursor of modern vetigastropods without nacre, i.e., the Scissurelloidea/Fissurelloidea or the Phasianellidae/Tricoliinae. It is the first known Palaeozoic vetigastropod with crossed lamellar shell structure. This shell structure was considered to be modern within the Vetigastropoda by HICKMAN & MCLEAN (1990). However, the Carboniferous age of this allegedly modern type of shell structure indicates that nacreous and non-nacreous archaeogastropods have belonged to separate evolutionary lines since the Palaeozoic. Therefore, both groups represent an equal level of evolution, as was previously suggested by BANDEL (1977, 1990). Even the Docoglossa (patellogastropods) have a non-nacreous, crossed lamellar shell structure (Bandel & Geldmacher 1996) and are considered to represent a very early evolutionary line of the Gastropoda (Ponder & Lindberg 1997). However, no shell structure of a Palaeozoic docoglossan gastropod has been reported to date.

Material: Ten specimens, SMF XII/10-3510 - SMF XII/10-3514.

## Family Microdomatidae WENZ 1938

Diagnosis: Shell trochiform, conical, elongated; sutures shallow; base convex, flattened; outer lip more or less straight, prosocline; shell with inner nacreous layer; protoconch of the archaeogastropod type, consisting of less than one whorl.

Remarks: The *Microdoma*-group (*sensu* BANDEL & GELDMACHER 1996) contains nacreous trochomorph genera with similar shells and a comparable shell microstructure. These genera were formerly classified in families distantly related to each other (WENZ 1938; KNIGHT et al. 1960a; SOHL 1987; HICKMAN & MCLEAN 1990). WENZ (1938) and KNIGHT et al. (1960a) placed the Microdomatidae in the superfamily Microdomatoidea, but MCLEAN (1981) and ERWIN (1988b) placed the Microdomatidae in the Trochoidea. BLODGETT & FRÝDA (1999) discussed Devonian members and classification of the *Microdoma*-group and FRÝDA et al. (2001) discussed the oldest (Ordovician) genera of the Microdomatoidea. The following genera can be placed in the *Microdoma*-group:

*Daidia* WILSON 1951 (Ordovician)
*Eopagodea* FRÝDA, ROHR, ROBARDET & MARCO 2001 (Ordov.)
*Pagodea* PERNER 1903 (Devonian)
*Copidocatomus* LINSLEY 1968 (Devonian)
*Petrochus* HORNÝ 1992 (Devonian)
*Dutrochus* BLODGETT 1992 (Devonian)
*Roemeriella* BLODGETT & FRÝDA 1999 (Devonian)
*Decorospira* BLODGETT & JOHNSON 1992 (Middle Devonian)
*Microdoma* MEEK & WORTHEN 1867 (Carboniferous)
*Euconodoma* KUES 1990 (Carboniferous)
*Anematina* KNIGHT 1933 (Carboniferous)
*Eucochlis* KNIGHT 1933 (Carboniferous)
*Glyptospira* CHRONIC 1952 (Permian)
*Pseudoclanculus* COSSMANN 1918 (Triassic)
*Eunemopsis* KITTL 1891 (Triassic)
*Eucycloscala* COSSMANN 1895 (Triassic)
*Ampezzotrochus* BANDEL 1993a (Triassic)
*Chilodontoidea* HUDDLESTON 1896 (Jurassic)
*Wilsoniconcha* WENZ 1939 (Jurassic)
*Planolateralus* SOHL 1960 (Jurassic).
*Chilodonta* ETALON 1862 (predominantly Cretaceous)
*Calliomphalus* COSSMANN 1888 (Cretaceous)

According to BLODGETT & FRÝDA (1999), the Devonian genus *Dongiovannia* HORNÝ 1992 is a junior synonym of *Decoros-*

*pira* BLODGETT & JOHNSON 1992. *Calliotropis* SEGUENZA 1903 or *Euchelus* PHILLIPPI 1847 could be modern representatives of the *Microdoma*-group.

### Genus *Microdoma* MEEK & WORTHEN 1867

Type species: *Microdoma conicum* MEEK & WORTHEN 1867, Pennsylvanian, Illinois, USA.

Diagnosis: Microdomatidae with an ornament on mature teleoconch whorls consisting of axial ribs and spiral cords with nodular intersections; in addition, the teleoconch may be ornamented with fine collabral threads.

Remarks: *Microdoma* from the Carboniferous of North America closely resembles the Triassic genera *Eunemopsis* KITTL 1891, *Pseudoclanculus* COSSMANN 1918, and *Ampezzotrochus* BANDEL 1993a – all are nacreous Archaeogastropoda with a similar shape and ornament (BANDEL 1993a; BANDEL & GELDMACHER 1996). However, *Eunemopsis* and *Pseudoclanculus* differ from *Microdoma* in having a distinct columellar denticle in the aperture. The predominantly Triassic/Jurassic Amberleyidae WENZ 1938 also appear to be closely related to *Microdoma* (NÜTZEL & SENOWBARI-DARYAN 1999). The Devonian-Permian genera *Anematina* KNIGHT 1933a and *Eucochlis* KNIGHT 1933a, *Dutrochus* BLODGETT 1992, *Devonospira* BLODGETT & JOHNSON 1992, and *Glyptospira* CHRONIC 1952 closely resemble *Microdoma*. The shells of the Triassic genus *Eucycloscala* COSSMANN 1895 are more slender. In contrast to other nacreous trochomorphs, the minute Triassic *Sabrinella* BANDEL 1993a has a thickened apertural lip.

### *Microdoma conicum* MEEK & WORTHEN 1867

Pl. 5 figs 40-48, Pl. 6 figs 49-50

Description: The shell is high-spired and of turbiniform shape. The early whorls have convex outlines while later whorls have nearly straight flanks. The sculpture of the teleoconch consists of fine lamellar opisthocline threads and a reticulate sculpture of broad rounded axial ribs and three spirals with nodular intersections. This reticulate sculpture gradually appears after the 3rd to 5th whorl. The axial ribs are not coincident with the fine lamellar threads of the growth increments. Only incomplete specimens were available for the present study. The largest specimen is a teleoconch fragment of six whorls with missing early whorls; it is 4.7 mm high and 2.7 mm wide. According to KNIGHT (1933a), *M. conicum* grows up to 12 whorls and a height of 14.6 mm. Our measurements agree with those of KNIGHT (1933a) and indicate that with the increase of the number of whorls, the ratio height/width increases from 0.9 to 2.8. The shell thus becomes more slender during ontogeny. The protoconch is smooth and consists of 0.7 to 0.8 whorls. It has a diameter of 0.23 mm to 0.25 mm. The first whorl measures 0.25 mm to 0.29 mm.

The shell has a thin outer layer that may appear homogenous, but is probably prismatic. The outer layer is succeeded by an aragonitic dissected crossed acicular layer. The latter is followed by an inner nacreous layer that grades into blocky prismatic inner callus glaze (sensu BANDEL 1979, 1990). With the exception of the outermost thin shell layer that may be calcitic, all other layers closely resemble the aragonitic, nacreous layers as found among modern trochoids, as in *Cittarium pica* L. with external calcitic layer described by ERBEN (1971).

Remarks: *Microdoma conicum*, the type species of *Microdoma*, is a common and well-known species in Carboniferous strata of North America. HOARE et al. (1980) reported a high degree of intraspecific variability for *M. conicum*. KNIGHT et al. (1960a) noted that the Microdomatoidea have an inner nacreous layer. The nacreous shell and protoconch of *M. conicum* are typical archaeogastropod features. If it were a modern species, its shell would place it in the Trochoidea. The Buckhorn specimens confirm the relation to Triassic genera like *Ampezzotrochus* BANDEL 1993a and the modern members of the Eucyclinae sensu HICKMAN & MCLEAN (1990). The thin outer, presumably calcitic layer might be responsible for the comparably good preservation of the *Microdoma* specimens from other Pennsylvanian strata in the USA. It is noteworthy that axial ribs and the collabral threads are not coincident as maintained by KNIGHT (1933a), but diverge at a small angle to the collabral threads and thus they are non-collabral.

Juvenile specimens may lack the typical knobby ornament of mature *Microdoma conicum* specimens. Such juvenile specimens show only the oblique axial threads on the teleoconch whorls. The specimen figured on Pl. 5 fig. 42-44 represents a comparatively large juvenile specimen of this kind. It is not sure whether it represents a juvenile *M. conicum* or a species of a genus like *Eucochlis* KNIGHT 1933. But the whorls of *Eucochlis* increase in diameter much faster and, as a result, its shape is more blunt. The typical nodular teleoconch ornamentation of *Microdoma* appears relatively late, as was mentioned by KNIGHT (1933a, 1941). To illustrate this, a specimen of *M. conicum* from the St. Louis outlier is figured here (Pl. 5 fig. 47-48); this specimen shows clearly the different ontogenetic sculptures. Seemingly, the onset of the typical knobby ornament during ontogeny is even subject to considerable intraspecific variability. The Lower Carboniferous *M. angulata* YOO 1988 from Australia displays a similar pattern; in this species the early teleoconch whorls are sculptured exclusively with axial threads, while the spirals appear somewhat later.

Material: Ten specimens from the Buckhorn Asphalt were studied with the SEM and documented here (SMF XII/10-3515 - SMF XII/10-3522), of which six specimens (SMF XII/10-3518 - SMF XII/10-3520) (Pl. 5 fig. 42-44) are only tentatively considered to be juveniles of *M. conicum*; an additional specimen (Pl. 5., Fig. 47-48) comes from the St. Louis Pennsylvanian outlier (Desmoinesian Labette Shale), collected by J. B. KNIGHT, housed in the Smithsonian Institution, Washington, D. C.

## Subclass Neritimorpha GOLIKOV & STAROBOGATOV 1975

Despite their rhipidoglossan radula, this group is excluded from Archaeogastropoda because Neritimorpha are able to have planktotrophic larval development and produce a larval shell formed during the planktotrophic phase of life (BANDEL

1982). This is also confirmed by the presence of sperm dimorphism and differences of sperm morphology (HEALY 1988).

## Family Neritopsidae GRAY 1847

The family is represented by three species belonging to the genera *Trachydomia* and *Naticopsis*. Both genera are well known from the Pennsylvanian of the United States.

### Genus ***Naticopsis*** MCCOY 1844

#### ***Naticopsis*** sp.

Pl. 6 figs 51-54, 58-59, Pl. 7 figs 60-62

Description: The shell is broad, globular and of naticiform shape. It is low-spired and has round, rapidly increasing whorls. The base is anomphalous. The sutures are adpressed but distinct. The aperture displays a thickened parietal inductura that bears transverse rugae. On late teleoconch whorls, growth lines tend to form transverse lirae in a subsutural zone of variable width. The early whorls are corroded and thus the number of whorls is not determined. The largest specimen is 16.8 mm high and 12.2 mm wide; the smaller specimens are approximately as high as wide.
The shell has a thin outer, prismatic, calcitic layer and a thick inner, aragonitic, crossed lamellar layer.

Remarks: The generic identity of the specimens at hand is quite clear. However, species identification is not recommended because of the insufficient preservation. Presumably, it is the same species that was described by SQUIRES (1976) as *Naticopsis (Naticopsis) wortheniana* KNIGHT 1933b from the Buckhorn Asphalt deposit. SQUIRES reported colour preservation of revolving bands from his specimens. We found no colour preservation in our material; two of them are uniformly dark and one is light coloured.

Material: Three specimens, SMF XII/10-3523 - SMF XII/10-3525.

### Genus ***Trachydomia*** MEEK & WORTHEN 1866

Type species: *Naticopsis nodosa* MEEK & WORTHEN 1861, Pennsylvanian, U.S.A.

Remarks: *Trachydomia* is very characteristic because of its naticiform shape and its coarse nodular ornamentation. KNIGHT (1933b) stated that accurate species identification is only possible in mature specimens, because diagnostic characters change during ontogeny. Since both specimens from the Buckhorn Asphalt deposit are incomplete, we designate them to *Trachydomia* sp. 1 and *Trachydomia* sp. 2. Both specimens display colour pattern, whereas all the other Buckhorn species do not, except for *Naticopsis (Naticopsis) wortheniana* KNIGHT 1933b (SQUIRES 1976). Colour preservation is probably due to the calcitic outer shell layer; it is quite common amongst fossil Neritimorpha (HAAS 1953; KŘÍŽ & LUKEŠ 1974; TICHY 1980) and seemingly favoured by the outer calcitic layer.

#### ***Trachydomia*** sp. 1

Pl. 6 fig. 55

Description: The shell is globose and moderately high-spired. Inductura and outer lip are thin. The whorls are round, oval in transverse section and higher than wide, increasing rapidly in diameter. The only specimen (incomplete) is 4.5 mm high and 4.0 mm wide and it has about 3 whorls (protoconch corroded). The growth lines are opisthocline. The shell is ornamented with pustules; a narrow subsutural band is bordered by a shoulder bearing a single row of pustules somewhat larger than those below. The shell displays colour pattern of dark irregular and poorly defined collabral bands.

Remarks: *Trachydomia* sp. 1 is not as globose as *Trachydomia* sp. 2 and its sutures are more deeply impressed. The shell seems to be much thinner. In addition, the two species have different colour patterns. A typical feature for some *Trachydomia* species is the pustule-bearing shoulder as described by KNIGHT (1933b).

Material: One specimen, SMF XII/10-3526.

#### ***Trachydomia*** sp. 2

Pl. 6 figs 56-57

Description: The shell is of globular, naticiform shape and rather large. The only specimen is 6.7 mm high and 5.5 mm wide. The spire is little protruding. The whorls are round and increase rapidly in size. The inner lip is straight and has a distinctly thickened inductura. The outer lip is thin. The whorls are adpressed and meet at shallow distinct sutures. The shell is ornamented with coarse pustules and displays a colour pattern – the pustules are dark and the background light. The early whorls are corroded.

Material: One specimen, SMF XII/10-3527.

## Subclass Caenogastropoda COX 1959

Diagnosis: The shell of Caenogastropoda is coiled in one direction throughout life (orthostrophic) and is usually dextral, rarely sinistral. The basic design is that of an embryonic shell composed of primary shell without growth lines succeeded by the larval shell with growth lines and different ornament pattern. When the planktotrophic larval stage of ontogeny is substituted by lecitotrophy, the primary and larval shell fuse to a single shell and ornament on the protoconch is simplified or lost. The teleoconch usually differs in shape and ornament from the protoconch. The caenogastropod shell is largely composed of aragonite with crossed lamellar structure and without nacre.

Remarks: This group was proposed to contain the Mesogastropoda and Neogastropoda. KNIGHT et al. (1960b) classified it as an order, PONDER & WARÉN (1988) as a superorder, BANDEL (1993b) as a subclass. Archaeogastropoda, Caenogastropoda, Neritimorpha, and Heterostropha are all present as distinct groups in the Carboniferous. The monophyly of the Caenogastropoda was corroborated by the phylogenetic analysis of PONDER & LINDBERG (1997). However, this analysis largely ignores fossil groups. Until recently, nearly all Palaeozoic Caenogastropoda were placed in the "catch all" Loxonematoidea. In its traditional composition, this is a heterogeneous assemblage and certainly not monophyletic (BANDEL 1991b; NÜTZEL 1998). It is not even clear whether *Loxonema* is a caenogastropod at all; FRÝDA & BANDEL (1997) claimed that some Devonian *Loxonema*-like genera are in fact archaeogastropods. The Early Devonian genus *Pragoscutula* FRÝDA 1998 has about 1.5 helicoidal initial whorls and then the shell becomes a limpet. FRÝDA (1998, 2001) interpreted these initial whorls as a caenogastropod larval shell. If this is true, we would face the perplexing fact that one of the earliest known caenogastropods is a limpet. FRÝDA (2001) reported the larval shell of the Early Devonian subulitiform gastropod *Balbiniconcha* HORNÝ 1992 and showed that it represents probably another early caenogastropod.

In the Late Palaeozoic, there are at least six caenogastropod families (with known protoconch): Goniasmidae, Orthonemidae, Pseudozygopleuridae, Meekospiridae, Soleniscidae, and Imoglobidae (NÜTZEL 1998; NÜTZEL et al. 2000; NÜTZEL & BANDEL 2000; NÜTZEL & COOK 2002). Therefore, the Palaeozoic caenogastropods were a rather diversified group at this time. However, the phylogenetic relationships between these groups are largely unresolved, as is their relation to post-Palaeozoic caenogastropod clades.

One of the highlights of this paper are the superbly preserved typical caenogastropod protoconchs and larval shells of the slit-bearing *Murchisonia*-like Goniasmidae. Now, there is no doubt that some early caenogastropods were slit-bearing, which sheds more light on the early evolution of the Caenogastropoda.

### Order Cerithimorpha GOLIKOV & STAROBOGATOV 1975

### Family Goniasmidae NÜTZEL & BANDEL 2000

Diagnosis: High-spired shells with a median slit generating a selenizone and a caenogastropod-type of protoconch, i.e., the protoconch has more than one whorl and a more-or-less pronounced sinusigera; the shell is crossed lamellar without nacre.

