

Higher classification and pattern of evolution of the Gastropoda

A synthesis of biological and paleontological data

With 1 table and 3 plates

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Kurzfassung

Gastropoda stammen von der gleichen Stammgruppe der Conchifera ab, von welcher sich parallel zu ihnen die Muscheln und Cephalopoden während des Kambriums entwickelten. Es wird davon ausgegangen, daß Schnecken einmal durch die Verdrehung des Eingeweidesackes dergestalt entstanden, daß sich das Ende des Verdauungstraktes wie auch die Kiemen und die mit ihnen verbundenen Drüsen und Sinnesorgane nach vorne unter die Schale und über den Kopf verlagerten. Die Spiralisierung der Schale folgte der Verdrehung des Eingeweidesackes nach, allerdings von der Schale des benthischen Tieres ausgehend, während die Embryonalschale und auch die Larvalschale anfänglich nicht oder nur offen eingerollt war. Der paläontologische Befund könnte auch Modelle stützen, die Schnecken als nicht monophyletischer Herkunft betrachten. Archaeogastropoda verdrehen ihren Körper während der Embryogenese erst nach der Bildung der Primärschale, verformen diese aber anschließend noch vor ihrer Mineralisierung. Auch wenn die Archaeogastropoda keine Larvalschale ausscheiden, können die Docoglossa unter ihnen dennoch eine Plankton-fressende Larve besitzen; alle anderen entwickeln sich direkt, viele über eine freischwimmende Larve, die jedoch keine Nahrung aus dem Plankton aufnimmt. Innerhalb der vom Kambrium bis in das Mitteldevon lebenden Mimospirina belegt der große glatte Protoconch, daß beschaltete Individuen nicht im Plankton schwammen. Der planspiralige Protoconch der Amphigastropoda (Bellerophontiden) weist eine sehr kleine Embryonalschale auf und umfaßt mehrere Windungen. Sie könnte sehr gut von einer planktotrophen Larve ausgeschieden worden sein, die dem Bodenleben vorgeschaltet war. Die *Bellerophon*-Verwandtschaft lebte vom späten Kambrium bis zur frühen Trias, und aus ihr heraus entstand keine der anderen Gastropodengruppen; zudem hat auch noch das Modell Bestand, demzufolge Bellerophontiden teilweise untordierte Mollusken und zum Teil Schnecken oder alle keine Schnecken waren. Bei den Vorfahren der Vertreter der modernen Unterklassen der Gastropoden Neritimorpha, Heterostropha und Caenogastropoda schied die planktotrophe Veligerlarve eine Larvalschale aus. Ihr Protoconch bestand während des Ordoviziums und Silurs noch aus einer gestreckten Embryonalschale und offen gekrümmter Larvalschale. Die Spiralisierung der Schale erfolgte erst während oder nach der Metamorphose zum benthischen Leben. Erst während des Devons rückte die Spiralisierung der Schale in die larvale Phase vor und erreichte zuletzt die Embryonalschale. Noch während des Karbon lebten Arten mit peruneloidem Protoconch mit solchen mit bereits vollständig eingerollem Protoconch zusammen. Die Neritimorpha spiralisierten ihre Embryonalschale nie vollständig. Bei den Heterostropha ist die Spiralisierung sekundär in einer Reihe von Gruppen (etwa unter den Pteropoden) wieder aufgehoben worden, nur bei den Caenogastropoda wurde sie in der Embryonalschale besonders stark fixiert, so daß bei keiner ihrer Gruppen wieder eine gestreckte Embryonalschale auftritt. Neritoidea unter den Neritimorpha und ihre terrestrischen Verwandten lösten spätestens während der Trias die Schaleninnenwände in Protoconch und Teleoconch auf. Die kambrischen bis spätpaläozoischen, eventuell noch triassischen Euomphalomorpha besaßen neben einer den Neritimorpha ähnlichen Schalenstruktur einen großen cyrtoconen Protoconch und mögen sich neben den Platyceratoidea mit offen gewundenem Protoconch parallel entwickelt haben.

Entweder entwickelten sie niemals die Planktotrophie oder legten sie frühzeitig ab. Innerhalb der Heterostropha entstanden während des Devons und Karbons verschiedene Gruppen der Allogastropoda aus denen heraus über Arten mit *Cylindrobullina*-ähnlicher Schalengestalt spätestens während der Trias sich Opisthobranchia wie auch Pulmonata herausbildeten. Die Basommatophoren mit ihrer charakteristischen Verzögerung in der Embryonalschalenbildung besiedelten erst im Jura die Süßgewässer, und Stylommatophoren breiteten sich erst in der Kreide auf den Kontinenten aus. Die linksgewundene frühontogenetische Schale der Heterostropha ist genetisch weniger fest verankert als jene der Caenogastropoda, so daß sie sich in einigen Gruppen wieder entspiralisieren ließ, wie bei einigen Pteropoden mit gestreckter Embryonalschale sowie den Ancyliidae mit sofortiger Bildung eines Schalennapfes. Während die Heterostropha ihren larvalen und embryonalen Schalenteil sinistral einrollten führten die Caenogastropoden diesen Prozess nach rechts herum durch, wobei die Spiralisierung vom Teleoconch her auf die Larvalschale vorgriff, und erst ganz zuletzt auch die Embryonalschale erfaßte. Hierbei entstanden nebeneinander mehrere Entwicklungsreihen, die von den Peruneloidea-ähnlichen silurischen und devonischen Arten mit offenem Protoconch zu den Ctenoglossa, Littorinimorpha, Cerithiimorpha oder Strombimorpha ähnlichen Vorformen des Karbon führten. Während des Mesozoikums erzeugten mehrere Evolutionsschübe in der Trias die eigentlichen Cerithiimorpha/Littorinimorpha, im Jura die Strombimorpha s.s., in der frühen Kreide die Neomeso- und Neogastropoda.

Abstract

Gastropoda had their ancestors among the Cambrian early Conchifera and evolved parallel to the Bivalva and Cephalopoda by torting their soft body. During this process the end of the digestive system as well as ctenidia and glands like mucus gland and osphradium connected to them came to lie in frontal position below the shell above the head. The spiralization of the shell followed body torsion during the transition from pelagic to benthic life. The paleontological evidence allows also the model of a non-monophyletic origin of the Gastropoda. A plankton-feeding larva provided only with primary embryonic shell is noted only within the Docoglossa of the Archaeogastropoda, all others of this taxon existing since Ordovician time develop without planktotrophy. Archaeogastropoda tort their body during embryogenesis and mechanically spiralize their embryonic primary shell before the onset of benthic life. Within the Mimospirina representing a gastropod group that existed from the Late Cambrian to the Mid-Devonian the large smooth protoconch indicates a non-planktotrophic development as well, but without potential of a shell bearing larval stage. The Amphigastropoda (Bellerophonitida), in contrast, with existence from Late Cambrian to Early Triassic probably could develop a planktotrophic larva that carried a bilaterally symmetrical shell, as did the adult. If they represent torted molluscs, they had their own independent evolution. The ancestors of the three modern subclasses Neritimorpha, Heterostropha and Caenogastropoda evolved planktotrophic larvae that secreted shell during their growth and carried out spiralization of the shell during or after metamorphosis to benthic life. Only during Devonian time spiralization of the shell took hold of the larval and the embryonic portion of the shell, with members of the old peruneloid larval types still present among some Carboniferous species. In the Neritimorpha the non-spiralized embryonic shell has been preserved in the ontogeny of extant species, and coiling of the larval shell is very tight. Internal wall dissolution gave rise to the Neritoidea and their terrestrial relatives by Triassic time. The Euomphalomorpha with large cyrtconic protoconch and similar shell structure may represent relatives to the early Neritimorpha (for example Platyceratoidea) that have abolished planktotrophy or failed to develop it. Members of this group lived from the Late Cambrian to Permian, perhaps Triassic time. Within the Heterostropha the Allogastropoda gave rise to species of *Cylindrobullina*-like shape in the Triassic from which Opisthobranchia as well as Pulmonata may have developed. In contrast to the Caenogastropoda the spiralization of the protoconch in Heterostropha was sinistral and less solidly genetically implanted so that among the Pteropoda, the shell became straight, or the Ancyliidae evolved limpet shape without trace of a spiral shell. In the Caenogastropoda the embryonic shell is well differentiated from the larval shell in regard to shape and ornament, and there may have been several lineages leading from Peruneloidea-like Silurian and Devonian forms to Ctenoglossa, and species with protoconchs resembling that of the Littorinimorpha, Cerithiimorpha or Strombimorpha. During the Mesozoic several evolutionary pushes produced the Cerithiimorpha/Littorinimorpha in the Triassic, the Strombimorpha with beginning of the Jurassic and the Neomeso- and Neogastropoda during late Early Cretaceous.

Keywords: Gastropodes, evolution, systematic palaeontology, ontogeny, phylogeny.

Introduction

"The present is the key to the past", is one of the general statements one uses as a common approach to palaeontological reconstructions. But when it comes to the reconstruction of the evolution of the gastropods the opposite is also true, and the past represents the key to their present classification. Whatever theory of evolution one may prefer in the analysis of the phylogeny of living gastropods, evidence to support it must come from the fossil record. Gastropods carry with them a shell with characters formed during almost all stages of ontogeny ranging from the embryo to the fully grown adult. The comparison of individual ontogenies in different gastropod taxa indicates that even though there is a basic course of development present many variations are superimposed onto it at all stages of development. In a complex and camouflaged way ontogeny, thus, reflects the historical course of evolution of the snail in question. This model proposed by HAECKEL (1866) can be implied as a useful tool to understand the evolution of the molluscs in general and the gastropods in special. BAER (1940) pointed out that animals resemble each other much more in their early developmental stages than when adult. As was noted by NAEF (1911, 1924) that BAER's rule according to which characters appear in the ontogeny in the sequence of their respective phylogenetic age, comes close to the observable truth. It can be confirmed that every stage in ontogeny and each level in ontogeny follows its own evolution (ANDRÉ 1988). Each stage of ontogenetic development has its own phylogeny, as was stated by GRANDJEAN (1957) in the study of insects. But it also has to be recognized that ontogenies never deliver data to the complete phylogeny and have been adapted to the needs of the individual of the growth stage in question.

