

Caenogastropoda during Mesozoic times

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The following groups of Mesozoic Caenogastropoda are discussed here: Cerithioidea and Littorinoidea-Rissooidea seemingly merging with each other during Triassic times; the fresh water and land snails of the Viviparoidae and Cyclophoroidea with unknown marine relatives but a Mesozoic history; the Vermetoidea, Turritelloidea and Campaniloidea with a late appearance in the Mesozoic; the Ctenoglossa with a continuous history from the Middle Palaeozoic to modern times; the Subulitoidea, Murchisonioidea and Loxonematoidea with Palaeozoic ancestors but unclear Middle Mesozoic relations; the Purpurinoidea as potential ancestors and relatives of the Stromboidea, the latter suddenly appearing in the Jurassic; the Heteropoda and Vanikoroidea with possible relation to each other but very uncertain relations to the others; and the Neomesogastropoda and Neogastropoda which begin their history in the Mid Cretaceous with still rather uncertain precursors.

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Introduction

The history of most groups of Caenogastropoda during Palaeozoic times is still uncertain. Only the Subulitoidea, Murchisonioidea, Loxonematoidea and Zygopleuroidea, and questionable Cerithioidea of the *Stegocoelia* type, can be traced through much of the Palaeozoic (Knight, 1931; Wenz, 1938-1944; Knight et al., 1960; Hoare & Sturgeon, 1978, 1980a, 1980b, 1981, 1985; Yoo, 1988, 1989; Bandel, 1991a; own data). The Subulitoidea have quite credible Ordovician representatives, the Loxonematidae are well traceable into the Devonian, and the Zygopleuroidea and Cerithioidea are present from the Early Carboniferous onwards. Many of their Palaeozoic genera still seem to have species or related genera in the Triassic (Bandel, 1991a, 1992b). The continuity of other groups of Caenogastropoda across the Palaeozoic-Mesozoic bounda-

ry is still problematic.

Only during the last decades taxonomic units of the Caenogastropoda have been cleansed from members of other groups, especially those belonging to forms with a heterostrophic protoconch. The morphology and sculpture of the protoconch enables us to expand anatomical studies supporting this process into the fossil record. It has also been demonstrated that the morphology of protoconchs of the Archaeogastropoda and the Neritomorpha differs from that of the Caenogastropoda (Bandel, 1982, 1991c, 1992a). Modern groups within the Caenogastropoda can usually easily be connected with their relatives that lived during Tertiary times, but when crossing over into the Mesozoic comparisons become increasingly more difficult due to convergence observed in regard to the teleoconch as well as the protoconch. But when a species has a planktrophic larva, it usually produced a characteristic protoconch that bears features not present on the teleoconch. This has been demonstrated to be of great help in tracing lineages sometimes across the whole time span into the Palaeozoic. But the number of species studied in this respect is still limited.

Based on the morphology of the protoconch Mesozoic Caenogastropoda are revised and the classification is re-evaluated. Data on fossil protoconchs are related to what is known about modern and Cenozoic species (Bandel, 1988b, 1992b). Since much fossil material is known only from teleoconch morphology, the evaluation is still in need of much further work.

Author and year of all taxa mentioned in this paper are given in Table 1.

Taxonomic discussion

Palaeo-Caenogastropoda

The heading Palaeo-Caenogastropoda unites large systematic groups of Caenogastropoda with ancestorship reaching back into Palaeozoic times. Within this unit ontogenies are simple and the modern fauna holds Cerithioidea, Littorinoidea and Rissoidae, which seem to merge into one and the same stock during the Mesozoic. The Sublitoidea, Murchisonioidea and Loxonematoidea represent independent superfamilies of the Caenogastropoda with Early to Middle Palaeozoic origin. They may show relations to the Campaniloidea, the Vermetidae and the Turritellidae, appearing late in Mesozoic times. The Architaenioglossa (Cyclophoroidea and Ampullarioidea) may have arisen from the marine Palaeo-Caenogastropoda still at Palaeozoic times.

The Cerithioidea characteristically have a low conical larval shell of c. 0.2 mm high and few whorls connected to an embryonic shell of c. 0.1 mm in diameter. The larval shells may have barrel-like shapes and a broad overlap to shapes seen in the Rissoidae and Littorinoidea. Commonly the aperture of the larval shell extends into a more or less wide, hook-like extension of the outer lip. The sculptural pattern on the larval shell is variable and can be utilised to differentiate units within this group. When the development is lecithotrophic the larval shell is absent and the embryonic shell usually is larger than one whorl (Pl. 1, fig. 6; Pl. 4, fig. 6).

The Procerithiidae have a larval shell with two strong spiral keels or ribs and resemble that of modern *Argyropeza* (Gründel, 1976; Houbriek, 1980a; Schröder, 1993;

Bandel & El Nakhal, 1993). These modern Indo-Pacific cerithioids may represent modern relatives of Jurassic procerithiids. Walther (1951) noted the characteristic feature of the early ontogenetic shell consisting of two sharp keels on the protoconch (Pl. 1, fig. 3). According to Cossmann (1906), Wenz (1938-1944), and Houbrick (1988) the Cerithioidea began their history during Mesozoic times with the family Procerithiidae. *Procerithium* is a representative of the Cerithioidea (Schröder, 1993). *Rhabdocolpus*, from the European Jurassic (Schröder 1993) as well as the Early Jurassic of New Zealand (Bandel & Maxwell, in prep.) (Pl. 2, fig. 1), also belongs here. This demonstrates the continuation of the Procerithiidae into the modern Cerithiidae (Pl. 1, fig. 4).

The Cerithiidae have larval shells with a combined spiral and axial sculpture like *Cerithium* (Houbrick, 1984, 1992), similar to *Bittium* from the Valangian of Poland (Schröder, 1992b) and *Tympanotonus (Exechocirsus)* from the Campanian of Mississippi (Dockery, 1991) (Pl. 3, figs. 1-2). Their sculpture also resembles that of the Late Triassic *Ampezzoscala* (Pl. 1, fig. 1) from the St Cassian Formation, which indicates a connection to the Ladinulidae. *Scaliola*, from the Maastrichtian of the southeastern USA, is also similar (Bandel, 1992b), as are more modern species of this genus (Pl. 1, fig. 5). Most genera of the Recent Cerithiidae (Pl. 3, fig. 1) appear during Tertiary time (Houbrick, 1988, 1992).

In regard to their larval shells the Ladinulidae, resemble modern Cerithiidae. The protoconch here consists of 2-3 whorls, is c. 0.2 mm high and bears an c. 0.1 mm wide embryonic shell in its apex. The sculpture consists of spiral ridges and rows of tubercles. *Ampezzoscala* and *Ladinula*, from the Late Triassic of St Cassian, represent members of a family that can be related to the Cretaceous Cassiopidae (Pl. 1, fig. 2; Pl. 2, fig. 3), as well as perhaps to modern Modulidae (Pl. 2, fig. 5) and Cerithiidae (Pl. 3, fig. 1).

The larval shell of the Cassiopidae is sculptured by several spiral keels, while the conical teleoconch is covered by wavy spiral striations and ribs, and has a rounded aperture with a short siphonal notch (Pl. 1, fig. 2; Pl. 2, fig. 3; Pl. 4, fig. 6). *Paraglauconia* appears at Barremian times and a whole group of related forms developed during the course of the Cretaceous and disappeared at its end. Mennessier (1984) distinguished 10 genera evolving and living during the Cretaceous. A maximum of genera was present at Mid-Cretaceous times like the name-giving *Cassiope*, and the group disappeared altogether during Maastrichtian times. The larval shell and the general shell shape of several members of this family resemble that of the Triassic *Ladinula* and *Ampezzoscala* (Pl. 1, fig. 1).

The Modulidae consists only of the modern genus *Modulus*, which can be traced back into the Tertiary (Houbrick, 1980b). Its supposed Cretaceous representative *Schizobasis* belongs to the Neomesogastropoda (Sohl, 1964a; own data). The Late Triassic Ladinulidae are similar to modern *Modulus* (Pl. 2, fig. 5), but also to *Bembicium*. This similarity in the case of *Modulus* includes the larval shell, while that of *Bembicium* is lost due to lecithotrophy (Reid, 1988).

Modern Diastomatidae were connected to the Paracerithiinae by Ponder & Warén (1988). A species of *Paracerithium*, from the Late Triassic of Peru, can be connected with the Purpurinidae based on the shape of its teleoconch and shows a smooth protoconch rather similar to the modern diastomatids and dialids (Haas, 1953; Bandel,

1994) and the modern *Plesiostrochus* (Houbrick, 1991) (Pl. 5, figs. 1-2). Larval shells of *Angularia* are simple and smooth, and bear a wide larval hook (Pl. 5, figs. 3-4; Pl. 14, figs. 2, 4). Only one species of *Diastoma* is still living in the coastal region of western Australia while most of the members of the family lived during Tertiary times. Houbrick (1981) found the group anatomically related to the Cerithiidae, Potamididae and Melanopsidae. A Jurassic *Paracerithium* from New Zealand, which is in shape close to the European genotype, probably belongs to the Stromboidea (Bandel & Maxwell, in prep.), as is the case with a very similar form from the Early Cretaceous (Pl. 14, fig. 7).

The Dialiidae, with a simple conical shell, sculptured by flat topped spiral ridges with linear interspaces, are equipped with an ovate aperture lacking an anterior canal. The larval shell is simple and smooth with the possible exception of a single spiral line on the last whorl portion, ending in the upper part of the pronounced apertural hook (Ponder, 1991). The cladistic analysis provided by Ponder (1991) indicates that this group of the Cerithioidea may be related to the Litiopidae. The lack of axial sculptural elements, as well as a smooth larval shell, may bring this modern group close to the Palaeozoic representatives of the genus *Stegocoeilia*, which is provided with a smooth sinusigera of two whorls as larval shell (Yoo, 1988, 1989).

The large protoconch of the Prostyliferidae has a characteristic barrel-shape and in some species it is attached to the top of the teleoconch inclined to the spiral axis of the teleoconch (Pl. 6, figs. 1-3). The sculpture of the larval whorls consists of strong spiral keels and rows of tubercles, and the outer lip forms a larval hook which can be

Plate 1

Fig. 1. The protoconch of *Ampezzoscala ornata*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.27 mm high (in the visible part), is ornamented by rows of tubercles, shows a strong projection of the lower outer lip and an embryonic whorl of 0.09 mm in diameter.

Fig. 2. The protoconch of *Cassiope kefersteini*, from the Late Cretaceous (Santonian-Campanian) Gosau Formation of Brandenberg, Tirol, is 0.26 mm high (in the visible part), is ornamented by two spiral ridges and a row of tubercles, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of 0.1 mm in diameter.

Fig. 3. The protoconch of a 3 mm high shell of *Procerithium culizkyi*, from the Early Cretaceous (Valanginian) of Wonwal near Tomaschow in Poland, is 0,6 mm high (in the visible part), is ornamented by two spiral keels, shows a strong projection of the lower outer lip and an embryonic whorl of 0.1 mm in diameter.

Fig. 4. The protoconch of a 0.5 mm high shell of *Pyrazus debile* (procerithiid species), from the Late Cretaceous (Santonian-Campanian) of the Gosau Formation near Brandenberg, Tirol, is 0.26 mm high (in the visible part), consists of 2.2 whorls, is ornamented by two spiral keels, shows a strong projection of the lower outer lip and an embryonic whorl of 0.09 mm in diameter.

Fig. 5. The protoconch of *Scaliola jansseni*, from the Middle Eocene of the Paris Basin, is 0.5 mm high (in the visible part), is smooth, shows a strong projection of the lower outer lip of the pediveliger shell that is thickened and an embryonic whorl of less than 0.1 mm in diameter.

Fig. 6. The 0.8 mm high shell of *Juramelanatria rugosa*, from the limnic transitional deposits of the Jurassic/Cretaceous boundary of the French Jura Mountains, has a 0.2 mm wide embryonic shell succeeded directly by the teleoconch.

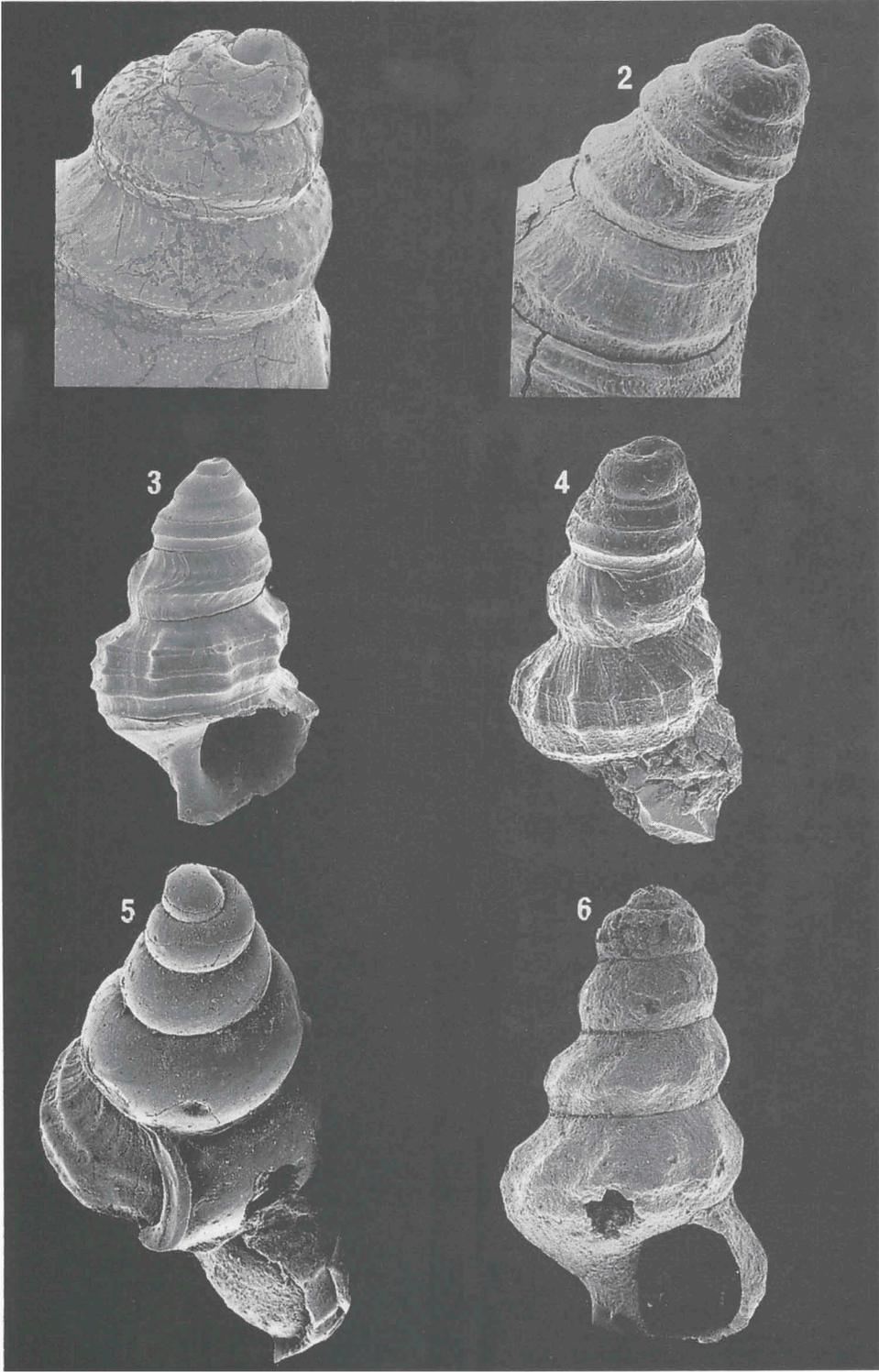


Plate 1

found near the middle or near the anterior base of the aperture. *Prostylifer* and *Ptychostoma* (Pl. 6, figs. 1-2) from the Late Triassic of the Dolomites form this family which could well represent the source for the Melanopsidae, but a connection with the Littorinidae or Pickworthiidae (Pl. 11, fig. 1) is also possible, since both have similar larval shells.

A larval shell of the Melanopsidae is only known from a fossil form from the Cretaceous (Maastrichtian) of the Pyrenees (Harbeck, 1989) and modern *Zemelanopsis* from New Zealand, while the other representatives have become lecithotrophic in their ontogenetic development. The protoconch is barrel-shaped and similar in shape to, but smaller in size (0.25 mm high) than that of the Prostyliferidae (0.5-1.2 mm high). Species similar to *Melanopsis* are found in the Campanian fresh water deposits of the Bakony Mountains, Hungary (Riedel, 1990). Transition of marine forms to such of fresh water might have occurred in Late Cretaceous times. Houbrick (1981) noted anatomical similarities between the Diastomatidae and Melanopsidae like *Zemelanopsis*.

The larval shell of the Planaxidae has a very characteristic pattern (Houbrick, 1987a), which is also found in *Fossarus* (Warén & Bouchet, 1988), but only known from the Neogene. Perhaps *Prisciphora* from the Mid-Cretaceous is related, as the sculpture of its larval shell seems to indicate (Pl. 3, fig. 3). But its sculpture also resembles that of the litiopids. Planaxids should have fossil representatives since they are considered to have risen from the same ancestors as the freshwater Thiariidae which also breed their eggs in a brood pouch behind their head (Ponder, 1980). The embryonic shell of the Thiariidae does not include a portion formed by a planktotrophic larva, since all or most representatives of this group possess a brood pouch from which crawling young hatch, usually provided with several whorls of the shell. Here the early ontogenetic embryonic shell can not be differentiated from the shell of the juvenile.

Juramelanatria and *Juramelanoides* from the Purbeckian facies of the Jura (Pl. 1, fig. 6) give evidence of the presence of these freshwater Cerithioidea in Jurassic times. *Pyrgulifera* can be traced back to the Purbeckian and is common in the Late Cretaceous freshwater deposits of the northern coasts of the Tethys (Bandel, 1991b). This lineage of the Thiariidae may have survived basically unchanged in the genera *Lavigeria* and *Paramelania* in Lake Tanganyika.

The larval shell of *Alaba* and *Litiopa* of the Litiopidae has a characteristic pattern (Houbrick, 1987b) that can in a similar way be found in *Prisciphora* from the Middle Cretaceous (Schröder, 1991, 1993) (Pl. 3, fig. 3). It resembles larval shell patterns as seen in *Cryptoptyxis* from the Early Jurassic of New Zealand (Bandel & Maxwell, in prep.) (Pl. 7, fig. 3). Both Mesozoic forms could also be placed in connection with the planaxid type of protoconch.

The Scaliolidae appear with *Scaliola* in the Late Cretaceous and have survived basically unchanged in the Indo-Pacific (Pl. 1, fig. 5). Bandel & El Nakhal (1993) recognised similarities to some modern Cerithioidea as well as the Triassic Ladinulidae and an Early Cretaceous species of *Bittium*.

The Coelostylinidae, with *Coelostylina*, *Ampezzoscala*, and *Omphaloptycha*, from the Late Triassic St Cassian Formation, have a simple smooth or tubercular larval shell (Pl. 5, fig. 6) resembling that of some modern Littorinidae but also that of *Cerithioidea*

(Bandel, 1992b). There is no similarity to *Loxonema* when its Triassic representative *Polygyrina* is taken into account (Bandel, 1991a) (Pl. 4, fig. 5). The shell resembles that of modern *Diala* in having a rounded aperture. Members have smooth larval shells with a large apertural projection. The small embryonic whorl can differentiate members of this group from early representatives of the Naticoidea (Pl. 12, fig. 3). Haas (1953) described some possible Coelostylinidae from the Late Triassic of Peru as members of the Zygopleuridae (Bandel, in press.).