Remarks: Until recently, high-spired shells of the genera *Goniasma*, *Cerithioides*, and *Stegocoelia*, with a slit in the outer lip generating a selenizone were included in the traditional family Murchisoniidae KOKEN 1896. Because of the presence of a slit, this family was placed in the Archaeogastropoda by most authors. Murchisoniids in general, were commonly considered to represent exceptionally high-spired pleurotomariids. FRÝDA & MANDA (1997) and FRÝDA (1999a) showed that species of the Devonian genus *Murchisonia* D' ARCHIAC & DE VERNEUIL 1841 have a typical archaeogastropod-type protoconch and therefore, the Murchisoniidae *sensu stricto* are probably archaeogastropods. However, other murchisoniid-like genera, *Goniasma*, *Cerithioides*, and *Stegocoelia* have a typical caenogastropod protoconch, as was shown by NÜTZEL (1998), NÜTZEL & BANDEL (2000), and as is shown here. The goniasmid gastropods described here are clearly caenogastropods, as can be inferred from protoconch morphology and the absence of nacre.

### Genus *Goniasma* TOMLIN 1930

Type species: *Murchisonia lasallensis* WORTHEN 1890, Upper Carboniferous, Illinois, USA

Diagnosis: Turriculate shell having whorls with smooth slope above an angular periphery that bears a short slit which generates a selenizone. Ornament consists of two spiral cords on the lower flank.

### *Goniasma* sp.

Pl. 8 figs 70-79, Pl. 9 figs 80-81

Description: The high-spired, small to medium-sized shell has a pleural angle of about 30°. Whorls are convex, angulated at the median spiral cords, and oval in transverse section (higher than wide). The base is anomphalous. Ornament of the teleoconch consists of four spiral cords, of which the uppermost is weak and lies in subsutural position. The spirals two and three are located at the periphery and are most prominent. The fourth spiral cord is weak or may be absent. It is partly or totally covered by the succeeding whorl. The third spiral cord appears immediately at the beginning of the teleoconch at the boundary with the protoconch while the other spiral cords appear later, jointly with the selenizone that lies between the median spiral cords. Delicate, regularly spaced pits are present on the three upper spirals. In addition, a spiral row of pits is developed in the middle of the selenizone. Spiral cords or threads may also be present on the base. Growth lines curve strongly backward between the adapical suture and the second spiral cord as well as between the abapical suture and the third spiral cord. Growth lines are strongly curving backwards at the margins of the selenizone.

The protoconch is orthostrophic, blunt and comprises a little more than one whorl. It is smooth and clearly demarcated from the teleoconch. A projection of the larval shell is present in a suprasutural position; this projection represents a larval hook formed by the outer lip of the aperture of the pediveliger shell. The protoconch is rather large, having a diameter of 0.32 mm, and the first whorl measures 0.30 mm across.

Remarks: *Goniasma* sp. has typical features of the slit-bearing true murchisoniids. It is high-spired, spirally ornamented and has a slit in the outer lip. However, Devonian species of *Murchisonia* have an archaeogastropod type protoconch (FRÝDA & MANDA 1997; FRÝDA 1999a) and therefore, *Murchisonia* and *Goniasma* are not closely related. The spirally arranged pits of *Goniasma* sp. are probably attachment points for periostracal hairs. Similar pits are also found in *Stegocoelia* (see below). This feature as well as the similar ornamentation and shell shape reflect a close phylogenetic relationship of the two genera. However, *Stegocoelia* has round, convex whorls instead of angular whorls and the selenizone in *Stegocoelia* is located much higher on the whorl.

*Goniasma* sp. closely resembles the type species of *Goniasma*, *G. lasallensis*. However, in *G. lasallensis*, the main angulation of the teleoconch whorls is situated distinctly lower on the whorls. Nevertheless, assuming a considerable variability, *Goniasma* sp. could be conspecific with *G. lasallensis* which is well-known from the Pennsylvanian of the United

States (e.g. YOCHELSON & SAUNDERS 1967; KUES & BATTEN 2001). NÜTZEL & BANDEL (2000) reported the protoconch of *G. lasallensis* which is similar to that of *Goniasma* sp. It comprises about 1.5 whorls, is relatively large and represents clearly a caenogastropod protoconch that reflects non planktotrophic early ontogeny.

Material: Several specimens; six specimens (SMF XII/10-3531 - SMF XII/10-3536) documented here with SEM-micrographs.

## Genus *Stegocoelia* DONALD 1889

Type species: *Stegocoelia compacta* DONALD 1889, Lower Carboniferous, Scotland.

Diagnosis: Slender, turriculate shell with a slit or deep notch at or above periphery; mature teleoconch whorls round, convex; protoconch consists of distinctly more than one whorl, is commonly of heliciform shape, and has a distinct sinusigera.

Remarks: The species that are here assigned to *Stegocoelia* are caenogastropods, as is indicated by a protoconch of more than one whorl that terminates in a deep sinusigera with a pronounced larval hook. YOO (1988) figured and described this type of caenogastropod protoconch from *Stegocoelia* species from the Early Carboniferous of Australia, but placed the genus nevertheless in the Archaeogastropoda (Murchisonioidea). In his second paper on this fauna, YOO (1994) placed *Stegocoelia* in the Loxonematoidea, since he realized that protoconch morphology indicates a placement within the Caenogastropoda. While the assignment to the Caenogastropoda is correct, the presence of a slit alone is a good argument against placing *Stegocoelia* in the Loxonematoidea. Therefore, NÜTZEL & BANDEL (2000) placed this genus in the Goniasmidae.

*Stegocoelia (Stegocoelia) nodosa* YOO 1988 from the Lower Carboniferous of Australia (YOO 1988: Figs. 67-71) has a smooth protoconch of two whorls with an apertural lip having a deep sinus. The teleoconch is ornamented with four dominant spiral cords and has a simple aperture without apparent slit. In *Stegocoelia (Hypergonia) elongata* YOO 1988 from Australia, the protoconch consists of one smooth whorl with a prominent varix between protoconch and teleoconch. *Stegocoelia (Hypergonia) tenuis* YOO 1988 has a protoconch with more than two whorls and 0.4 mm height (YOO 1994). It has a large larval projection of the aperture, which is half covered by the first whorl of the teleoconch. The first whorl is about 0.15 – 0.2 mm wide.

### *Stegocoelia* sp. 1

Pl. 7 figs 63-69

Description: Several juvenile specimens are characterized by broad, strongly convex teleoconch whorls. A relatively large specimen (Pl. 7 fig. 66) comprises about 5 whorls, is 1.8 mm high and 1.1 mm wide. The teleoconch has a broad selenizone above the periphery and can have a faint spiral ornament.

The protoconch consists of 1.2-1.3 whorls and ends in a pronounced sinusigera with a large larval projection that emerges just above the lower suture. The sinus of the sinusigera is strengthened by a varix. The protoconch is largely smooth, has a diameter of about 0.25-0.26 mm, and an initial whorl with a diameter of 0.24-0.25 mm.

The shell structure is exclusively crossed lamellar, with two layers that differ from each other in the orientation of the crystallites.

Remarks: The protoconch of *Stegocoelia* sp. 1 closely resembles that of *Goniasma* sp. However, the second and third whorls of *Goniasma* sp. are already distinctly angular and carinated while comparable growth stages of *Stegocoelia* sp. 1 are round and convex. Moreover, the selenizone of *Goniasma* sp. is located considerably lower on the whorl. The distinct sinusigera, paucispirality, and the relatively large size of the protoconch indicate non planktotrophic larval development.

Material: Several specimens; three specimens (SMF XII/10-3528 - SMF XII/10-3530) documented here with SEM-micrographs.

### *Stegocoelia* sp. 2

Text-fig. 3, Pl. 9 figs 82 -90, Pl. 10 figs 91-92

Description: The shell is high-spired turriculate and of small to medium size with the largest specimen consisting of 6.5 whorls at a height of 2.5 mm and 0.9 mm width. Whorls are convex and somewhat angulated at the spiral cords. The sutures are impressed and flat. The aperture is not well preserved but has a rounded outline with concave columellar lip and indistinct apertural notch at its anterior end. Whorls are higher than wide and in transverse section of oval outline. The ornament of the teleoconch in the seventh whorl (mature teleoconch whorl) consists of six spiral cords, of which cord 4 and 5 are most prominent and occur near the periphery. Spiral 1 and 3 are weak and sometimes missing, especially in the early teleoconch whorls. The suprasutural spiral 6 is weak and sometimes covered almost completely by the next whorl. Spiral 2 and 4 border the broad selenizone, and spiral 3 lies within it. Small pits are present on spiral 1 and 3, and often very indistinct pits are present at the abapical slope of spiral 4 and the adapical slope of spiral 5. The selenizone can only be seen in extremely well preserved shells, because its growth lines are delicate. In the early whorls, the selenizone is not obvious and growth lines seem to be parasigmoidal. Generally, they run almost straight below spiral 4.

The protoconch consists of 1.2 to 1.3 whorls, has a diameter between 0.25 mm and 0.27 mm, with a diameter of the first whorl between 0.23 mm and 0.25 mm. A deep sinusigera-like apertural projection clearly demarcates the protoconch from the teleoconch. This larval hook is thin and was commonly broken away before the onset of the teleoconch. A varix-like ridge, in contrast, strengthens the sinus. The whole protoconch is covered by a Hammerschlag-microsculpture ("Hammerschlag" is a German word that was used by HERHOLZ (1990) to characterize this type of micro-ornament that resembles hammered metal).

The composition of the shell is aragonitic and consists exclusively of crossed-lamellar microstructure (Pl. 9 fig. 83).

Remarks: *Stegocoelia* sp. 2 can be confused with *Goniasma* sp., especially in its early growth stages. However, the mature teleoconch is quite distinct. The whorls of *Goniasma* are much more angular and its selenizone lies lower. In addition, *Goniasma* has just two distinct spiral cords. The protoconchs of *Stegocoelia* sp. 1, *Stegocoelia* sp. 2 and *Goniasma* sp. are basically the same, but *Stegocoelia* sp. 2 has a pronounced Hammerschlag-micro-ornament while the protoconchs of *Goniasma* sp. and *Stegocoelia* sp. 1 are smooth. *Stegocoelia* sp. 3 has more (about two) protoconch whorls (see below).

The relatively large paucispiral protoconch of *Stegocoelia* sp. 2 with its deeply lobed apertural outer lip indicates that it belonged to a free-swimming planktonic larva. The large embryonic whorl is evidence for a yolk rich embryonic development before hatching. Therefore, it may have metamorphosed from the larval phase without feeding on plankton, but planktotrophy is more likely. The Hammerschlag-microsculpture is present in *Stegocoelia* sp. 2, *Cerithioides* sp., *Orthonema* sp., and in *Palaeostylus batteni*. This seems to be an old caenogastropod feature that is still present in modern representatives of this group (BANDEL 1975). The spirally arranged pits on the teleoconch indicate the former presence of periostracal hairs or spines. Such pits are also found on the shell of *Goniasma* sp. Characters like those of embryonic shells, microsculpture of pits on the teleoconch, and minute details of growth line pattern can only be studied here, because of the exceptionally good preservation found among the fossils of the Buckhorn Asphalt deposit.

Material: Several specimens; six specimens (SMF XII/10-3537 - SMF XII/10-3542) documented here with SEM-micrographs.

### *Stegocoelia* sp. 3

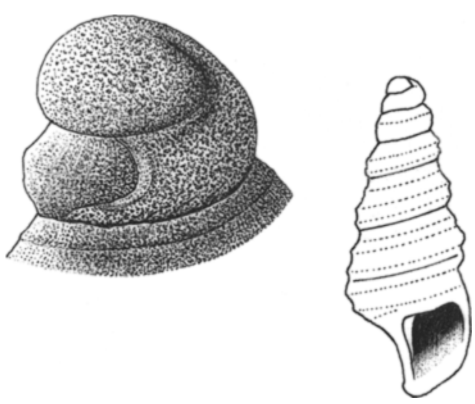
Text-Fig. 4, Pl. 10 figs 93-100

Description: The juvenile specimens at hand have convex early teleoconch whorls with more-or-less pronounced spiral ornamentation. The largest available specimen is 0.9 mm high and 0.7 mm wide. A slit is present and seems to be situated above the periphery, except on the specimen illustrated in Pl. 10 figs 93, 94, 100, in which the slit is lower on the whorl.

The protoconch consists of about two whorls and has a heliciform shape. It has a diameter of 0.27 mm and is 0.25 mm high. The first whorl has a diameter of 0.17-0.18 mm. The protoconch is clearly demarcated from the teleoconch by a deep sinusigera apertural lip. It is largely smooth but has a fine spiral thread that accompanies the upper edge of the larval hook. In addition, the protoconch may be ornamented with very fine pustules.

Remarks: In teleoconch morphology, this species is most similar to *Stegocoelia* sp. 1. However, *Stegocoelia* sp. 1 has a paucispiral protoconch of a little more than one whorl. Both species are certainly closely related but had different larval strategies, i.e., a yolk-rich lecitotrophic ontogeny in *Stegocoelia* sp. 1 and a planktotrophic ontogeny in *Stegocoelia* sp. 3. The protoconch of *Stegocoelia* sp. 3 is very similar to that of *Cerithioides* and *Orthonema* as described below. This corroborates a close phylogenetic relationship of these Palaeozoic cerithimorphs.

Material: Three specimens, SMF XII/10-3543 - SMF XII/10-3545.



Text-fig. 3. *Stegocoelia* sp. 1; left protoconch side view, x 100; right apertural side view, x 40; the protoconch of this caenogastropod probably reflects non planktotrophic larval development because it is relatively large, paucispiral, and has a distinct larval projection (sinusigera).

### Genus *Cerithioides* HAUGHTON 1895

Type species: *Glyptobasis telescopium* DEKONINCK 1881, Lower Carboniferous, Ireland.

Diagnosis: The shell is smooth and high-spired; the outer lip displays a deep labral sinus or slit. The protoconch has a heliciform shape and is of the caenogastropod type.

### *Cerithioides* sp.

Text-fig. 5, Pl. 11 figs 101-104

1998 *Cerithioides* sp. – NÜTZEL: 203, Textfig. 36, Pl. 32, Fig. J-K
2000 *Cerithioides* sp. – NÜTZEL & BANDEL: 559, Fig. 1

Description: The shell is high-spired conical to turriculate, with a pleural angle of 30°. The larger specimen comprises about seven whorls, is 2.0 mm high and 0.8 mm wide. The whorls are convex and sutures are impressed. The base is anomphalous. The aperture is not well preserved – seemingly, it may have had a slightly concave columellar lip and a broad short anterior notch. Growth lines indicate that the outer lip of the aperture in the fifth whorl of the teleoconch has a distinct sinus at about mid-whorl. The surface of the teleoconch is smooth with strongly sinuous growth lines. The basal portion of the whorl has weak spiral threads which cover the somewhat flattened anomphalous base. In the first teleoconch whorl, the sinus is located rather high on the whorl face and on the third whorl of the teleoconch it has moved into a central position.

The protoconch is bluntly heliciform and clearly demarcated from the teleoconch by a strongly lobed apertural lip (sinusigera). Its ornament consists of a fine Hammerschlag-microsculptural pattern and a suprasutural spiral thread that accompanies the adapical edge of the larval hook. The second whorl is moderately adpressed. The embryonic part of the protoconch measures about 0.12 mm across and is smooth while the Hammerschlag-pattern covers shell that was formed by the planktotrophic larva. When metamorphosis occurred, the shell was about 0.35 mm high and consisted of 2.3 whorls.

The shell is composed of aragonite and has a crossed-lamellar microstructure.

Remarks: *Cerithioides* sp. was illustrated and discussed by NÜTZEL (1998) and NÜTZEL & BANDEL (2000). Uninterrupted growth lines document that the early teleoconch whorls in the present specimens have only a pronounced labral sinus and not a deep slit. Nevertheless, the presence of this pronounced labral sinus indicates that this species belongs to the Goniasmidae, although the teleoconch lacks an ornament of revolving cords. The protoconch of *Cerithioides* sp. is similar to those of *Orthonema* sp. and in *Stegocoelia* sp. 3. The protoconch morphology and dimensions suggest a planktotrophic larval development. HERHOLZ (1990) described isolated larvae of very much the same type from the Westphalian of the Ruhr Area in western Germany. HERHOLZ applied to them the preliminary name "*Kryptomorpha malleata*" because the teleoconchs are unknown. Thus, the present species is a representative of a Palaeozoic group of caenogastropods with a wide distribution and a long existence in the geological record.

Material: Two specimens, one specimen lost (Pl. 11, Fig. 101-103), the other SMF XII/10-3546.

## Family Orthonemidae NÜTZEL & BANDEL 2000

The family Orthonemidae is characterized by the same types of protoconchs that are present in the Goniasmidae, but they have no slit or pronounced notch in the outer lip. WENZ (1938) placed *Orthonema* MEEK & WORTHEN 1862 in the Acanthonematidae WENZ 1938. The genus *Acanthonema* SHERZER & GRABAU is based on the type species *A. newberryi* MEEK 1873 that is known from external casts from the Devonian; it is a moderately high-spired to trochiform, minutely phaneromphalous shell with a knobby ornament (KNIGHT 1941). The protoconch of *Acanthonema* is unknown. KNIGHT (1934b) placed the Palaeozoic genus *Orthonema* into the Turritellidae and this family assignment was retained for a long time (e.g. KNIGHT et al. 1960b; ANDERSON et al. 1985). However, it is very unlikely that the genera *Orthonema* and *Turritella* belong to the same family (NÜTZEL 1998; NÜTZEL & BANDEL 2000). *Turritella* has a Tertiary type species and the family Turritellidae has its first appearance in the Early Cretaceous (SCHRÖDER 1995). Many modern turritellids are highly specialized infaunal filter-feeding gastropods which have reduced their radula. TRACEY et al. (1993) again used the family Acanthonematidae for the Palaeozoic 'turritellids' sensu KNIGHT et al. (1960b). Based on protoconch morphology, NÜTZEL (1998) redefined the family Acanthonematidae and placed all Palaeozoic caenogastropod genera having a largely smooth heliciform larval shell in this family and included the family in the Cerithimorpha. This type of larval shell is distinct from the axially ribbed larval shell of the other highly diverse Late Palaeozoic caenogastropod clade: the Pseudozygopleuridae. The genus *Acanthonema* is insufficiently known and differs considerably from the well-known Palaeozoic cerithimorphs. Therefore NÜTZEL & BANDEL (2000) placed Palaeozoic caenogastropod genera with a heliciform larval shell but without slit in the new family Orthonemidae and included the genera *Orthonema*, *Palaeostylus*, *Spiromphalus*, *Metorthonema*, and *Knightella*. KUES (2002) included the genus *Hermosanema* KUES & BATTEN 2001 in this family. The genus *Trepsipleura* KUES 2002 which was placed in the Pseudozygopleuridae by KUES (2002) could also belong to the Orthonemidae (see below).