Unquestionable fossils of gastropods come from rocks of Ordovician age, and thus, gastropod evolution spans a time of at least 400 million years. The morphology of the shell reflects general trends in gastropod phylogeny, but it needs to be deciphered. Among the four supertaxa of Gastropoda living today the Archaeogastropoda and here selenimorph groups as the Pleurotomarioidea and trochomorph groups like the Trochoidea can be recognized in species that lived during the Ordovician period. Neritimorpha are safely determined from Silurian deposits and most probably also developed during the Ordovician (BANDEL 1992a). The earliest recognized protoconch of a species of the Heterostrophia comes from Mid Devonian rocks (BANDEL 1994a). With the Early Carboniferous the Caenogastropoda become recognizable (BANDEL 1993a). It has to be taken into account that there are still large gaps in our knowledge of Paleozoic gastropods. A review of some species of the seemingly well established gastropod superfamilies Murchisonioidea, Subulitoidea and Loxonematoidea reveals that they are not monophyletic, but that some of their members belong to different supertaxa (FRYDA & BANDEL in press). The name giving type spe-

cies to *Murchisonia* from the Mid Devonian may be an archaeogastropod or a caenogastropod. *Murchisonia*-like species in the Early Devonian of the Prague Basin proved to represent archaeogastropods and others from the Carboniferous of the USA are caenogastropods (own observations). The type of *Subulites* is an Ordovician fossil without closer systematic relation revealed, while Carboniferous representatives are in part Caenogastropoda, Heterostrophia and a still unknown taxon probably close to the Peruneloidea (FRYDA & BANDEL in press). *Loxonema* is based on a Later Silurian type, which may never be known closely, but Mid-Devonian and Carboniferous species of this genus belong to the Caenogastropoda and Heterostrophia, earlier ones probably are Archaeogastropoda of the order Stylogastropoda (FRYDA & BANDEL in press). The excellent fauna of the Late Triassic St. Cassian Formation of the Italian Dolomites is evidence for a long history of the class gastropoda preserved from a reef at the tropical sea of that time in which ancestors and relatives of many still living taxa can be recognized (BANDEL 1991a,b, 1992a,b, 1993a,b,c, 1994a, 1995, 1996a). From there on the fossil record becomes much more detailed, and the revolution in the Early Cretaceous during which Neomeso- and Neogastropoda evolved is quite well established with fossils.

Ontogenies of many ancient gastropods can be related to modern ones that have been studied in detail in the living fauna. When the early parts of the shell are preserved, fossils can be clearly recognized by characters of their shell. Carboniferous gastropods for example hold representatives of the four extant subclasses, but also such of extinct groups such as the Euomphalomorpha. In the Early Devonian in contrast only the Archaeogastropoda can be recognized, while the others are represented by species of stem groups. With our present knowledge it is up to date impossible to indicate those species that may be ancestral to most of the Carboniferous and later Neritimorpha, Caenogastropoda and Heterostrophia (FRYDA & BANDEL in press). It is sure to state that fossil gastropods must be included into a system of the phylogenetic relationships of Recent gastropods, if the resulting system is to be considered the evolutionary truth. Gastropods known only from the fossil record are just as real components of the evolution of this class as are modern gastropods. Without considering the fossil forms a representation of the phylogenetic relationships of modern gastropods would be quite incomplete.

What is a gastropod?

The development of the rudiment of the mantle on the gastropod embryo can be interpreted as the accelerated formation of mantle and shell as it occurred in the aculiferan ancestors after they had established themselves as benthic animal. Like modern Placophora the primitive molluscs developed a shell only after the free swimming

larval stage had been completed and during the transition and establishment to the benthic stage of life. Placophora produce a dorsal mucous layer into which a mineral shell is secreted and continued growth of the post larva is more organized for it (for references see BANDEL 1982). It is quite possible that some of the small limpet-like shells found in the early Cambrian produced their shell in a similar way as is seen in modern chitons. Relatives of Cambrian aculiferan molluscs may well have had one univalve shell of cap-like shape and calcareous construction. If so this shell remained attached to the mantle edge throughout life. The mantle margin may also have held calcareous spines and scales as is found in the mantle of the Aplacophora and the girdle of the Placophora. An Early Cambrian transitional species may have transferred the process of shell formation from the young adult organizational stage into its larval stage. The larval stage probably was like a "trochophora" as found in the Placophora, like the non-shelled veliger seen in some bivalve larvae before formation of a shell gland (BANDEL 1987), or like that seen in the early ontogeny of some Docoglossa (MORSE 1910, SMITH 1935). In Placophora a well organized periostracum as found in the Conchifera with appearance of the first shell forms only after first mineralization has occurred, while this process is reverted in the Conchifera. Deposition of mineral shell may have been retarded, and thus, the sequence of events changed so that the production of a well organized organic shell (periostracum) was carried out by the cells of the mantle in advance of their mineralization. This proterogenetic process may have resulted in a rather prominent functional change that eventually gave rise to the Conchifera. Their appearance in time is indicated by the first true bivalves in late Lower Cambrian times (POJETA & RUNNEGAR 1985, BENGTSON et al 1990, HINZ-SCHALLREUTHER 1995) and first undoubted cephalopods in Late-Cambrian times (YEN & TEICHERT 1983). Cambrian gastropods still remain problematic (PEEL 1991, own observations).

Torsion of the soft body changing the position of the anus and the pallial complex as well as crossing the nervous system has been considered the main feature of the gastropods since last century and GARSTANG (1929) reached the opinion that torsion made its first appearance in the veliger larva. He suggested that torsion arose as a larval adaptation that was carried over into the adult stage, the adults being then compelled to cope with the resulting situation. If this idea is correct, torsion should be more advantageous to the larva than to the adult. A handicap in GARSTANG's idea is his assumption that prior to torsion the protective value of the larval shell was limited because the delicate head and velum could not be withdrawn into the posterior mantle cavity until the foot had been withdrawn. Torsion supposedly facilitated the withdrawal of the head and velum, because the mantle cavity moved into a more favourable position. According to STANLEY (1979) it is nearly impossible for an untorted gastropod-like mollusc to evolve an operculum. STANLEY's problem can be

comprehended when his fig.6 is taken into reconsideration. Here the operculum and head foot have to enter the mantle cavity when the retractor muscle contracts. In real life the head foot is not retracted into the mantle cavity (BANDEL 1982). The argument of GARSTANG (1929) has thus lost its base. JÄGERSTEN (1972) had also regarded this scenario as an unlikely one, but suggested that the phylogenetic appearance of the phenomenon of torsion occurred gradually in the adult phase to be shifted later to the pelagic larva. His view was confirmed by BANDEL (1982) when the embryonic development of several archaeogastropods was analysed. The predominance of not well spiralized larval shells in Early Devonian and older species of gastropods that could represent relatives to the stratigraphically younger Caenogastropoda and Heterostropha also points in that direction (FRYDA & BANDEL in press) as do the interpretations of torsion suggested by RIEDEL (1996).

The most simple ontogeny of the Archaeogastropoda

The embryo of a member of the Archaeogastropoda first forms a bilaterally symmetrical primary shell that detaches from the glandular cells of the mantle as soon as it has grown to a size that is sufficient to contain the soft body in its shelter and retractor muscles have formed (BANDEL 1982). Only afterwards the visceral mass is twisted by about 180° due to differential growth of its epidermis. Thus, head foot are rotated in relation to the shell. During the process of body torsion the growing foot changes its position from lateral/dorsal to ventral. The shell is later transformed into the trochospiral, usually dextral coil aided by the activity of muscles. Two muscle bundles are usually attached to the inner side of the shell and continue into body and foot. The shell is deformed when the foot with its dorsal operculum is pressed against the outer side of the shell while muscle fibres pull being attached to the inner side. Muscles are usually attached asymmetrically to the inside of the shell, a lateral twist, thus, results in a dextral, rarely in a sinistral coil during the deformation process. After the shell has been pulled into spiral shape it is mineralized from within and, thus, fixed in shape. During this rapid process aragonitic crystallites grow into the organic material of the primary shell which is mineralized thoroughly. The weaker of the two muscle bundles detaches from the shell, and the stronger transforms into the columellar retractor muscle (BANDEL 1982, HASZPRUNAR 1993).

This mode of shell coiling due to mechanical deformation and subsequent stabilization in shape by mineralization represents a key innovation in the archaeogastropod branch of the gastropods that is recognized since the Ordovician period. Aside from the portion of ontogeny reflected in the shell some other features characterize Archaeogastropoda. Their eggs are surrounded by an envelope when fertilization occurs. Commonly eggs are fer-

tilized outside their body. Spermatozoans of the archaeogastropods resemble those of the bivalves and the scaphopods, but also those of other bilateral metazoans which fertilize their eggs in the sea water outside of the body (HEALY 1988). Sperma has to enter through the cover of the egg and the egg envelope to fertilize the ovum. This kind of fertilization can be considered as basic one among molluscs and is observed in Placophora, Bivalvia, Scaphopoda, and slightly altered in Cephalopoda. Since the egg envelope of the archaeogastropods is porous, no liquid albuminous yolk is stored around the egg. All the yolk that is used in development of the embryo is contained within the egg itself. In the order Vetigastropoda (= Rhipidoglossa without Neritimorpha) the smallest size of eggs lies near to 0.1 mm and the largest near 0.8 mm with average between 0.2 and 0.5 mm. The shell, thus, reflects the size of the embryonic shell so that egg size of fossil species can be evaluated from the dimension of the first shell whorl.