The larval shell of some modern Obtortionidae from the Pacific Ocean (Bandel, 1991e) (Pl. 2, figs. 2, 4) may prove to be related to the Triassic Popenellidae, with *Popenella* and *Cerithiozyga* (Pl. 3, fig. 5) from the Late Triassic St Cassian Formation. They carry a characteristic larval shell with an inclined pattern of collabral ribs. Some modern small sized cerithioideans are similar (W.F. Ponder, pers. communication), but also the *Hemizyga* group from the Carboniferous of Australia (Yoo, 1988) and the Triassic *Cassianozyga* from the Alps (Pl. 4, fig. 1) can be compared. It is possible that some species of the Carboniferous Pseudozygopleuridae rather belong here than with the Ctenoglossa.

The Settsassiidae, with *Lacunina* and *Settsassia*, represent Late Triassic genera which could be placed near to the modern Cerithioidea as well as to the Littorinoidea. Their smooth larval shells (Pl. 4, fig. 2; Pl. 5, fig. 5) connect with modern Lacunidae.

The Littorinoidea, consisting of the Littorinidae and Lacunidae, can only be traced to the beginning of Tertiary times. The Lacunidae may be related to genera like *Lacunina* from the Late Triassic St Cassian Formation (Pl. 5, fig. 5) that is similar to modern *Lacuna* and a similar juvenile shell was noted in the Early Cretaceous of Poland by Schröder (1993). The Settsassiidae (Pl. 4, fig. 2) therefore have similarities with the modern Lacunidae, but could just as well belong to the Cerithioidea.

Modern Littorinidae may have larval shells resembling those of the Prostyliferidae (Pl. 6, figs. 1-3) (Bandel & Kadolsky, 1982), but also of the modern Assimineidae and such larval shells were found in the Valangian of Poland (Schröder, 1993). But modern littorinids as a group of characteristically intertidal gastropods seem to have appeared in the earlier Tertiary (Palaeogene). According to a model offered by Ponder (1988) the Littorinoidea arose from a common ancestor with the eatoniellids in the cold water of southern Pangea and migrated from there northwards, possibly reaching European waters by the beginning of the Cretaceous. Fossil evidence to support this hypothesis is so far missing.

The landsnails Pomatiasidae are according to Wenz (1938-1944) present in the Late Cretaceous of southern France with *Bauxia*, which was confirmed by Hrubesch (1965). He found in the terrestrial deposits from the Campanian of Gosau the oldest representatives with *Anapomatias*. It belongs to the group formed by the modern genera *Tudorella*, *Pomatias*, and Tertiary *Dissostoma*.

Rissooidea can only be traced to the middle part of the Mesozoic. Rissoidae are thought to be represented by *Rissocerithium* and *Zebinostoma* from the Middle Jurassic of Italy (Conti & Fischer, 1983) and these have also a relative in the Early Jurassic of New Zealand (Bandel & Maxwell, in prep.). Ponder (1988) sees the origin of the rissoids in barleeid or prebarleeid ancestors. Marine Rissoidae are considered to have given rise to various families that have entered the brackish water and evolved into

non marine habitats (Ponder, 1988). Sohl (1960) noted a Late Cretaceous rissoid with smooth larval shell, redescribed by Dockery (1991) as *Alvania*. Dockery (1991) also noted species of *Stosicia* and *Cossmannia* from the Campanian of Mississippi.

According to Knight et al. (1960) the Hydrobiidae range back in time to the Permian. The shells of most members of this group are rather uncharacteristic in shape, especially when belonging to a species with young hatching without planktotrophic veliger phase. Records of Late Jurassic species of *Hydrobia* are confirmed (Bandel, 1991b) (Pl. 6, fig. 4), older ones must be checked. But some forms from the Late Permian Zechstein of northern Germany certainly look just like modern relatives of fresh water species of the hydrobiids. Other fresh water members of the rissoidaeans as found among the Pomatiopsidae, Hydrococcidae, Stenothyridae and Iravadiidae, all having their origin in marine forms, are convergent in shell shape. According to Ponder (1988) invasion of the non-marine habitats occurred at least at three different times. According to his model the first hydrobiid invasion is documented by the Purbeckian faunas in Europe. The assimineid-pomatiopsid-truncatellid radiation occurred at about the same time on the southern side of the Pangea continent (Ponder, 1988). The stenothyrids finally invaded freshwater during the Tertiary. Marine Iravadiidae with *Hyala*, *Ceratia*, and *Nozeba* are present in the Late Campanian Coffee Sand in Mississippi (Dockery, 1991) (Pl. 6, fig. 5).

The Bithyniidae, with *Bithynia* from the Purbeckian, resembles the shell of modern species in all respects. Thus we can trace the Bithyniidae with as much confidence as can be placed on shell morphology in a freshwater species to the Jurassic/Cretaceous

Plate 2.

Fig. 1. The protoconch of *Rhabdocolpus* sp., from the Early Jurassic of southern New Zealand, is 0.4 mm high (in the visible part), is ornamented by spiral ridges, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 2. The protoconch of a species of *Obtortio*, from a shallow lagoon on Lizard Island, southern Australian Barrier Reef, is 0.2 mm wide, is sculptured by collabral ribs that reflect the presence of a rounded projection of the lower outer lip of the veliger shell that is thickened at its end and has an embryonic whorl of c. 0.1 mm in diameter.

Fig. 3. The protoconch of cf. *Cassiope* (*Glauconia*) *ornata*, from the Late Cretaceous (Santonian-Campanian) Gosau Formation in Brandenberg, Tirol, is c. 0.3 mm high (in the visible part), has two strong spiral keels like a procerithiid species, has a much smaller apical angle than the teleoconch, and an embryonic whorl of 0.11 mm in diameter.

Fig. 4. The protoconch of modern *Obtortio*, from the Pacific Ocean near Cebu City, Philippines, is 0.2 mm high (in the visible part), is ornamented with collabral costae reflecting the outline of a rounded apertural projection of the lower outer lip of a veliger shell as is shown in Fig. 2.

Fig. 5. The 2.2 mm high juvenile shell of modern *Modulus*, from the Pacific Ocean near Cebu City, Philippines, has a protoconch of c. 3 whorls and 0.6 mm height (in the visible part) that is sculptured by undulating spiral ridges, shows a strong apertural projection and an embryonic whorl of 0.12 mm in diameter.

Fig. 6. The 2.7 mm high shell of *Pyrgulifera purbeckiensis*, from the limnic Jurassic-Cretaceous boundary deposits of Portland in England, has a 0.3 mm wide embryonic first whorl and an embryonic shell of 2 whorls succeeded directly by the teleoconch.

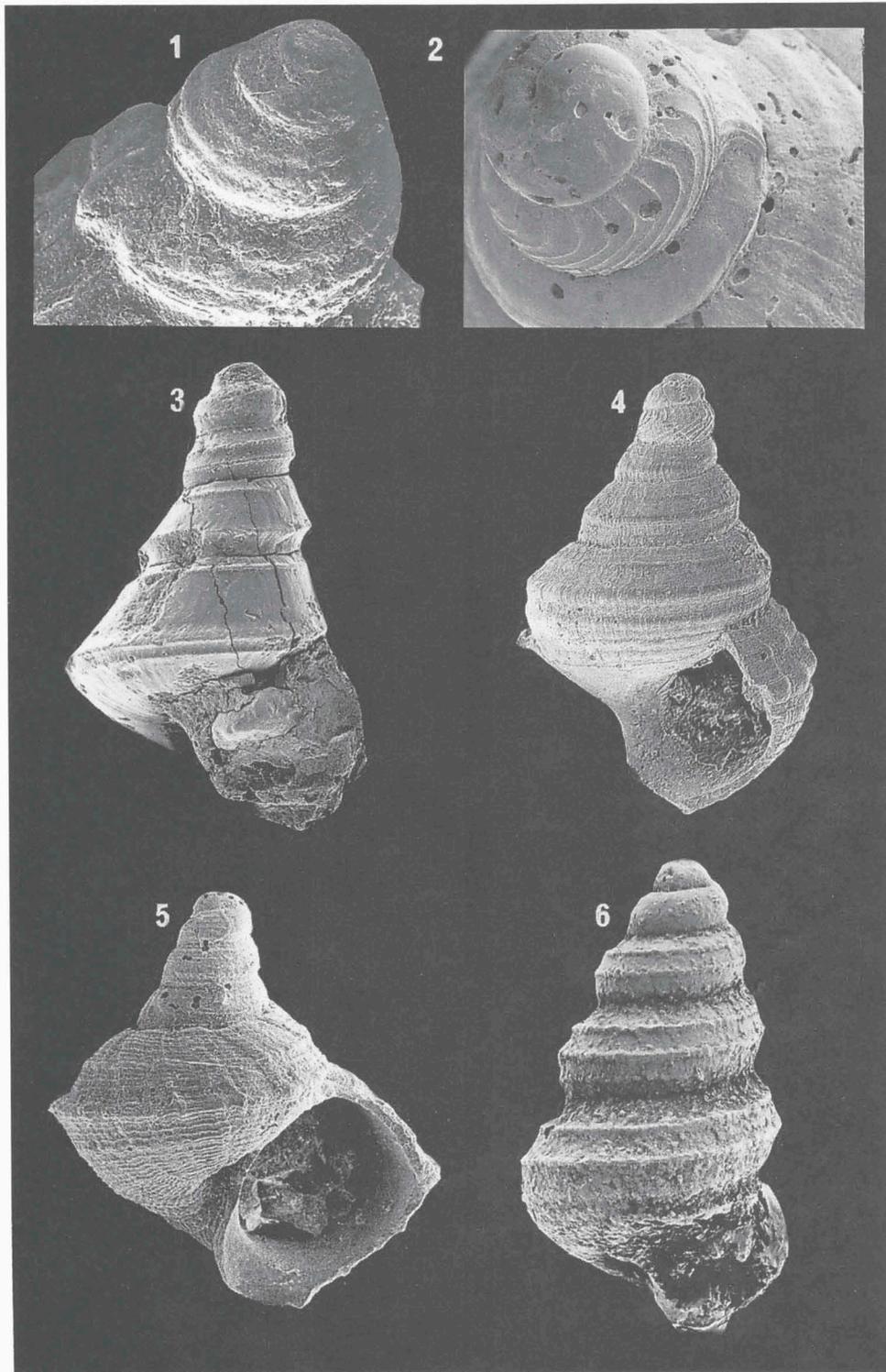


Plate 2

boundary (Bandel, 1991b).

The Assimineidae developed on the southern shores of the Tethys Ocean (Ponder, 1988). According to Wenz (1938-1944) assimineids did not occur in Europe before Tertiary times, but Hrubesch (1965) found *Turbacmella* in the Campanian of Gosau representing a member of a group now living in southeastern Asia. According to Ponder (1988) the Falsicingulidae, and Truncatellidae come from the same ancestors and have up to now provided recognisable fossils only in Tertiary times.

The oldest reliable species of the Vitrinellidae are from the Campanian Coffee Sand in Tennessee and Mississippi (Pl. 6, fig. 6). Sohl (1960) and Dockery (1991) attribute them to the genera *Teinostoma* and *Solariorbis*. Members of this group are easily confused with the Skeneidae (own data) and small Architectonicoidea when the early shell is not well known (Wenz, 1938-1944).

The Architaenioglossa hold two possibly quite unrelated groups of primitive Caenogastropoda. Up to now it is quite unknown which marine group of gastropods have been the ancestors to the landsnails represented by the Cyclophoroidea and the freshwater snails of the Ampullarioidea.

Cyclophoroidea may range back to the Carboniferous, since the Dendropupinae with *Anthracopupa*, *Maturipupa*, and *Dendropupa* from the Carboniferous have been placed in the Cyclophoridae (here Cyclophoroidea) by Knight et al. (1960). This placement has been doubted by Solem & Yochelson (1979). These authors suggested that the members of this group are more likely related to the Pulmonata. In the case of *Anthracopupa* and *Maturipupa* this may be so (Harbeck, 1993), but *Dendropupa* closely resembles cyclophorid shells, as Wenz (1938-1944) suggested.

The next less ancient Cyclophoroidea known up to date seem to be represented by *Diplommatoptychia*, *Loriolina*, and *Maillardinus* from the Purbeckian (latest Jurassic,

Plate 3

Fig. 1. The protoconch of a cerithiid, from the Gulf of Aqaba, is c. 0.35 mm high (in the visible part), is ornamented by spiral and axial elements, shows a strong projection of the lower outer lip that is thickened in the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 2. The protoconch of *Tympanotonus* sp., from the Late Cretaceous (Campanian) of Coffee Sand in Mississippi, is 0.7 mm high (in the visible part), is ornamented by spiral ridges, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 3. The 1.7 mm high juvenile shell of *Prisciphora beyschlagi*, from the Early Cretaceous (Aptian) of Algermissen in northern Germany, has a 0.7 mm high protoconch, consisting of 4.5 whorls ornamented by axial ribs crossed by fine spiral striae, shows a strong projection of the lower outer lip and an embryonic whorl of c. 0.15 mm in diameter.

Fig. 4. The juvenile shell of *Cerithiozyga* sp., from the Late Triassic St Cassian Formation of the Dolomites near Cortina d'Ampezzo is 2.7 mm high. Its protoconch is shown in Fig. 6.

Fig. 5. The protoconch of *Cerithiozyga bittneri*, from the same formation, is 0.35 mm wide (in the visible part), is ornamented by collabral ribs crossed by fine spiral lirae, shows an apertural projection of the pediveliger shell and an embryonic whorl of c. 0.12 mm in diameter.

Fig. 6. The protoconch of *Cerithiozyga* sp. in the detail to Fig. 4 is 0.3 mm high (in the visible part), is feebly ornamented, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.09 mm in diameter.

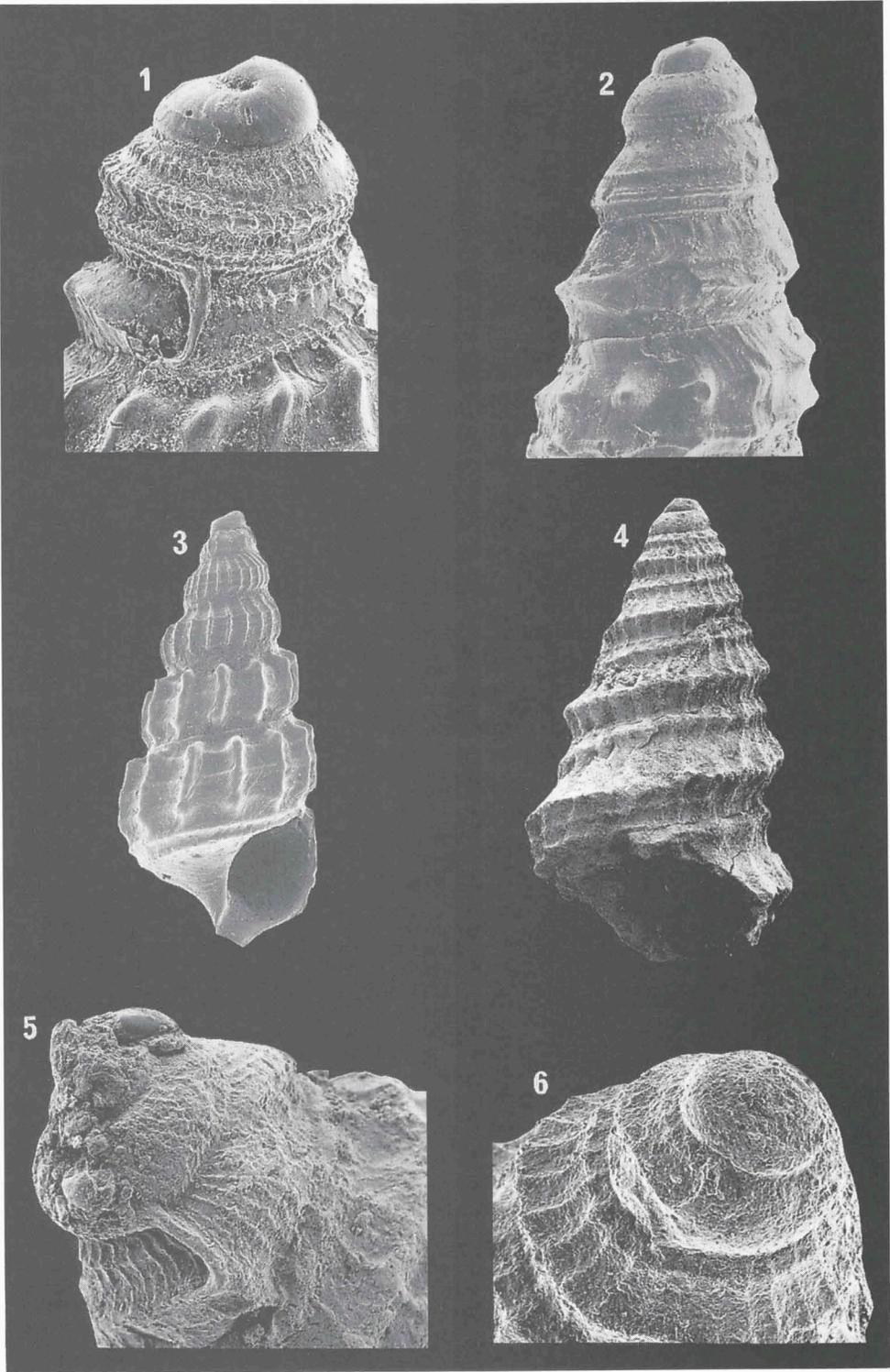


Plate 3

earliest Cretaceous) of the Jura Mountains (Pl. 4, fig. 4). The position of these genera in the Cyclophoroidea has been confirmed by the presence of a characteristic embryonic shell of landsnails, as well as a calcified operculum (Bandel, 1991b). They resemble the Late Cretaceous species placed in the genus *Leptopoma* of the modern Cyclophoridae by Hrubesch (1965) from Campanian terrestrial deposits of the Austrian Gosau. *Cyclomastoma* of the Pupinidae, *Pseudonicida*, *Entypogyra*, and *Ajkaia* of the Diplommatinidae are of the same age and similar occurrence. *Proelektraea* is considered a Cretaceous precursor of the amber snail *Elektrea* from the Eocene.

The Ampullarioidea with the Viviparidae have a representative of the genus *Viviparus* in the Purbeckian with *Viviparus arkelli*, confirmed by the morphology of its early ontogenetic shell by Bandel (1991b), based on a specimen from England (Pl. 7, fig. 1). The species ranges into the Kimmeridgian, whilst older representatives from the Carboniferous are questionable (Knight et al., 1960; Huckriede 1967).

Kase (1984) noted the occurrence of *Pila*, and thus of Ampullariidae in the Early Cretaceous of Japan, but specimens are imperfectly preserved and remain doubtful in their systematic assignment. *Lanistes* appears near the Cretaceous-Tertiary boundary in freshwater deposits of Pakistan and Sudan.

Houbrick (1988) excluded the Campanilidae from the Cerithioidea. Sohl (1987) supposed the modern and Tertiary *Campanile* to be related with *Procampanile* from Coniacian age, but this Cretaceous fossil is somewhat doubtful. This independent caenogastropod group has no Mesozoic connection so far, which certainly must be expected to be there, and stands out from other groups.

The Vermetidae characterised by an attached and irregularly oriented shell, could well represent a polyphyletic unit. There are very different protoconch types connec-

Plate 4

Fig. 1. The protoconch of *Cassianozyga seelandica*, from the Late Triassic St Cassian Formation in the Italian Dolomites is 0.3 mm high (in the visible part), is ornamented by fine collabral lirae, shows a projection of the lower outer lip and an embryonic whorl of c. 0.11 mm in diameter.

Fig. 2. The protoconch of *Settsassia obliquecostata*, from the same formation, is 0.22 mm high (in the visible part), is ornamented only by indistinct growth lines, shows a large apertural projection of the outer lip and an embryonic whorl of c. 0.12 mm in diameter.