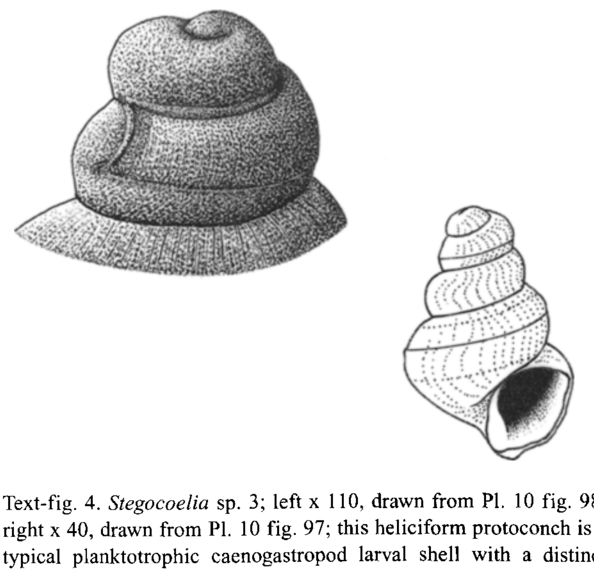
### Genus ***Orthonema*** MEEK & WORTHEN 1862

Type species: *Eunema? salteri* MEEK & WORTHEN 1860, Carboniferous, USA.

Diagnosis emended from ANDERSON et al. (1985): High-spired, turriculate shell; whorl profile commonly with subsutural shelf; sides of mature teleoconch whorls nearly straight, parallel below shelf; thread or carina just below subsutural shelf, below this more threads, colour bands, or carinae may be present; base anomphalous. Planktotrophic protoconchs are of heliciform shape, largely smooth but with a Hammerschlag-microsculpture and a spiral thread at the upper edge of the larval projection (larval hook, sinusigera); non-planktotrophic protoconchs similar with a little more than one whorl.

Remarks: According to ANDERSON et al. (1985), growth line pattern is no longer regarded as key character and it is only sporadically mentioned in their species descriptions (seemingly due to poor preservation). These authors did not regard characters of the protoconch as diagnostically important. In their species descriptions, ANDERSON et al. (1985) mention orthostrophic conispiral protoconchs with up to three whorls as well as planispiral and heterostrophic ones, but based no taxonomic conclusions on these observations.

*Orthonema* is a high-spired gastropod with revolving ornament and without slit in the outer lip. It has an orthostroph-



Text-fig. 4. *Stegocoelia* sp. 3; left x 110, drawn from Pl. 10 fig. 98; right x 40, drawn from Pl. 10 fig. 97; this heliciform protoconch is a typical planktotrophic caenogastropod larval shell with a distinct sinusigera.

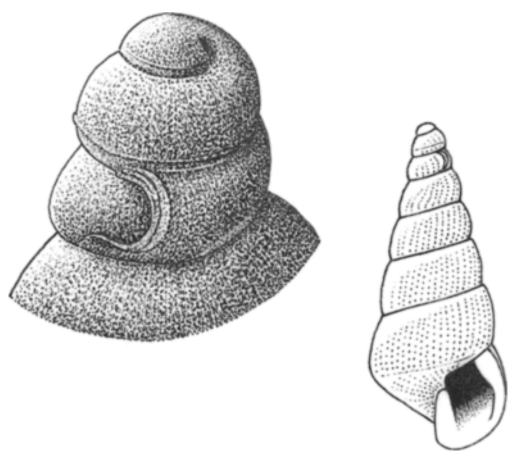
ic, heliciform caenogastropod protoconch resembling that of *Cerithioides* and *Stegocoelia*. This indicates a close relationship of the Orthonemidae and the slit-bearing Goniasmidae (NÜTZEL 1998; NÜTZEL & BANDEL 2000).

The concept of the genus *Orthonema* as well as its systematic position has changed. According to KNIGHT (1934b), the original concept was predominantly based on a nearly straight outer lip and revolving ornamentation (ridges, carinae, angulations) typically arranged in two groups separated by a wide band. KNIGHT (1934b) supplemented the diagnosis by stating that there may be a complex sinuosity of the outer lip and that there is an orthostrophic and simple protoconch. KNIGHT (1934b) and KNIGHT et al. (1960b) placed the genus in the family Turritellidae WOODWARD 1851 (= Turritellidae LOVÉN 1847) and in the superfamily Cerithioidea FLEMING 1822. Even ERWIN (1988b) placed *Orthonema* in the family Turritellidae but assigned this family to the Loxonematoidea. Since the modern Turritellidae represent Cerithioidea (e.g. HOUBRICK 1988), this would imply that Loxonematoidea are a synonym of Cerithioidea or that they are closely related to each other. Cerithioidea have been shown to be present in the Late Triassic (BANDEL 1992, 1993b; NÜTZEL & SENOWBARI-DARYAN 1999), while the concept of the Loxonematoidea remains an unresolved problem (BANDEL 1991b, 1993b, 1994a; NÜTZEL 1998). The Late Silurian type species of the genus *Loxonema* could be closely related to the Palaeozygopleuridae, as suggested by FRÝDA(1993) or to the Archaeogastropoda (FRÝDA & BANDEL 1997). It could just as well represent a member of the Heterostropha, as is the case for a mid-Devonian species attributed to *Loxonema* (BANDEL 1994b; NÜTZEL 1998). As long as the protoconch of the type species of *Loxonema* is not known, the placement of the extant Abyssochrysidae and Provannidae to the superfamily Loxonematoidea (HOUBRICK 1979; WARÉN & BOUCHET 1993) is premature.

### *Orthonema* sp.

Pl. 11 figs 105-110, Pl. 12 figs 111-113

1998 *Orthonema* sp. – NÜTZEL: 203, Pl. 33, Figs H-I



Text-fig. 5. *Cerithioides* sp., left x 22, drawn from Pl. 11 fig. 101; right drawn from Pl. 11 fig. 103; heliciform protoconch of a typical planktotrophic caenogastropod larval shell with distinct sinusigera.

Description: The shell is high-spired and the largest (incomplete) specimen consists of seven whorls. It is 1.9 mm high and 0.9 mm wide. Early teleoconch whorls are convex, oval, and higher than wide. The outline of the later whorls is characteristic for *Orthonema*, with a subsutural ramp and nearly straight parallel sides. Sutures are moderately deeply impressed and the base is round and anomphalous. The teleoconch is ornamented with three spiral cords and a weak fourth one that is commonly covered by the succeeding whorl. Growth lines are fairly straight (orthocline) or may be somewhat sinuous in adapical portion of whorls.

The protoconch is orthostrophic and blunt. It consists of two whorls with 0.25 mm to 0.26 mm in diameter (one specimen that probably represents another species has a protoconch diameter of 0.31 mm); the first whorl measures 0.14 mm to 0.18 mm in width. The first 0.8 whorls are smooth and represent the embryonic shell. Beyond it, a submedian to suprasutural spiral thread appears that demarcates the adapical edge of the larval hook. The larval shell is sculptured with minute granules and granulation tends to become denser on the last part of the larval shell. It is denser below the spiral thread than above it. The specimen with the bigger protoconch displays Hammerschlag-microsculpture. The protoconch is clearly demarcated from teleoconch by a strongly lobed outer lip (sinusigera). The shell microstructure is exclusively crossed-lamellar.

Remarks: The protoconch of this species reflects planktotrophic larval development. As mentioned above, protoconch shape and ornament resemble that found in *Cerithioides* sp. and *Stegocoelia* sp. 3. A close relationship of *Orthonema* with the slit-bearing Goniasmidae is therefore likely.

Material: Three specimens were studied with the SEM (SMF XII/10-3547 - SMF XII/10-3549).

### *Orthonema? sinistrorsa* (KNIGHT 1934b)

Pl. 12 figs 114-118

pars 1930 *Orthonema liratum* n. sp. – SAYRE: 151, Pl. 17, Figs 2-3

1934b *Murchisonia sinistrorsa* n. sp. – KNIGHT: 443-444, Pl. 56, Fig. 5

Description: The shell is high-spired and sinistrally coiled. The whorl profile is gently convex and sutures are lightly impressed. Whorls are round in transverse section and approximately as high as wide. The largest (incomplete) specimen with five whorls is 1.2 mm high and 0.8 mm wide. Teleoconch ornamentation consists of four spiral cords of which spiral 2 and 3 are most prominent and situated at a median position while spiral 1 is weak and spiral 4 is indistinct and covered by the next whorl. Growth lines are clearly orthocline. The aperture has been fractured and the base is anomphalous. The protoconch is orthostrophic and consists of 1.2 smooth whorls. It is clearly demarcated from the teleoconch and has a diameter of 0.28 mm to 0.29 mm. The first whorl diameter measures 0.25 mm to 0.26 mm. The shell is aragonitic in composition and has a crossed-lamellar microstructure.

Remarks: The most unusual feature of this species is its sinistral coiling. The rather large protoconch of more than one whorl shows that this species is a caenogastropod with yolk-rich (lecitotrophic) early development. SAYRE (1930) proposed the species *Orthonema liratum* from the Pennsylvanian (Missourian) of Kansas and figured two sinistral specimens under that name. However, sinistrality is not mentioned in SAYRE'S (1930) description. KNIGHT (1934b) re-examined the type material of this species and found four specimens, the two sinistral specimens figured by SAYRE (1930) and two additional dextral specimens. KNIGHT (1934b) based a new species (*Murchisonia sinistrorsa* KNIGHT 1934) on the sinistral specimens that previously had been illustrated by SAYRE (1930). Moreover, KNIGHT (1934b) designated one of the dextral specimens of SAYRE's material as holotype of *Orthonema liratum* and figured this specimen. The sinistral specimens figured by SAYRE (1930) and KNIGHT (1934b) agree well with our specimens from the Buckhorn Asphalt deposit in shape, size and in the arrangement of the spiral cords. KNIGHT (1934b) reported a selenizone between the upper two spiral cords of *Orthonema? sinistrorsa* and therefore, he placed that species in the genus *Murchisonia*. However, in our specimens, a selenizone is not seen. The reason for that might be that the types of *O. sinistrorsa* represent more mature growth stages. However, a placement in *Murchisonia* is not recommended because *Murchisonia* has a Middle Devonian type species and Early and Middle Devonian species of the genus have an archaeogastropod-type protoconch (FRÝDA & MANDA 1997; FRÝDA 1999a). In contrast, *O.? sinistrorsa* has a caenogastropod protoconch. Sinuous growth lines were also reported from the dextral type species of *Orthonema* and other species of this genus (KNIGHT 1934b; ANDERSON et al. 1985), and therefore we prefer to place *Orthonema? sinistrorsa* in this genus. However, this placement is somewhat doubtful because of the sinistral coiling and KNIGHT's (1934b) report of a selenizone.

This is the first report of *Orthonema? sinistrorsa* apart from SAYRE's initial collection of that species. Protoconch and shell microstructure of this species are reported for the first time.

*Metorthonema sinistrale* ERWIN 1988 (Early Permian, Wolfcampian, South-western United States) is another *Orthonema*-like sinistral gastropod. It differs from *O.? sinistralis* in having a predominantly smooth teleoconch. Left coiled species occur within several Recent and fossil caenogastropod taxa (sometimes within the same genus).

Material: Two specimens, SMF XII/10-3550 - SMF XII/10-3551.

## Genus *Palaeostylus* MANSUY 1914

Type species: *P. pupoides* COSSMANN 1918, Lower Permian, Cambodia

Diagnosis: High-spired anomphalous shells of cyrtoconoid shape. Spire whorls are rather low and wide. They are sculptured with axial ribs. Planktonic protoconchs are of heliciform shape.

Remarks: KNIGHT (1930) and KNIGHT et al. (1960b) included this genus in the Pseudozygopleuridae although the protoconch of its type species is still unknown. Nevertheless, KNIGHT et al. (1960b: I314, fig. 7) reconstructed *Palaeostylus* to have a protoconch with axial ribs, and therefore regarded the genus as member of the pseudozygopleurids. Moreover, KNIGHT et al. (1960b) considered *Pseudozygopleura* KNIGHT 1930 to represent a junior synonym of *Palaeostylus*. HOARE & STURGEON (1981) suspected that *Palaeostylus* is not a pseudozygopleurid because they found a smooth and paucispiral protoconch in the seemingly closely related genus *Spiromphalus*. Thus, they placed both genera in the family Palaeozygopleuridae HORNÝ 1955. HORNÝ (1955) defined the Palaeozygopleuridae as having a paucispiral smooth protoconch in order to distinguish them from the Pseudozygopleuridae, which were defined by having an axially ribbed protoconch of the planktotrophic type. Later, BANDEL (1991) assumed that *Palaeozygopleura* had non-planktotrophic larval development and NÜTZEL (1998) corroborated this with measurements of the protoconch. Therefore, *Palaeozygopleura* is not comparable with pseudozygopleurids in protoconch morphology, regardless of the true phylogenetic affinities of that genus. NÜTZEL discussed several possibilities for the systematic placement of the palaeozygopleurids, e.g. that they represent non-planktotrophic pseudozygopleurids or that they form an independent lineage. FRÝDA & BANDEL (1997) even suggested that the protoconchs of the Devonian palaeozygopleurids are of the archaeogastropod type and placed them in the order Stylogastropoda FRÝDA & BANDEL 1997 which comprises exceptionally high-spired archaeogastropods. Therefore, according to these authors, the teleoconch morphology of the palaeozygopleurids is convergent to that of the pseudozygopleurids.

BATTEN (1985) recognized that *Palaeostylus* is not closely related to the Pseudozygopleuridae because it has a siphonal canal. Hence, BATTEN (1985) placed *Palaeostylus* into the Cerithioidea (Procerithiidae). NÜTZEL (1998) confirmed this placement near the modern Cerithioidea based on the observation of a heliciform planktotrophic larval shell in *Palaeostylus*-like gastropods from the Pennsylvanian of the United States. This type of protoconch is also present in the genera *Orthonema* and *Stegocoelia* (see above) (NÜTZEL 1998). Thus, the results of BATTEN (1985) and NÜTZEL (1998) suggest that *Palaeostylus* is not closely related to Pseudozygopleuridae; certain characters of the aperture and the protoconch show that this genus is closer to the Cerithioidea, which are represented in the Palaeozoic by the family Orthonemidae. BATTEN (1985) showed that the Southeast Asian type species of *Palaeostylus*, *P. pupoides*, has a relatively complex teleoconch ornament. In contrast, the North American species have simple, straight ribs. However, *P. pupoides* shares the cyrtoconoid shape and the stout teleoconch whorls with the North American species. The protoconch of *P. pupoides* is unknown. The procerithiids in a strict sense are a Mesozoic group; the type species of the genus *Procerithium* is from the Early Jurassic. Generally, the protoconch of most Jurassic procerithiids consists of a carinated larval shell (e.g. GRÜNDEL 1974; NÜTZEL & KIESSLING 1997; BANDEL 1993b; SCHRÖDER 1995) and therefore it differs from the orthonemid protoconch.

The genus *Trepsipleura* KUES 2002 comprises sinistral high-spired gastropods from the Pennsylvanian of Texas. Apart from the sinistral coiling, these gastropods closely resemble *Palaeostylus*. They have stout teleoconch whorls with an axial ornament and a cyrtoconoid shape. Although the protoconch of *Trepsipleura* is smooth, KUES (2002) placed it in the Pseudozygopleuridae. Previously, NÜTZEL (1998) reported the smooth caenogastropod protoconch of the sinistral zygopleuroid species *Palaeozygopleura*? *perversa* (KNIGHT 1930). KUES (2002) discussed the systematic placement of *Trepsipleura* intensively and considered the convergent shell shape in various zygopleuroid gastropods. He acknowledged that the protoconch of *Trepsipleura* is uncommon within the Pseudozygopleuridae. In our opinion, a placement of *Trepsipleura* in the Orthonemidae and a close relationship to *Palaeostylus* is more likely.