The rudiment of the mantle (shell gland) consists of a flat disk of cells which differ from the other ectodermal cells by being higher and closer to each other. The first cells of the mantle secrete the shell. Cells and shell remain connected to each other until the shell has grown to a size that is large enough to hold the body in its shelter. Before dissolution of glandular cells from shell margin the mantle attaches to the shell at two spots, where muscular fibres find their attachment to connective tissue below the mantle cells. With this new attachment in place the shell can be put into its function serving as exoskeleton. The primary or embryonic shell of the Archaeogastropoda is succeeded by the teleoconch. (pl. 1, fig. 1)

The larval shell enables marine species to construct a shell that serves and grows on a free-swimming larva that feeds on planktonic organisms. A first trace of such a larval shell (or rudiment of the former presence of a larval shell) is found among such Archaeogastropoda that swim in the sea for a while after hatching from their egg capsule. (pl. 1, fig. 2) Here a narrow additional growth of shell occurs that is added to the rounded margin of the primary shell and reshapes the outer lip of the aperture with a median lobe and two lateral sinuses (BANDEL 1982, 1993b). These rhipidoglossan larvae did not feed while swimming in the plankton. In all other gastropod subclasses an additional shell may be secreted between embryonic shell and teleoconch. The ontogeny is, thus, extended by a planktotrophic larval phase. The larval shell differs from the shell of the embryo, and the shell produced after metamorphosis. The presence of a larval shell is quite visible in Neritimorpha, Caenogastropoda and Heterostrophia even when transformed and fused with the embryonic shell due to yolk uptake within the egg mass or the body of the female. Also cleavage patterns and mesoblast formation within the archaeogastropod ontogeny differs from that of the Caenogastropoda, Neritimorpha and Heterostrophia (mesoblast forms later in archaeogastropods) (BIGGELAAR & HASZPRUNAR 1996)

thus supporting the evolutionary pattern suggested by the fossil record.

Members of the archaeogastropod order Docoglossa (= Patellogastropoda) produce an embryonic shell like that of the Archaeogastropoda in general, but in addition may feed on plankton (DODD 1955). Docoglossa own a "trochophora" stage of larval development during which there is a mouth and anus, but no shell (pseudotrochophora according to SALVINI-PLAWEN 1980, praeveliger according to FIORONI 1979). Species of *Patella* and *Acmaea* may feed on plankton even though they have no velar lobes when starting their pelagic larval stage. *Patella vulgata* for example has young hatching from the egg without shell and swim with two ciliary rings, and one of the rings disappears during embryonic development (NIELSEN, 1987). Within the first days of their development they grow a shell just like that of the other Archaeogastropoda and will also metamorphose without enlarging this shell. Docoglossan larvae may feed with simple ciliary corona and some cilia that surround the mouth (SCHARENBERG, pers. com.), in contrast to all Vetigastropoda with known ontogeny. JÄGERSTEN (1972) and STRATHMANN (1978) emphasized the concept that an evolutionary loss of the planktotrophic larva is irreversible. Such a loss may have occurred during the evolution of the Vetigastropoda while the pelagic feeding capacity is still found among the Docoglossa. Only the Docoglossa have a feeding larva that can remain free swimming beyond the reserves provided to them by the egg yolk (DODD 1955, KESSEL 1964). Thus, modern Archaeogastropoda can be divided by reasons of differences in their ontogeny into the two subtaxa Docoglossa and Vetigastropoda (SALVINI-PLAWEN & HASZPRUNAR 1987). While a chitinous supporting rod in the ctenidium is a character of the Vetigastropoda it has retained the original unsupported hydroskeleton in the Docoglossa (SALVINI-PLAWEN & HASZPRUNAR 1987). The Docoglossa (= Patellogastropoda) represent the sister group to the Vetigastropoda (including most Cocculiniformia), and both together represent the Archaeogastropoda that may find their closest relatives in the Amphigastropoda on one side and the other three subclasses (Neritimorpha, Caenogastropoda, Heterostrophia) on the other side (BANDEL & GELDMACHER 1996). FRYDA & BANDEL (in press) recognized a third group, the Stylogastropoda, that represent archaeogastropods with slender turritiform shells of the type found in *Loxonema* and *Palaeozygopleura*. This group has lived in Ordovician to Devonian time and has since disappeared.

The simple but feeding larva of the Docoglossa and the even more simple larva that occurs in the bivalve *Teredo* (BANDEL 1987) can be taken as evidence for the presence of an original planktotrophic phase in the development of conchiferan molluscs even before the food sorting velum had evolved. Therefore a direct homology between the metatrochal ciliary bands of the veliger larva and the annelid/echiurid trochophore as suggested by

NIELSEN (1985, 1987) could only be supported if the larva of Docoglossa are to be regarded as secondarily simplified, having lost their veliger mode of feeding and utilizing a more ancient and simple feeding mode. Vetigastropoda among the gastropods and as well as Protobranchia among the bivalves may have lost their planktotrophic feeding and substituted it by yolk reserves. Docoglossa and Scaphopoda may still have simple planktotrophic larvae (SCHARENBERG in prep.), the eulamellibranchiate bivalves and higher gastropods can still activate this old constructional plan, if needed (BANDEL 1982, 1987).

Inclusion of the model *Bellerophon* as gastropod: Amphigastropoda

Archaeogastropoda perform torsion of the body after the shell has been formed. All other extant gastropods secrete a shell only after the shell-less soft body has been tortured due to differential growth of its tissues. Thus, Archaeogastropoda differ from all other living gastropods by the timing of torsion of the visceral mass in relation to shell formation. The sister group of the Gastropoda, the Cephalopoda still have retained the type of mineralization that is found among the Archaeogastropoda (BANDEL 1982, 1986, 1990). Archaeogastropoda reflect in their ontogeny the difference in timing between torsion of the soft body and spiralization of the shell. Thus, a stage of gastropod evolution can be imagined in which the soft body torsion occurred even later in ontogeny as is the case in Archaeogastropoda. NAEF (1911) considered the bellerophonitids (Amphigastropoda SIMROTH, 1906) to represent gastropods in which torsion of the body occurred during the early benthic stage while the shell remained to grow in a totally symmetrical way. Thus, bellerophonitids may represent such gastropods where the soft body tortured after embryogenesis was completed and the shell mineralized. But since they became extinct during Early Triassic time anatomy can no longer be analysed directly.

Bellerophon and its relatives are gastropods, the presence of crossed lamellar structure in Fissurellidae/Scissurellidae, the Phasianellidae and their relation and some Skeneidae could represent a very old character of shell structure that formed very early in gastropod evolution (MAC CLINTOCK 1967, ROLLINS et al. 1971, BATTEN 1972, BANDEL & GELDMACHER 1996). McLEAN (1984) suggested that the Fissurellidae are the logical limpet derivatives of the Bellerophonitoidea. WENZ (1938) and among the more recent authors among others RUNNEGAR (1981, 1983) considered Bellerophonitoidea to represent untorted molluscs that may be related to the Monoplacophora. KNIGHT et al. (1960) and among other more recent authors PEEL (1980, 1991) presented arguments for their gastropod nature. Muscle scars have been considered as indicator for the tortured as well as the untorted nature of the Amphigastropoda, but number and position of muscle scars are related primarily to shell form and mode of life (FRETTER & GRAHAM 1962, HARPER & ROLLINS 1982,

BANDEL 1982). WAHLMANN (1992) considered the presence of a slit generating a selenizone as strong evidence of a close affinity between the bellerophonitoids and the pleurotomaroids. This later author suggested that Bellerophonitoidea represent Archaeogastropoda that had arisen from trochispirally coiled ancestors by secondarily becoming planispirally coiled again. This idea can be rejected based on the morphology of the early ontogenetic shell. In members of bellerophonitid molluscs from the Ordovician, the Silurian, and the Carboniferous the early ontogenetic shell was analysed, and it is bilaterally symmetrical, has no fold or other feature of deformation on it. The protoconch consists of more than one whorl and may well have formed by a planktotrophic larva. There is no transition noted between an embryonic and a larval shell, but preservation may not be good enough to be sure of that (see also DZIK 1994). If Amphigastropoda characterized by *Bellerophon* and related genera were tortured molluscs, they could represent the sister group of the Archaeogastropoda (BANDEL & GELDMACHER 1996). Only due to selective reading omitting much of the controversial discussion concerned with gastropod torsion RUNNEGAR (1996) assumed that torsion is unobservable and can not be used in tracing the potential stem group gastropods. He suggested that tighter coiling present in Cambrian helcionellids, bellerophonitids and gastropods provided the rotational flexibility required for the initiation of torsion, but that it is unclear which of the early coiled univalves did in fact tort their body. RUNNEGAR (1981) stated that torsion is directly linked to the evolution of asymmetrical coiled shell and therefore RUNNEGAR (1996) concluded that the bilateral symmetry of the bellerophonit shell must be secondarily evolved if bellerophonitids are to be placed within the gastropods. This reasoning fails due to the mode of ontogeny of modern archaeogastropods as well as to the occurrence of openly coiled protoconchs of the Paleozoic Peruneloidea (see in the following).

Slit bearing bellerophonitoids seem to have appeared in the Late Cambrian with a single genus *Chalarostrepsis* KNIGHT and in the Early Ordovician only *Eobucania* KOBAYASHI is present. Radiation begins with the late Middle Ordovician. WINGSTRAND (1985) united the Gastropoda, Cephalopoda and Bellerophonitida within the hypothetical superclass Cyrtosoma. If this concept is correct, the proposed separate class by SIMROTH (1903) of molluscs for the bellerophonitids which he termed Amphigastropoda could be accepted.

Gastropoda with planktotrophic veligers

The taxa that can be considered as of about equal level in the system, Neritimorpha, Caenogastropoda and Heterostrophina consist of species that have a planktotrophic veliger that produces a spirally coiled larval shell or such species that have ancestors with such a larval phase in their ontogeny. From the paleontological record there is

no reason to assume that all three taxa have the same ancestor, but HASZPRUNAR (1995) suggested that the similarity of the metatrochal ciliary bands proven to exist among Caenogastropoda and Heterostrophia and assumed to be also present in the Neritimorpha represent a direct homology and, thus, a indication for a common origin of planktotrophy and a common ancestor. The primary or embryonic shell of the Archaeogastropoda is succeeded by the teleoconch. In all other gastropod groups an additional shell may be secreted that lies between the embryonic primary shell and the teleoconch. In these cases ontogeny is extended, and the larval shell differs from the primary shell and from the postmetamorphic shell. Such larval shells can be found on gastropods since Early Carboniferous times (KNIGHT 1930, HERHOLZ 1992, YOO 1989, 1994, BANDEL 1991a,c, 1993a, 1994a).

It still remains mysterious how Caenogastropoda with their right coiled shell and Heterostrophia (= Heterobranchia) with the left coiled protoconch and right coiled teleoconch are related to each other. They certainly are different taxa by about Mid Devonian and safely by Early Carboniferous time (BANDEL 1994a, 1995, 1996a), but they have not been found prior to that, for example in Early Devonian time (FRYDA & BANDEL in press).