Fig. 3. The protoconch of *Protuba winkleri*, from the same formation, is 0.27 mm high (in the visible part), is ornamented by spiral ridges, shows a strong projection of the outer lip of the pediveliger shell and an embryonic whorl of c. 0.08 mm in diameter.

Fig. 4. The c. 2 mm high shell of *Maillardinus sanctusclaudius*, from the Purbeck facies (Jurassic-Cretaceous transition) in the French Jura Mountains, has an embryonic whorl of c. 0.4 mm width that is connected to the teleoconch without visible change in sculpture.

Fig. 5. The c. 2.1 mm high shell of *Polygyrina lommelli*, from the Late Triassic St Cassian Formation in the Italian Dolomites, has a 1.3 mm high protoconch that consists of 4.25 whorls, is ornamented by a tubercular collabral pattern of ribs, shows a weak projection of the outer lip of the pediveliger shell, and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 6. The 7 mm high shell of *Cassiope ? giebeli*, from the Late Cretaceous (Santonian-Campanian) Gosau Formation of Brandenberg, Tirol, has an over 0.2 mm large embryonic shell of 1.5 whorls that is succeeded by the teleoconch.

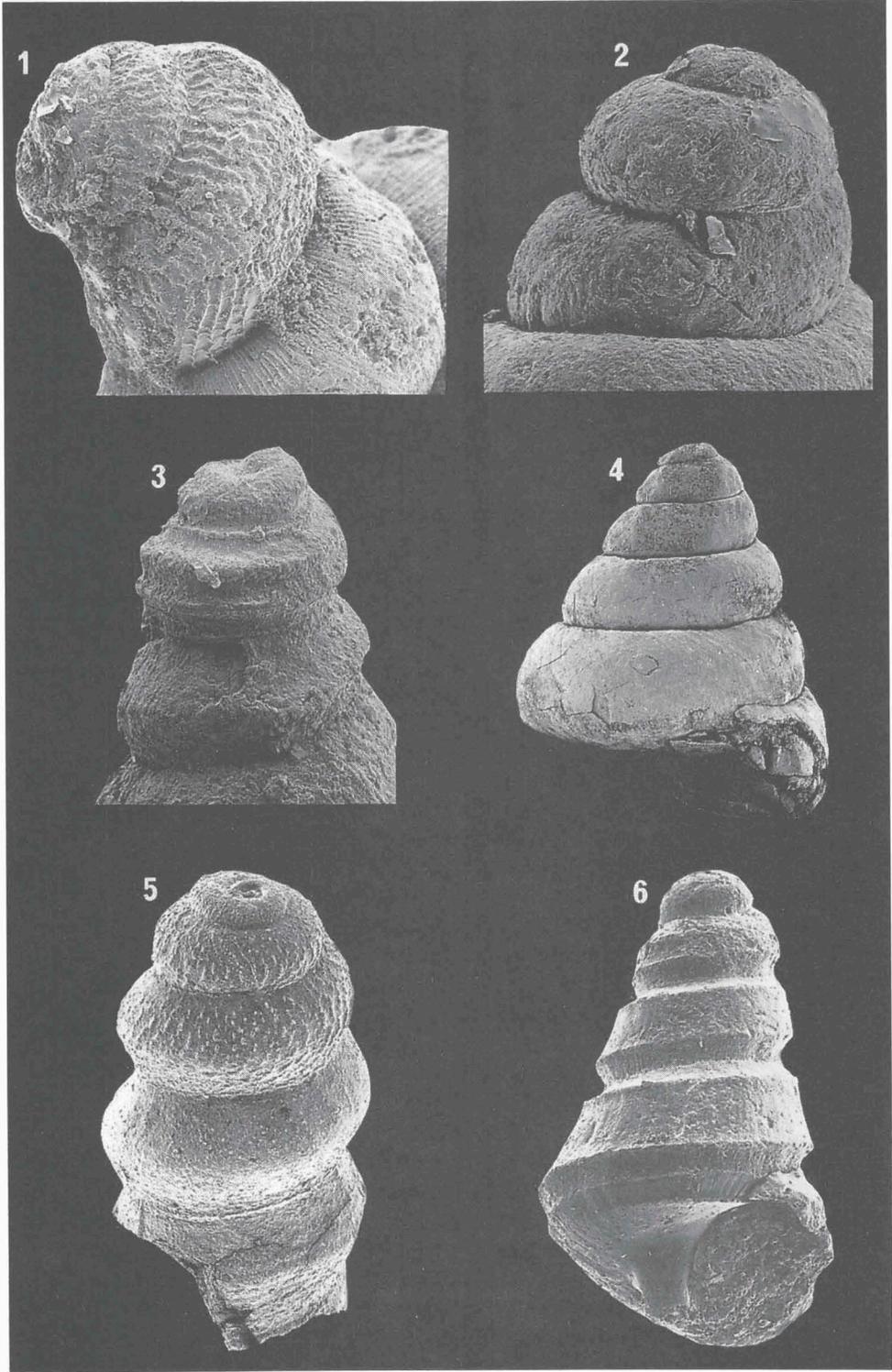


Plate 4

ted to a vermetid teleoconch. A form from the Eocene of Gan in southern France has a larval shell resembling the Protorculidae (Pl. 7, fig. 2), *Petalococonchus* and *Vermetus* are provided with a sinusigera of cerithioid shape, whilst *Stephopoma* has a characteristic shell covered with large rounded tubercles, quite unknown from other Caenogastropoda (Pl. 7, fig. 4). The same type of protoconch has been described by Lozouet (1986) from the Oligocene of France. Thus modern Vermetidae may be derived from different ancestors. The Late Cretaceous genus *Laxispira* from the Gulf Coast (Mississippi) of the USA (Pl. 7, figs. 5-6) and the Western Desert of Egypt seems to have come from a cerithiid stock (Dockery, 1991). It is convergent with modern *Vermicularia* that comes from a turritellid stock (Pl. 8, fig. 3). Haszprunar (1988) considers the Vermetoidea to represent a superfamily of its own, belonging to the Neotaenioglossa.

The Turritellidae were thought to appear first in the Early Cretaceous (Wenz, 1938-1944), which was confirmed by Schröder (1992, 1993). *Haustator* (Pl. 8, fig. 1) appears in the Valanginian of Poland. *Turritella* is common from there on (Dockery, 1991). The Palaeozoic genera placed in this family by Knight (1934) and Knight et al., (1960) do not belong in this group, which according to Houbrick (1988) is more closely related to the Vermetidae and Campanilidae than to the Cerithioidea. Some of the older species supposedly belonging into the Turritellidae belong to the Allogastropoda (Bandel, 1991c).

The Subulitoidea according to Wenz (1938-1944), are represented by fossils with more or less elongated fusiform to egg-shaped, usually smooth shells with a rounded base. A varying number of whorls with shallow sutures between them may be coiled around a straight or somewhat bend axis. The columella may be plicate and, if so, usually with a central swelling or ridge extending into the shell interior and an anterior thickening running nearly parallel to the siphonal notch. The aperture is

Plate 5

Fig. 1. The protoconch of *Plesiotrochus*, from the Pacific Ocean near Cebu City, Philippines, is similar to that of the Triassic *Angularia* (Fig. 3), 0.3 mm wide, ornamented by a weak spiral ridge only in the last portion of the larval shell, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.15 mm in diameter.

Fig. 2. The 2.8 mm high juvenile shell *Plesiotrochus*, from shallow lagoon Lizard Island on the Barrier Reef of Australia, resembles in shape the shell of Triassic *Angularia* (Fig. 4). The protoconch is like that shown in Fig. 1.

Fig. 3. The protoconch of *Angularia subpleurotomaria*, from the St Cassian Formation (Late Triassic, Italian Dolomites), is 0.35 mm high (in the visible part), is smooth and shows a large projection of the outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 4. The juvenile shell of *Angularia subpleurotomaria*, from the same formation, is 2.6 mm high.

Fig. 5. The juvenile shell of *Lacunina bronni* (Settsassiidae), from the same formation, is 1.5 mm high and has a larval shell of 3 whorls that is sculptured by a subsutural row of tubercles, is 0.3 mm high, shows a projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 6. The protoconch of *Omphaloptycha muensteri*, from the same formation, is 0.55 mm high (in the visible part), is ornamented by granulae, shows a large rounded projection of the outer lip of the 3,7 whorls large pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

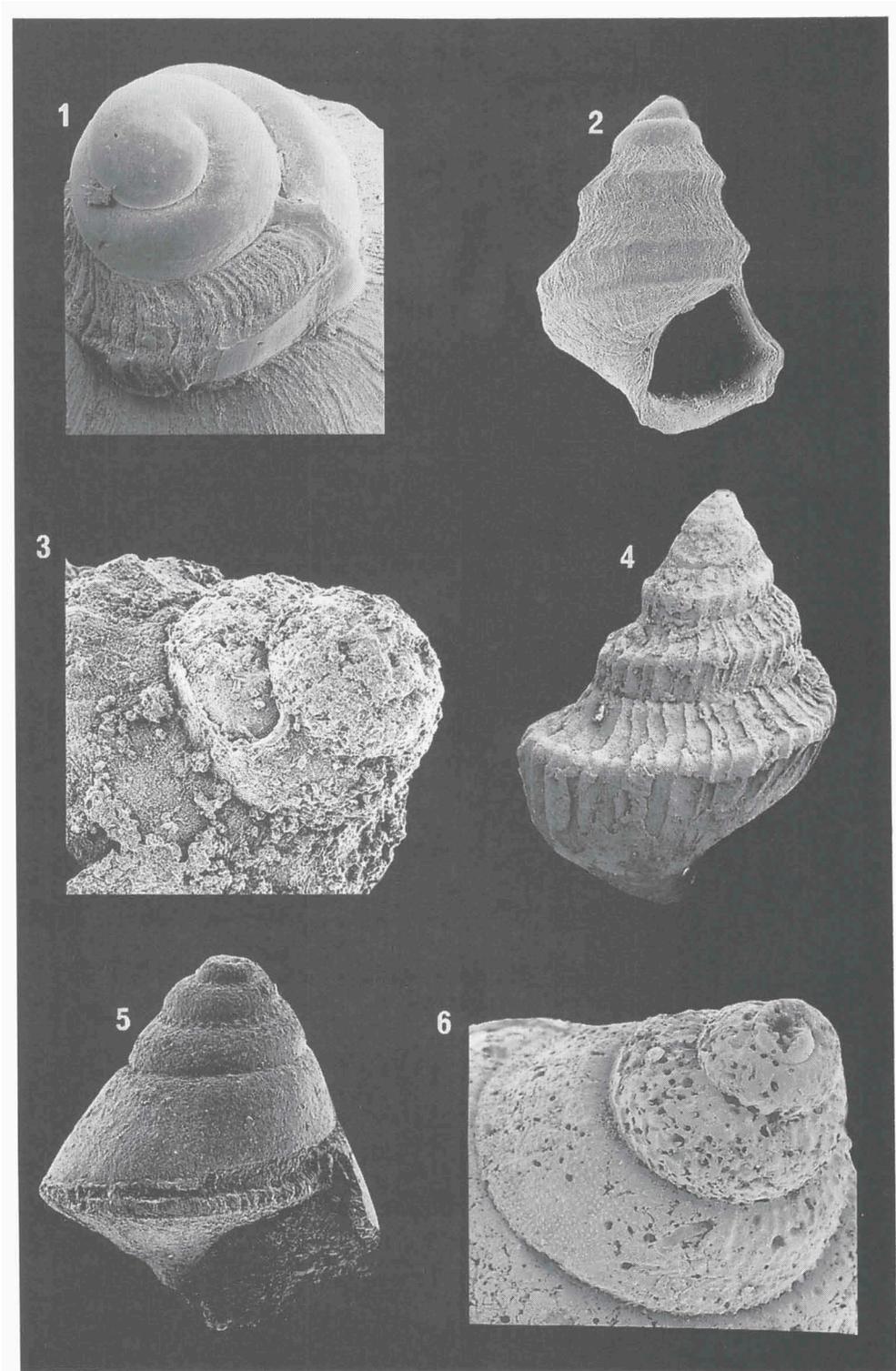


Plate 5

egg-shaped, more narrow above and rounded below, and may extend into a shallow, short siphon to form a pronounced siphonal notch.

The Subulitoidea are subdivided into the Meekospiridae, without columellar folds and only a broad shallow siphonal notch, the Subulitidae, with a siphonal notch and associated siphonal fold, and the Ischnoptygmididae, with a thin, plate-like columellar fold. Harper (1977) considered the Subulitidae with siphonal notches and siphonal folds as of equal rank as the Soleniscidae, which have strong columellar folds in addition to the siphonal notch and siphonal fold. The larval shell of possible Triassic representatives of the Subulitoidea is smooth, has rounded whorls, and the aperture is provided with a sinusigera larval hook (Pl. 8, figs. 4-5; Pl. 14, fig. 6.). *Euchrysalis*, from the Late Triassic St Cassian Formation (Zardini, 1978) (Pl. 14, fig. 6), could be a synonym of the genus *Ceraunocochlis*, as Harper (1977) described it from the Carboniferous. The same can be said for *Cylindritopsis* from the Permian (Erwin, 1988), with the Late Triassic *Cylindritopsis rimbianchi* (Pl. 8, figs. 4-5). Yoo (1988, 1989) demonstrated the probably caenogastropod nature of *Soleniscus* and *Ceraunocochlis* from the Early Carboniferous of Australia with species that may have hatched without planktotrophic larvae and that have only one whorl of the protoconch. Ponder (1973) assumed that the Neogastropoda had their origin in the Subulitoidea, a hypothesis which still needs to be evaluated.

The Triassic Subulitoidea and Late Cretaceous Neogastropoda are connected only by the Pseudomelaniidae of Wenz (1938-1944) representing a group of genera most of which belong to different systematic units that need to be re-evaluated. The genus *Pseudomelania* consists of slender eulimiform shells with straight sides, a non-umbilicate rounded base and a simple aperture (Pl. 8, figs. 6-7), as found among the caenogastropods as well as the Heterostropha (own data). *Oonia*, with species from New Zealand similar to the French type and of the same Early Jurassic age, may be related to the Subulitoidea, and certainly belongs to the Caenogastropoda (Bandel & Maxwell, in prep.). *Ianthinopsis*, from the Early Carboniferous of the USA (Harper, 1977, pl. 14, figs. 1-13) and from Australia (Yoo, 1988, fig. 103) resembles *Ampezzoella* (Coelostylinidae) with a smooth sinusigera larval shell (Knight, 1932, 1941). Thus it remains quite unsolved whether Palaeozoic Subulitoidea and Mesozoic forms of similar shape are related and whether the Pseudomelaniidae do not represent a composite group of unrelated species with a similarly smooth teleoconch.

The Murchisonioidea are based on a Mid-Devonian type, the protoconch of which is still unknown. But morphologically close species from the Early Carboniferous have a sinusigera-like protoconch with a rounded apertural projection and an embryonic shell larger than 0.1 mm. Their shell is composed of material in aragonitic crossed lamellar structure, as is the case in the Late Triassic *Cheilotomona* with its type-species from the St Cassian Formation. Also *Trypanocochlea* (= *Verania*) from the Pucará Group of Peru is a characteristic murchisoniid (Haas, 1953). Characteristic slit-bearing species and groups of the murchisoniids merge with forms having only a deep apertural sinus. It is quite unclear what happens to this group after the end of the Triassic and whether it has slit-less descendants among later Caenogastropoda.

The Loxonematoidea survive up to the Triassic. The Palaeozoic Loxonematidae have evolved into the Polygyrinidae with *Polygyrina* (Bandel, 1991a) (Pl. 4, fig. 5), which has a characteristic barrel-shaped protoconch with flattened apical portion

into which the small embryonic shell is imbedded. The sculpture of the larval shell consists of collabral rows of tubercles and a ridge pattern reflecting the position of the large larval hook during growth. A similar characteristic protoconch shape was noted for a Mid-Devonian species from western Germany resembling the Triassic polygyrinids (own observation).

Ctenoglossa

The fossil *Ctenoglossa* can be traced through time by their characteristic larval shell, which is presently known back to the Carboniferous (Knight, 1931; Hoare & Sturgeon, 1978-85; Yoo, 1988, 1989; Bandel, 1991a). The Zygopleuroidea are represented in Palaeozoic times by the Pseudozygopleuridae, with rounded larval whorls and a collabral axial sculpture, which reflects the presence of a larval hook at the middle of the outer lip (Pl. 9, figs. 1, 2, 4). This type of ornamentation is still found in species which lived in the Zechstein Sea (Pl. 9, fig. 4), whilst it is replaced by the Zygopleuridae, with the larval hook present further down on the apertural lip and thus usually covered by succeeding whorls (Pl. 10, fig. 6). *Zygopleura* is represented by a number of species in the Triassic St Cassian Formation. *Zardinistylus* is a close relative with a very similar larval shell that reminds one of that of some more modern Cerithiopsidae (Bandel, 1991a) (Pl. 9, fig. 3).

The Protorculidae, with *Protorcula* and *Ampezzopleura* from the Triassic St Cassian Formation, are characterised by a larval shell that is similar to those found in forms of the Early Cretaceous of Poland (Schröder, 1991) and in some more modern forms that can in part be placed within the Janthinoidea (Pl. 9, figs. 5-6; Pl. 10, figs. 2, 3, 5) (Bouchet, 1976; Bouchet & Warén, 1979; Bandel, 1991a).

Houbrick (1979) regards the deep water members of the Abysochrysidae, with *Abysochrysos*, as modern relatives of the Triassic Zygopleuridae and the Carboniferous-Permian Pseudozygopleuridae. The radula presents features which can be noted among modern Cerithiopsidae as well (Houbrick, 1979; Bandel, 1984). Abysochrysidae may thus represent modern intermediates between the Zygopleuroidea and the Triphoroidea. A larval shell is not known. The Triphoroidea with the modern Triforidae and Sherborniidae have not yet produced Mesozoic representatives (Bouchet, 1985; Marshall, 1978, 1983, 1984). Triphoridae, with a characteristic sinistral shell, are first known from the Danian of Denmark. Perhaps precursors can be traced back to a form that is close to the European Late Jurassic *Cryptoptyxis*, also known from the Early Jurassic of New Zealand (Bandel & Maxwell, in prep.) (Pl. 7 fig. 3).

The Cerithiopsidae may with *Teutonica* confirm this group in the Jurassic (Pl. 9, fig. 3) as supposed by Gründel (1980). In the Late Cretaceous of the Gulf Coast of the USA, several species of cerithiopsids are present (Dockery, 1991; Bandel, 1991a) (Pl. 10, figs. 2, 5) and with the beginning of the Tertiary representatives of the family Cerithiopsidae had become common (Pl. 8, fig. 2).

The Janthinoidea with the Epitoniidae according to Wenz (1938-1944) appeared in the Jurassic. In the Late Cretaceous of the US Gulf Coast larval shells of the characteristic epitoniid type are found (Dockery, 1991; Bandel, 1991a). The reported species have to be rechecked but the group could be very ancient since Herholz (1990, 1992) found larval shells in the Late Carboniferous of West Germany which had the char-

acteristic shape as present in modern *Epitonium*, but they may also represent a juvenile subulitid.

Whether the Eulimoidea with the Eulimidae are related to the epitoniids can not yet be demonstrated with fossil shells which make their first appearance with *Eulima* and *Niso* during the Late Cretaceous of the US Gulf Coast (Sohl, 1960; Dockery, 1991) (Pl. 10, figs. 1, 4). Modern representatives of these genera are primitive in regard to their anatomical features (Warén, 1983).