### ***Palaeostylus batteni*** n. sp.

Text-figs 6-7, Pl. 12 figs 119-120, Pl. 13 figs 121-122

1998 *Palaeozygopleura*? sp. – NÜTZEL: 201, Pl. 32, Figs A-C

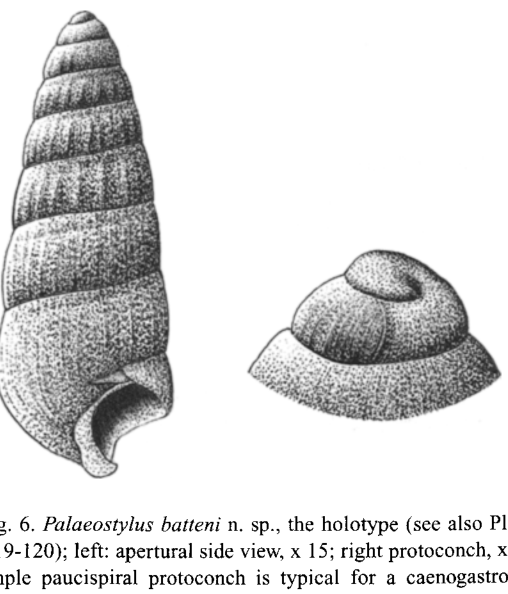
Diagnosis: Species with zygopleuroid habitus, low spire whorls, and cyrtoconoid shape. The teleoconch is sculptured with broad axial ribs. The protoconch is paucispiral and blunt (non-planktotrophic type).

Derivatio nominis: In honour of ROGER L. BATTEN
Stratum typicum: Boggy Formation, Deese Group, Late Carboniferous, Desmoinesian Stage (Moscowian)

Locus typicus: Buckhorn Asphalt quarry south of Sulphur, Murray County, Oklahoma (SE 1/4, sec. 23, T. 1S., R. 3E., Indian Baseline and Meridian)

Types: Seven specimens, holotype: SMF XII/10-3552, and six paratypes: SMF XII/10-3553 (one specimen) and SMF XII/10-3554 (five specimens)

Description: The shell is high-spired, cyrtoconoid to turriculate and small. The largest of the studied specimens consists of 7.5 whorls is 3.6 mm high and 1.3 mm wide. The base is rounded and anomphalous and the whorl profile is straight to gently convex, with the early whorls more convex than later ones. The sutures are adpressed to weakly impressed, distinct but rather flat. Whorls are a little higher than wide and of rounded subrectangular shape in transverse section. Spire whorls are rather low and stout. The aperture is not preserved, but the growth lines are orthocline indicating a straight outer lip. The growth lines are overprinted by broad straight ribs on the teleoconch (up to 20 on the 4th whorl) that do not continue onto the base. The ribs are faint or absent on early and late teleoconch whorls. Three or four spiral furrows may be present on the upper portion of the whorls.



Text-fig. 6. *Palaeostylus batteni* n. sp., the holotype (see also Pl. 12 figs. 119-120); left: apertural side view, x 15; right protoconch, x 66; the simple paucispiral protoconch is typical for a caenogastropod with non planktotrophic early ontogeny.

The protoconch is orthostrophic, heliciform, consisting of 1.1 whorls having a diameter of up to 0.3 mm. The initial part of the protoconch is up to 0.1 mm wide. The whole protoconch is covered by a Hammerschlag-microsculpture, which tends to become finer abapically. The transition between protoconch and teleoconch is abrupt and adapically marked by a distinctly rolled-up edge that outlines a broad sinus. The abapical portion of the apertural lip of the protoconch is thin, frequently broken and projects in an indistinct larval hook of which the lower portion is covered by the first whorl of the teleoconch.

Difference: *Palaeostylus batteni* n. sp. resembles *Spiromphalus pervius* HOARE 1980 regarding teleoconch shape and ornament, but *P. batteni* has an anomphalous base.

Remarks: *Palaeostylus batteni* is a caenogastropod, as shown by teleoconch features and by the protoconch, which is of non-archaeogastropod-type. It consists of an embryonic shell of more than one whorl and an apertural lip reflecting a larva of the sinusigera type. The size of the protoconch and the low number of whorls reflect a lecitotrophic larval development. This and the presence of a larval hook on the outer lip of the fully grown protoconch indicate that the embryo hatched as pediveliger (BANDEL 1975, 1982; NÜTZEL 1998). The large diameter of the first whorl of about 0.3 mm indicates that *Palaeostylus batteni* is non-planktotrophic (NÜTZEL 1998); NÜTZEL (1998) showed that lower caenogastropods with planktotrophic larval development have a diameter of the first whorl of about 0.15 mm. This author placed *Palaeostylus batteni* tentatively in the genus *Palaeozygopleura* (as *Palaeozygopleura*? sp.). But *Palaeozygopleura* has finer ribs, the shape is not cyrtoconoid, and the whorls are not as stout as in *Palaeostylus batteni*. Both, *Palaeozygopleura* and *Palaeostylus batteni* have non-planktotrophic protoconchs. But the protoconch of *Palaeozygopleura* has a different shape (NÜTZEL 1998; FRÝDA & BANDEL 1997; FRÝDA 1999b).

*Palaeostylus batteni* has a teleoconch that is similar to *Pseudozygopleura* and therefore, it could be interpreted as a non-planktotrophic species of the pseudozygopleurids (see NÜTZEL 1998 for a discussion). Studies on Recent gastropods have shown that larval strategy alone is not necessarily of taxonomical relevance above species level, because planktotrophic and lecitotrophic strategies commonly occur within a single genus in many marine gastropods including the Ptenoglossa (MARSHALL 1983; BANDEL 1975, 1982, 1991b; NÜTZEL 1998). However, we will demonstrate that *Palaeostylus batteni* probably does not belong to the Pseudozygopleuridae. Lecitotrophic and planktotrophic protoconchs of congeneric species are often sculptured in a basically similar way. The protoconch of *Palaeostylus batteni* lacks ribbing - even traces of an axial ornament are absent. In contrast, non-planktotrophic pseudozygopleurids commonly have a few ribs at the end of the protoconch (NÜTZEL 1998). Furthermore, the Hammerschlag-microsculpture of *Palaeozygopleura batteni* has not been reported from any pseudozygopleurid. Preservation of such microsculptures is possible only under favourable conditions, as is the case in the Buckhorn material. The well preserved *Pseudozygopleura peoriense* of the Buckhorn Asphalt deposit shows no microsculpture on the embryonic shell (see below). Moreover, there are Pennsylvanian species with a cyrtoconoid shape, axial ribs on the teleoconch, and a planktotrophic heliciform larval shell which is very similar to the planktotrophic larval shells of *Orthonema*, *Cerithioides*, and *Stegocoelia*. Such a species (*Palaeostylus* sp. 1) was described and illustrated by NÜTZEL (1998: 201, Pl. 32, Fig. G-Q). The protoconch of this species is clearly distinguished from those of the pseudozygopleurids. Therefore, *Palaeostylus batteni* is probably a non-planktotrophic species of the Cerithimorpha that represents the genus *Palaeostylus*.

## Order Ptenoglossa GRAY 1853

This highly diverse group of high-spired small to medium sized caenogastropods contains the Recent superfamilies Janthinoidea, Triphoroidea and Cerithiopsoidea. It is likely that the group originates in the Palaeozoic and was already separated from the precursors of modern Cerithioidea by the Early Carboniferous. The stem line of modern Ptenoglossa is hidden in the Loxonematoidea in a traditional sense - a group which is certainly poly- or paraphyletic (BANDEL 1991b, 1993b; NÜTZEL 1998). Shell morphology, especially that of the protoconch suggests that Pseudozygopleuridae KNIGHT are close relatives of the Mesozoic Zygopleuroidea (BANDEL 1991b; NÜTZEL 1998). In each of the Recent superfamilies of the Ptenoglossa, a larval shell with collabral axial ribs represents the plesiomorphic state (NÜTZEL 1998). Similar larval shells can also be found in the Mesozoic and Palaeozoic Zygopleuroidea (Zygopleuridae, Protorculidae, and Pseudozygopleuridae). For this reason, NÜTZEL (1998) proposed that the Pseudozygopleuridae are the extinct sister group of the Mesozoic Zygopleuroidea and the Recent Ptenoglossa.

## Family Pseudozygopleuridae KNIGHT 1930

The Pseudozygopleuridae were defined by a characteristic protoconch (KNIGHT 1930). The larval shell has an ornament of collabral axial ribs that reflect a strong median apertural projection of the outer lip. The Pseudozygopleuridae are very diverse and many species are known, especially from the Pennsylvanian of the U.S.A. (KNIGHT 1930; HOARE & STURGEON 1978, 1980, 1981, 1985; ANDERSON & BOARDMAN 1989; KUES & BATTEN 2001). There are also records from Australia (YOO 1994), Europe (HERHOLZ 1992; BANDEL 1993b; NÜTZEL 1998) and Russia (LICHAREW 1970). Only species with known protoconchs can be assigned to the family with certainty. The oldest known pseudozygopleurid protoconchs are of Tournaisian age (YOO 1994), the youngest from the Upper Permian Zechstein of Germany (BANDEL 1993b; NÜTZEL 1998). Thus, the family existed at least for 120 million years and represents one of the most important groups of Palaeozoic caenogastropods.

Text-fig. 7. *Palaeostylus batteni* n. sp., protoconch, x 110.

## Genus *Pseudozygopleura* KNIGHT 1930

Type species: *Loxonema attenuata semicostata* MEEK 1872, Pennsylvanian, Illinois, USA.

### *Pseudozygopleura peoriense* (WORTHEN 1884)

Pl. 13 figs 123-125

1985 *Pseudozygopleura (Pseudozygopleura) peoriense* (WORTHEN) – HOARE & STURGEON: 76, Fig. 4 P-R; see for prior synonymy.

Description: The only specimen consists of 5.3 whorls, is 1.8 mm high and 0.9 mm wide. The high-spired shell is of conical shape. The whorls are higher than wide, have rounded subrectangular shape in transverse section, a slightly convex outline, and meet in adpressed, moderately deepened sutures. The protoconch consists of 2.4 whorls, is 0.5 mm high and 0.38 mm wide. The embryonic shell consists of 0.7 smooth whorls with a diameter of 0.20 mm (first whorl diameter 0.21 mm). The larval shell displays the typical collabral ornament of pseudozygopleurids with curving ribs forming a median spiral thread. The aragonitic shell is rather thick and composed of a crossed lamellar layer and a thin inner prismatic glaze.

Remarks: Pseudozygopleurids are diverse and are frequently abundant in Pennsylvanian strata of North America. Their characteristic protoconch shows typical features of planktonic development, in the case of *Pseudozygopleura peoriense* planktotrophic larval development is indicated by the number of whorls and the diameter of the first whorl (see NÜTZEL 1998). Our juvenile specimen closely resembles *Pseudozygopleura peoriense* as illustrated and described by HOARE & STURGEON (1985) from the Pennsylvanian of the Appalachian Basin.

Material: One specimen, SMF XII/10-3555.

## Superfamily Subulitoidea LINDSTRÖM 1884

The Subulitoidea in a traditional sense are a heterogeneous assemblage of Palaeozoic gastropods that are commonly fusiform to high-spired and generally devoid of teleoconch ornament. In a phylogenetic analysis of the Late Palaeozoic Subulitoidea, NÜTZEL et al. (2000) recognized three clades (families), the Soleniscidae KNIGHT, the Meekospiridae KNIGHT, and the Imoglobidae NÜTZEL, ERWIN & MAPES. Each of these families is characterized by a particular protoconch morphology. The protoconch of the Soleniscidae is smooth and coni-

Text-fig. 8. Protoconch of the subulitid *Girtyspira minuta*, x 70; this blunt protoconch comprises distinctly more than one whorls. It is smooth and ends abruptly at an oblique prosocline line. The teleoconch has distinct growth lines. This is a caenogastropod protoconch that reflects non planktotrophic larval development (drawn after Pl. 13 fig. 126).

cal; the protoconch of the Meekospiridae is blunt and smooth; the protoconch of the Imoglobidae has an openly coiled initial whorl and a larval shell with non-collabral ornament. NÜTZEL et al. (2000) showed that the phylogenetic relationships of these three families are unclear, i.e. there is no support for a monophyly of the Subulitoidea. NÜTZEL et al. (2000) preliminarily retained the Late Palaeozoic families in the Subulitoidea because the protoconchs of the Early Palaeozoic subulitids are still unknown. FR+DA (2001) reported smooth high-spired larval shells in some Middle Palaeozoic subulitoid gastropods and assigned them to the Soleniscidae. These represent the oldest known protoconchs of subuliltoid gastropods.

## Family Meekospiridae KNIGHT 1954

Diagnosis: Shell is turriculate or fusiform; anterior notch weakly developed or absent; columellar fold absent or indistinct; protoconch smooth and blunt.

Remarks: NÜTZEL et al. (2000) included the genera *Meekospira* KNIGHT, *Girtyspira* KNIGHT, and *Ceraunocochlis* KNIGHT in this family. They found a blunt, smooth protoconch in these genera i.e. the protoconch has a much lower spire than the teleoconch. In Meekospiridae, both teleoconch and protoconch are smooth and therefore, the transition from the protoconch to the teleoconch is not determinable in 'normal' recrystallized material. Thus, NÜTZEL et al. (2000) could not determine the nature and position of the protoconch/teleoconch transition. This transition can be shown here for the first time, well-preserved in a representative of the Meekospiridae.

## Genus *Girtyspira* KNIGHT 1936

Type species: *Bulimella bulimiformis* HALL 1858, Spergen Hill Limestone, Indiana, USA, Mississippian.

Remarks: NÜTZEL et al. (2000) discussed the genus *Girtyspira* and showed that the protoconch is not heterostrophic. Therefore, *Girtyspira* probably does not belong to the Opisthobranchia as was suggested by KOLLMANN & YOCHELSON (1976).

### *Girtyspira minuta* (STEVENS 1858)

Text-fig. 8, Pl. 13 figs 126-130

See YOCHELSON & SAUNDERS (1967) and NÜTZEL et al. (2000) for the extensive prior synonymy.

Description: The fusiform shell has abutting whorls that are much higher than wide, oval in transverse section and have a gently convex profile. The largest specimen illustrated here (Pl. 13 fig. 129) comprises about five whorls, is 2.1 mm high and 1 mm wide. The sutures are lightly impressed. Increments of growth are prosocline to prosocyrt. The surface of the whole shell is polished and shining in well-preserved specimens. The ornament of the teleoconch consists of very faint spiral lirae which are normally corroded on the median portions of the whorls and are more distinct in the vicinity of the sutures and at the anomphalous base. The aperture has a small siphonal notch.

The protoconch is orthostrophic, bluntly rounded and smooth except for indistinct, wrinkle-like growth-increments on its last part. It consists of about 1.3 whorls, has a diameter of 0.25 mm to 0.26 mm; the first whorl has a diameter of 0.22 mm to 0.23 mm. The protoconch is clearly demarcated from teleoconch by a strongly prosocline suture that is marked by a faint, thread-like thickening. Beyond it, on the early teleoconch, distinct growth lines appear which are oriented at an angle to it. The shell is composed of aragonite with exclusively crossed lamellar microstructure.

Remarks: KNIGHT (1932) and NÜTZEL et al. (2000) reported a high intraspecific variability for *Girtyspira minuta* that includes presence or absence of a subsutural ramp as well as overall shell shape. The present specimens have no ramp. KOLLMANN & YOCHELSON (1976) and NÜTZEL et al. (2000) suggested an infaunal mode of life for *Girtyspira*, and the smooth polished shell surface in our specimens of *Girtyspira minuta* could indicate an infaunal mode of life. Polished shells are also present in the modern Eulimidae that feed on echinoderms. Several eulimids resemble the Palaeozoic Meekospiridae and therefore a carnivorous parasitic life habit seems possible for the Meekospiridae. However, polished shells also occur in epifaunal species (BANDEL & WEDLER 1987). It is probably a strategy to reduce friction and represents an adaptation to environments in which friction is a handicap.

The very fine spiral striation of the teleoconch represents an interesting feature that can be studied only in extremely well preserved specimens like those from the Buckhorn Asphalt deposit. A similar micro-striation was reported by HERHOLZ (1990) from "*Bulimorpha germanica* HERHOLZ 1990" (invalid species that was proposed in an unpublished thesis) from the Late Carboniferous of Germany. This species probably also belongs to *Girtyspira* as is suggested by the small size and the overall shape (NÜTZEL et al. 2000; NÜTZEL & MAPES 2001).

The protoconch shows only few characters. We can assume that it represents the protoconch of caenogastropod with non-planktotrophic development because it is orthostrophic with more than one whorl and it is rather large. The first whorl diameter of the present specimens of about 0.22 mm is similar to the diameter of 0.20 mm reported for *G. minuta* from the Pennsylvanian of Texas (NÜTZEL et al. 2000:

table 1). The opisthocline, straight transition from the protoconch to the teleoconch is unique among the Palaeozoic caenogastropods, as known at the present time. However, this type of protoconch is not unusual among modern caenogastropods with lecitotrophic early ontogeny.

Material: Eight specimens, SMF XII/10-3556 - SMF XII/10-3558.

Subclass Heterostropha FISCHER 1885
Order Allogastropoda HASZPRUNAR 1985
Superfamily Streptacidioidea KNIGHT 1931

Diagnosis: Streptacidioidea (Streptacididae *sensu* KNIGHT et al. 1960b) comprise high-spired shells with sinistral protoconchs, a rounded labral sinus high on the whorl and simple oval aperture. Their ornament consists of growth lines and, in case of the Donaldinidae, of spiral cords or threads. The protoconch is a discoidal (initially sinistral) whorl that caps the spire flatly or is deviated.