Eggs of all living gastropods with exception of archaeogastropods are covered with an additional capsule after fertilization. They have been fertilized in the interior of the femal genital tract. Three groups of spermatozoan morphologies can be distinguished. One encompasses the Caenogastropoda, the second the Heterostrophia and the third the Neritimorpha (HEALY 1988). It seems as if all three have developed independently from each other starting out with sperm morphology as found among the archaeogastropods. JÄGERSTEN (1972) suggested that the storage of an abundance of yolk in the egg or of special nutrients in the egg capsule has allowed the entire larval phase of the life cycle to take place inside the envelope in many evolutionary lines of the gastropods. Within the Neritimorpha and the Caenogastropoda many eggs may be contained within one and the same egg capsule, so that they may in part be used as nurse eggs during development. Semipermeable egg capsules also allow the egg case to hold back yolk and have an embryo swimming in liquid nutrients, as may be found in all three taxa.

The plankton feeding veligers have several ciliary ribbons on the velar lobes as described by WERNER (1955) and FRETTER & MONTGOMERY (1968). These ribbons consist of two rows of cells with single cilia and two rows of cells with compound cilia (NIELSEN 1987). These later cilia produce the water current that keeps the larva swimming and produce a downstream current from which food particles are collected in a groove between the composite ciliary bands. Thus, larvae move through the water, and at the same time collect particles which become entrapped between the ciliary bands. Food particles are concentrated in the groove and taken hold of by the shorter adoral cilia that transport them to the mouth.

Neritimorpha independence and its problematic Paleozoic relation

Neritimorpha with free larval development, during their embryonic development secrete a shallow concave and smooth primary shell. The shell detaches from the gland cells before it has grown to half a sphere. It is consequently mineralized and connects to the tissue at the same location which later is used for the attachment of the retractor muscle. Further shell growth is by accretion of shell increments. Mineralization is by aragonitic crystallites added to the outer organic shell wall on the inside of the shell. When the larva is ready to hatch, the embryonic shell resembles an egg with the upper part cut off obliquely. During the larval stage a convolutedly coiled shell is secreted that covers much of the embryonic shell and also covers much or most of the whorls produced by the younger larva. Thus, the protoconch is strongly convolute, and much of the former whorls are hidden below the last one (pl. 2, figs. 1, 2, 3).

Neritimorpha are commonly considered to represent archaeogastropods especially due to their complex rhipidoglossate radula. But the unique mode of development of the neritoid larval shell (BANDEL 1982, 1991c, 1992a) indicates the establishment of larval planktotrophy in the Neritoidea as an independent event in gastropod evolution. *Nerita* and *Neritina* form the first mantle and shell at a stage of development in which there is no anus or mouth present, but a slight trochospiral twist of the visceral mass indicates body torsion. The muscle cells of the retractor muscle begin to function even before the shell has grown large enough to cover the whole body. A pallial cavity may be present before or after hatching, and before hatching the animal can withdraw into its shell and seal the aperture with an operculum. The hatched larva remains in the plankton for weeks and feeds on algal cells. The inner walls of the larval shell are resorbed with the result that the shell interior does not change much in shape but becomes successively larger. Within the pallial cavity a current of water is kept going by a ribbon of cilia from the neck into the end of the cavity and from here on the roof to the shell margin. The velum of the pediveliger has four narrow lobes, and during metamorphosis it is resorbed and not discarded as in some caenogastropods.

Neritopsoidea are the most primitive Neritimorpha which occur from Early Devonian (*Naticopsis*-like species), Mid Devonian and Carboniferous in a greater number of genera (pl. 2, figs. 5, 6). *Neritopsis*-like species form a peak of diversity during the Triassic just to decrease in number of species and shell diversity during Jurassic and Cretaceous to only a few species today. Neritopsoidea have a characteristic calcareous angular operculum with two attachment scars of the retractor muscle on their inside and they retain inner shell walls.

The Platyceratoidea have been specialized parasitic forms that lived attached to crinozoans since Ordovician times. They developed limpet shell form and lost the oper-

culum. In *Orthonychia* from the Triassic St. Cassian Formation with teleoconch that closely resembles platyceratids of the Paleozoic, the earliest whorl is largely covered by the following whorl (pl. 2, fig. 1). The shape of the larval shell is spherical naticoid with dextral coiling and rapid expansion of whorl diameter. The margin of the shell of the fully grown planktotrophic veliger (pediveliger) is thickened and forms 6 thorn-like projections (BANDEL 1992a). The larval shell measures about 0.7 mm in diameter and consists of aragonitic shell material in crossed lamellar structure. A very similar species of *Orthonychia* lived in the shallow sea at Late Carboniferous times in Missouri, but has a protoconch with the shape of a vermiform hook consisting of one openly coiled whorl (KNIGHT 1934, own observations). (pl. 2, fig. 4). This may indicate that Neritimorpha also began to coil their protoconchs during Precarboniferous times as was made plausible for the ancestral Caenogastropoda (FRYDA & BANDEL in press).

The Cortinellidae (BANDEL in prep.) based on the small planispirally coiled genus *Cortinella* BANDEL, 1989 with the type *Euomphalus aries* LAUBE, 1868 from the Late Triassic St. Cassian Formation (BANDEL 1993b, pl. 3, figs. 5, 9) represent an independent lineage of the Neritimorpha as is indicated by its characteristic protoconch. (pl. 2, figs. 2, 3). This genus with small species only known from the Late Triassic may have larger relatives and Paleozoic ancestors in *Spirina* and similar forms that lived for example in the Silurian sea of the Prague Basin.

The terrestrial branch of the neritimorphs Helicinoidea may be present since Carboniferous times with *Dawsonella*. They represent land snails having a lung and a shell commonly resembling that of some pulmonate land snails like *Helix* (Heterostropha), but in contrast to the later having a calcareous operculum and a neritimorphan type of radula. They resorb the internal wall of their shell as is the case in the Neritoidea. Hydrocenoidea also resorb all inner shell walls but have a smaller and more high spired shell with a protoconch resembling that of *Theodoxus* or *Neritilia*. (pl. 2, figs. 7, 8). They live in the litter and among mosses in warm, wet climate and their fossil record is unknown.

A Paleozoic supertaxon, the Euomphalomorpha

The core group of Euomphalidae with the genera *Euomphalus*, *Straparollus*, *Serpulospira*, *Phymatifer*, *Schizostoma*, and *Philoxene* from Devonian to Permian strata are characterized by a cyrtconic openly coiled protoconch. (pl. 1, figs. 3, 4). This distinguishes them from members of the other four extant subclasses of the Gastropoda (Archaeogastropoda, Neritimorpha, Caenogastropoda, and Heterostropha) and places Euomphalidae at similarly high taxonomic level, the subclass Euomphalomorpha BANDEL & FRYDA, in press. With *Euomphalopsis* the group may have made its first appearance in the Late Cambrian (WEBERS et al. 1992) and with *Serpulo-*

spira it may still have been living at Upper Triassic time (BANDEL 1988, 1993b). Throughout existence of the Euomphaloidea other gastropod units developed convergent shell forms which can be detected by the morphology of the protoconch and, in some cases, the structure of the shell. In *Euomphalus* and relation the shell consists of an outer calcitic layer and an inner non-nacreous aragonitic layer (BATTEN 1984). It is important to note, that there are also other Paleozoic Gastropoda with open coiling in their initial part, but these differ by a more delicate protoconch size and morphology.

The Paragastropoda or Mimospirina

LINSLEY & KIER (1984) proposed to create the taxon Paragastropoda to hold the sinistral Onychochilidae KOKEN, 1925 and Clisospirinae MILLER, 1925 that lived from the Late Cambrian to the Mid-Devonian along with some other Paleozoic snail-like fossils. According to WÄNGBERG-ERIKSSON (1979) and DZIK (1983) their protoconch is simple and smooth, consists of about one and a half whorls and is of rather large size (about 0.5 mm). (pl. 1, fig. 5). Onychochilid/clisospirid teleoconchs are of conical shape with strongly inclined aperture and collar ornament. DZIK proposed the suborder Mimospirina to include Onychochilida and Clisospirida and considered them to represent gastropods as had done WENZ (1938). LINSLEY & KIER (1984) reconstructed them as being untorted and, thus, not gastropods, but some other type of molluscs. *Mimospira* is a characteristic Ordovician fossil found in all parts of the world. To our knowledge up to now these sinistral gastropod-like fossils may have been gastropods or not, and they seem to have arisen from unknown relation. They disappeared in the Devonian without successors. The Carboniferous *Onychochilus minutissimus* described by YOO (1988) is so small that even though its shape resembles that of early Paleozoic species of *Onychochilus* it probably represents the larva of a member of the Heterostropha or is the larval shell of a sinistral caenogastropod.

A puzzling ontogenetic shift in coiling direction during early ontogeny: Heterostropha (= Heterobranchia)

Heterostropha FISCHER, 1885 have a sinistral embryonic shell and a sinistral larval shell that may change coiling direction within the larval portion of the shell or at its end in transition to the teleoconch. (pl. 3, figs. 1, 2). Three larger units can be recognized within this subclass, the Allogastropoda HASZPRUNAR, 1985, the Opisthobranchia MILNE & EDWARDS, 1848 and the Pulmonata CUVIER, 1817, all of which have this character of the protoconch in such species that have a free marine feeding larval stage. The presence of heterostrophic protoconchs in Streptacidoidea (Allogastropoda) in the Mid-Devonian (BANDEL 1994a) demonstrates the antiquity of the taxon.