Meta-Mesogastropoda

The heading Meta-Mesogastropoda unites Caenogastropoda of first appearance in Mid-Mesozoic times. They encompass the Purpurinoidea and their possible offshoots the Stromboidea, as well as the Heteropoda and their potentially closest benthic relatives, like Pickworthidae and Vanikoridae.

The Pickworthiidae are first seen with *Urceolabrum* from the Late Cretaceous of the southeastern USA. This form certainly does not represent a member of the Angariidae, not even a suspect one as suggested by Hickman & McLean (1990). Its smooth larval shell (Dockery, 1991) differs from that of Palaeocene (Pl. 11, fig. 1) and modern Pickworthiidae. The protoconch of the latter in turn resembles that of some Vanikoridae (Warén & Bouchet 1988), of which no Mesozoic representatives are known up to the moment, as well as *Prostylifer* (Prostyliferidae) of the St Cassian Formation (Late Triassic) (Pl. 6, figs. 1-3). This may indicate some kind of relation of Prostyliferidae with Vanikoridae and Pickworthiidae which are considered questionable representatives of the Rissooidea by Ponder & Warén (1988). The modern genera *Sansonia* and *Pickworthia* occur in the Danian chalks of Denmark (Pl. 11, fig. 1).

The Heteropoda, with the Atlantidae and Firolidae, have no known fossil repre-

Plate 6

Fig. 1. The protoconch of *Prostylifer paludinaris*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.5 mm high (in the visible part), is ornamented by strong spiral ridges, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 2. The protoconch of *Ptychostoma pleurotomoides*, from the same formation, is 1 mm high, is ornamented by spiral rows of tubercles, shows a repaired outer lip of the pediveliger shell and an embryonic whorl of c. 0.08 mm in diameter.

Fig. 3. The larval shell of a member of the Prostyliferidae, from the same formation, is 0.35 mm wide and is ornamented by spiral ridges.

Fig. 4. The 1 mm high juvenile shell of *Hydrobia chopardiana*, from the Berriasian (Early Cretaceous) of the French Jura Mountains has a first embryonic whorl of 0.2 mm width.

Fig. 5. The protoconch of the iravadiid *Nozeba crassa*, from the Campanian (Late Cretaceous) Coffee Sand in Mississippi, consists of 2.5 whorls of which the embryonic shell is 0.1 mm wide and the illustrated shell 0.8 mm in diameter.

Fig. 6. The protoconch of the 1.3 mm large vitrinellid *Solariorbis clara*, from the same deposit, has 2.5 whorls with 0.45 mm width, is smooth, shows a straight, simple outer lip of the pediveliger shell and a granulated, embryonic whorl of c. 0.1 mm in diameter.

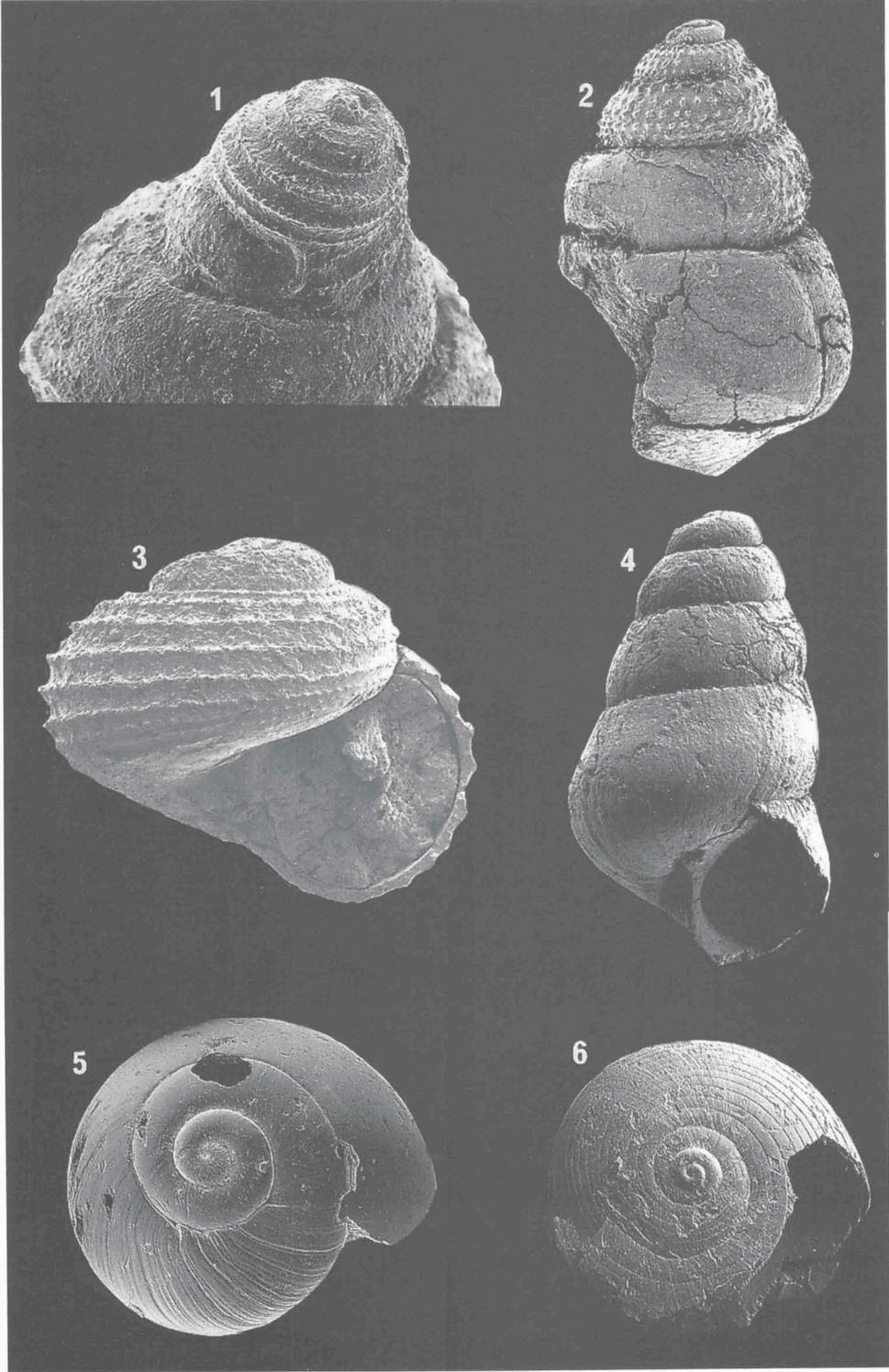


Plate 6

sentatives from the Mesozoic. The larval shells of the Atlantidae are of diverse shape. The most simple of these resemble those of the Pickworthiidae and some Vanikoriidae. The Carinariidae, in contrast, have been noted in the Early Jurassic with *Coelodiscus* from the Toarcian of Germany (Bandel & Hemleben, 1987) (Pl. 13, fig. 2). Here also Pterotracheidae are found, with the genus *Pterotrachea* which develops only an embryonic and larval shell that is discarded during metamorphosis (Bandel & Hemleben, 1987) (Pl. 13, fig. 1).

Taylor et al. (1980) suggested that the Purpurinoidea, with the Purpurinidae, represent the ancestors of the Neogastropoda. Wenz (1938-1944) considered them to represent Littorinoidea, which was accepted by Ponder & Warén (1988). *Angularia* and *Pseudoscalites* from the Late Triassic St Cassian Formation are close to *Purpurina* from the Jurassic in general shape of the shell (Pl. 5, fig. 4; Pl. 14, fig. 2). *Angularia* is a member of the Caenogastropoda as its protoconch consists of a sinusigera larva (Pl. 5, fig. 3; Pl. 14, fig. 4), as is characteristic for many Neogastropoda (Bandel, 1988b, 1991c). But in dimension the embryonic and larval shells resemble those found among the Littorinoidea, Rissooidea, and Stromboidea. The Purpurinoidea include *Maturifusus* from the Jurassic, which resembles neogastropods in teleoconch shape (Schröder, 1992, 1993), but regarding to its larval shell it is a purpurinid (Pl. 14, fig. 1). Species considered to belong to the genera *Protofusus*, *Paracerithium*, and *Rhabdocolpus* from the Late Triassic of Peru (Haas, 1953) may also belong here. Their protoconchs resemble those of the Purpurinidae and their teleoconchs are provided with a siphonal canal or notch (Bandel, in press).

The Stromboidea make their first appearance at the beginning of the Jurassic (Wenz, 1938-1944). Bandel (1991a) suggested that *Hemizyga* from the Carboniferous and *Cassianozyga* from the Late Triassic (Pl. 4, fig. 1) represent members of an evolutionary lineage that leads to the Stromboidea with similar larval shells found in the

Plate 7

Fig. 1. The 1.9 mm high juvenile shell of *Viviparus arkei*, from the Middle Purbeckian (Jurassic-Cretaceous transition) of Dorset in England, has a 0.2 mm wide earliest shell with irregularly wrinkled pattern, whilst later shell surface shows spiral rows of pits.

Fig. 2. The protoconch with 4 whorls of a vermetid shell of 1 mm height, from the Eocene of Gan in southern France (northern Pyrenees near Pau) is 0.5 mm high, is ornamented by strong axial ribs and weak spiral threads, shows a smooth outer lip of the pediveliger shell and an embryonic whorl of c. 0.16 mm in diameter.

Fig. 3. The protoconch of *Cryptoptyxis* sp., from the Early Jurassic of southern New Zealand, is 0.4 mm high (in the visible part) and ornamented by spiral and collabral ridges forming a reticulate pattern.

Fig. 4. The protoconch of *Stephopoma* sp., from the Late Oligocene of southern France is c. 1 mm wide and ornamented by large tubercles. Embryonic and larval shell form a single planispiral whorl that differs strongly from the teleoconch. Illustrated shell measures 3 mm across.

Fig. 5. The juvenile shell *Laxispira lumbricalis*, from the Late Campanian Coffee Sand in Mississippi, uncoils, while the protoconch (Fig. 6) consists of a regular, trochospiral shell with 3.5 whorls.

Fig. 6. The protoconch of *Laxispira lumbricalis* (Fig. 5) is 0.5 mm high, ornamented by spiral rows of tubercles, shows a weak projection of the lower outer lip of the veliger shell and an embryonic whorl of c. 0.12 mm in diameter.

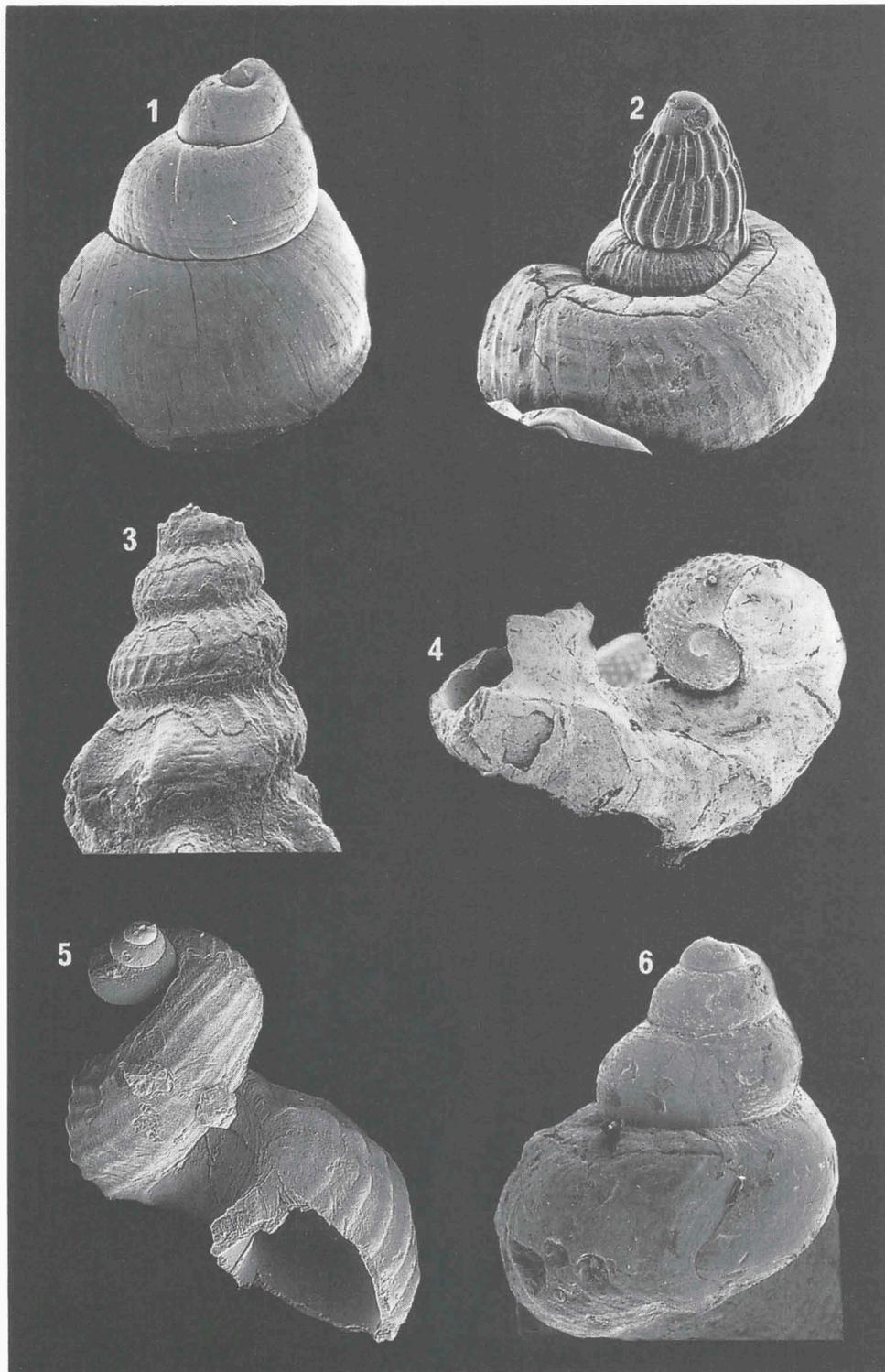


Plate 7

aporrhaid genus *Dicroloma* from the Jurassic (Pl. 11, fig. 4) (Schröder, 1992). Some species from the Early Jurassic placed in the genus *Paracerithium* probably represent members of the stromboids (Schröder, 1992, 1993) which disintegrates the Paracerithiinae as a supposed subgroup of the Procerithiidae (Wenz, 1938-1944).

From the Early Jurassic onwards the Aporrhaidae developed explosively with a number of genera such as *Alaria*, *Aporrhais*, *Anchura*, *Dicroloma*, and others which according to Schröder (1992) are used in the literature in a confused manner so that they need to be revised. Typical larval shells of the *Aporrhais*-type are present in the Middle Jurassic strata of North Germany and can also be found in the Early Cretaceous of Poland (Schröder, 1992) (Pl. 11, figs. 2-3) and the Late Cretaceous of Mississippi (Dockery, 1991, pl. 16, fig. 9).

The Colombellinidae with *Colombellina* from the Late Cretaceous of Tennessee and Mississippi (Sohl, 1960, 1964a, b) resemble *Columbellaria* from the Late Jurassic of Europe. Dockery (1991) described its protoconch as dome-shaped with a flat top and two convex whorls. *Zittelia* from the Late Jurassic of Europe resembles a cypraeid shell and is considered to have given rise to the Cypraeidae (Wenz 1938-1944). Colombellinidae are also assumed to represent the basic group from which the Cassoidea have developed. Taylor et al. (1980) include the Colombellinidae in the Cassoidea as earliest family appearing early in the Cretaceous and derived from the Stromboidea during Jurassic times. Taylor & Morris (1988) suggest that this group, including some cowry and cymatiid-like species, represents the stem group for the Cypraeoidea and Cassoidea. All this needs careful checking before the model of a transition from the Stromboidea into the different groups of the Neomesogastropoda

Plate 8

Fig. 1. The protoconch of *Haustator polonica*, from the Valanginian (Early Cretaceous) of Wonwal near Tomaschow in Poland, is 0.5 mm high (in the visible part), smooth, has a much larger apical angle than the teleoconch, shows a projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.09 mm in diameter. The shell is 1.6 mm high.

Fig. 2. The protoconch of the 1.7 mm high shell of a cerithiopsid species, from the Danian (earliest Tertiary) of Denmark, consists of 5.3 whorls, is 0.7 mm high (in the visible part), is ornamented by strong spiral ridges and interrupted axial lirae, shows a strong projection of the outer lip of the pediveliger shell and an embryonic whorl of c. 0.11 mm in diameter.

Fig. 3. The protoconch of modern *Vermicularia spirata*, from Florida, is 0.7 mm high with 2.5 whorls, ornamented by a spiral keel as commonly found among turritellids, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.2 mm in diameter.

Fig. 4. The protoconch of *Cylindritopsis rimbianchi*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.25 mm wide, ornamented only by growth lines, shows a rounded thickened projection of the outer lip of the pediveliger shell and an embryonic whorl of c. 0.12 mm in diameter.

Fig. 5. The teleoconch of *Cylindritopsis rimbianchi*, from the same formation, is 3.2 mm high. Details see Fig. 4.

Fig. 6. The 0.8 mm high juvenile shell of *Pseudomelania turrita*, from the Late Cretaceous (Santonian-Campanian) Gosau Formation at Brandenberg (Tirol), shows a sculptured protoconch (Fig. 7).

Fig. 7. Detail of Fig. 6, showing the 0.35 mm high protoconch with 2.7 whorls ornamented by strong spiral ridges in the larval part and an embryonic whorl of c. 0.1 mm in diameter.

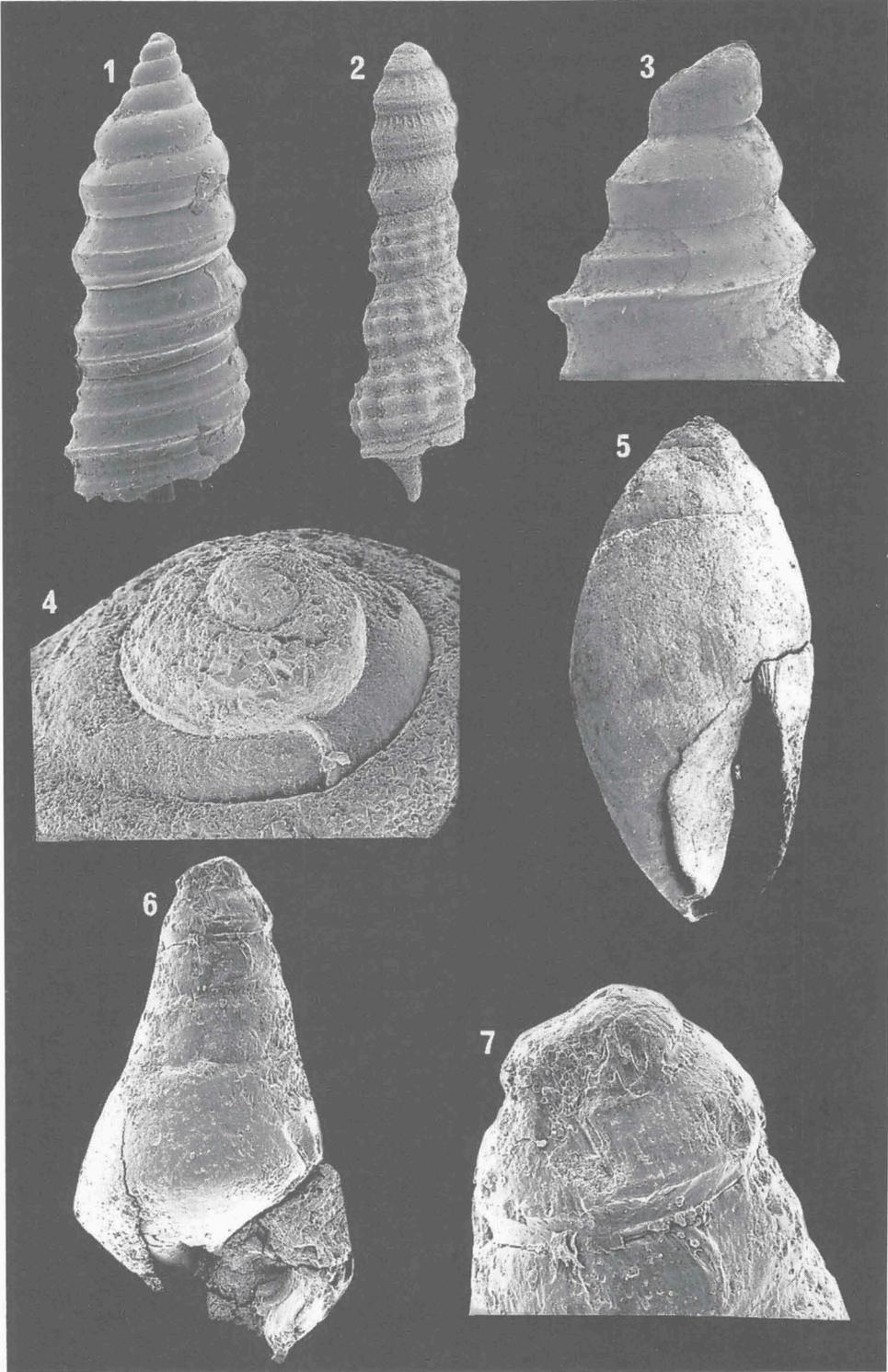


Plate 8

can be accepted.