Differences: The Mathildoidea usually have a highly ornamented shell (BANDEL 1995), differing from the smooth Cassianebalidae BANDEL 1996 and Ebalidae BANDEL 1994 (= Ebalidae WARÉN 1994) with shallow sutures and Streptacididae with deep sutures, as well as from the spirally ornamented Donaldinidae BANDEL 1996. The Pyramidelloidea ORBIGNY 1840 commonly bear columellar folds and have more pronounced ornament. They are not known in the geological record before the Cretaceous.

## Family Donaldinidae BANDEL 1996

Diagnosis: Streptacidioidea with a teleoconch ornament of revolving cords or threads. The protoconch is commonly nearly planispiral and its initial part is sinistrally coiled.

Remarks: The oldest *Donaldina*-like species and other alleged members of the Heterostropha with known protoconchs were reported from the Early and Middle Devonian (BANDEL 1994; NÜTZEL 1998; FRÝDA 2000; FRÝDA & BLODGETT 2001). However, these Devonian examples are not really convincing because heterostrophy is not very distinct in the illustrated specimens due to poor preservation. *Donaldina* is abundant in the Carboniferous (e.g. ANDERSON et al. 1990; YOO 1988, 1994) and Permian (ERWIN 1988a) and they have worldwide distribution. The other Streptacidioidea (Streptacididae, Ebalidae, and Cassianebalidae) are not ornamented by prominent spiral cords. The ornament of Mathildoidea includes spiral cords and axial ribbing, while the morphology of the protoconch may be quite similar to that of the Streptacidioidea (BANDEL 1995a). Anoptychiidae have a change of ornament on their teleoçonchs, but juvenile teleoconchs may resemble those of Donaldinidae (BANDEL 1994b, 1996).

## Genus *Palaeoalvania* YOO 1994

Type species: *Palaeoalvania talenti* YOO 1994, Early Carboniferous (Tournaisian), Australia

Diagnosis: Hydrobiform small shell with ornament of spiral cords and simple growth lines. The protoconch is smooth and sinistral and the aperture simple.

Difference: YOO (1994) erected two genera (*Palaeoalvania* and *Pseudoaclisina*) to encompass heterostrophic species with an ornament of spiral cords. Both genera are present in the Buckhorn Asphalt deposit (see below). *Palaeoalvania* is broader and has an open umbilicus, while the *Pseudoaclisina* is anomphalous and more slender. In both genera, the protoconch is bulbous, paucispiral, and deviated whereas the protoconch of *Donaldina* is not bulbous. *Palaeoalvania* and *Pseudoaclisina* could represent close relatives of *Donaldina* with a lecitotrophic early ontogeny. In the Triassic, similar forms of the Heterostropha exist in the genus *Neodonaldina* BANDEL 1996 but this genus has a more deviated and clearly heterostrophic protoconch. The genus *Aclisina* DEKONINCK 1881 increases in shell width more rapidly than species of *Pseudoaclisina*.

### ***Palaeoalvania*** sp.

Pl. 14 figs 131-133

Description: The high-spired shell has a convex whorl profile and impressed sutures. The largest specimen comprises about 5.5 whorls, is 1.9 mm high and 1 mm wide. The whorls are rounded and oval in transverse section, a little higher than wide. The aperture is fractured, but according to the growth line pattern appears to be round with arched columellar lip and simple outline. The base is rounded anomphalous. Teleoconch ornamentation consists of four spiral cords with the fourth spiral cord near the abapical suture. Ornamentation of the teleoconch starts after a relatively narrow subsutural smooth ramp is developed. Growth lines are opisthocyrt.

The protoconch consists of one smooth planispiral whorl with only the most apical rounded embryonic portion demonstrating a twist below apical surface. The protoconch is demarcated from teleoconch by a faint suture, which is only visible on well preserved specimens. It measures 0.21 mm to 0.22 mm in diameter. Its heterostrophy (if present at all) appears indistinct because of its paucispiral appearance reflecting a lecitotrophic development and hatching from the egg as crawling young or as a veliger swimming only ashort time.

Remarks: *Palaeoalvania* sp. resembles *Donaldina* sp., but it has fewer spiral cords which are distributed evenly on the whorl flanks. Although heterostrophy is indistinct because of paucispirality, this species is most probably a member of the Heterostropha as are the species of this genus described by YOO (1994) from the Early Carboniferous of eastern Australia.

Material: Five specimens, SMF XII/10-3559 - SMF XII/10-3561.

## Genus ***Donaldina*** KNIGHT 1933

Type species: *Donaldina grantonensis* (DONALD 1898), Carboniferous, Scotland

Diagnosis: The high-spired shell is ornamented with spiral cords or threads generally confined to the lower part of the whorl.

Remarks: *Donaldina* differs from the Triassic genus *Neodonaldina* BANDEL 1996 as well as from the Carboniferous genera *Palaeoalvania* YOO 1994 and *Pseudoaclisina* YOO 1994 by the presence of a subsutural ramp. The shell of *Streptacis* is smooth. The Early Devonian genus *Bouskaspira* FRÝDA 1999 could be closely related to *Donaldina* or it could even represent a synonym (FRÝDA, written communication 2002). It has the same shape and teleoconch ornament. FRÝDA (1999b) reported the protoconch of *Bouskaspira* which could be heterostrophic but its preservation is not sufficient for a certain assignment.

### *Donaldina* sp.

Pl. 14 figs 134-137

Description: The shell is high-spired, turriculate with distinctly convex whorls and impressed sutures. The specimen on Pl. 14 fig. 135 comprises about 5.5 whorls, is 1.2 mm high and 0.6 mm wide. Whorl flanks are rounded and whorls are oval in transverse section (little higher than wide). The aperture is not well preserved but seems to have been round and simple in outline. The base is rounded and anomphalous. Ornament of the teleoconch consists of four to five distinct spiral cords. The lowermost spiral cord is covered in part or as a whole by the succeeding whorl. The revolving ornamentation is restricted to the abapical portion of whorls and the adapical portion is smooth and ramp-like. Growth lines are opisthocyrt.

The sinistral, almost discoidal protoconch consists of about 1.5 whorls, that lie flatly to moderately obliquely upon the succeeding whorl. It is clearly demarcated from the teleoconch by a distinct suture and a gentle varix. In one specimen a very fine mesh-work is preserved in the deepening at protoconch sutures (Pl. 14 fig. 137). The protoconch diameter is 0.21 mm to 0.22 mm and the diameter of the first whorl measures 0.14 mm to 0.17 mm. In another specimen, the protoconch is broken open and reveals some septa that were formed during subsequent shell growth (Pl. 14 fig. 136).

Remarks: This species is similar to *Donaldina swallowiana* (GEINITZ 1866), especially in having a comparably strong revolving ornamentation restricted to the abapical portion of the whorls. Judging from figures of ANDERSON et al. (1990), *Donaldina swallowiana* differs in having a more rounded whorl profile. Furthermore ANDERSON et al. (1990) described the protoconch of *D. swallowiana* as comprising two whorls.

Material: Three specimens, SMF XII/10-3562 - SMF XII/10-3564.

## Genus *Pseudoaclisina* YOO 1994

Type species: *Aclisina turgida* YOO 1988, Lower Carboniferous (Tournaisian), Australia

Diagnosis: The minute, high-spired shell with convex whorls is covered by an ornament of numerous spiral threads. The protoconch is deviated and smooth.

Remarks: Affinities and differences were discussed under *Palaeoalvania* (see above).

### *Pseudoaclisina* sp.

Pl. 14 figs 138-140

Description: The shell is high-spired and has distinctly convex whorl profile. The only specimen comprises about six whorls, is 1.8 mm high and 0.8 mm wide. The sutures are impressed and whorls are round with oval transverse section. The aperture is thus a little higher than wide and of simple outline, but is not well preserved. The base is rounded and anomphalous. Teleoconch ornamentation consists of five to six fine spiral threads that are more or less evenly spaced. Growth lines are opisthocyrt with the labral sinus culminating at adapical portion of the whorls. The protoconch is smooth and consists of only one whorl that has a diameter of 0.2 mm. The embryonic shell is clearly raised up and appears to dip into the apical surface. The coiling of the protoconch may represent oppressed heterostrophy due to paucispirality and non-planktotrophic larval development.

Remarks: The sinistrality of the protoconch of *Pseudoaclisina microspirulata* YOO 1994 is more distinct than in *P. turgida* (YOO 1988: Figs. 11-13). The protoconch of *Pseudoaclisina* sp. from the Buckhorn Asphalt deposit is intermediate between these species. It has fewer spiral threads on the teleoconch than *P. turgida*. The features of *Pseudoaclisina* sp. fit fairly well into the descriptions of *Donaldina stevensana* (MEEK & WORTHEN 1866) given by KNIGHT (1931a) and by ANDERSON et al. (1990). KNIGHT (1931a, p. 8) described the protoconch of as follows: "The plano-spiral nucleus lies flat upon the succeeding whorl". The description given by ANDERSON et al. (1990, p. 559) is: "... one whorl, smooth, nearly planispiral, initial end slightly upturned, with more rounded whorl profile than teleoconch". The protoconch of the present specimen is closer to the description of ANDERSON et al. (1990). A planispiral or near planispiral protoconch of only one whorl looks orthostrophic, especially when it is situated oblique in relation to the teleoconch. This type of protoconch is also known from *Donaldina minutissimia* YOO 1994 and *Streptacis elegantissima* (YOO 1988). It probably indicates that these species had a yolk-rich ontogenesis and no or a very short larval phase.

Material: One specimen, SMF XII/10-3565.

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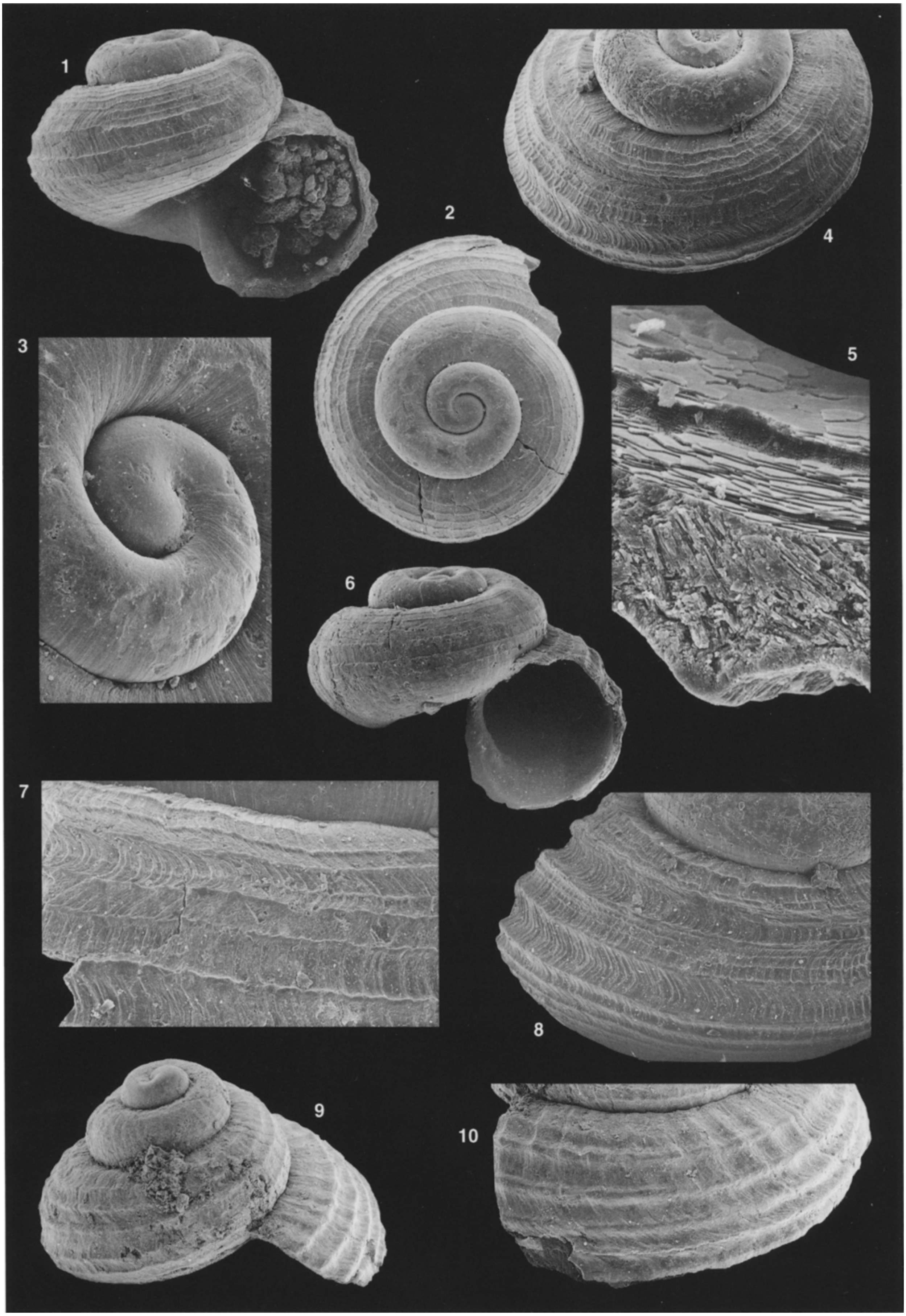
# Plate 1

Figs 1-8. *Salterospira* sp.

1. Apertural, SMF XII/10-3500, × 40.
2. Apical, SMF XII/10-3501, × 50.
3. Protoconch oblique, SMF XII/10-3501, × 200.
4. Teleoconch detail oblique view, SMF XII/10-3500, × 55.
5. Shell structure, inner nacreous layer in upper part, SMF XII/10-3500, × 880.
6. Apertural, SMF XII/10-3501, × 50.
7. Teleoconch detail, selenizone on upper whorl face relatively close to suture, SMF XII/10-3501, × 120.
8. Teleoconch detail, SMF XII/10-3500, × 50.

Figs 9-10. *Paragoniozona nodolirata* NELSON 1947

9. Oblique side view, SMF XII/10-3503, × 50.
10. Teleoconch detail, growth lines curve backward strongly and form selenizone that in lower part of figure, whorl broken, SMF XII/10-3503, × 60.

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# Plate 2

Figs 11-16. *Paragoniozona nodolirata* NELSON 1947

11. Shell structure, inner nacreous layer in lower part of figure, SMF XII/10-3503, × 570.
12. Shell structure, inner nacreous layer in upper part of figure and inner glaze in lower part, SMF XII/10-3503, × 1000.
13. Apertural, no selenizone in this early teleoconch, SMF XII/10-3504, × 60.
14. Apical, SMF XII/10-3504, × 48.
15. Teleoconch detail with distinct notch at about mid-whorl, SMF XII/10-3504, × 73.
16. Apical, SMF XII/10-3505, × 70.

Figs 17-20. *Anomphalus* sp. 1, SMF XII/10-3506

17. Apical, × 40.
18. Oblique apertural, × 45.
19. Teleoconch detail, × 125.
20. Protoconch apical, × 200.


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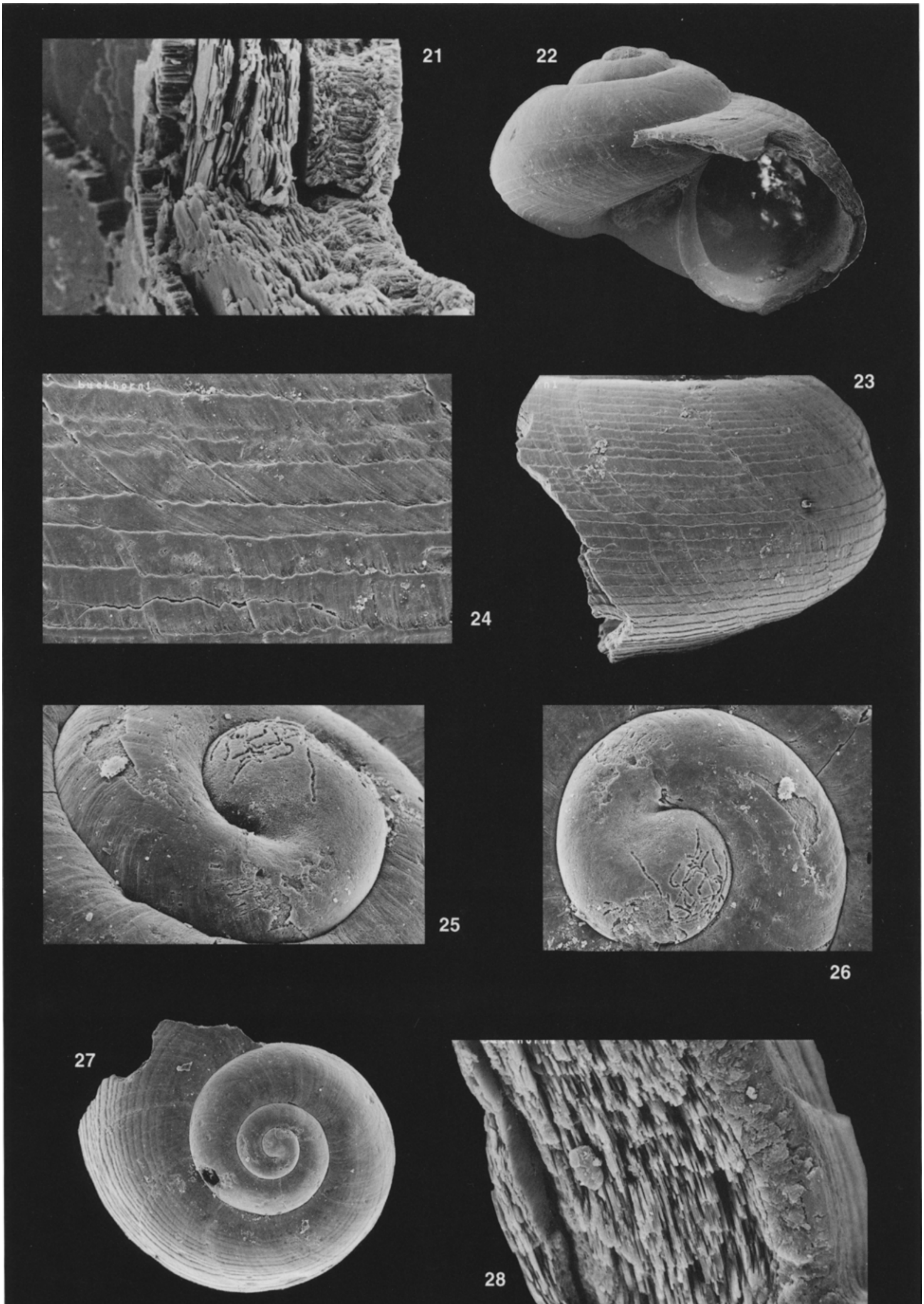
# Plate 3

Fig. 21. *Anomphalus* sp. 1

21. Shell structure, SMF XII/10-3506, × 600.

Figs 22-28. *Anomphalus* sp. 2, SMF XII/10-3508

22. Apertural, × 70.
23. Teleoconch detail, × 80.
24. Teleoconch detail, × 217.
25. Protoconch oblique side view, × 280.
26. Protoconch apical view, × 260.
27. Apical, × 55.
28. Shell structure, × 1100.