Carboniferous and Permian species of the Streptacidae are usually minute (KNIGHT, 1931) and resemble modern *Ebala* of which Triassic and Jurassic representatives are known (SCHRÖDER 1995, BANDEL 1996a). Donaldinidae from the Carboniferous differ by having a prominent spiral ornament, and protoconch position is flat on the apex (YOO 1988, 1994). Representatives of this ancient family are still alive (BANDEL 1996a). Mathildoidea and Architectonicoidea had numerous species living in the tropical sea in the Late Triassic, and here without transitional forms to connect them (BANDEL 1988, 1994a,b, 1995, 1996a). They can be grouped in the families Architectonicidae, Sturaxidae, Cassianaxidae, Amphitomariidae, Omalogyridae, and Glacidorbiidae among the low to planispirally coiled Architectonicoidea and Mathildidae, Anoptychiidae, Tofanellidae, Ampezzanildidae, and Trachoeidae among the Mathildoidea which demonstrated their rich differentiation in Late Triassic time. The allogastropodan branch Pyramidelloidea with the many extant parasitic species appears quite late in the geological record (SOHL 1964, DOCKERY 1995, BANDEL 1996a) and Nerineidae are a characteristic group of lagoonal species from Jurassic and Cretaceous tropical seas (VAUGHAM 1988, KOWALKE & BANDEL 1996) that disappeared at the end of the Cretaceous.

A basic change occurred when heterostrophic families settled fresh water and land, and the shell was simplified during the process of liquid egg yolk feeding in exchange for the planktotrophic larval phase. Valvatidae live in fresh water and still have extant marine relatives united in the family Cornirostridae (PONDER 1990a,b). The marine branch has been living in Tethyan waters at late Triassic times (BANDEL 1996a), the Jurassic Sea (GRÜNDEL 1997) and the Early Cretaceous of Poland (SCHRÖDER 1995). Provalvatidae represent transitional species that lived in brackish and freshwater during Late Jurassic times (BANDEL 1991d) and forms similar to modern *Valvata* with simplified planispiral protoconch are found with *Ariomphalus* from the Late Cretaceous (BANDEL & RIEDEL 1994a).

Among the Pulmonata the Basommatophora are the more ancient appearing in the Jurassic while the Stylommatophora diversified during the Cretaceous. Archaeopulmonates with the Ellobiidae are usually found in the intertidal mud flats, rubble zones, coastal forests, and swamps. They can safely be traced to the Late Jurassic (BANDEL 1991d). Perhaps Misurinellidae from the late Triassic with *Misurinella* which is very close in shape to the modern *Blauneria* of the Ellobiidae H. & A. ADAMS, 1855 belong here (BANDEL 1994a). The Ellobiidae represent the modern core group of the Archaeopulmonata MORTON, 1955 (= Mesommatophora HUBENDICK, 1947), and are the least specialized of the three suborders of the Pulmonata. In their ranks many species are found with a planktotrophic larva and the characteristic heterostrophic protoconch, and if development is lecithotrophic, a veliger stage can be recognized to occur within the egg

capsule. Two groups of the Archaeopulmonata have entered the fresh water. The first are the Chiliniidae which are found in rivers and lakes of southern South America and their limpet-like relatives, the Latiidae, live in river rapids of New Zealand. The second are the Carychiidae which may even be present on land since Upper Carboniferous time with the genera *Anthraxopupa*, *Maturipupa* and *Dendropupa*. *Carychium* during its ontogeny still forms a sinistral embryonic shell, but no operculum as is the case in Chiliniidae (DOLL & SANDER 1985, own observations). The small snails live in wet litter and moss in springs and forests. Their potential presence in the Late Carboniferous contrasts to the comparatively late appearance of pulmonates like Basommatophora and Ellobiidae in the early Mesozoic.

Also the evolution of another lung bearing group of Heterostrophia is problematic. Amphibolidae occupy a similar amphibious environment in the Eastern Pacific area and most abundantly in Australian and New Zealand as do the Ellobiidae, but no paleontological record is available of these. This is probably due to their convergent shell shape with naticoid species of the Caenogastropoda. The limpet-like Siphonariidae and Trimusculidae that live on rocky shores may be represented by a number of genera from the Jurassic and Cretaceous. Their characteristic sinistral protoconch has been recognized from the Campanian of Mississippi by (DOCKERY 1995). Their close relation to the other archaeopulmonates has recently been questioned (TILLIER et al. 1996), which accounts also for the Amphibolidae.

The Basommatophora KEFERSTEIN, 1864 live in fresh water, and the Stylommatophora SCHMITT, 1855 live on land. The Basommatophora during early ontogeny invaginate the shell gland coupled with a retardation of the secretion of the primary shell (heterochroneously due to neotony). Thus, the early ontogenetic shell has peculiarities separating them from all other Gastropoda and also the other Heterostrophia. A larval phase is totally omitted, and the shell has, thus, become coiled in the mode of the adult. The veliger stage is reflected by only a ribbon of cilia that have semicircular shape on the head and end in the mouth without forming lobes. The foot has lost the operculum.

Stylommatophora SCHMITT, 1855 become recognizable during the Late Mesozoic with some doubtful species (BANDEL 1991d), but with better recognized taxa in the Late Cretaceous (HRUBESCH 1965, SOLEM 1978, BANDEL & RIEDEL 1994a). Thus, in contrary to WENZ & ZILCH (1960) and SOLEM & YOCHELSON (1979) stylommatophoran snails have no Paleozoic origin; which was supported by rRNA sequence studies carried out by TILLIER et al. (1996) and confirmed a Late Mesozoic derivation of this large group of gastropods.

Members of the Opisthobranchia are not recognized among Paleozoic Heterostrophia, but Cephalaspidea FISCHER, 1883 (= Architectibranchia HASZPRUNAR, 1985) are represented by members of the Cylindrobullinoidea

from the Late Triassic and Jurassic (SCHRÖDER, 1995, BANDEL 1991c, 1994a). Actaeonoidea and Ringiculidae can be traced from the Jurassic (SCHRÖDER 1995, GRÜNDEL 1997a,b) in a continuous lineage to the modern species. Bullomorph opisthobranchs appear in the Cretaceous and pteropods as well as nudibranchs appear during the early Tertiary. Pteropods differ from the normal way of the Heterostropha by retaining the originally sinistral larval shell throughout adult life (BANDEL et al. 1984). Early pteropods may have become pelagic by production of a mucus raft on which all extant thecosomatous pteropod species drift through the sea (GILMER & HARBISON 1986, LALLI & GILMER 1989).

The idea expressed by STANLEY (1979) that modern opisthobranch snails like *Acteon* seem frozen at grades of evolution intermediate between the ancestral prosobranch state and the derived opisthobranch condition is not confirmed by the paleontological record. It cannot be supported that opisthobranchs and their ancestors among the allogastropods actually had caenogastropod ("prosobranch") ancestors. There is no fossil known that could represent such a transition of species and it would have to be a species that lived prior to the Mid-Devonian. HASZPRUNAR (1988) proposed a common ancestor of Caenogastropoda and Heterobranchia (= Heterostropha) with metatrochal ciliary bands in the veligers of both groups. This possibility is still open, but these veligers may have had an openly coiled shell as found in the Late Silurian and Early Devonian Peruneloidea. PONDER (1991) proposed the derivation of the Heterostropha from a small sized stem species with lecithotrophic development. Accordingly PONDER assumed an independent evolution of larval planktotrophy in Caenogastropoda and Heterostropha. This interpretation can also not be supported by paleontological evidence.

Within the Heterostropha groups evolved that secondarily simplified their early ontogenetic shell by uncoiling larval and embryonic shell, as for example in the case of many Pteropoda BANDEL et al. 1984, BANDEL & HEMLEBEN 1995). Thecosomatous pteropods also continue to construct their larval shell throughout life and this shell may even become reshaped in some Cavolinidae. Within some eolidid nudibranchs embryos construct a shell that is large enough that the larva after hatching can grow into it. Thus, these species produce only an embryonic shell and no larval shell, even though they have an ontogenetic phase as planktotrophic veliger, before they discard their shell as a whole. Other nudibranchs among the opisthobranchs produce a larval shell before the shell is discarded during metamorphosis. Among the basommatophoran pulmonates shell coiling can be totally abandoned, as is the case in *Ancylus* and relation since Late Cretaceous (BANDEL & RIEDEL 1994a). This flexibility in some of the more modern groups of the Heterostropha contrasts to what we know from the Caenogastropoda where embryonic shells remain coiled and a reconstruction and change in constructional timing of the shell is much more fixed.

Early Devonian Peruneloidea as potential ancestors to the Caenogastropoda and Heterostropha with openly coiled protoconch

The Peruneloidea were created by FRYDA & BANDEL (in press) to hold Early Devonian gastropods from marine deposits of the Prague Basin with small dextrally coiled teleoconch and a planispirally and openly coiled protoconch (pl. 1, fig. 6). Besides members of the Perunelidae with hydroboid teleoconch Chuchlinidae with subulitiform teleoconch are represented by this group. The initial (embryonic) portion of the protoconch is straight and small (about 0.1 mm), and curving of the shell begins later. In many cases only the protoconchs not connected to a teleoconch are found which measure fully grown about 0.5 mm in diameter. This can be interpreted in two ways. The first is that this small shell was calcified when it was embedded and could thus fossilize. The second is that the young, probably freshly metamorphosed animal did not find the right conditions to live and grow a teleoconch. This is a very common feature seen in almost all modern species with a planktotrophic larva. When these have to perform metamorphosis at a late stage of their larval existence they have to do so whether conditions are good for further growth or not. The larval shell is usually only slightly mineralized as long as the animal swims within the plankton, but rapidly mineralizes when the animal settles for benthic life. If the shell is deposited prior to metamorphosis its mainly organic shell is usually rapidly decomposed by bacteria. But after metamorphosis and shell mineralization the juvenile can only grow on when it has settled in the right environment that allows the young to feed and grow. Preservation of such freshly settled but starved animals is common now and has been so in Ordovician and Silurian times, and if preservation due to special conditions of diagenesis were right, many of these small shells were preserved as described by BOCKELIE & YOCHELSON (1979) and DZIK (1994). They were usually not connected to a teleoconch and thus not recognized as belonging to the apex of a normally trochospirally coiled shell.

The Early Devonian fauna from the Prague Basin bears many species of gastropods, among them many archaeogastropods and the Peruneloidea. With all caution this can be interpreted that during this time and prior to the presence of well recognizable Heterostropha and Caenogastropoda potential ancestors of these had a planktotrophic larva that started to coil its shell only when close to metamorphosis to the benthic animal. In contrast to Heterostropha and Caenogastropoda the embryonic shell was still uncoiled, and coiling began within the larval shell. If the interpretation is correct that Peruneloidea belong in the stem group of the Caenogastropoda and/or Heterostropha, spiral coiling can be interpreted as a process that developed in the benthic stage and migrated into successively younger ontogenetic stages, reaching that of the embryonic shell last. It also is evidence for a long last-

ing split between Archaeogastropoda on one side and the others with larval phase of shell growth preserved from Ordovician rocks. (pl. 1, figs. 7, 8).