The Strombidae according to Wenz (1938-1944) and Sohl (1960) start to appear with *Pugnellus* in the Late Cretaceous. The characteristic larval shell of the type found with modern *Strombus* can be traced back into the Early Jurassic, where *Mesostrombus* occurs (Pl. 11, fig. 5; Pl. 14, fig. 3) and marks the evolution of the Strombidae parallel to the Aporrhaidae. The Seraphsidae according to Jung (1974) consist of *Seraphs* and *Paraseraphs*. Modern *Terebellum* developed as a burrowing branch of the Stromboidea during the Late Cretaceous and flourished in the Tertiary.

The Xenophoridae supposedly include the genera *Jurassiphorus* and *Lamelliphorus*. These are still problematic gastropods and therefore cannot be used to extend the range of the Xenophoridae into the Jurassic. *Jurassiphorus triadicus*, from the Late Triassic of Peru, most probably represents an archaeogastropod, related to some forms found in the St Cassian Formation (Bandel, 1993, in press). *Xenophora* occurs first in the Late Cretaceous (Wenz, 1938-1944; Sohl, 1960). Sohl (1960) found that the genus *Endoptygma* can be united with *Xenophora*, so that only this genus remains in the Cretaceous. Its protoconch (described by Dockery, 1991, pl. 20, fig. 4) is in all essential features like that of the modern forms (Pl. 12, fig. 1).

Neomesogastropoda

The Neomesogastropoda contain the superfamilies Calyptraeoidae, Naticoidea, Cypraeoidea, Cassoidea, and Scaphoconchoidea, which make their first appearance within the Early Cretaceous and are united also by an extended ontogeny (Bandel, 1991c).

Plate 9

Fig. 1. The protoconch of a pseudozygopleurid of 0.8 mm height, from the Late Carboniferous Kendrick Shale Member (Late Westfalian B) of Kentucky, is ornamented by collabral ribs reflecting a strong projection of the outer lip of the veliger shell. The embryonic whorl is c. 0.15 mm in diameter.

Fig. 2. The 0.8 mm high protoconch of a pseudozygopleurid, from the same member, has a collabral ornament and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 3. The protoconch of *Teutonica gramanni*, from the Middle Jurassic of Osterfeld near Goslar (northern Germany), is 0.65 mm high (in the visible part), is ornamented by tubercular axial ridges, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 4. The protoconch of a pseudozygopleurid, from the Late Permian Zechstein of western Germany, consists of almost 4 whorls, is 0.55 mm high (in the visible part), and ornamented by the characteristic pattern of collabral ribs. The embryonic whorl measures c. 0.1 mm in diameter.

Fig. 5. The protoconch of *Protorcula subpunctata*, from the Late Triassic St Cassian Formation of the Dolomites, consists of 6.5 whorls, is 1.3 mm high, is ornamented by strong axial ridges crossed by fine spiral striae, shows a strong projection very low on the outer lip of the aperture and an embryonic whorl of c. 0.13 mm in diameter.

Fig. 6. The protoconch of *Ampezzopleura tenuis*, from the same formation, consists of 5.5 whorls, is c. 1 mm high (in the visible part), ornamented by strong axial ribs, shows a projection of the lowermost outer lip of the veliger shell and an embryonic whorl of c. 0.1 mm in diameter.

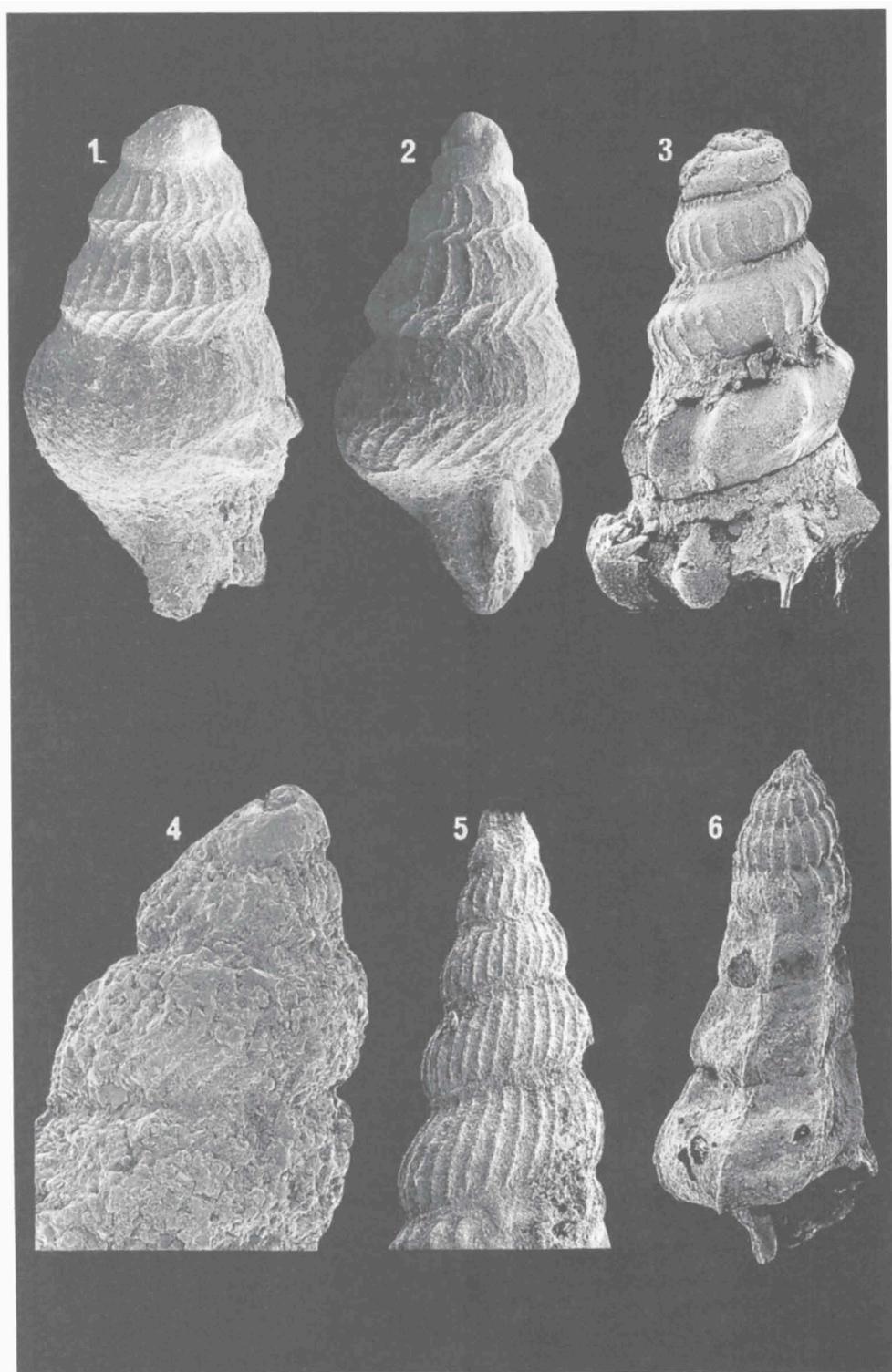


Plate 9

Of the Calyptraeidea the Hipponicidae are present at Late Cretaceous times with *Thylacus*, which was interpreted to represent a member of the Capulidae by Sohl (1960), but its globular larval shell clearly places it with the modern Hipponicidae such as *Cheilea*, *Sabia*, and *Antisabia* (Dockery, 1991, pl. 18, fig. 2; own data) (Pl. 12, fig. 2). *Hipponix* is reported from the Late Cretaceous, but this needs confirmation. *Thylacus* looks like modern *Neojanacus* and like it lived on the inside of shells that might also have been carried around by hermit crabs. The Calyptraeidae with *Calyptraea* are found in the Late Cretaceous at different places in Europe (Wenz, 1938-1944). In the Maastrichtian of the Western Desert of Egypt the subgenus *Sigapatella* is common (own data).

Wenz (1938-1944) traced the Naticidae into the Triassic. Taylor (1981), without presenting additional evidence, noted representatives of the Naticoidea first in the Early Jurassic. This can not be confirmed. All assumed naticids of the Triassic St Cassian Formation represent members of the Neritomorpha (Bandel, 1992a). The adult shells of many Naticoidea show very few characteristic features while the larval shells are easy to recognise and differentiate (Bandel, 1991c, e). None of these features were noted by Schröder (1992) in any of the Jurassic gastropods from north Germany and Poland. The characteristic protoconch shape can be used to check problematic species into which all those have to be included that lived before the Early Cretaceous and many later fossil forms too.

Taylor (1981) noted that in England Naticidae started drilling prey by Albian

Plate 10

Fig. 1. The protoconch of *Eulima laevigata*, from the Late Cretaceous Coffee Sand (Campanian, Mississippi), is 0.3 mm high (in the visible part), is smooth, has c. 3 rounded whorls that indistinctly grade into the teleoconch and an embryonic whorl of c. 0.15 mm in diameter.

Fig. 2. The protoconch of *Cerithiopsis meeki*, from the same deposit, is 0.75 mm high (in the visible part), consists of c. 4.3 whorls, is ornamented by strong radial ribs, shows a strong projection of the outer lip near the base of the veliger shell and an embryonic whorl of c. 0.1 mm in diameter. The teleoconch resembles that of modern *Seila*.

Fig. 3. The protoconch of a ctenoglossan species, from the Early Cretaceous (Valanginian) of Wonwal near Tomaschow in Poland intermediates in characters between cerithiopsids and protorculids, is 0.5 mm high, is ornamented by strong axial ribs that twist at the top of the strong projection of the lower outer lip of the veliger shell and an embryonic whorl of c. 0.2 mm in diameter.

Fig. 4. The protoconch of *Eulima gracilistylis*, from the Late Cretaceous Coffee Sand (Campanian, Mississippi), has a larval shell that merges with the teleoconch and an embryonic whorl of c. 0.15 mm in diameter. The illustrated shell is 1.4 mm high.

Fig. 5. The protoconch of cf. *Cerithiella* sp. (Bandel, 1991a), from the same deposit, is slender, consists of 6 whorls, is almost 1 mm high (in the visible part), is ornamented by strong collabral ribs in the upper whorl flank and a spiral keel in its lower portion, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.16 mm in diameter.

Fig. 6. The protoconch of *Zygopleura* cf. *haueri*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.55 mm high (in the visible part), consists of c. 4.2 whorls, is ornamented by a subsutural row of tubercles, shows a strong projection of the lower outer lip of the pediveliger shell and an embryonic whorl of c. 0.1 mm in diameter.

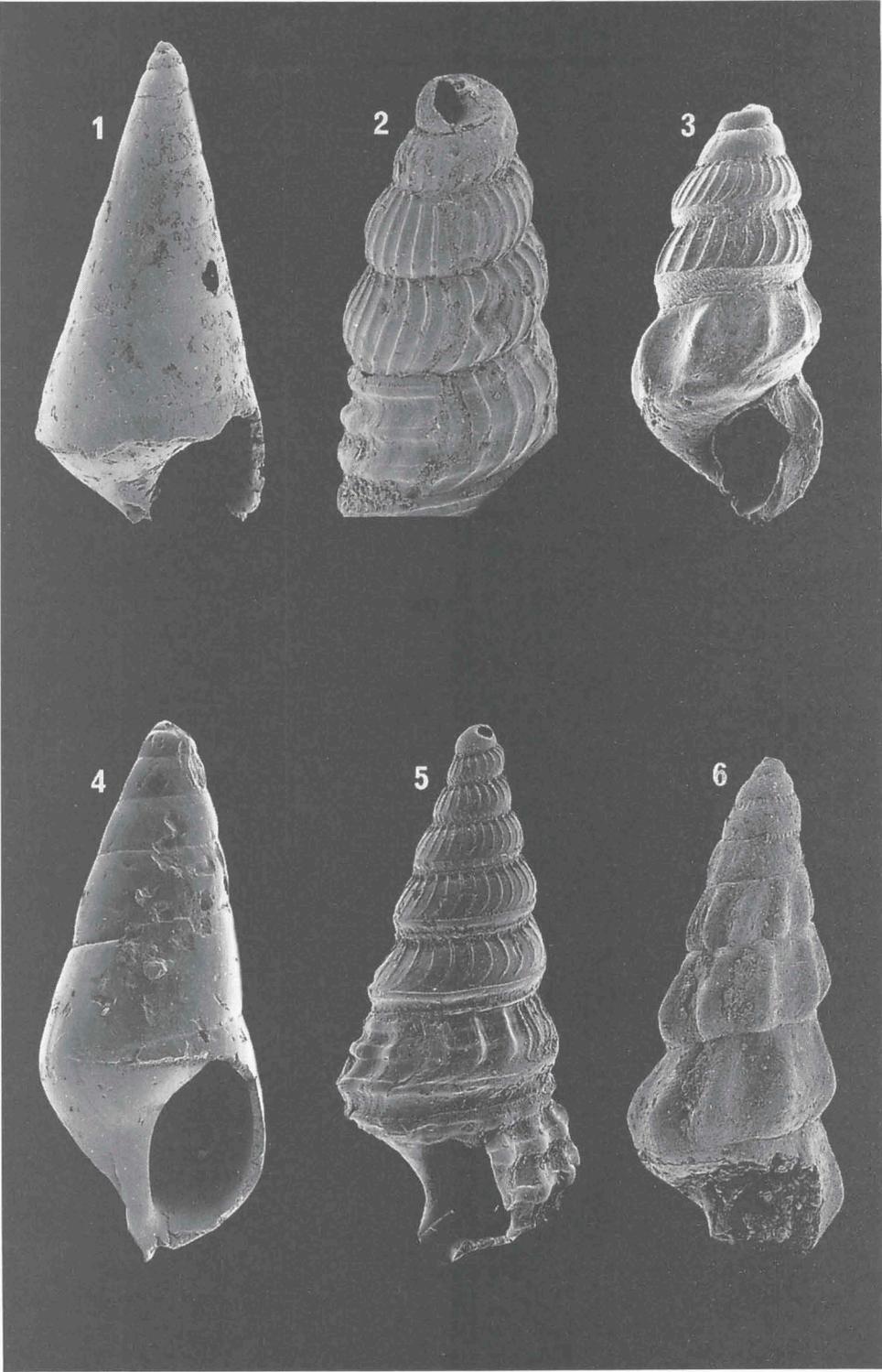


Plate 10

times which was confirmed by Kollmann (1982, upper Early Cretaceous). Popenoe et al. (1987) noted on the American West Coast the same behaviour only from Maastriichtian times onwards. They supposed that West Coast naticids appear to lag behind Atlantic basin naticids, even though *Gyrodes* is present here from the Albian onwards.

A globular shell of general naticoid shape with a large larval shell of the naticid type was found in the Early Cretaceous (Valangian) of Poland (Schröder, 1992) and may represent a member of the Naticidae. *Gyrodes* of the Gyrodinae is a common form in the Late Cretaceous and found in practically all Late Cretaceous marine faunas (Sohl, 1960). According to Dockery (1991) its protoconch consists of 2.25 whorls of the same shape as the adult shell, which is characteristic for naticid larvae. It is also preserved from the Senonian-Campanian Amman Formation in Jordan (Pl. 12, fig. 3).

Wenz (1938-1944) lists a number of extinct genera under the term Globularidinae which is synonymous with Ampullinidae (Sohl, 1960). All of the genera here included need careful checking. The species from the Late Triassic St Cassian Formation, that by Zardini (1978) and others were considered to belong to *Ampullina* and *Amauropsis*, belong into the Neritomorpha (Bandel, 1991d, 1992a). Several species of the genus *Amaurellina* may also belong to the Amphibolidae of the Archaeopulmonata (Harbeck, 1993). Sohl (1960) reports their presence and that of *Ampullina* (= *Pseudamaura*) from the Late Cretaceous of the US Gulf Coast.

As Sohl (1960) stated, most Cretaceous Naticinae have involved synonymies with

Plate 11

Fig. 1. The fully grown shell of *Sansonia* sp., from the Danian (earliest Tertiary) of Denmark, is 0.3 mm high. Its protoconch is c. 0.3 mm high and of typically pickworthiid shape with an ornament of spiral ribs and inclined position on the apex.

Fig. 2. The protoconch of an aporrhaid species, from the Valangian (Early Cretaceous) of Wonwal near Tomaschow in Poland is 0.4 mm high (in the visible part), consists of c. 3.3 whorls, is ornamented only in the last portion of the larval shell with spiral lines which are continuous into the teleoconch. The embryonic whorl measures c. 0.12 mm in diameter.

Fig. 3. The protoconch of an aporrhaid species from the Middle Bajocian of northern Germany with 3 whorls and 0.45 mm width shows sculpture continuous over the transition into the teleoconch. The embryonic whorl measures c. 0.1 mm in diameter.

Fig. 4. The protoconch of *Dicroloma subpunctata*, from the early Middle Jurassic (Aalenian) of northern Germany, is 0.5 mm high (in the visible part), consists of c. 3.3 whorls, and is ornamented by a collateral sculpture crossed by inclined lirae. A broadly rounded projection of the outer lip of the pediveliger shell is present.

Fig. 5. The protoconch of *Mesostrombus vetustus*, from the early Middle Jurassic (Aalenian) of northern Germany is 0.55 mm high (in the visible part), consists of c. 4 whorls, is ornamented by fine inclined ridges and tubercles in the first larval whorl, shows a low projection of the lower outer lip of the veliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 6. The juvenile shell of *Spirocyclus eucyclus*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.4 mm wide, consists of c. 2 whorls, is smooth and flattened apically, shows a straight apertural margin and an embryonic whorl of c. 0.2 mm in diameter.