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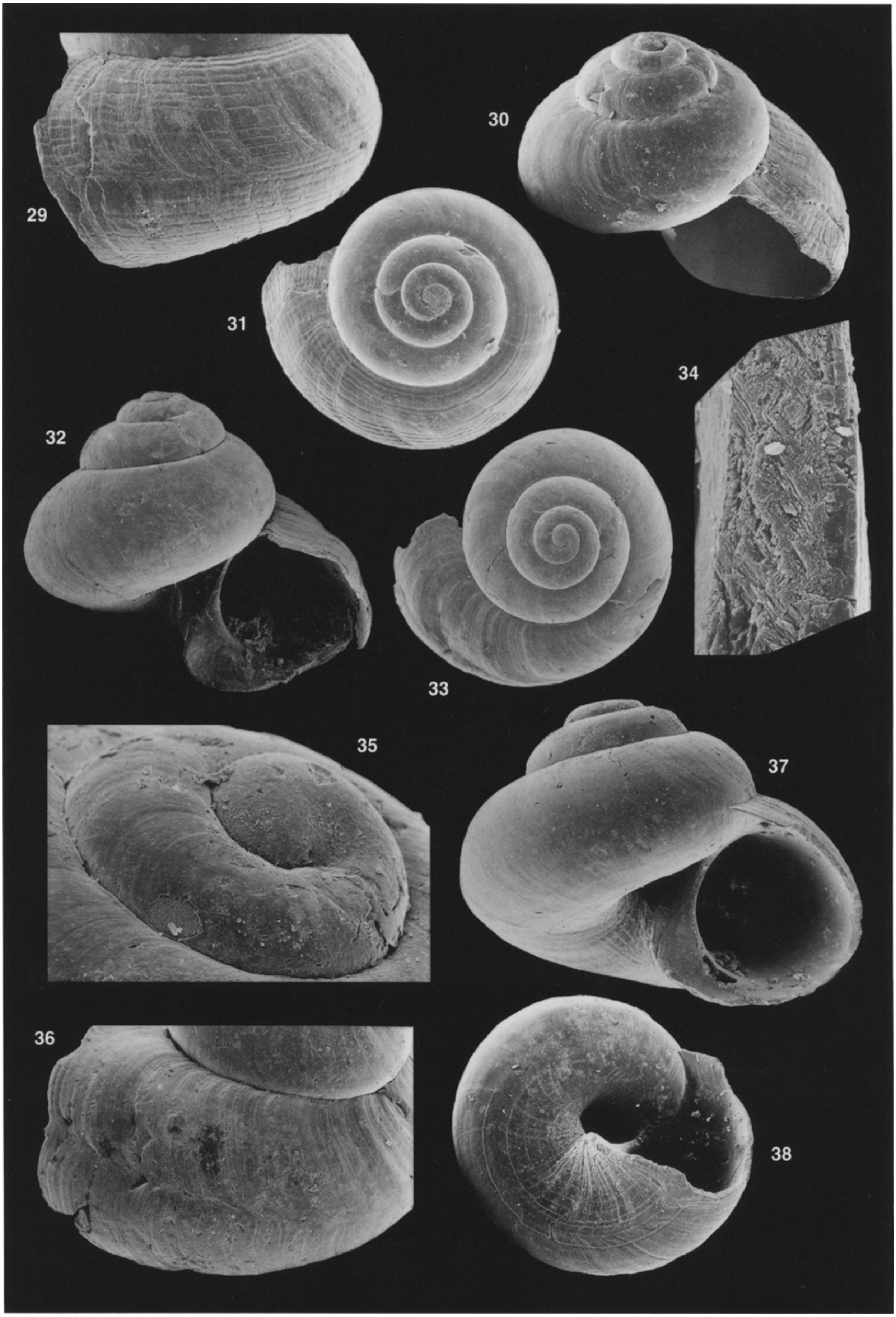
# Plate 4

Figs 29-38. Trochomorph archaeogastropod with crossed lamellar structure

29. Teleoconch detail, SMF XII/10-3510, × 60.
30. Oblique side view, SMF XII/10-3510, × 55.
31. Apical, SMF XII/10-3510, × 48.
32. Apertural, SMF XII/10-3511, × 40.
33. Apical, SMF XII/10-3511, × 40.
34. Shell structure, SMF XII/10-3512, × 800.
35. Protoconch, oblique side view, SMF XII/10-3511, × 283.
36. Teleoconch detail, SMF XII/10-3511, × 55.
37. Apertural, SMF XII/10-3513, × 68.
38. Basal, SMF XII/10-3513, × 60.

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# Plate 5

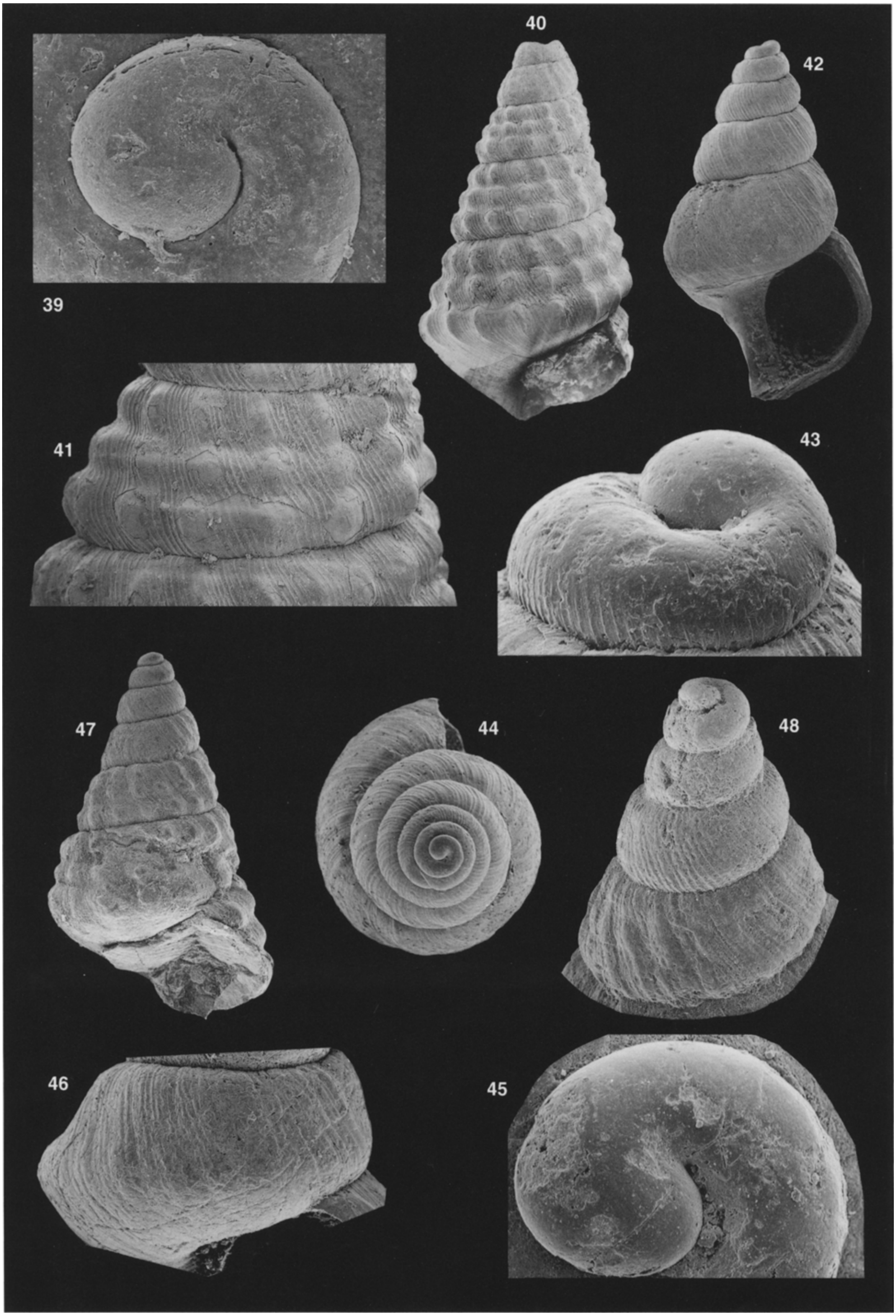
Fig. 39. Trochomorph archaeogastropod with crossed lamellar structure; protoconch apical, SMF XII/10-3511, × 276.

Figs 40-45. *Microdoma conicum*
40. Apertural, SMF XII/10-3515, × 15.
41. Teleoconch Detail, SMF XII/10-3515, × 33.

Figs 42-45. *Microdoma*? cf. *conicum* (juvenile specimens)
42. Side view, apertural, SMF XII/10-3518, × 22.
43. Protoconch side view, SMF XII/10-3518, × 217.
44. Apical view, SMF XII/10-3518, × 30.
45. Protoconch apical view, SMF XII/10-3519, × 230.

Fig. 46. *Microdoma conicum*, detail early teleoconch whorl, SMF XII/10-3521, × 50.

Figs 47-48. *Microdoma conicum* from the Desmoinesian Labette Shale, material collected by J. B. Knight, housed in the Smithsonian Institution, Washington, D. C.
47. Side view, apertural, × 33.
48. Protoconch and early teleoconch, formation of mature ornament, × 50.

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# Plate 6

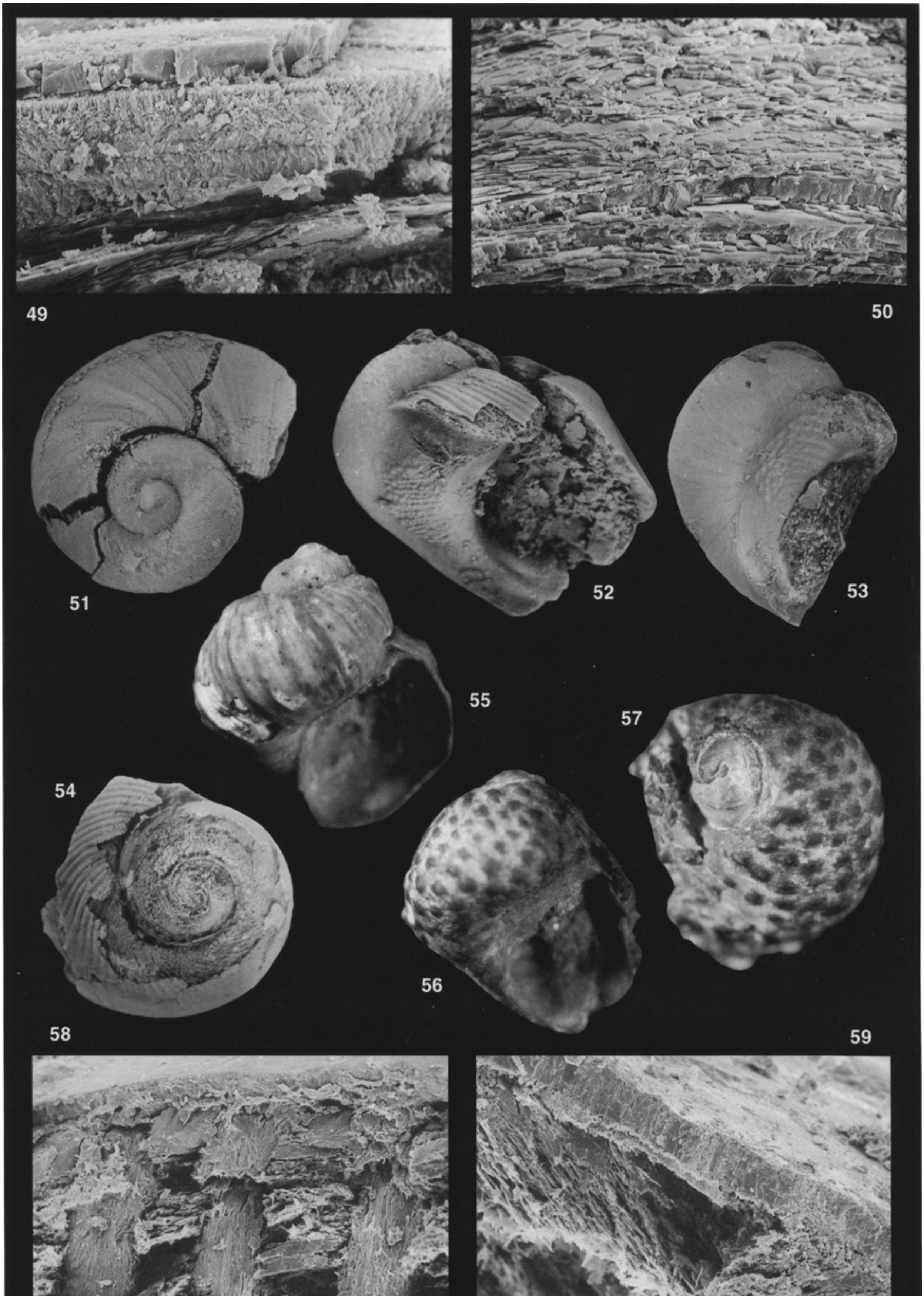
Figs 49-50. *Microdoma conicum* shell structure
49. SMF XII/10-3518, × 700.
50. SMF XII/10-3515, × 800.

Figs 51-54. *Naticopsis* sp.
51. Apical, SMF XII/10-3523, × 5.
52. Apertural, SMF XII/10-3524, × 5.
53. Apertural, base, oblique, SMF XII/10-3524, × 5.
54. Apical, SMF XII/10-3524, × 5.

Fig. 55. *Trachydomia* sp. 1, apertural, note colour preservation, SMF XII/10-3526, × 16.

Figs 56-57. *Trachydomia* sp. 2, SMF XII/10-3527
56. Apertural, × 8.
57. Oblique apical, × 9.

Figs 58-59. *Naticopsis* sp. shell structure, a thick aragonitic, crossed lamellar shell layer is overlain by a thin prismatic, calitic layer
58. × 110.
59. × 233.

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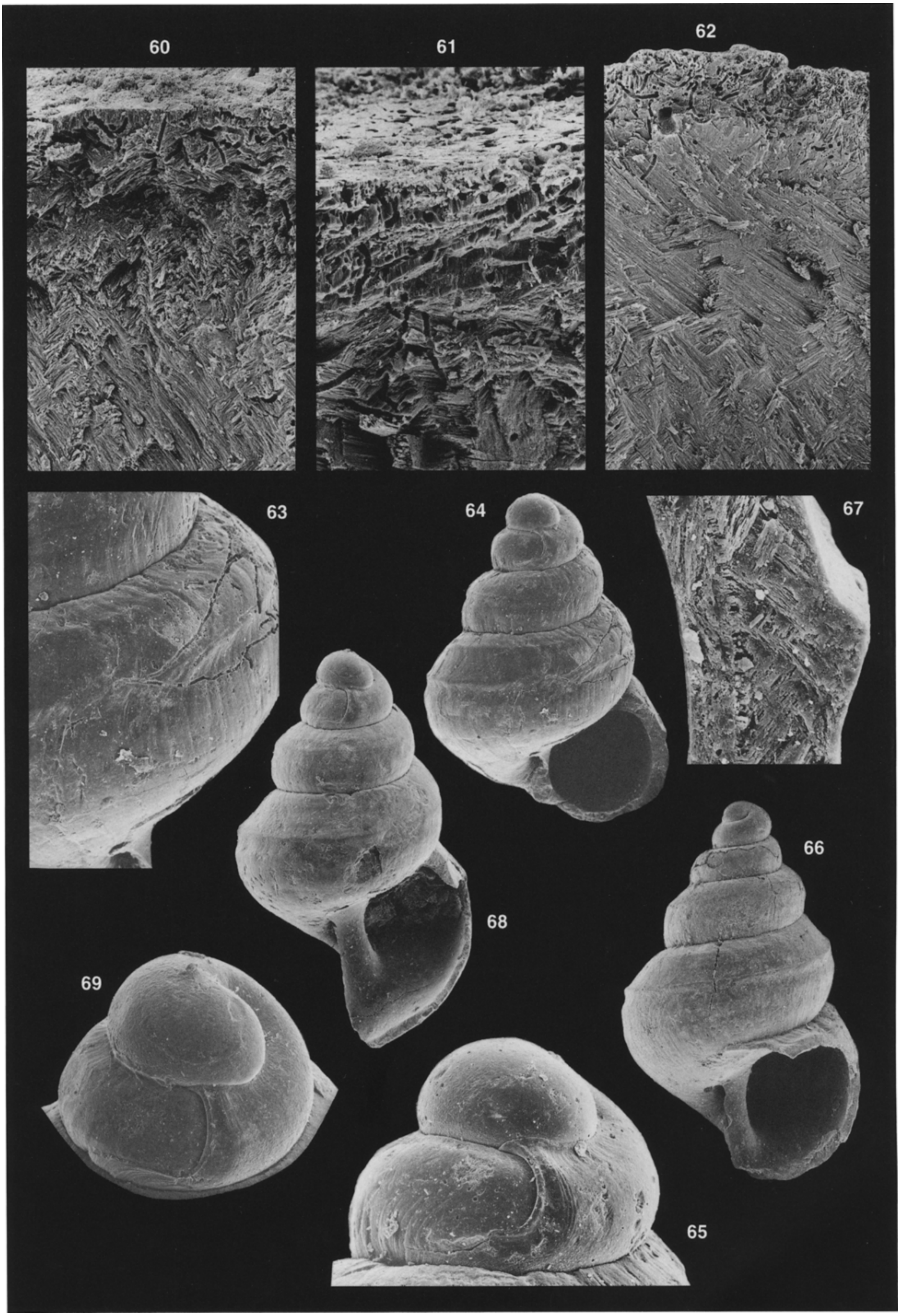
# Plate 7

Figs 60-62. *Naticopsis* sp. shell structure
60. × 233.
61. × 390.
62. × 167.