Caenogastropoda and their complex evolution and timing

Caenogastropoda have an embryonic shell formed after body torsion is completed. After hatching a larval shell with characteristic shape and ornament forms in those groups that have a free planktotrophic larval life. The alternative to exchange larval existence to parental care or yolk rich spawn was always present in marine groups, documented since the Carboniferous (BANDEL 1991a,c, YOO 1988, 1994). But almost all marine genera and suprageneric taxa have species that have a planktotrophic development, thus produce a larval shell that jointly with the embryonic shell provide useful information for phylogenetic reconstructions. Caenogastropoda with clear evidence from preserved protoconchs exist from the early Carboniferous onward. It can now be firmly established that well known Palaeozoic taxa such as Loxonematoidea, Murchisonioidea and Subulitoidea (pl. 1, figs. 7, 8) are not natural and monophyletic taxa, but represent a mixture of convergent species belonging to different subclasses. Some species from the Carboniferous that were placed in these taxa are Caenogastropoda, but at present in no case the type to the genus on which the name of these superfamilies is based (*Loxonema*, *Murchisonia*, *Subulites*) can be classified with accuracy.

From the Triassic onward many systematic units can be traced more or less faithfully to their modern descendants (BANDEL 1993a); (pl. 3, fig. 4). It can, for example, be clearly demonstrated that Neogastropoda and Neomesogastropoda (= higher Mesogastropoda) have the same origin in the Early Cretaceous (BANDEL & RIEDEL 1994b, RIEDEL 1994, 1995). The superfamily Calyptraeoidae is on equal ranks with the other superfamilies of the Neomesogastropoda and the Neogastropoda all having evolved from a stem group that lived at Aptian/Albian time and had the option to form a long term planktotrophic veliger with large embryonic and larval shell. (pl. 3, figs. 5-8). The Neogastropoda in contrast probably represent only a stage group that appeared after the Cretaceous/Tertiary faunal crises eradicated transitional forms between groups of species with taenioglossate and rachiglossate radula.

Data on the morphology of the sperma have helped grouping some of the Caenogastropoda with each other like the Littorinimorpha holding Littorinoidea, Rissoidea and Heteropoda (HEALY 1988, 1990) or the Vermetidae which according to HEALY (1988, 1990) are grouped closer to the Ctenoglossa rather than with the Cerithioidea. Some of these data can be supported with fossil evidence (KOWALKE & BANDEL 1997, NÜTZEL in prep.). The history of the Ctenoglossa has been traced from their modern representatives within the Cerithiopsoidae,

Triphoroidea and Janthinoidea to the Mesozoic Zygopleuroidea and the Paleozoic Pseudozygopleuroidea (NÜTZEL in prep.). (pl. 3, fig. 3). Judging from Carboniferous species with caenogastropod protoconchs it appears possible, that several lineages evolved parallel to each other starting with openly coiled peruneloid protoconch and evolving trochospirally coiled ones with the embryonic shell the last to become coiled tightly. Ornament of the larval shell appears to have been adopted from the teleoconch during this process. Thus, the Caenogastropoda appear to be split in several quite ancient lineages each of which based on a different branch of the Silurian and Devonian Peruneloidea.

Where caenogastropods left the marine environment they may have more or less strongly altered their ontogeny. This has rather strong impact on the shape of the protoconch (RIEDEL 1993). When embryonic nourishment is liquid yolk the egg can become quite a bit smaller than 0.1 mm which seems to be about the size needed for an embryo to hatch as shelled planktotrophic larva (BANDEL 1975, 1982). The smallest embryos are developed in extremely yolk rich cases as in *Viviparus* with only 0.03 mm large eggs. Here the embryo begins feeding on albumen by a first opening of the sac-like digestive system that will later in development be transformed in the anus. The formation of the first opening of the body through which food comes into the digestive system of an embryo usually has a very prominent value in phylogenetic discussions. Protostomia are usually considered to keep the functions of their openings to the digestive system constant. In *Viviparus* and related *Bellamyia* the primary opening, thus, turns into the anus. If molluscs are grouped with the Gastroneuralia (Protostomia) as is the case in the gastraea theory of HAECKEL (1874) and its modern new version by NIELSEN (1985, 1987) and NIELSEN & NORREVANG (1985), the blastoporus should be partitioned into a mouth and an anus portion. There is no evidence to be found so far that the first body opening occurring in gastropods will be the mouth of the adult. But the opposite can be stated (BANDEL 1982). A formation of mouth and anus at the same time by stretching of the blastoporus during its growth has also not been noted. Mouth and anus may form at the same time, but at a later stage of embryology than formation of a single mouth (later anus).

Conclusions and suggested evolutionary scenario

The comparison of the ontogeny of individual species of gastropods indicates that a strict sequence of events features each species of a genus. Within the genus there is a wider range of variations present than is found within individual species. In marine genera for example there is usually a pair of species present in which one utilizes a planktotrophic mode of development, while the other relies more on yolk reserves and is lecithotrophic, with clearly visible results seen in the protoconch morphology. In each ontogeny additions and short cuts are superimposed onto

each other with heterochronies present. Thus, the basic steps in the embryogenesis need to be uncovered in order to clarify the construction of the elementary structure of the organisation. They are camouflaged by those alterations that lead to the characteristic features of a species or even an individual. Smaller variations may to some degree be reversible. Variations in the basic constructional program have deep impacts and are irreversible. It is not easy to differentiate small steps in evolution from larger changes, especially when only shell changes are evaluated. This is especially so in groups like the Euomphalomorpha, the Amphigastropoda or the Mimaspirida which have become extinct so that only shell features can be evaluated. Where ontogenies are still available, success in their interpretation can sometimes be extrapolated from the fossil record of a group. In order to reveal the basic program, the description and characterisation of the construction of homologous organs have to be cleansed from their camouflage of variations. Individual steps in the ontogeny and their possible minor alterations have to be recognized and the general course of phylogeny unraveled. Taxonomy of gastropods has been based to much upon a single stage in the life cycle which is the adult stage. It has proven very fruitful to look at the entire life cycle and to the relationships between different stages. The interpretation of ontogenies of living gastropods and their expression into morphology of the shell helps to understand the fossil record. The combination of features from ontogenies studied in living species with features seen in the protoconchs of fossil species are united in a model depicted in a diagram with numbers indicating characteristics of the succeeding branch.

1) During embryogenesis all gastropods detach their mantle tissue from the margin of the shell as soon as the primary shell has been formed. This feature places them into the Conchifera, a subphylum of the Mollusca and into the relation with the Cephalopoda, Bivalvia, Monoplacophora and Scaphopoda. Conchifera have principally the same development of the embryonic shell, and its detachment from the mantle edge prior to shell mineralization distinguishes from the other subphylum of the Mollusca. In the Amphineura (Aculifera) shell and mantle remain attached to each other during life. With the late Early Cambrian the conchiferan condition was well established.

2) The only uniting factor of the class Gastropoda is their body torsion. The ontogeny of modern Archaeogastropoda demonstrates that body torsion and shell spiralization represent separate processes. The presence of uncoiled embryonic and larval shells in ancestral gastropods to the three extant subclasses Neritimorpha, Heterostropha and Caenogastropoda can be taken as evidence, that body torsion was originally carried out at begin of the benthic stage of life.

3) The first body opening acts as mouth only in very special cases of yolk feeding intracapsular ontogenies, as is the case in *Anodonta* or *Viviparus*. The planktotrophic

case displays the construction of a complete intestine with mouth stomach and anus when it begins to function. Among gastropods only Docoglossa have feeding larvae still without shell while it occurs more commonly among Bivalvia (*Teredo*). Larvae of this type among the Docoglossa indicate either the very basal position of this group among the Archaeogastropoda and the occurrence of planktotrophic larvae among basal gastropods or represent a reinvention of planktotrophy in the docoglossate group of archaeogastropods.

4) The change from external to internal fertilization as a fixed ontogenetic trend caused a change in the morphology of the spermatozoa and did not occur in the archaeogastropods. External fertilization postulates the accessibility of sperms to the eggs and, thus, inhibits the enclosure of eggs within a capsule that can hold back salt and yolk. This limited the Archaeogastropoda to water of normal marine salinity and inhibits to enclose eggs in liquid yolk.