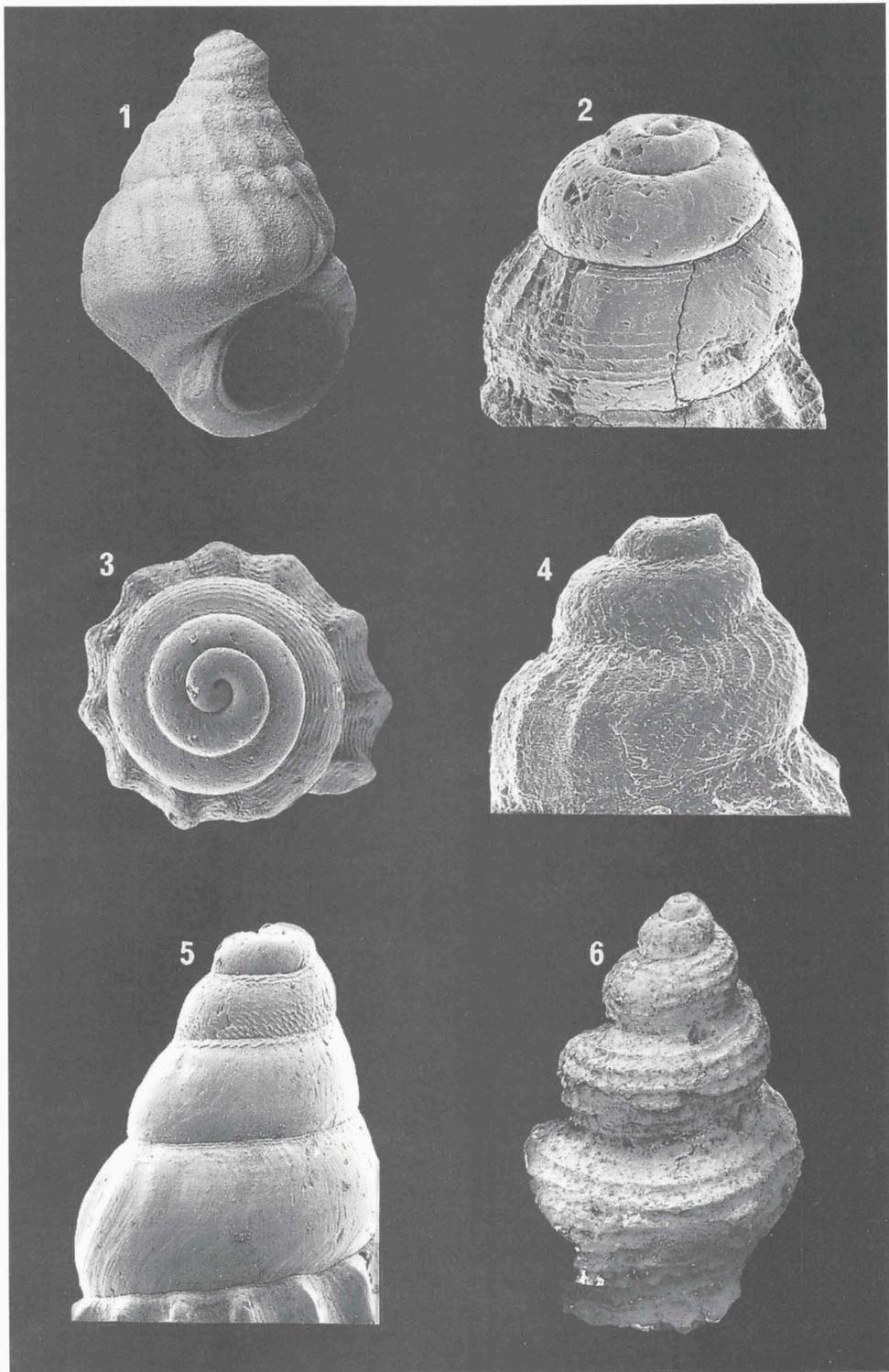


Plate 11

the genera *Polinices*, *Natica*, *Lunatia*, and *Euspira* being in use for the same species. Sohl (1960) recognised species of the genera *Polinices* and *Euspira* from the Gulf Coast Cretaceous; Popenoe et al. (1987) recognised *Natica* from the Turonian onwards on the US West Coast.

The Cypraeoidea have supposedly come from the stromboid (Colombellinidae) stock. According to Wenz (1938-1944), who refers to data originally presented by Schilder in a number of publications, the colombellinid *Columbellaria* gave rise to *Zitelia* and *Colombellina* which presented the base to the Eratoidea and these to the actual *Cypraea* relatives. This scenario cannot be considered to be concise since the Eratoidea have proven to be a group convergent to the Cypraeidae (Fretter & Graham, 1962), and belong to the Scaphoconchoidea. The larval shells of the Stromboidea, Cypraeoidea and Scaphoconchoidea differ from each other (Bandel, 1991c; Bandel et al., 1993), so that they may be used to unravel the history of each of these groups.

Quite a number of Cypraeidae range back into the Late Cretaceous, most from the Campanian to Maastrichtian beds. *Palaeocypraea* with a Palaeocene type species has been reported from the Albian of California and Texas (Groves, 1990) and is supposedly ranging back into the Late Jurassic (Wenz, 1938-1944), which needs, however, verification. *Bernaya* and *Protocypraea* have been reported from different Late Cretaceous localities (Groves, 1990; Dockery, 1991). The latter still has a living representative in the Gulf of Oman.

Wenz (1938-1944) expressed the opinion, that the Ovulidae made their appearance

Plate 12

Fig. 1. The protoconch of modern *Xenophora* sp., from the Pacific Ocean near Borneo, is 1.2 mm wide, consists of c. 3.5 low trochospiral whorls, ornamented by growth lines and one spiral ridge ending in the upper edge of the apertural projection of the outer lip. The same morphology is present in this genus since the Late Cretaceous. The illustrated shell is 4.5 mm wide.

Fig. 2. The protoconch of *Thylacus cretaceus*, from the Late Cretaceous Coffee Sand (Late Campanian, Mississippi), is 0.5 mm high, has a rounded larval shell with a 0.12 mm large embryonic whorl and is attached to a limpet-like teleoconch.

Fig. 3. The protoconch of a naticid species, from the Santonian Amman Formation of Amman in Jordan, is c. 1 mm wide, sculptured only by smooth straight growth lines and has an embryonic whorl of c. 0.15 mm in diameter.

Fig. 4. The protoconch of an unknown caenogastropod, from the Eocene Claiborn Formation of Brazos River near College Station in Texas, is 0.5 mm high, consists of c. 3.5 whorls, is ornamented by strong straight axial ribs crossed by fine spiral ribs, shows a straight simple aperture. It resembles protoconchs as seen in *Cypraea*.

Fig. 5. The pediveliger shell of an ovulid, from the Eocene Claiborn Formation of Brazos River near College Station in Texas, is 0.5 mm high, is ornamented by inclined ribs forming a reticulate pattern, shows a strong projection of the outer lip of the pediveliger shell and an embryonic whorl of c. 0.11 mm in diameter.

Fig. 6. The protoconch of *Cerithioderma* sp., from the Late Cretaceous Coffee Sand (Late Campanian, Mississippi), is 1.7 mm high, consists of c. 3.5 whorls, is ornamented by a regular pattern of axial and spiral ribs, shows a simple, straight outer lip of the pediveliger shell and an embryonic whorl of c. 0.25 mm in diameter.

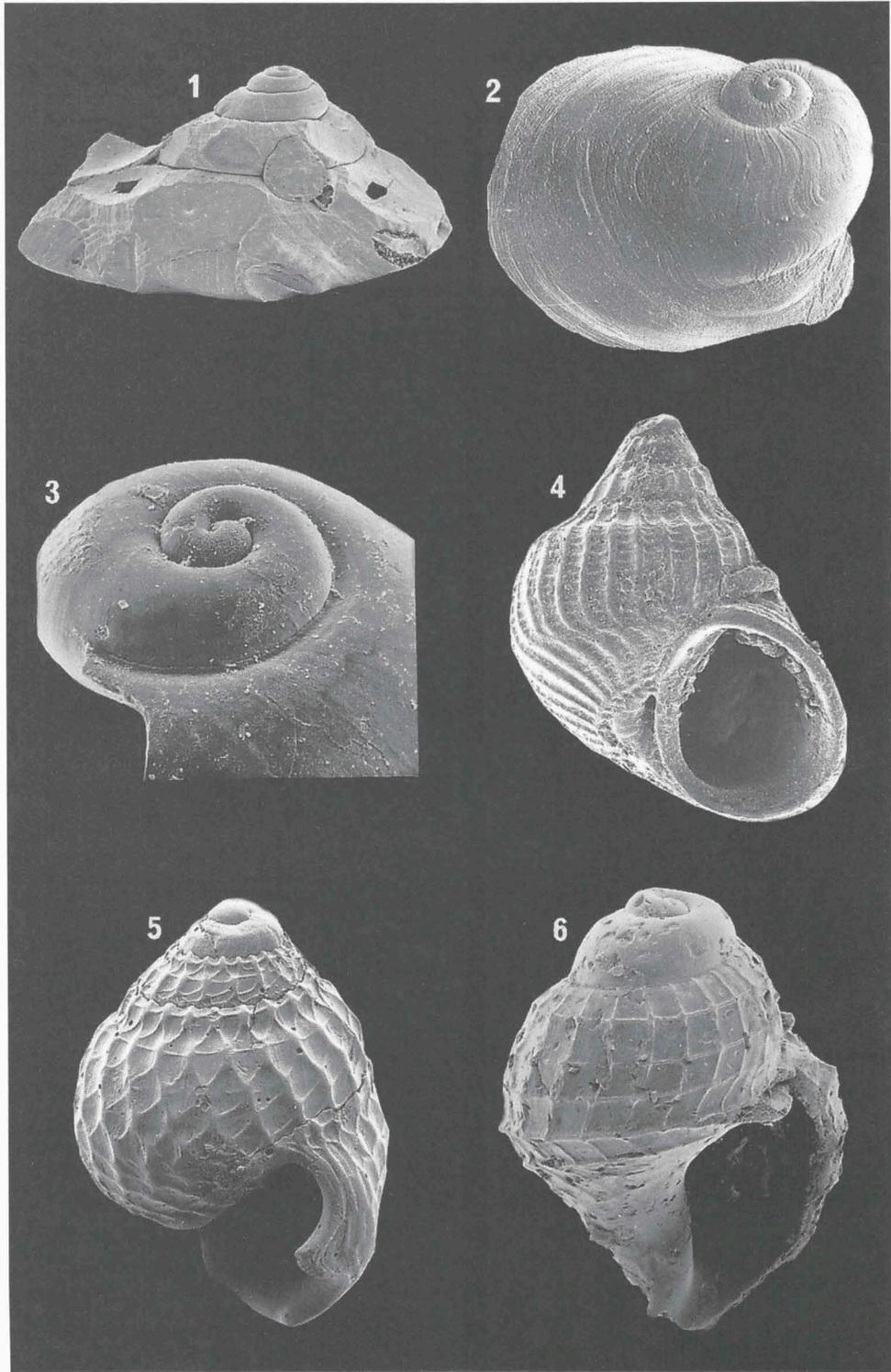


Plate 12

in the Late Jurassic. Groves (1990) reports the presence of *Eocypraea* in the Late Cretaceous of California, Oregon and Alabama and it has also been reported from India. The larval shells of the Ovulidae and Cypraeidae offer a chance to distinguish clearly both groups with convergent teleoconchs (Pl. 12, fig. 5).

The Scaphoconchoidea combine Neomesogastropoda with echinospira and limacosphaera larvae. Among these the Trichotropidae with *Trichotropis*, *Turbinopsis* and *Cerithioderma* are present in the Late Cretaceous of the US Gulf Coast deposits (Sohl, 1960; Dockery, 1991, pl. 18, fig. 5) (Pl. 12, fig. 6). Capulidae with *Capulus* can be recognised by their larval shell while the teleoconch is commonly convergent with that of members of the Calyptraeidea. *Capulus* is present in the Tertiary and may have representatives in the Late Cretaceous, which needs confirmation. According to Ponder & Warén (1988) the Capulidae represent the sessile branch of the Trichotropidae. The larval shell of *Sargana* resembles that of the Trichotropidae/Capulidae. Thus *Sargana*, and the whole group of the Sarganidae, are considered to represent potential members of the Scaphoconchoidea (Pl. 13, figs. 3, 4).

Erato and *Trivia* of the Triviidae have shells convergent with the Cypraeidae and Marginellidae. Late Cretaceous representatives need to be rechecked, both are clearly present within the Tertiary. The Lamellariidae and Marseniopsidae have no Mesozoic representatives.

The Cassoidea include the Cassidae, Ranellidae and the Personidae. The Ficidae anatomically resemble some modern neogastropods on the one side and in conchological respect Cretaceous forms like the Perissityidae, on the other (Riedel, 1992). According to Popenoe & Saul (1987) the Perissityidae represent a part of the Late Cretaceous siphonate gastropod radiation documented by Sohl (1964b) and Taylor et al. (1980). Popenoe & Saul (1987) suggest that *Tudicla* should be considered a close relative to the Perissityidae. Modern *Tudicla* is a representative of the Neogastropoda, but the fossil forms *Tudiclana* and *Heteroterma* from New Zealand are connected to the Perissityidae and only occur in the Palaeocene (Beu & Maxwell, 1990). They are similar to *Pyropsis* from the Late Cretaceous (Sohl 1964b), which like members of the Late Cretaceous genera *Schizobasis*, *Lowenstamia*, *Morea*, *Paramorea*, *Hippocampoides*, *Weeksia*, and *Sargana* have similar early ontogenetic shells (Bandel 1988a) (Pl. 13, figs. 3-4) that bring them close to the Neomesogastropoda, especially the most basic Cassoidea and Scaphoconchoidea (Trichotropidae). *Lowenstamia* closely resembles the modern deep-sea cassoidean *Thalassocyon* from the southern Pacific.

The characteristics of the Perissityidae, according to Popenoe & Saul (1987), are intermediate between those of the colombellinids and the buccinids. According to these authors they were derived from colombellinid ancestors, probably in advance to the cymatiids and perhaps in consort with the Tudiclidae and Colubrariidae. Late Cretaceous genera according to Popenoe & Saul (1987) are *Perissitys*, *Pseudocymia*, *Murphitys*, and *Christitys* from Western America, with relations to related forms in Pacific areas such as Japan and New Zealand.

The Cassidae, Personidae and Ranellidae according to Taylor et al. (1980) appeared in the Mid Cretaceous. Riedel (1992) considers them as separate units from the Campanian onwards, well characterised by their larval shells (Pl. 13, figs. 5-6). An Aptian/Albian ancestral form has a rectangular network pattern (Pl. 13, fig. 5) (Schroder, 1992), which in later species is reduced to the early larval whorls and may in even

younger species disappear, while a smooth organic shell is added (Bandel, 1981, 1991c; Riedel, 1992). Riedel (1992) recognised clearly defined members of the Cassidae from the Mid-Tertiary onwards, whilst the Ranellidae according to Taylor et al. (1980) appeared in the Mid Cretaceous. This was confirmed by Schröder (1992) who found the characteristic larval shells in the Aptian/Albian transition zone in northern Germany (Pl. 13, fig. 5). Beu (1988) mentioned *Triton kabanense* from the Turonian of Utah. *Gyrineum*, from the Campanian Coffee Sand of Mississippi, was well described and its larval shell documented by Dockery (1991) and Riedel (1992). *Charonia*, *Plesiotriton*, and *Tintorium* were described from the Campanian and Maastrichtian of the US Gulf Coast deposits. The Personidae appear with *Eutritonium* in the Campanian of Madagascar (Beu, 1988). Bursidae according to Taylor et al. (1980) appeared in the Mid Cretaceous, but Cretaceous representatives that may belong here can currently not be differentiated from other cassidoidean (= tonnoidean) species.

Neogastropoda

It has long been considered that some Late Triassic gastropods of the Purpurinoidea represent the earliest members of the Neogastropoda. The features of the protoconch do not confirm this assumption, since embryonic and larval shells are smaller than is usual among the Neogastropoda (Bandel, 1975). Kollmann (1982) and Taylor & Morris (1988) suggested that the first Neogastropoda occur in the Early Cretaceous. Kollmann (1982) considered the boreal seas of the Barremian as a possible place of origin of this group. Based on German and Polish material Schröder (1992) could not confirm the presence of neogastropods in the Early Cretaceous. Taylor (1981) mentions their first appearance in the Aptian Stage of the Cretaceous which also still needs confirmation. It is still unsolved which systematic units of the Neogastropoda appear first, even though Taylor et al. (1983) report the first appearance of the Muricoidea from the Albian, the Cancellarioidea in the Cenomanian and the presence of most groups in the Campanian. Sohl (1987) assumed that with exception of the Columbelloidea all neogastropod families had appeared during the course of the Cretaceous. Taylor (1981) recognised all groups with exception of the Harpidae in the Late Cretaceous.

The Muricoidea (= Rachiglossa) according to Wenz (1938-1944) appear with the Muricidae, genus *Pseudorapa*, in the Cenomanian of Aachen. *Ecphora* is supposedly present in the Late Cretaceous of the US Gulf Coast (Wenz, 1938-1944; Sohl, 1964b), but its larval shell with low spire and flat apex (Pl. 14, fig. 5) is very different from the true muricid *Ecphora* of the Miocene with the characteristic high conical larval shell of that group (Cool, pers. comm.). Sohl (1964a, b) reports the presence of several genera of the Muricidae from the Campanian and Maastrichtian of Tennessee and Mississippi. Of these only members of the genus *Morea* may represent neogastropods while others, like *Sargana* (see above), have a larval shell as found among the Trichotropidae of the Neomesogastropoda (Pl. 13, fig. 3). All so-called muricids from the Late Cretaceous of the US Gulf Coast that have been checked show a larval shell that is not typical for the neogastropods. The differentiation of the Muricidae began with the onset of the Tertiary (Pl. 15, fig. 4) and all older reports need careful rechecking.

The stratigraphically earliest report of the Coralliophilidae is from the Maastricht-

ian of Tennessee and Mississippi (Sohl, 1964a-b) with the genera *Hippocampoides* and *Lowenstamia*, both of which show larval shells similar to those of *Sargana* and *Ecphora* (Pl. 13, fig. 3; Pl. 14, fig. 5), without similarities to those generally found among Cenozoic and Recent Coralliophilidae (Pl. 15, fig. 6).

The Turbinellidae, such as *Protobusycon*, *Pyropsis*, *Harpovoluta*, *Lupira*, and *Lomirosa*, have been described from the Late Cretaceous of the USA by Sohl (1964b). Members of the first three genera as well as *Tudicla* have also been living in the shallow sea of the Maastrichtian in Egypt (own data). Taylor & Morris (1988) report the presence of Melongenidae from the Albian onwards. Regarding the Buccinidae Jablonski & Bottjer (1990) reviewed several Early Cretaceous members of the genera *Fusus* and *Buccinum*, just to note that they are problematic. Taylor et al. (1980) also state that buccinids appear in the Early Cretaceous and are common during the Late Cretaceous. *Stantonella*, from the Campanian and Maastrichtian, *Aliofusus*, *Buccinopsis*, *Anomalofusus*, *Deussenia*, *Hercorhyncus*, *Ornopsis*, and *Odontobasis*, as described by Sohl (1964b), represent neogastropods probably related to the Buccinidae. Observations on their protoconchs revealed only rather simple embryonic whorls sometimes with a tubercular ornament connected to fairly large, basically smooth larval whorls with a low projection of the outer lip of the aperture (Pl. 15, fig. 1). *Palaeopsephaea* can be traced back into the Cenomanian and occurs almost world wide (Sohl, 1964b).

Maturifusus, from the Middle Jurassic, may represent an early buccinid species as assumed by Schröder (1992), but more likely is related to the Purpurinoidea (Pl. 14, fig. 1). Wenz (1938-1944) mentioned only Cenozoic genera of the Columbellinae.

Plate 13

Fig. 1. The larval shell of *Pterotrachea liassica*, from the Toarcian of Unterstürmig (Early Jurassic, southern Germany), is 2 mm wide, consists of c. 2.5 whorls, is ornamented by simple axial costae and was probably shed at metamorphosis. \

Fig. 2. The shell of the Jurassic heteropod *Coelodiscus minutus*, from the same locality, is 1.2 mm wide, consists of c. 4 whorls, is ornamented by fine spiral ridges, shows a smoothly rounded ovoid aperture and an embryonic whorl of c. 0.13 mm in diameter.