Figs 63-69. *Stegocoelia* sp. 1.
63. Teleoconch detail showing selenizone somewhat below upper suture; SMF XII/ 10- 3528, × 115.
64. Side view, apertural, SMF XII/10-3528, × 55.
65. Protoconch side view with pronounced sinusigera, SMF XII/10-3528, × 193.
66. Side view, apertural, SMF XII/10-3529, × 40.
67. Shell structure, SMF XII/10-3528, × 633.
68. Side view, apertural, SMF XII/10-3530, × 60.
69. Protoconch side view with pronounced sinusigera, SMF XII/10-3530, × 160.

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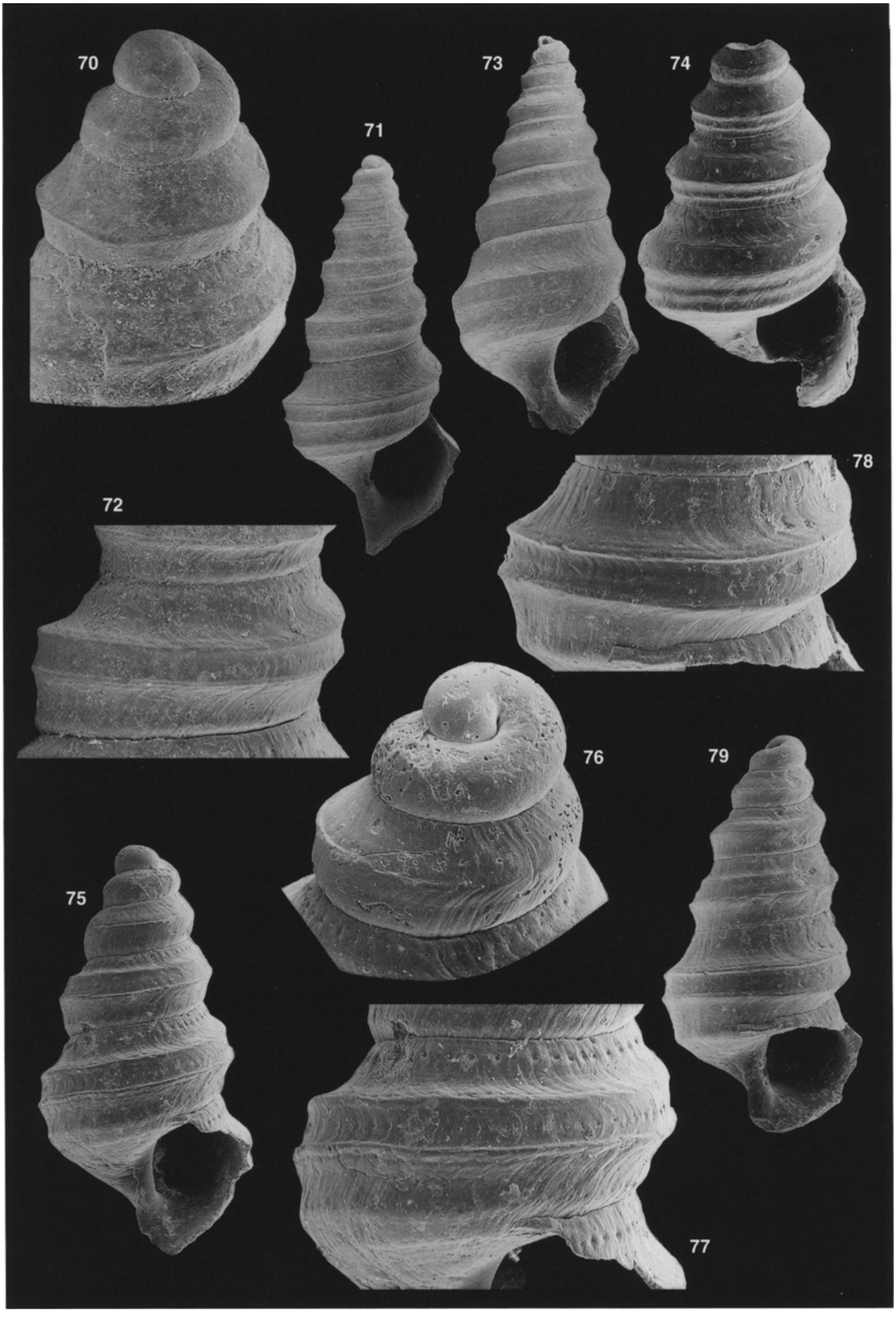
# Plate 8

Figs 70-79. *Goniasma* sp.

70. Apex with protoconch, side view SMF XII/10-3531, × 88.
71. Apertural side view, SMF XII/10-3531, × 20.
72. Teleoconch whorl, detail, selenizone bordered by two threads with distinct angulations, SMF XII/10-3531, × 50.
73. Apertural side view, SMF XII/10-3532, × 20.
74. Apertural side view, SMF XII/10-3533, × 43.
75. Apertural side view, SMF XII/10-3534, × 40.
76. Apex with protoconch, side view, SMF XII/10-3534, × 105.
77. Teleoconch whorl, detail, selenizone bordered by two threads with distinct angulations, SMF XII/10-3534, × 75.
78. Teleoconch whorl, detail, selenizone bordered by two threads with distinct angulations, SMF XII/10-3535, × 70.
79. Apertural side view, SMF XII/10-3535, × 42.

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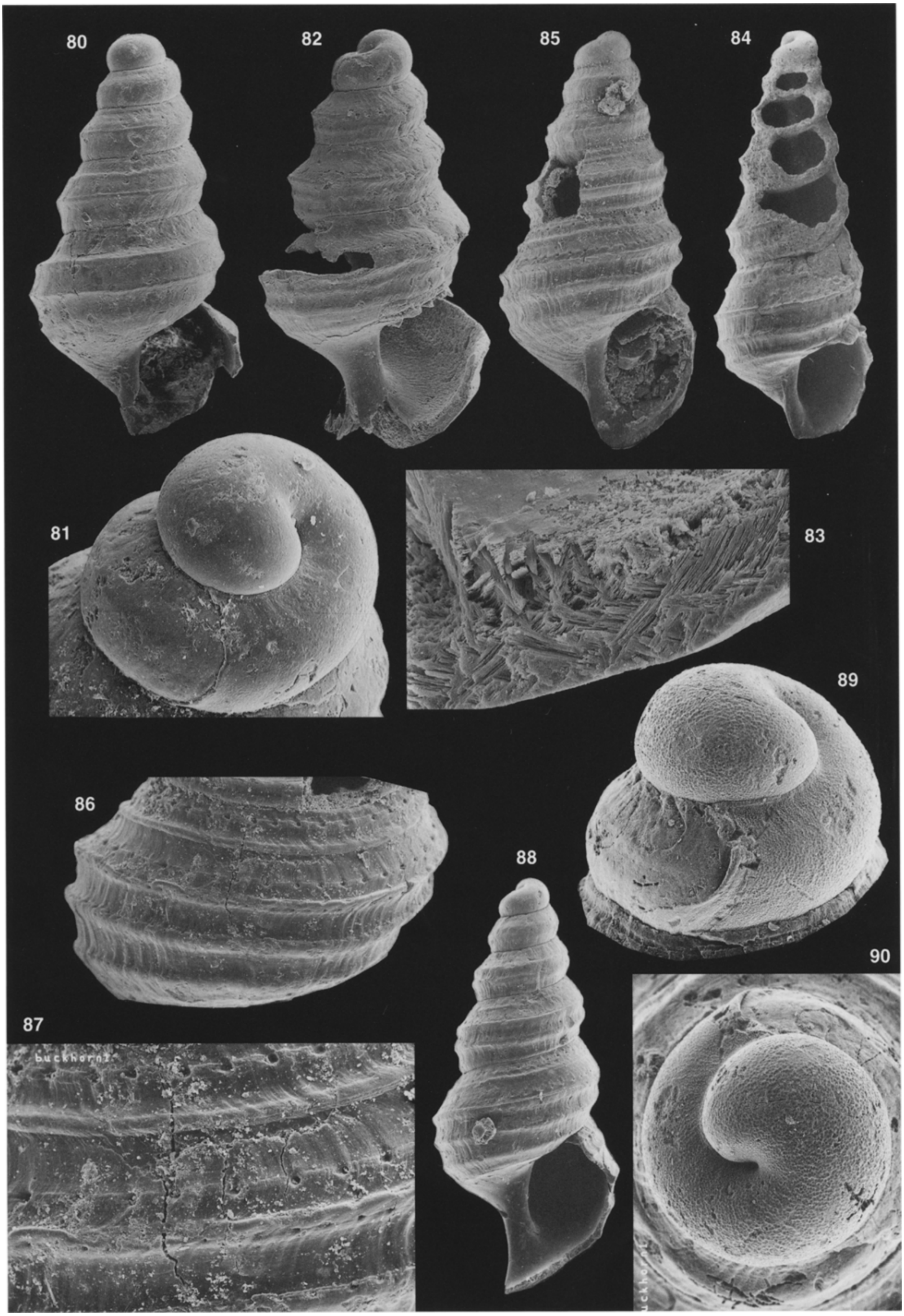
# Plate 9

Figs 80-81. *Goniasma* sp., SMF XII/10-3536
80. Apertural side view, × 40.
81. Protoconch, oblique side view, × 140.

Figs 82-90. *Stegocoelia* sp. 2
82. Apertural side view, SMF XII/10-3537, × 52.
83. Shell structure, SMF XII/10-3537, × 440.
84. Apertural side view, SMF XII/10-3538, × 30.
85. Apertural side view, SMF XII/10-3539, × 38.
86. Teleoconch whorl, SMF XII/10-3539, × 78.
87. Teleoconch whorl, detail, SMF XII/10-3539, × 150.
88. Apertural side view, SMF XII/10-3540, × 35.
89. Protoconch, side view, SMF XII/10-3541, × 150.
90. Protoconch, apical view, SMF XII/10-3541, × 150.

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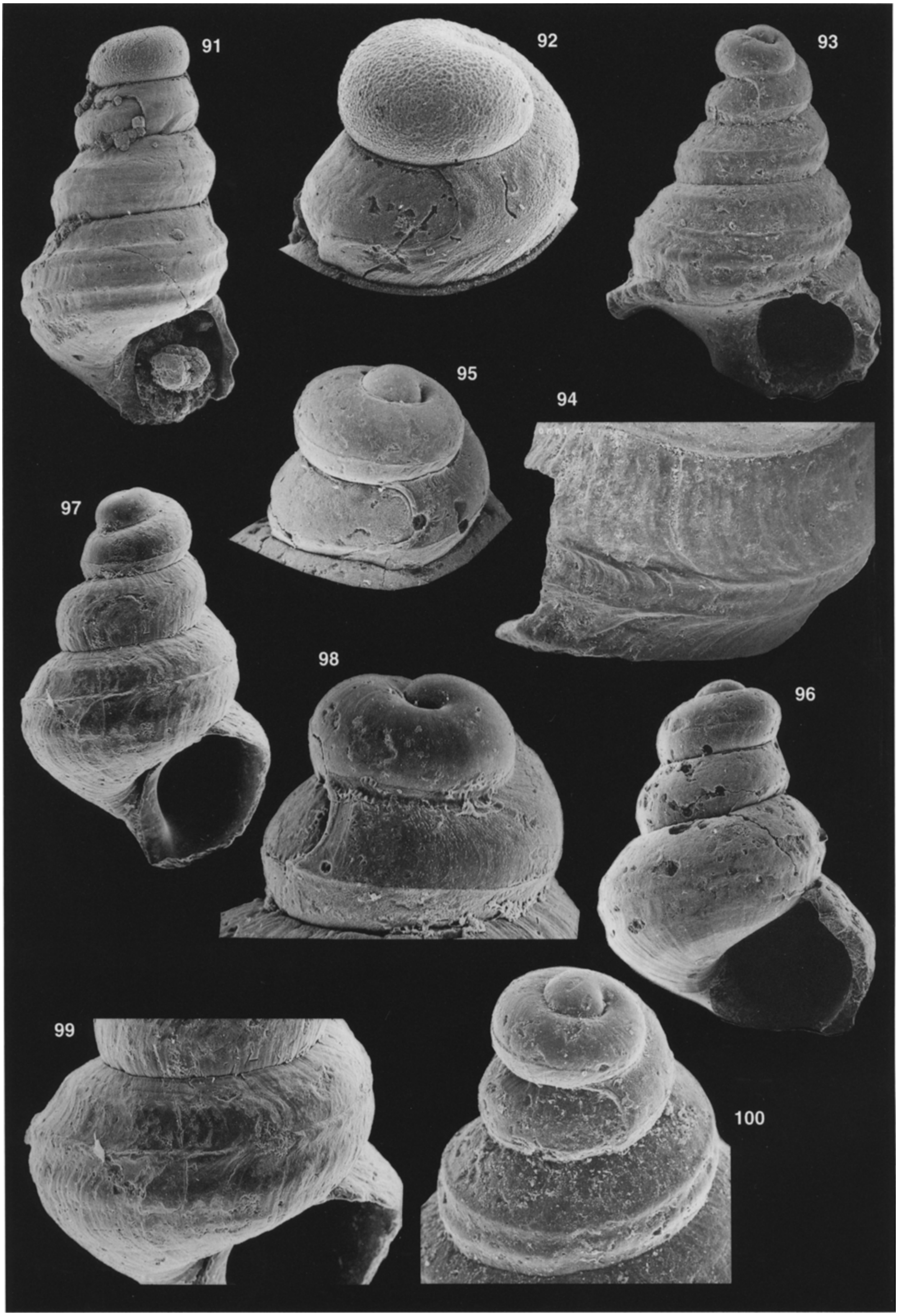
# Plate 10

Figs 91-92. *Stegocoelia* sp. 2, SMF XII/10-3542

91. Juvenile shell, apertural side view, × 60.
92. Protoconch side view, distinct sinusigera and Hammerschlag-microsculpture, × 150.

Figs 93-100. *Stegocoelia* sp. 3

93. Apertural side view, SMF XII/10-3543, × 78.
94. Teleoconch whorl detail, submedian selenizone between spiral cords, SMF XII/ 10-3543, × 130.
95. Protoconch, side view, heliciform shell with distinct sinusigera, SMF XII/10-3544, × 135.
96. Juvenile shell, apertural side view, SMF XII/10-3544, × 90.
97. Juvenile shell, apertural side view, SMF XII/10-3545, × 80.
98. Protoconch, side view, heliciform shell with distinct sinusigera, SMF XII/10-3545, × 200.
99. Teleoconch whorl, SMF XII/10-3545, × 120.
100. Protoconch, side view, heliciform shell with distinct sinusigera, SMF XII/10-3543, × 130.