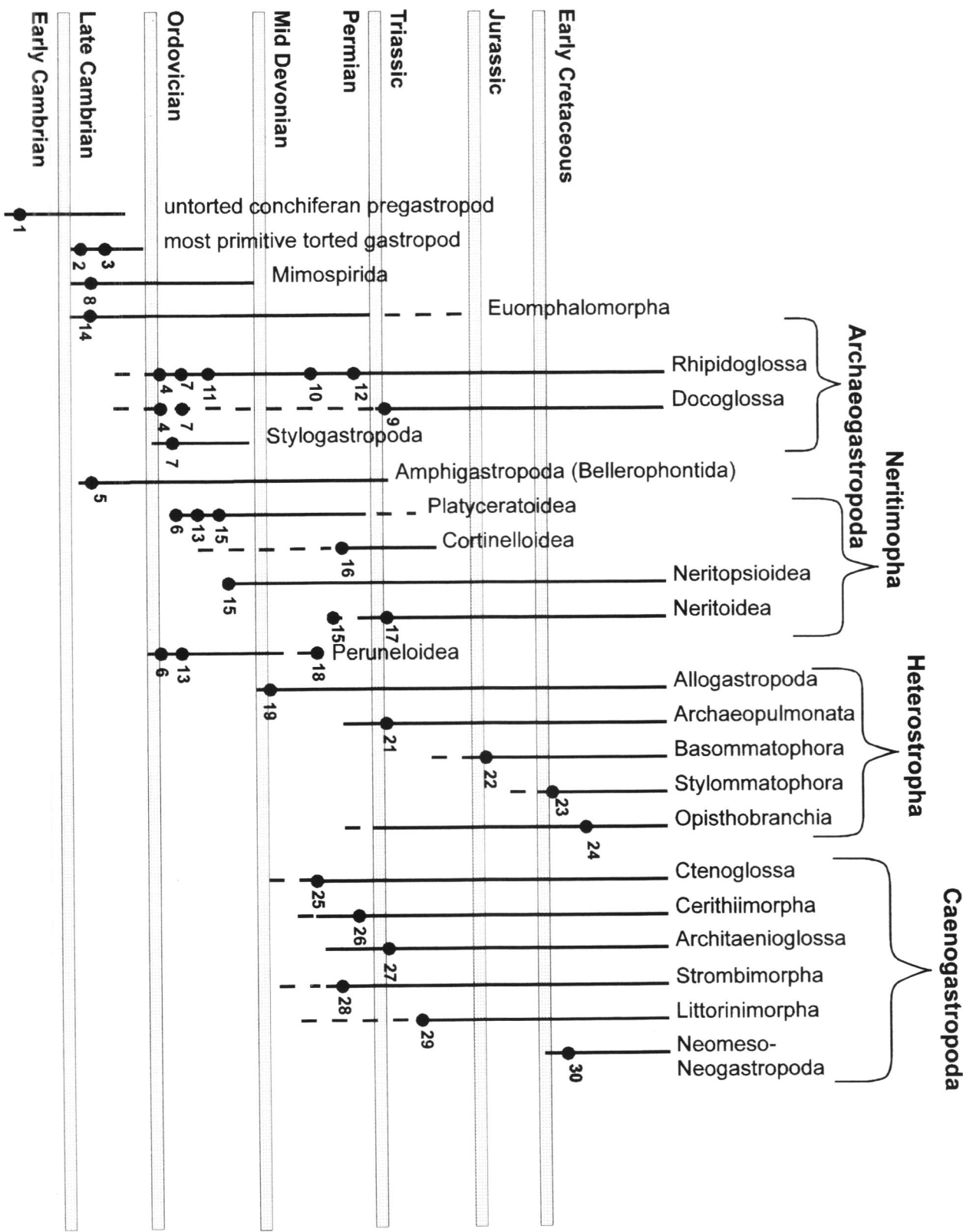
5) The Amphigastropoda had a totally planispirally coiled, non chambered, and bilaterally symmetrical shell, which differentiates them from all other molluscs. Their protoconch consists of more whorls than that of the Archaeogastropoda, and its initial portion is small, so that it may well have been carried by a plankton-feeding larva. If the adult body was tortoise, Amphigastropoda can be regarded as independent subclass of the Gastropoda. They did not give rise to any of the other groups of the gastropods during their Precambrian existence.

6) Internal fertilization allows to cover fertilized eggs with an egg capsule that can prevent salts and yolk from leaking out. Thus, environments with higher or lower salinity could be conquered as has been the case among some of the groups contained within the Neritimorpha, Caenogastropoda and Heterostropha. The change from external to internal fertilization as a fixed ontogenetic trend caused a change in the morphology of the spermatozoa. Three types of basic morphologies are evidence for independent development of the three internally fertilizing groups of Neritimorpha, Caenogastropoda and Heterostropha. Their existence can clearly be demonstrated to range back to the Early Carboniferous and in part of the Mid Devonian.

7) The primary shell of the Archaeogastropoda is deformed before it becomes mineralized. Aragonite crystallites grow into the organic shell here while the other gastropods have an embryonic and larval periostracum that forms the base to mineral deposits, but does not mineralize. Thus, periostracum in Archaeogastropoda has a different composition as that found in the other taxa of the Gastropoda. Spiralization of the shell in archaeogastropods occurs after a bilateral symmetrical shell has formed, but before begin of benthic life. The resulting type of protoconch has been documented from Ordovician onward.

8) In the extinct sinistral Mimospirida the early ontogenetic shell is large and consists of more than one

Tab. 1



whorl. It was, thus, most probably not constructed during larval life, but during the benthic existence of these gastropods. This group is quite characteristic, existed from Late Cambrian to Mid-Devonian and can not well be placed with any other less enigmatic taxon of the Gastropoda.

9) During the larval stage feeding may occur in the Docoglossa even though there is no velum with ciliary feeding groove, and there is no larval shell being added to the archaeogastropod type of protoconch. Modern Docoglossa are limpets and their occurrence can be documented without doubt only to the Triassic. Their simple anatomy, the basic shell design with calcitic outer shell layer, crossed lamellar inner aragonitic layer has not yet been recognized among the Paleozoic gastropods with spiral shell.

10) The larvae of the Rhipidoglossa (= Vetigastropoda) may swim in the plankton, but do not feed on plankton.

11) Apparently Rhipidoglossa with nacreous shell structure (pleurotomarioidea, Trochoidea, Seguenzioidea, Cirroidea etc.) are recognized from the Ordovician onward and appear to have developed independently from all other archaeogastropods.

12) Rhipidoglossa with crossed-lamellar shell (Fissurelloidea, Scissurelloidea, Phasianelloidea, etc). These can presently only be traced to the Late Paleozoic.

13) The openly coiled protoconch of some Paleozoic Neritimorpha and the Early Devonian and older Peruneloidea demonstrated that embryos and larvae secreted and carried no trochospiral shell. They may have also had an untorted body during much of early ontogeny. Coiling of the shell was established with begin of the construction of the teleoconch and, thus, the transition to the benthic gastropod. In the ancestors of Neritimorpha, Heterostropha, and Caenogastropoda the originally adult feature of shell coiling successively moved into the larval stage and even later later into the embryonic stage. The larva was plankton-feeding and constructed similar to the modern veliger.

14) Euomphalomorpha have a large and uncoiled protoconch that differs from all other gastropods. Its openly curving shape indicates that shell-coiling occurred late in ontogeny. Its large size is evidence for not having been carried by a free swimming larva. Euomphalomorphs have a similar shell construction to Neritimorpha with external calcitic shell and internal crossed lamellar shell, but a non spiralized and large embryonic shell. It appears that this group can be recognized from the Late Cambrian into the Triassic.

15) The most ancient and primitive of the groups of gastropods with a larval shell in addition to the embryonic one are represented by the modern Neritimorpha with a radula resembling that of the Rhipidoglossa, shell structure and gill resembling that of the Docoglossa. Within its older branch the planktotrophic larva constructed a shell with open coiling in the time before the Mid-Devonian. This is carried into the Platyceratoidea

and apparently disappeared in Carboniferous/Permian time.

16) During Mid Devonian coiling of the shell transgressed into the larval phase und led to the formation of the Neritimorpha as they still occur, but also developed into groups which have since disappeared, like the Cortinelloidea.

17) At least during the Triassic internal wall resorption characterized larval and adult phase in Neritoidea which developed land snails as well.

18) Within the anatomically more modern branch of the internally fertilizing Gastropoda with probably taenioglossate radula, shell spiralization moved into the larval and embryonic stage. Thus, a peruneloid protoconch was transformed into the spiral protoconch of the Heterostropha and Caenogastropoda.

19) Heterostropha become recognizeable with the appearance of the sinistrally coiled allogastropod protoconch connected to dextrally coiled teleoconchs at Mid-Devonian time.

20) The fixation of embryonic coiling in the Caenogastropoda was genetically more strongly fixed than that in the Heterostropha. When shells by secondary development became uncoiled again the embryonic shell remained spiralized as for example in the Caecidae (BANDEL 1996b). In Heterostropha a similar development uncoiled also the embryonic shell (BANDEL et al. 1984, BANDEL & HEMLEBEN 1995).

21) Archaeopulmonata may appear with the Carychiidae in the Late Carboniferous, with the Misurinellidae in the Triassic and well documented with the Ellobiidae in the Jurassic, mostly in amphibious environment.

22) The shell gland forms due to an interaction of cells of the entoderm with such of the ectoderm. The latter induces the growth of mantle tissue usually forming in a pit. Shell is at first firmly attached to the glandular cells of the mantle that form a simple cap. The fresh water pulmonate taxon Basommatophora differs by invaginating the mantle cells extremely deep into the visceral mass during embryonic development and later evaginating them especially rapid. The early shell is, thus, produced very rapidly around the embryo in a late stage of development.

23) Truly terrestrial pulmonate Stylommatophora with simplified and enlarged embryonic shell appear with begin of the Cretaceous.

24) Within the Opisthobranchia there was a development toward shell reduction visible from the Cretaceous onward and and despiralization as seen in pteropods since the Paleogene. The modern nudibranchs discard the shell and exposing the inner mantle surface in the dorids or even discard their mantle during metamorphosis as is the case in the aeolidids.

25) The caenogastropod branch of the Ctenoglossa appears with the Pseudozygopleuridae in the Early Carboniferous with characteristic ornamental pattern on the larval shell and from there on a well documented history

connecting to modern groups as Ianthinoidea, Cerithio-
psioidea and Triphorioidea.

26) Cerithiimorpha may have their origin in "murchi-
soniid" species found in the Carboniferous with charac-
teristic larval shell resembling that of some modern ones.

27) Architaenioglossa with embryonic development
adapted to terrestrial (Cyclophoroidae) or limnic life
(Viviparoidea) appear as early as Late Carboniferous,
recognizeable due to the simplified protoconch.

28) The ornamental pattern as developed in the
strombimorph larval shell appears first during the Car-
boniferous in subulitoid shells which may still have an
apical opening resembling peruneloid "ancestors".

29) The littorinimorph larval shell patterns are recog-
nized in Triassic forms.

30) Neomesogastropoda and Neogastropoda added an
extra larval shell to the shell of the veliger or moved adult
shell patterns onto the larval shell, thus, acquiring a poten-
tially longer embryonic and larval development which
was utilized in staying in the plankton for a more extended
time than their caenogastropod ancestors and by develop-
ing more extended ontogenies within the egg capsule.