Fig. 3. The protoconch of *Sargana stantoni*, from the Late Cretaceous (Maastrichtian) Coon Creek, Tennessee, resembles that of members of the Scaphoconchoidea with almost planispiral coiling and c. 0.7 mm in diameter, c. 2 smooth whorls and 0.2 mm wide embryonic whorl. The illustrated shell is 1.6 mm wide.

Fig. 4. The protoconch of *Weeksia* cf. *amplificata*, from the Early Maastrichtian of Mississippi (Ripley Formation), is 0.6 mm wide, consists of c. 3.2 whorls, is ornamented only by growth lines, shows a simple aperture and an embryonic whorl of c. 0.22 mm in diameter.

Fig. 5. The protoconch of the oldest known cassoidean species *Rapana gracillima*, from the late Early Cretaceous (Aptian/Albian-transition) of Algermissen in northern Germany, is c. 1 mm high, consists of c. 3 whorls, is ornamented by a regular network of axial and spiral ribs, and shows a weakly projecting outer lip of the pediveliger shell.

Fig. 6. The protoconch of *Sassia* sp., from the Late Cretaceous Coffee Sand (Late Campanian, Mississippi), is 1.3 mm high, consists of c. 3.5 whorls, is ornamented by a regular pattern of axial and spiral lirae, shows a smooth apical outer lip of the pediveliger shell and an embryonic whorl of c. 0.15 mm in diameter.

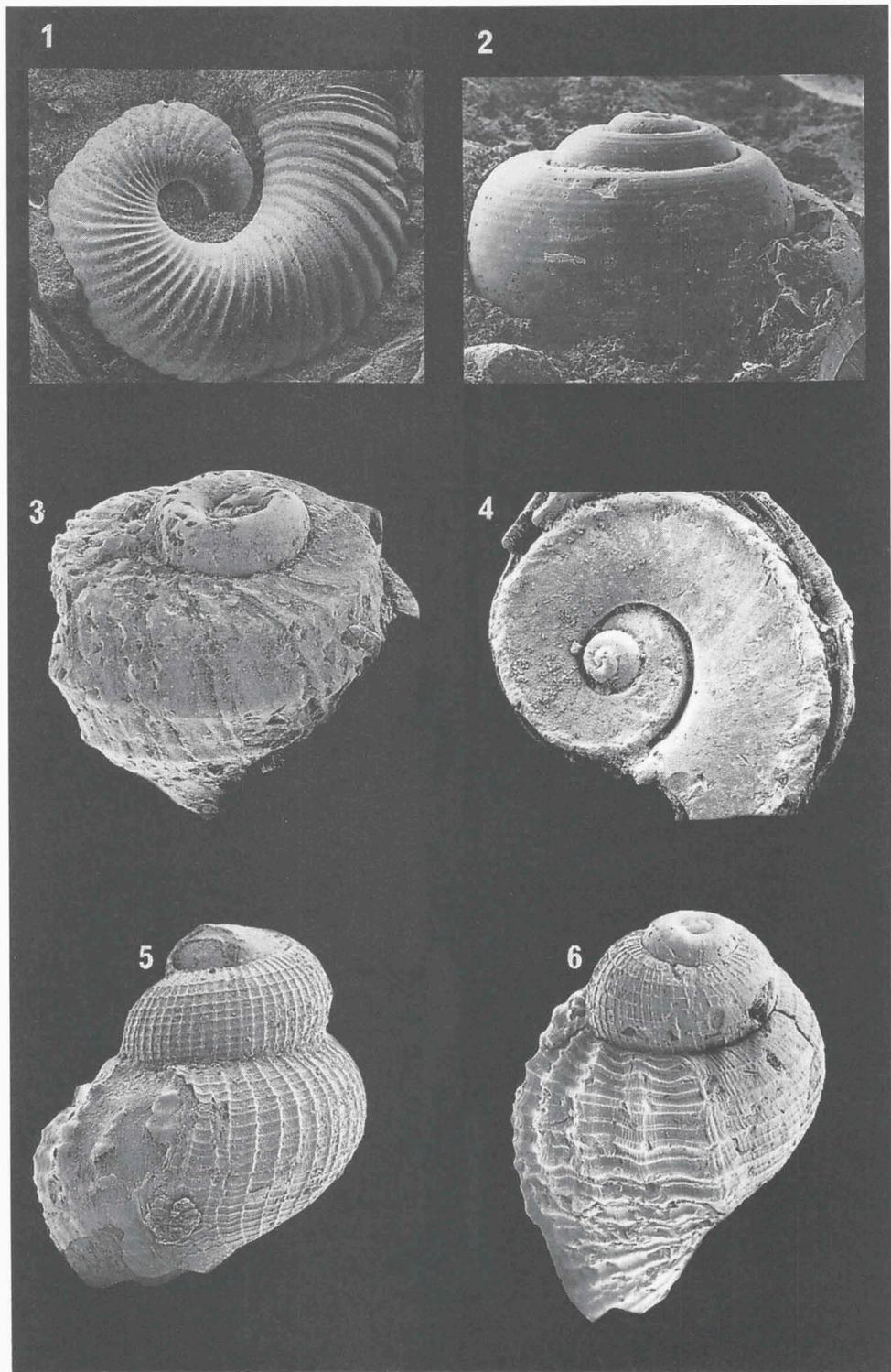


Plate 13

Shell shapes found within this group are largely convergent to other groups of the neogastropods so that this may not reflect the true history of members of this group. Also the characteristic Nassariinae appeared only after the Cretaceous within the Cenozoic, whilst the Fascioliariinae according to Taylor & Morris (1988) are present from the Albian onwards.

The Volutidae with *Longoconcha*, from the Late Cretaceous of the US East Coast, are replaced by *Volutoderma* on the US West Coast (Sohl, 1964b). *Volutomorpha* is also common in the Late Cretaceous of western Egypt and its young hatched with a large embryonic shell as miniature adults (Pl. 15, fig. 5) just like their Neogene and modern relatives.

Pseudoliva, *Ptychosyca*, and *Hydrotribulus* represent the Olividae from the Late Cretaceous of the USA, Europe and North Africa (Wenz, 1938-1944; Sohl, 1964b). The *Oliva*-type with a very long narrow aperture also lived during the Maastrichtian in Egypt (own data).

Only *Mitridomus* seems to represent the Mitridae in the Late Cretaceous (Wenz, 1938-1944; Sohl, 1964b).

The Cancellarioidea (= Nematoglossa) with the Cancellariidae supposedly represented by the Cretaceous genus *Mataxa* is placed here by Sohl (1964b) (different place in Wenz, 1938-1944), who also recognised Cretaceous members of the genera *Trigonostoma* and *Cancellaria*. Wenz (1938-1944) and Sohl (1964a, b) name several other genera from the Late Cretaceous. The characteristic larval shell, as seen in a member from the Palaeocene of Alabama (Pl. 15, fig. 3), supports such an opinion.

Plate 14

Fig. 1. The 3 mm high juvenile shell of *Maturifusus szaboi*, from the Bajocian of northern Germany, has a 1.4 mm high protoconch that consists of c. 4.5 whorls, is smooth with an apertural projection of the lower outer lip of the veliger shell.

Fig. 2. The 3.5 mm high juvenile shell of *Angularia subpleurotomaria*, from the Late Triassic St Cassian Formation of the Dolomites, has a protoconch as in Fig. 4.

Fig. 3. The protoconch of *Mesostrombus* sp. (Schröder, 1992), from the middle Early Jurassic of Hambühren in northern Germany, is 1 mm high, consists of c. 4.4 whorls, is ornamented by spiral rows of minute tubercles, shows a weak projection of the lower outer lip of the veliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 4. The protoconch of *Angularia*, as shown in Fig. 2, is 0.35 mm high (in the visible part), consists of c. 3 whorls, is smooth with a well rounded projection of the outer lip of the aperture and has an embryonic whorl of c. 0.07 mm in diameter.

Fig. 5. The protoconch of *Ecphora proquadricostata*, from the Late Cretaceous Coffee Sand (Late Campanian, Mississippi), is 0.8 mm high (in the visible part), consists of almost 3 smooth whorls, has flatly coiled first 1.5 whorls, shows a simple aperture and an embryonic whorl of c. 0.2 mm in diameter.

Fig. 6. The protoconch of *Euchrysalis alata*, from the Late Triassic St Cassian Formation of the Dolomites, is 0.3 mm high (in the visible part), consists of c. 3.5 whorls, is smooth with a strong projection of the outer lip of the veliger shell and an embryonic whorl of c. 0.1 mm in diameter.

Fig. 7. The protoconch of *Dicroloma* sp., from the Early Cretaceous (Valanginian) of Wonwal in Poland, is 0.45 mm high, smooth, has a strong projection of the outer lip of the veliger shell and an embryonic whorl of c. 0.12 mm in diameter. The illustrated shell is 0.85 mm high.

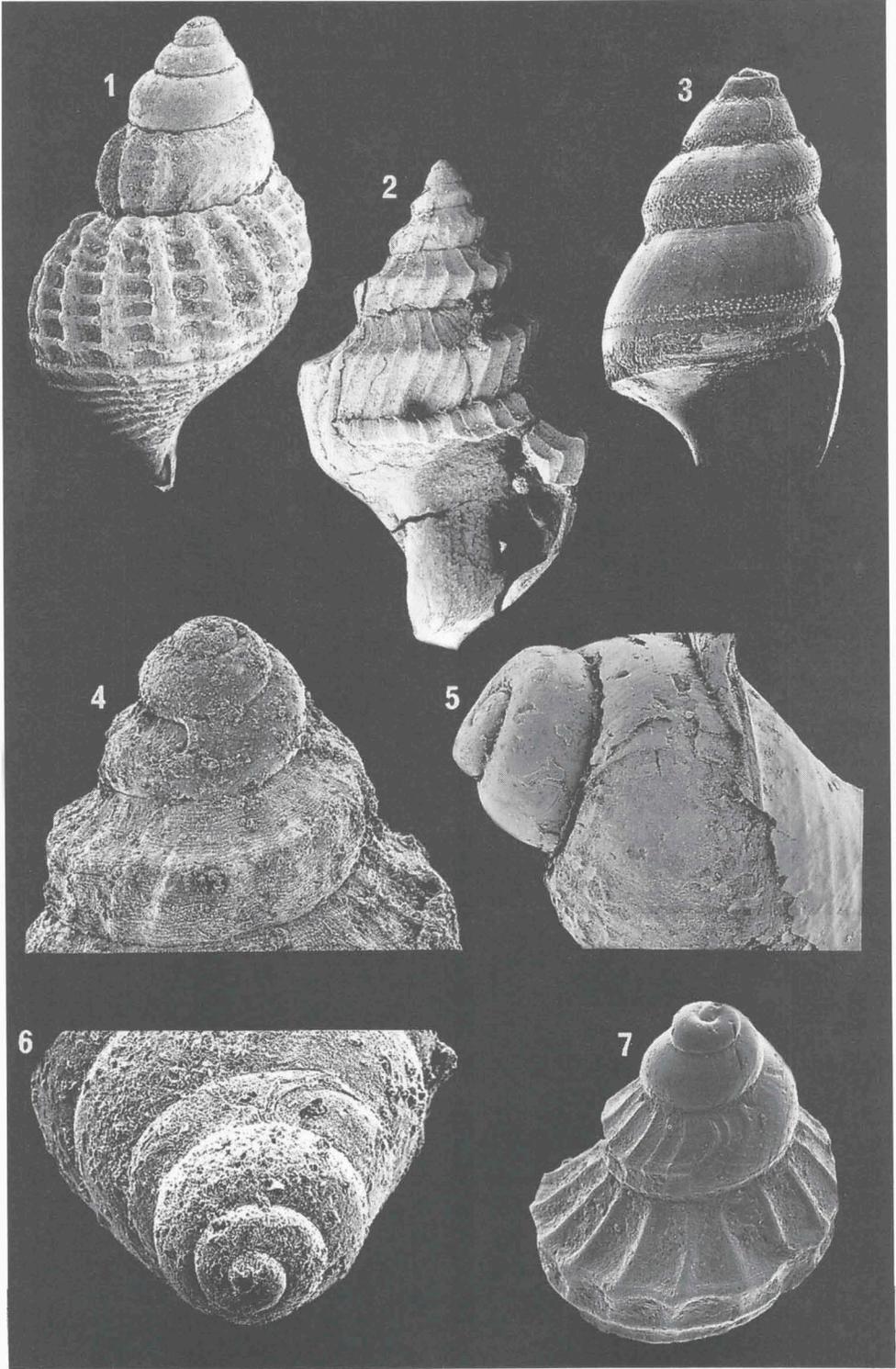


Plate 14

The Conoidea (= Toxoglossa), with the Turridae, are found in the Campanian and Maastrichtian deposits of the Gulf Coast area in the USA and hold the genera *Amuletrum*, *Lutema*, *Remnita*, *Beretra*, and *Fusimilis*, which, according to Sohl (1964b), all are members of a related group. They all have rather similar larval shells with rather simple ornament (Pl. 15, fig. 2) which differs from the rather complex sculptures found among many of the later forms.

Conclusions

This course through taxonomic connections that may be seen among Mesozoic caenogastropods indicates that knowledge is still limited and many suggested links are questionable. The tracing of lineages across the Palaeozoic-Mesozoic boundary has just begun, but the provisional data indicate that probably several independent units of Caenogastropoda can be traced all the way back into the Ordovician.

Studies concerned with Late Triassic gastropods of the Alpine St Cassian Formation revealed (Bandel, 1988b; 1991a, d; 1992a, b, 1993) that genera commonly combine a number of species, which differ considerably from each other when their protoconch and shell structure are known. All established genera thus have to be re-evaluated before their place in larger taxonomic units can be confirmed. Seemingly well known taxonomic units like Loxonematoidea and Euomphaloidea disappear largely when their numerous representatives in the Late Triassic are better known (Bandel, 1988a, 1993). Other taxonomic units, like Cerithioidea and Ctenoglossa reveal a rich diversification at St Cassian times, reflecting an evolutionary history that is much older than was thought. Jurassic gastropods with early ontogenetic shell preserved show that all established genera have to be re-evaluated. This process has only been started (Gründel, 1976, 1980; Schröder, 1991, 1992, 1993; Bandel & Maxwell, in prep.), and most

Plate 15

Fig. 1. The protoconch of a neogastropod, from the Late Cretaceous Coffee Sand (Late Campanian, Mississippi), is 0.9 mm high, consists of c. 4 whorls, is ornamented by tubercles in the 0.2 mm wide embryonic whorl and a subsutural row of tubercles in the larval part of the shell.

Fig. 2. The protoconch of a buccinid-type neogastropod of a different species as shown in Fig. 1, from the same deposit, is almost 1.2 mm high, consists of c. 4 whorls, is ornamented by tubercles in the 0.18 mm wide embryonic whorl and only growth lines in the larval part of the shell reflecting a wide projection in the lower part of the aperture.

Fig. 3. The protoconch of a cancellariid species, from the Palaeocene of Matthews Landing at the Alabama River in Alabama, is flattened in its upper portion with the 0.15 mm wide embryonic whorl. The larval shell has a simple aperture and smooth surface. The illustrated shell is 1.8 mm high.

Fig. 4. The protoconch of this *Typhis*-like muricid from the Palaeocene of Matthews Landing in Alabama, is 1 mm high (in the visible part), consists of c. 4 smooth whorls and has an embryonic whorl of c. 0.2 mm in diameter. The illustrated shell is 4 mm high.

Fig. 5. The protoconch of the 5 mm high volutid neogastropod, from the Maastrichtian of Ammonite Hill in the Western Desert of Egypt, consists of a single whorl of 4 mm width.

Fig. 6. The 3 mm high juvenile shell of *Coralliophila*, from the reef environment of the Pacific Ocean near Cebu City, Philippines, carries a larval shell of c. 1.2 mm height that is highly sculptured.

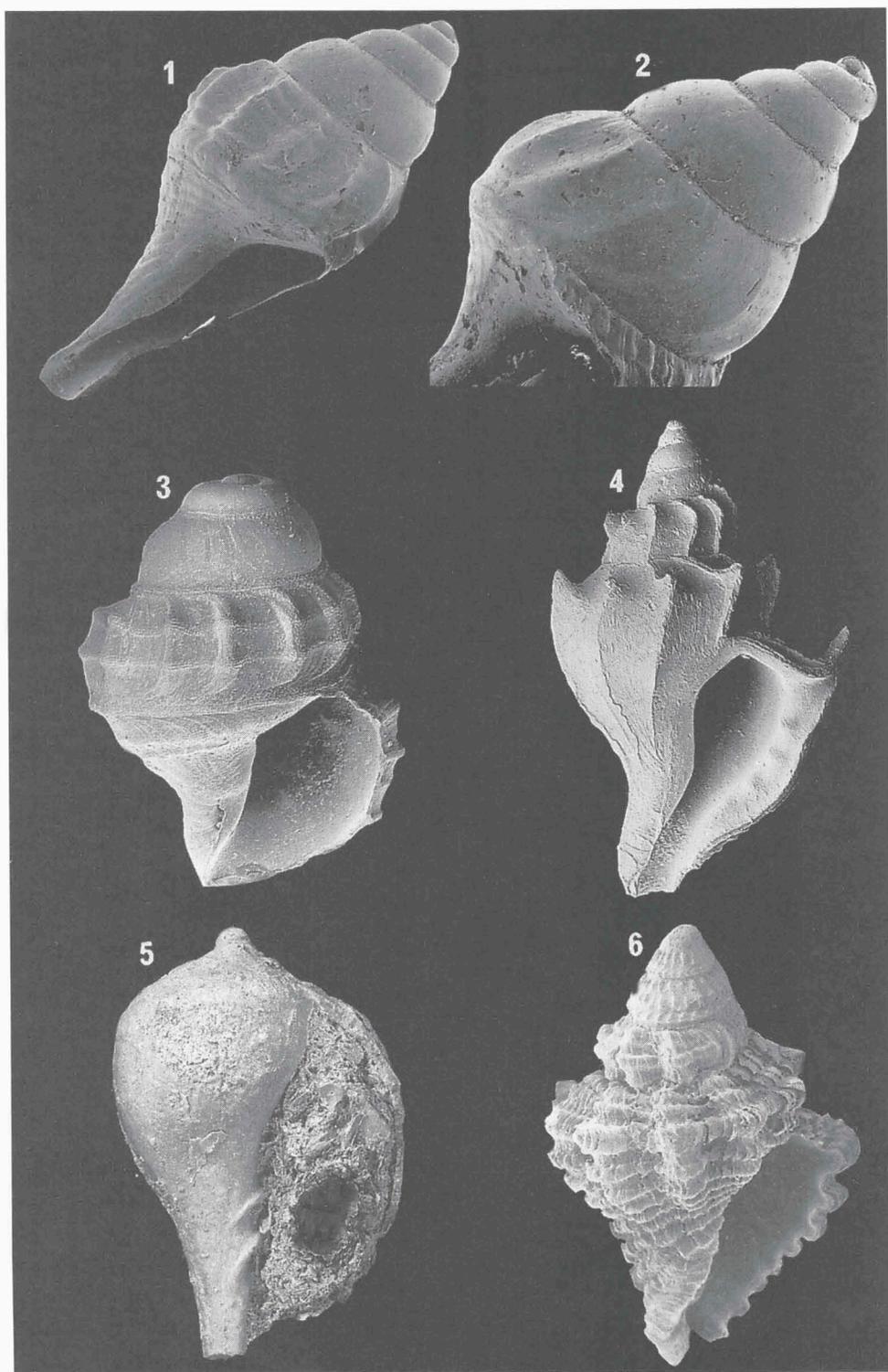


Plate 15

taxonomic units are still good for surprises. Due to the extensive studies on Cretaceous gastropods from Mississippi Dockery (1991) increased our knowledge of protoconch morphology for many caenogastropod species, but most other faunas are still untouched in this respect. Own studies in the Alpine Gosau facies indicate that the change across the Mesozoic-Cenozoic boundary is larger than commonly expected.