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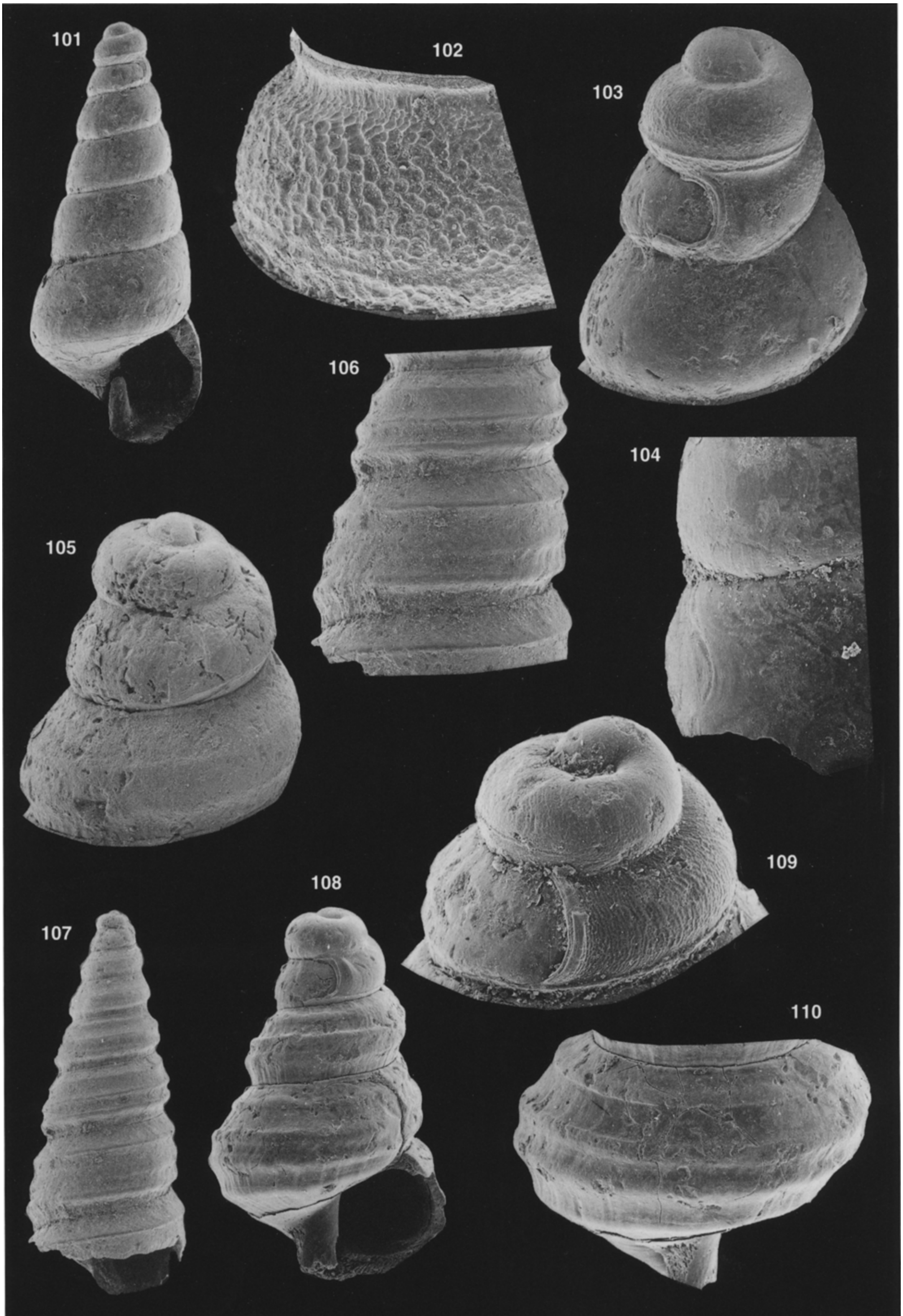
# Plate 11

Figs 101-104. *Cerithioides* sp.

101. Apertural side view, × 40 [specimen lost].
102. Detail larval shell, × 367 [specimen lost].
103. Protoconch, side view, × 160 [specimen lost].
104. Detail teleoconch whorl with distinct labral sinus, SMF XII/10-3546, × 120.

Figs 105-110. *Orthonema* sp.

105. Protoconch, side view, SMF XII/10-3547, × 140.
106. Detail teleoconch whorls, SMF XII/10-3547, × 50.
107. Apertural side view, SMF XII/10-3547, × 20.
108. Apertural side view, SMF XII/10-3548, × 70.
109. Protoconch, side view, SMF XII/10-3549, × 150.
110. Detail teleoconch whorl, SMF XII/10-3548, × 110.

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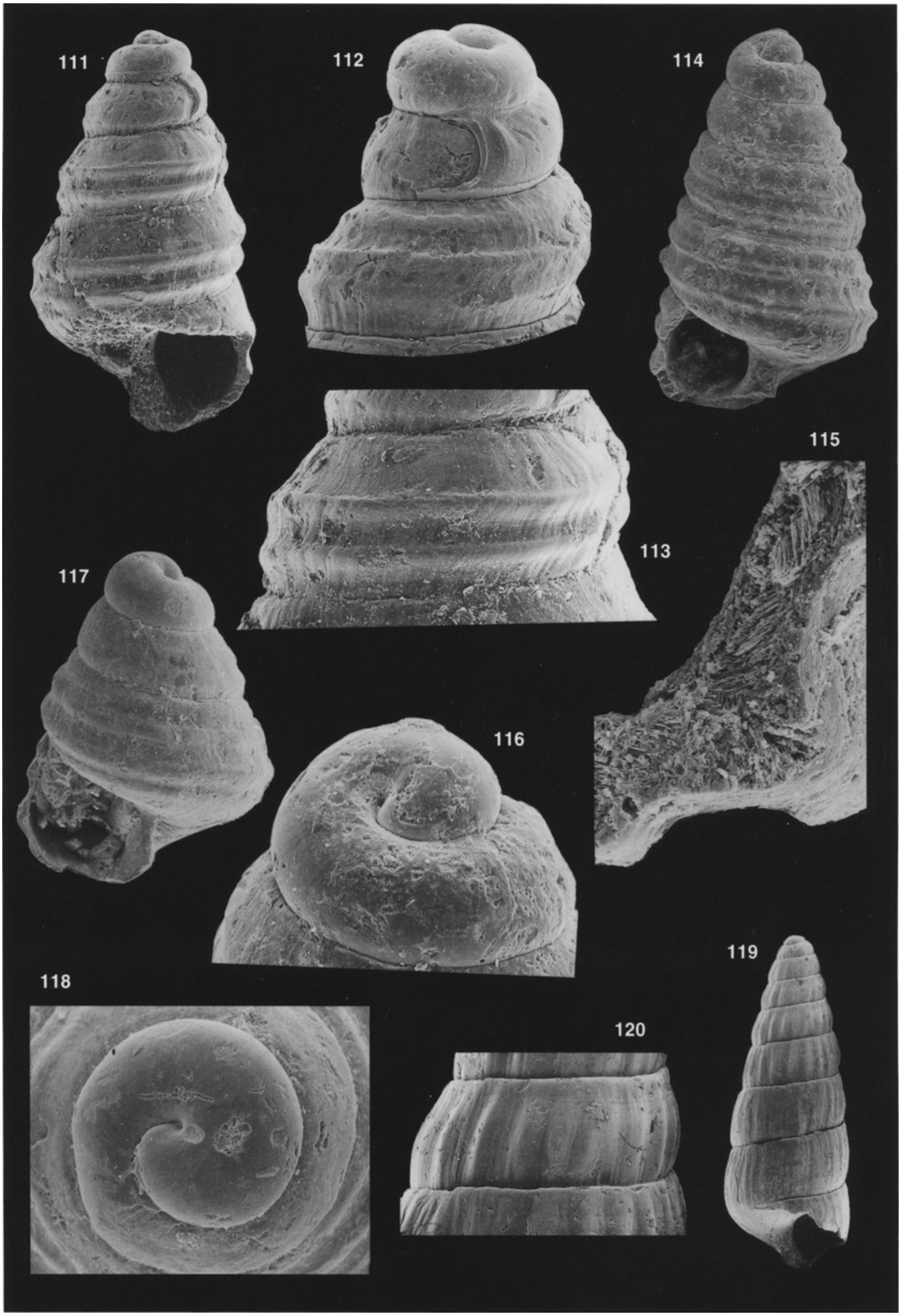
# Plate 12

Figs 105-110. *Orthonema* sp.
111. Apertural side view, SMF XII/10-3549, × 55.
112. Protoconch, side view, SMF XII/10-3548, × 120.
113. Detail teleoconch whorl, SMF XII/10-3549, × 120.

Figs 114-118. *Orthonema*? *sinistrorsa* (KNIGHT 1934b)
114. Apertural side view, SMF XII/10-3550, × 58.
115. Shell structure, SMF XII/10-3551, × 500.
116. Protoconch, side view, SMF XII/10-3550, × 170.
117. Apertural side view, SMF XII/10-3551, × 80.
118. Protoconch apical, SMF XII/10-3551, × 150.

Figs 119-120. *Palaeostylus batteni* n. sp., Holotype, SMF XII/10-3552
119. Apertural side view, × 15.
120. Detail teleoconch whorl, × 50.

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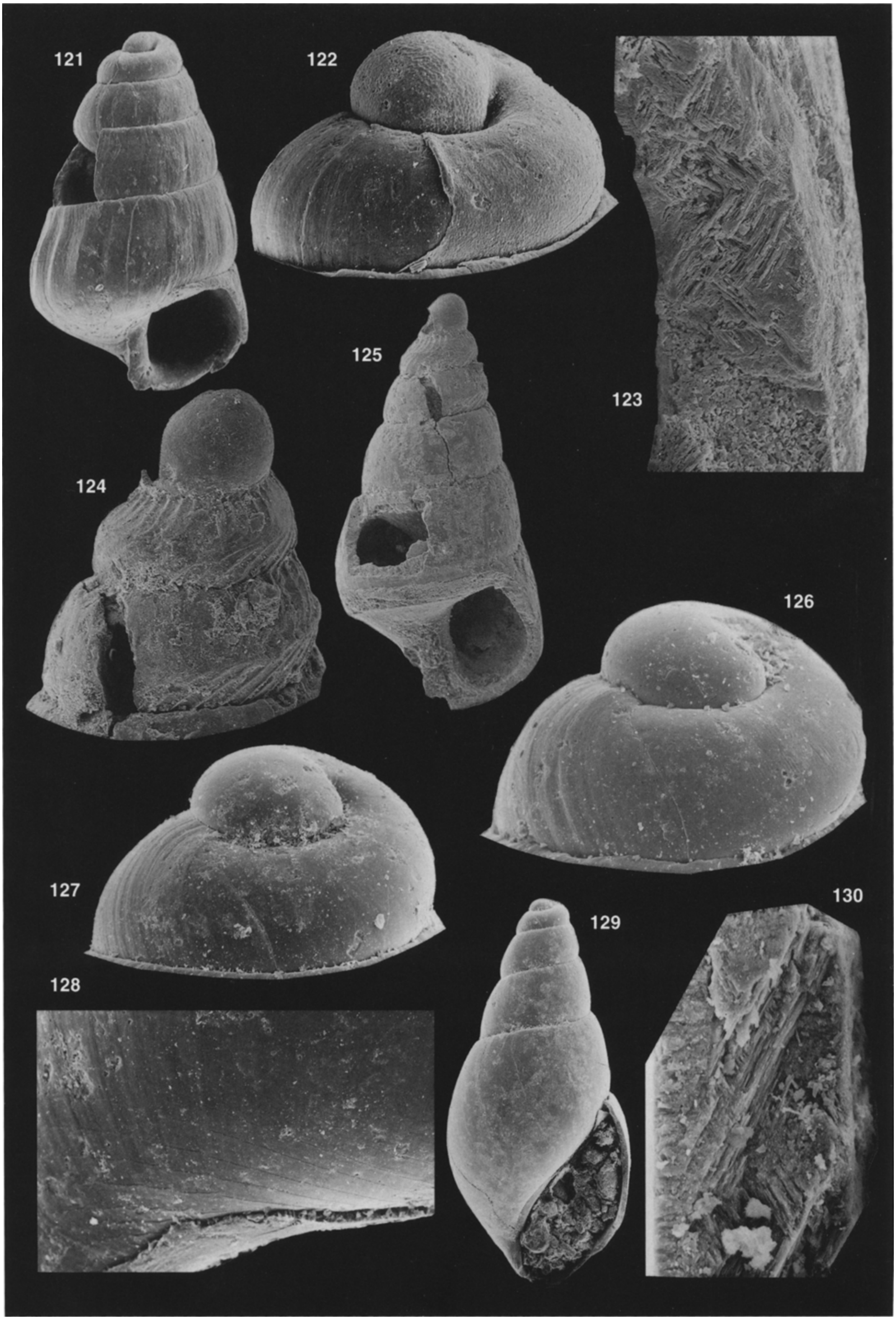
# Plate 13

Figs 121-122. *Palaeostylus batteni* n. sp., paratype, SMF XII/10-3553
121. Apertural side view, × 50.
122. Protoconch, side view, × 200.

Figs 123-125. *Pseudozygopleura peoriense* (WORTHEN 1884), SMF XII/10-3555
123. Shell structure, × 500.
124. Protoconch, side view, × 115 .
125. Apertural side view, × 43.

Figs 126-130. *Girtyspira minuta* (STEVENS 1858)
126. Protoconch, side view, SMF XII/10-3556, × 223.
127. Protoconch, side view, SMF XII/10-3557, × 227.
128. Detail body whorl near aperture with fine spiral striation, SMF XII/10-3556, × 200.
129. Apertural side view, SMF XII/10-3557, × 34.
130. Shell structure, SMF XII/10-3557, × 1200.

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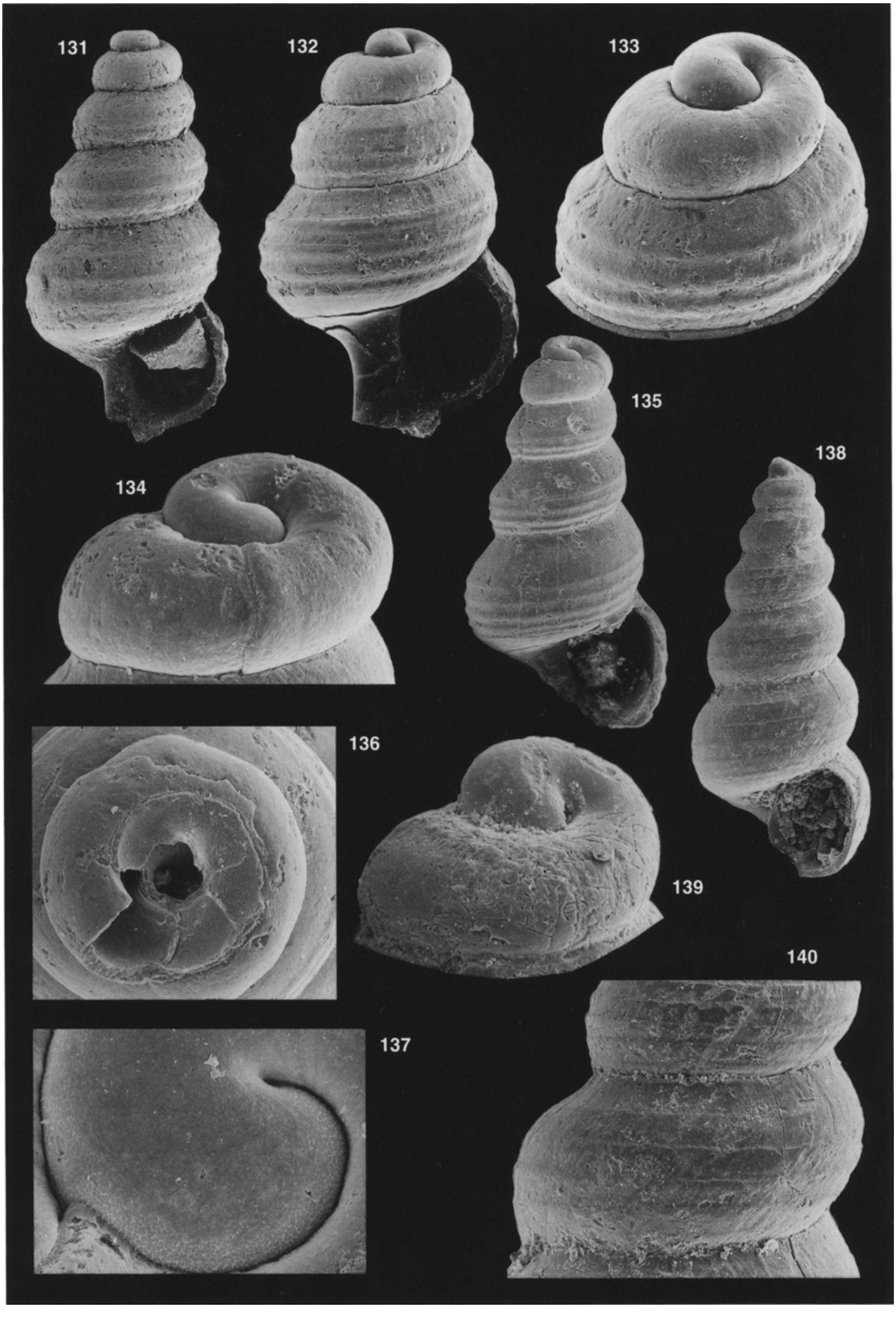
# Plate 14

Figs 131-133. *Palaeoalvania* sp.
131. Apertural side view, SMF XII/10-3559, × 40.
132. Apertural side view, SMF XII/10-3560, × 80.
133. Protoconch, side view, SMF XII/10-3560, × 130.

Figs 134-137. *Donaldina* sp.
134. Protoconch, side view, SMF XII/10-3562, × 233.
135. Apertural side view, SMF XII/10-3562, × 60.
136. Broken protoconch in apical view with septation, SMF XII/10-3563, × 170.
137. Initial whorl of protoconch in apical view, SMF XII/10-3562, × 780.

Figs 138-140. *Pseudoaclisina* sp., SMF XII/10-3565
138. Apertural side view, × 43.
139. Protoconch, side view, × 200.
140. Detail teleoconch whorl, × 100.

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