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Plate 1

- Fig. 1: Typical protoconch of Archaeogastropoda as in the case of *Wortheniella* from the Late Triassic St. Cassian Formation.
- Fig. 2: Archaeogastropod protoconch from *Eucycloscala* from the Late Triassic St. Cassian Formation with aperture with indications of growth during free swimming planktic stage.
- Fig. 3: Representative of the Euomphalomorpha from the Permian German Zechstein with protoconch openly coiled.
- Fig. 4: Euomphalomorpha from the Late Carboniferous of the USA with wide and uncoiled protoconch, merging with a coiled teleoconch.
- Fig. 5: Mimospirinid from the Lower Devonian of Prague with large smooth protoconch and ornamented teleoconch, both sinistrally coiled.
- Fig. 6: Peruneloid protoconch from the Lower Devonian near Prague.
- Fig. 7: The protoconch of the subulitid *Globozyga* from the Late Carboniferous in the USA has an ornamented larval portion of the protoconch.
- Fig. 8: The same *Globozyga* as in Fig. 7 with initial shell portion uncoiled.

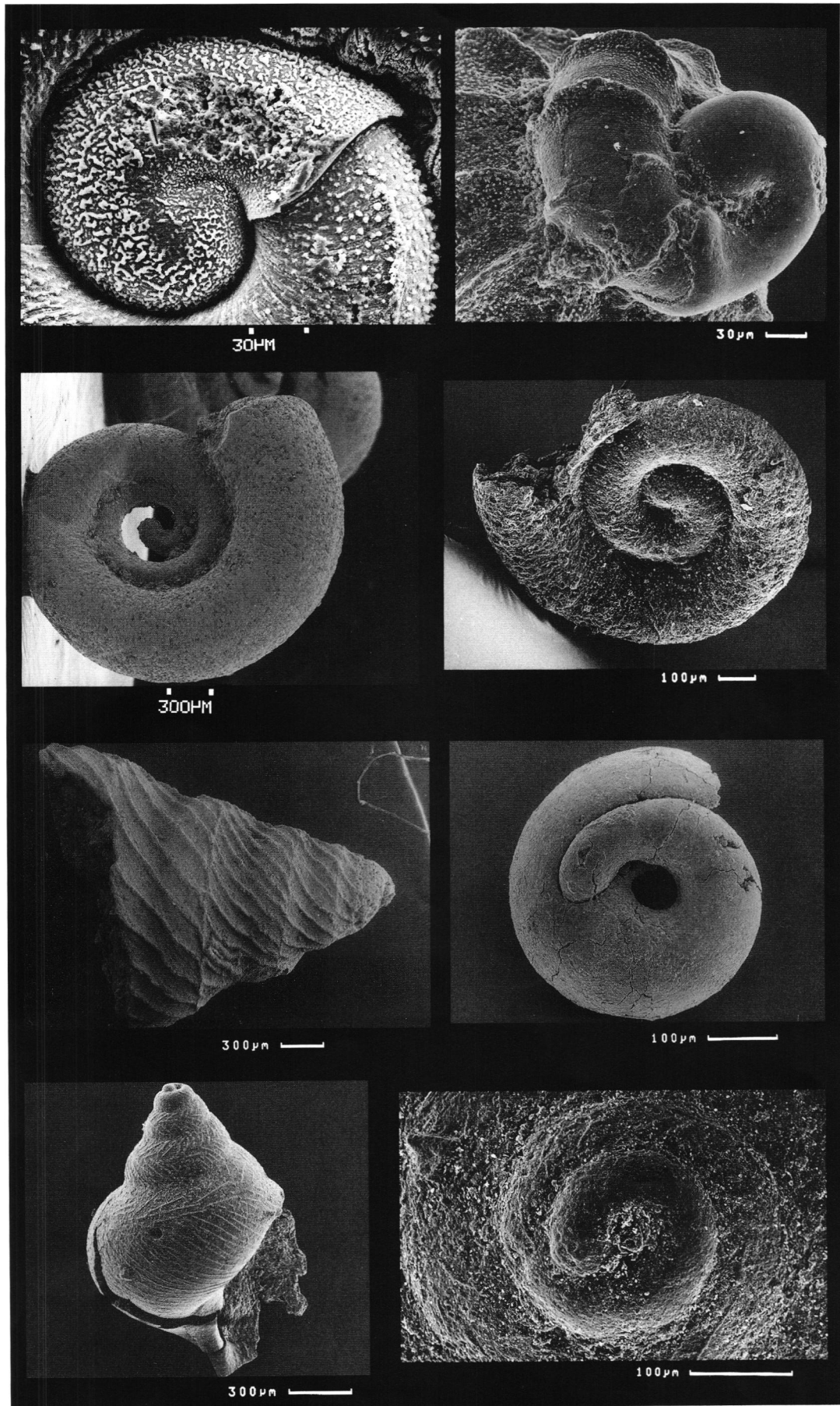


Plate 2

- Fig. 1 The protoconch of "*Orthonychia*" *alata* with its apertural hooks is characteristic to neritimorphs from the Late Triassic St. Cassian Formation.
- Fig. 2 *Cortinella* has a neritimorph protoconch and a shell differing from other known Neritimorpha. St. Cassian Formation.
- Fig. 3 *Cortinella acutecostata* from the St. Cassian with juvenile teleoconch hiding part of the neritimorph protoconch. St. Cassian Formation.
- Fig. 4 Platyceratoid protoconch from the Early Devonian near Prague.
- Fig. 5 Protoconchs of a neritopsid genus from the St. Cassian Formation with ornament.
- Fig. 6 As Fig. 5, but seen in apical view.
- Fig. 7 Hydrocaenid protoconch with simplified neritimorph shape.
- Fig. 8 As Fig. 7, but seen in apical view. (Indonesia)

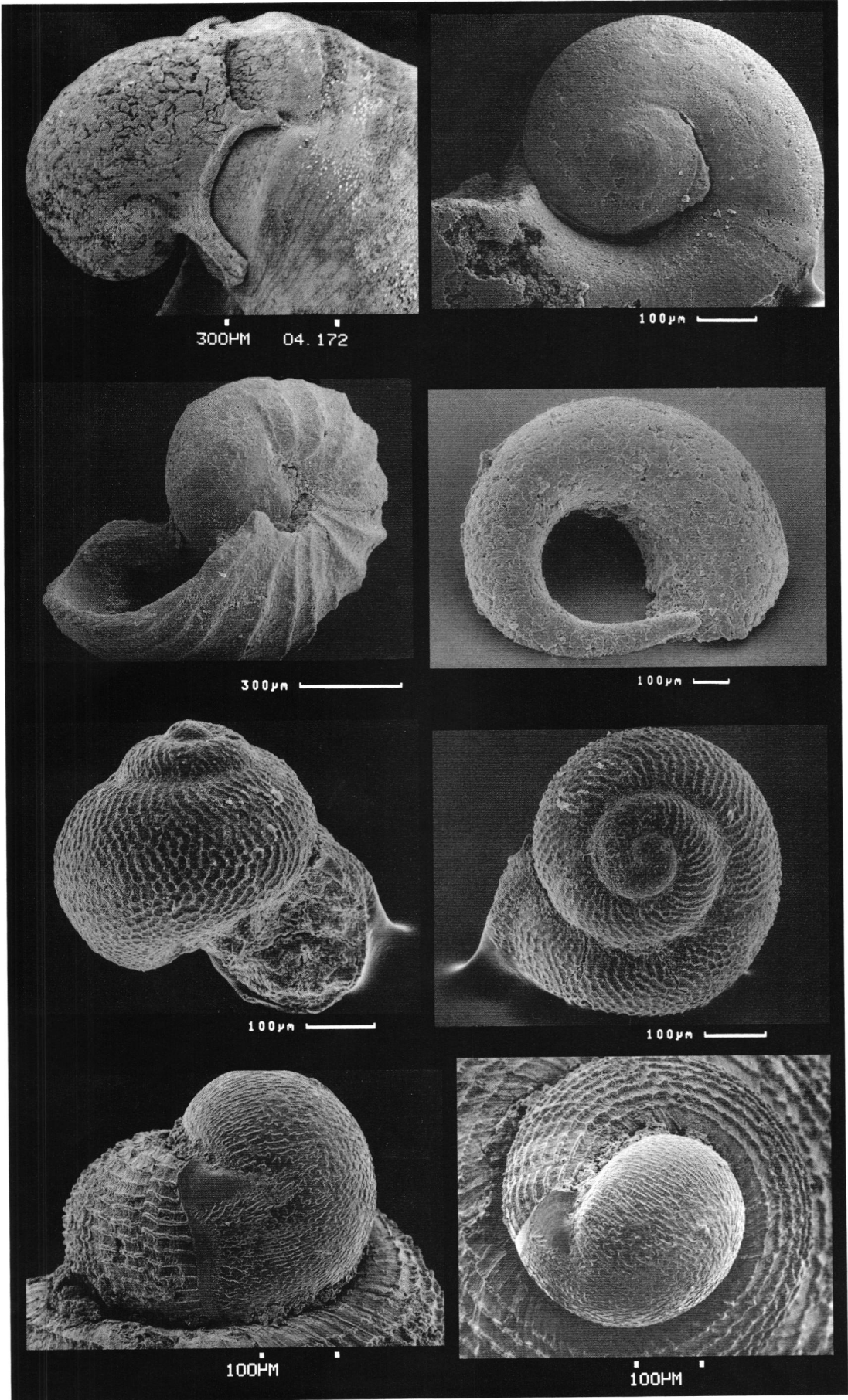


Plate 3

- Fig. 1 Streptacid gastropod from the Late Carboniferous from the USA with heterostrophic protoconch.
- Fig. 2 *Cylindrobullina* from the Late Triassic St. Cassian Formation with sinistral protoconch and dextral teleoconch.
- Fig. 3 Characteristic ornamental pattern of the pseudozygopleurid protoconch from a Late Carboniferous shell from the USA.
- Fig. 4 The protoconch of *Prostylifer* of the Prostyliferidae of still unresolved relation to modern Caenogastropoda is strongly ornamented and reflects long existence in the plankton. St. Cassian Formation.
- Fig. 5 The protoconch of *Maturifusus* from the Middle Jurassic of northern Germany reflects long life in the plankton and resembles that of Neogastropoda from the Late Cretaceous, as in Fig. 6 and 8.
- Fig. 6 The protoconch of an Albian neomesogastropod from northern Germany with the characteristic reticulate pattern of the larval shell that is still found in some modern relatives.
- Fig. 7 Neogastropod-like protoconch from Late Cretaceous Ripley Formation in Mississippi, USA.
- Fig. 8 Neogastropod or stromboid protoconch of the Late Cretaceous Ripley Formation indication a long larval phase during ontogeny.