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Table 1. Alphabetic list of taxa mentioned in this paper

<i>Abyssochrysidae</i> Tomlin, 1927	<i>Campanilidae</i> Douvillé, 1904
<i>Abyssochrysos</i> Tomlin, 1927	<i>Cancellaria</i> de Lamarck, 1799
<i>Ajkaia</i> Tausch, 1886	<i>Cancellariidae</i> Gray, 1853
<i>Alaba</i> H. & A. Adams, 1853	<i>Cancellarioidea</i> Gray, 1853
<i>Alaria</i> Morris & Lycet, 1850	<i>Capulidae</i> Fleming, 1822
<i>Aliofusus</i> Stephenson, 1941	<i>Capulus</i> de Montfort, 1810
<i>Alvania</i> Risso, 1826	<i>Carinariidae</i> de Blainville, 1818
<i>Amaurellina</i> P. Fischer 1895	<i>Cassianozyga</i> Bandel, 1991
<i>Amauropsis</i> Mörch, 1857	<i>Cassianozyga seelandica</i> Bandel, 1991
<i>Ampezzoella</i> Bandel, 1992	<i>Cassidae</i> Latreille, 1825
<i>Ampezzopleura</i> Bandel, 1991	<i>Cassiope</i> Coquand, 1865
<i>Ampezzopleura tenuis</i> (von Münster, 1841)	<i>Cassiope ? giebeli</i> (Zekeli, 1852)
<i>Ampezzoscala</i> Bandel & El Nakhal, 1992	<i>Cassiope (Glauconia) ornata</i> (Drescher, 1868)
<i>Ampezzoscala ornata</i> (von Münster, 1841)	<i>Cassiope kefersteini</i> (von Münster, 1844)
<i>Amphibolidae</i> Gray, 1840	<i>Cassiopidae</i> Kollmann, 1979
<i>Ampullariidae</i> Gray, 1824	<i>Cassoidea</i> Latreille, 1825
<i>Ampullarioidea</i> Gray, 1824	<i>Ceratia</i> H. & A. Adams, 1852
<i>Ampullina</i> Bowdich, 1822	<i>Ceraunocochlis</i> Knight, 1931
<i>Ampullinidae</i> Cossmann, 1918	<i>Cerithiella</i> Verrill, 1882
<i>Amuletrum</i> Stephenson, 1941	<i>Cerithiidae</i> Fleming, 1822
<i>Anapomatias</i> Hrubesch, 1965	<i>Cerithioderma</i> Conrad, 1860
<i>Anchura</i> Conrad, 1860	<i>Cerithioidea</i> de Férussac, 1819
<i>Angariidae</i> Thiele, 1921	<i>Cerithiopsidae</i> H. & A. Adams, 1853
<i>Angularia</i> Koken, 1892	<i>Cerithiopsis meeki</i> Wade, 1926
<i>Angularia subpleurotomaria</i> (von Münster, 1841)	<i>Cerithiozyga</i> Bandel, 1992
<i>Anomalofusus</i> Wade, 1916	<i>Cerithiozyga büttneri</i> (Kittl, 1894)
<i>Anthracopupa</i> Whitfield, 1881	<i>Cerithium</i> Bruguière, 1789
<i>Antisabia</i> Iredale, 1937	<i>Charonia</i> Gistel, 1848
<i>Aporrhaidae</i> Gray, 1850	<i>Cheilea</i> Modeer, 1793
<i>Aporrhais</i> da Costa, 1778	<i>Cheilotomona</i> Strand, 1928
<i>Architectonicoidea</i> Gray, 1840	<i>Christiys</i> Popenoe & Saul, 1987
<i>Argyropeza</i> Melvill & Standen, 1901	<i>Coelodiscus</i> Brösamlen, 1909
<i>Assimineidae</i> H. & A. Adams, 1856	<i>Coelodiscus minutus</i> (von Zieten, 1832)
<i>Atlantidae</i> Rang, 1829	<i>Coelostylina</i> Kittl, 1894
<i>Bauxia</i> Caziot, 1890	<i>Coelostylinidae</i> Cossmann, 1909
<i>Bembicium</i> Philippi, 1846	<i>Colombellina</i> d'Orbigny, 1842
<i>Beretra</i> Stephenson, 1941	<i>Colombellinidae</i> Fischer, 1884
<i>Bernaya</i> Jousseau, 1884	<i>Colubrariidae</i> Dall, 1904
<i>Bithynia</i> Leach, 1818	<i>Columbellaria</i> Rolle, 1861
<i>Bithyniidae</i> Gray, 1857	<i>Columbellidae</i> Swainson, 1840
<i>Bittium</i> Leach, 1847	<i>Columbellinae</i> Swainson, 1840
<i>Buccinidae</i> Rafinesque, 1815	<i>Conoidea</i> Rafinesque, 1815
<i>Buccinopsis</i> Conrad, 1857	<i>Coralliophila</i> H. & A. Adams, 1853
<i>Buccinum</i> Linné, 1758	<i>Coralliophilidae</i> Chenu, 1859
<i>Bursidae</i> Thiele, 1925	<i>Cossmannia</i> Newton, 1891
<i>Calyptraea</i> de Lamarck, 1799	<i>Cryptoptyxis</i> Cossmann, 1906
<i>Calyptraeidae</i> de Lamarck, 1809	<i>Cryptoptyxis</i> sp.
<i>Calyptraeoidea</i> de Lamarck, 1809	<i>Cyclomastoma</i> Hrubesch, 1965
<i>Campanile</i> Bayle, 1884	<i>Cyclophoridae</i> Gray, 1847
	<i>Cyclophoroidea</i> Gray, 1847

Table 1 (continued)

<i>Cylindritopsis</i> Gemmellaro, 1889	<i>Haustator</i> de Montfort, 1810
<i>Cylindritopsis rimbianchi</i> (Zardini, 1978)	<i>Haustator polonica</i> Schröder, 1993
<i>Cypraea</i> Linné, 1758	<i>Hemizyga</i> Girty, 1915
Cypraeidae Rafinesque, 1815	<i>Hercorhyncus</i> Conrad, 1868
Cypraeoidea Rafinesque, 1815	<i>Heteroterma</i> Gabb, 1869
<i>Dendropupa</i> Owen, 1861	<i>Hippocampoides</i> Wade, 1916
Dendropupinae Wenz, 1938	Hipponicidae Troschel, 1861
<i>Deussenia</i> Stephensen, 1941	Hipponix Defrance, 1819
<i>Diala</i> A. Adams, 1861	<i>Hyala</i> H. & A. Adams, 1852
Dialidae Ludbrook, 1941	<i>Hydrobia chopardiana</i> (de Loriol, 1865)
<i>Diastoma</i> Deshayes, 1861	<i>Hydrobia</i> Hartmann, 1821
Diastomatidae Cossmann, 1893	Hydrobiidae Troschel, 1857
<i>Dicroloma</i> Gabb, 1868	Hydrococcidae Thiele, 1928
<i>Dicroloma subpunctata</i> (von Münster, 1844)	<i>Hydrotribulus</i> Wade, 1916
Diplommatinidae Pfeiffer, 1856	<i>Ianthinopsis</i> Meek & Worthen, 1866
<i>Diplommatoptychia</i> Maillard, 1884	Iravadiidae Thiele, 1928
<i>Dissostoma</i> Cossmann, 1888	Ischnoptygmidae Erwin, 1988
<i>Echphora</i> Conrad, 1843	Janthinoidea de Lamarck, 1810
<i>Echphora proquadricostata</i> Wade, 1917	<i>Juramelanatria</i> Bandel, 1991
<i>Elektrea</i> Klebs, 1886	<i>Juramelanatria rugosa</i> (Dunker, 1843)
<i>Endoptygma</i> Gabb, 1877	<i>Juramelanoides</i> Bandel, 1991
<i>Entypogyra</i> Hrubesch, 1965	<i>Jurassiphorus</i> Cossmann, 1815
<i>Eocypraea</i> Cossmann, 1903	<i>Jurassiphorus triadicus</i> Haas, 1953
Epitoniidae Berry, 1910	<i>Lacuna</i> Turton, 1827
<i>Epitonium</i> Röding, 1798	Lacunidae Gray, 1857
<i>Erato</i> Risso, 1826	<i>Lacunina bronni</i> (Wissmann, 1841)
Eratoidae Gill, 1871	<i>Lacunina</i> Kittl, 1891
<i>Euchrysalis alata</i> Kittl, 1894	<i>Ladinula</i> Bandel, 1992
<i>Euchrysalis</i> Laube, 1869	Ladinulidae Bandel, 1992
<i>Eulima gracilistylis</i> Sohl, 1964	Lamellariidae d'Orbigny, 1841
<i>Eulima laevigata</i> (Wade, 1926)	<i>Lamelliphorus</i> Cossmann, 1815
<i>Eulima</i> Risso, 1826	<i>Lanistes</i> de Montfort, 1810
Eulimidae Troschel, 1853	<i>Lavigeria</i> Bourguignat, 1888
Eulimoidea H. & A. Adams, 1854	<i>Laxispira</i> Gabb, 1877
<i>Euspira</i> Agassiz, 1838	<i>Laxispira lumbricalis</i> Gabb, 1877
<i>Eutritonium</i> Cossmann, 1904	<i>Leptopoma</i> L. Pfeiffer, 1847
<i>Exechocirsus</i> Cossmann, 1906	<i>Litiopa</i> Rang, 1829
Falsicingulidae Slavosheveskaya, 1976	Litiopidae Gray, 1847
Fasciolarinae Gray, 1953	Littorinidae Gray, 1840
Ficidae Meek, 1854	Littorinoidea Gray, 1840
Firolidae Rang, 1829	<i>Lomirosa</i> Stephenson, 1941
<i>Fossarus</i> Philippi, 1841	<i>Longoconcha</i> Stephenson, 1941
<i>Fusimilis</i> Stephenson, 1941	<i>Loriolina</i> Huckriede, 1967
<i>Fusus</i> Helbling, 1779	<i>Lowenstamia</i> Sohl, 1964
Globularidinae Wenz, 1941	<i>Loxonema</i> Phillips, 1841
<i>Gyrineum</i> Link, 1807	Loxonematidae Koken, 1889
<i>Gyrodes</i> Conrad, 1860	Loxonematoidea Koken, 1889
Gyrodinae Wenz, 1941	<i>Lunatia</i> Gray, 1847
Harpidae Bronn, 1949	<i>Lupira</i> Stephenson, 1941
<i>Harpovoluta</i> Wade, 1918	<i>Lutema</i> Stephenson, 1941

Table 1 (continued)

<i>Maillardinus</i> Bandel, 1991	<i>Paramorea</i> Wade, 1817
<i>Maillardinus sanctusclaudius</i> Bandel, 1991	<i>Paraseraphs</i> Jung, 1974
Marginellidae Fleming, 1828	Perissityidae Popenoe & Saul, 1987
Marseniopsidae Bandel et al., 1993	<i>Perissitys</i> Steward, 1927
<i>Mataxa</i> Wade, 1916	Personidae Gray, 1854
<i>Maturifusus</i> Szabó, 1983	<i>Petalococonchus</i> H.C. Lea, 1843
<i>Maturifusus szaboii</i> Schröder, 1993	<i>Pickworthia</i> Iredale, 1917
<i>Maturipupa</i> Pilsbry, 1926	Pickworthiidae Iredale, 1917
Meekospiridae Knight, 1959	<i>Pila</i> Röding, 1798
Melanopsidae H. & A. Adams, 1854	Planaxidae Gray, 1850
<i>Melanopsis</i> de Férussac, 1807	<i>Plesiotriton</i> Fischer, 1884
Melongenidae Gill, 1871	<i>Plesiotrochus</i> Fischer, 1878
<i>Mesostrombus</i> Schröder, 1993	<i>Polinices</i> de Montfort, 1810
<i>Mesostrombus</i> sp.	<i>Polygyrina</i> Koken, 1892
<i>Mesostrombus vetustus</i> (Phillips, 1829)	<i>Polygyrina lommelli</i> (von Münster, 1841)
Mitridae Swainson, 1831	Polygyrinidae Bandel, 1991
<i>Mitridomus</i> Sohl, 1964	<i>Pomatias</i> Studer, 1789
Modulidae Fischer, 1884	Pomatiasidae Gray, 1852
<i>Modulus</i> Gray, 1842	<i>Popenella</i> Bandel, 1992
<i>Morea</i> Conrad, 1860	Popenellidae Bandel, 1992
Murchisonioidea Koken, 1896	Potamididae H. & A. Adams, 1854
Muricidae Rafinesque, 1853	<i>Prisciophora beyschlagi</i> (Wolleman, 1903)
Muricoidea Rafinesque, 1815	<i>Prisciphora</i> Schröder, 1991
<i>Murphitys</i> Popenoe & Saul, 1987	<i>Procampanile</i> Hacobjan, 1976
Nassariinae Iredale, 1916	Procerithiidae Cossmann, 1905
<i>Natica</i> Scopoli, 1777	<i>Procerithium</i> Cossmann, 1902
Naticidae Forbes, 1838	<i>Procerithium culizkyi</i> Schröder, 1993
Naticinae Forbes, 1838	<i>Proelektraea</i> Hrubesch, 1965
Naticoidea Forbes, 1838	<i>Prostylifer</i> Koken, 1889
<i>Neojanacus</i> Suter, 1907	<i>Prostylifer paludinaris</i> (von Münster, 1841)
Neomesogastropoda Bandel, 1991	Prostyliferidae Bandel, 1992
Neotaenioglossa Haller, 1882	<i>Protobusycon</i> Wade, 1917
<i>Niso</i> Risso, 1826	<i>Protocypraea</i> Schilder, 1927
<i>Nozeba crassa</i> Dockery, 1991	<i>Protofusis</i> Bonarelli, 1921
<i>Obtortio</i> Hedley, 1899	<i>Protorcula</i> Kittl, 1894
Obtortionidae Thiele, 1925	<i>Protorcula subpunctata</i> (von Münster, 1841)
<i>Odontobasis</i> Meek, 1876	Protorculidae Bandel, 1991
<i>Oliva</i> Martyn, 1786	<i>Protuba winkleri</i> (Klipstein, 1841)
Olividae Latreille, 1825	<i>Pseudamaura</i> Fischer, 1885)
<i>Omphaloptycha</i> Ammon, 1892	<i>Pseudocymia</i> Popenoe & Saul, 1987
<i>Omphaloptycha muensteri</i> (Wissmann, 1841)	<i>Pseudoliva</i> Swainson, 1840
<i>Oonia</i> Gemmellaro, 1878	<i>Pseudomelania</i> Pictet & Campiche, 1862
<i>Ornopsis</i> Wade, 1916	<i>Pseudomelania turrata</i> (Zekeli, 1852)
Ovulidae Fleming, 1822	Pseudomelaniidae Fischer, 1885
<i>Palaeocypraea</i> Schilder, 1928	<i>Pseudonicida</i> Hrubesch, 1965
<i>Palaeopsephaea</i> Wade, 1926	<i>Pseudorapa</i> Holzapfel, 1888
Paracerithiinae Cossmann, 1906	<i>Pseudoscalites</i> Kittl, 1894
<i>Paracerithium</i> Cossmann, 1902	Pseudozygopleuridae Knight, 1930
<i>Paraglauconia</i> Steinmann, 1929	<i>Pterotrachea</i> Forskål, 1775
<i>Paramelania</i> E.A. Smith, 1881	<i>Pterotrachea liassica</i> Bandel & Hemleben, 1987

Table 1 (continued)

Pterotracheidae Gray, 1843	Stenothyridae Fischer, 1885
<i>Ptychostoma</i> Laube, 1868	<i>Stephopoma</i> Mörch, 1860
<i>Ptychostoma pleurotomoides</i> (Wissmann, 1841)	<i>Stosicia</i> Brusina, 1870
<i>Ptychosyca</i> Gabb, 1877	Strombidae Rafinesque, 1815
<i>Pugnellus</i> Conrad, 1860	Stromboidea Rafinesque, 1815
Pupinidae H. & A. Adams, 1850	<i>Strombus</i> Linné, 1758
<i>Purpurina</i> d'Orbigny, 1850	Subulitidae Lindström, 1884
Purpurinidae Zittel, 1895	Subulitoidea Lindström, 1884
Purpurinoidea von Zittel, 1895	<i>Teinostoma</i> H. & A. Adams, 1853
<i>Pyrazus debile</i> (Zekeli, 1852)	<i>Terebellum</i> de Lamarck, 1799
<i>Pyrgulifera</i> Meek, 1877	<i>Teutonica gramanni</i> Schröder, 1991
<i>Pyrgulifera purbeckiensis</i> Bandel, 1991	<i>Teutonica</i> Schröder, 1991
<i>Pyropsis</i> Conrad, 1860	<i>Thalassocyon</i> Barnard, 1960
Rachiglossa Gray, 1853	Thiaridae Troschel, 1857
Ranellidae Gray, 1854	<i>Thylacus</i> Conrad, 1860
<i>Rapana gracillima</i> Wollemani, 1903	<i>Thylacus cretaceus</i> Conrad, 1860
<i>Remnita</i> Stephenson, 1941	<i>Tintorium</i> Sohl, 1960
<i>Rhabdocolpus</i> Cossmann, 1906	Toxoglossa Troschel, 1847
<i>Rhabdocolpus</i> sp.	Trichotropidae Gray, 1850
<i>Rissocerithium</i> Conti & Fischer, 1981	<i>Trichotropis</i> Broderip & Sowerby, 1829
Rissoidea Gray, 1847	Triforidae Jousseume, 1884
Rissooidea Gray, 1847	<i>Trigonostoma</i> de Blainville, 1827
<i>Sabia</i> Gray, 1847	Triphoridae Gray, 1847
<i>Sansonia</i> Jousseume, 1892	Triphoroidea Gray, 1847
<i>Sansonia</i> sp.	<i>Triton kabanense</i> Stanton, 1893
<i>Sargana stantoni</i> (Weller, 1907)	<i>Trivia</i> Broderip, 1837
<i>Sargana</i> Stephenson, 1923	Triviidae Troschel, 1863
Sarganidae Stephenson, 1923	Truncatellidae Gray, 1840
<i>Sassia</i> Bellardi, 1872	<i>Trypanocochlea</i> Tomlin, 1931
<i>Scaliola</i> A. Adams, 1860	<i>Tudicla</i> Röding, 1798
<i>Scaliola jansseni</i> Bandel, 1993	<i>Tudiclana</i> Finlay & Marwick, 1937
Scaliolidae Iredale & McMichael, 1962	Tudicidae Cossmann, 1901
Scaphoconchoidea Bandel, 1993	<i>Tudorella</i> P. Fischer, 1885
<i>Schizobasis</i> Wade, 1916	<i>Turbacmella</i> Thiele, 1927
<i>Seila</i> A. Adams, 1861	Turbinellidae Swainson, 1835
<i>Seraphs</i> de Montfort, 1810	<i>Turbinopsis</i> Conrad, 1860
Seraphsidae Gray, 1853	Turridae Swainson, 1840
<i>Settsassia</i> Bandel, 1992	<i>Turritella</i> de Lamarck, 1799
<i>Settsassia obliquecostata</i> (von Münster, 1841)	Turritellidae Lovén, 1847
Settsassiidae Bandel, 1992	<i>Tympanotonus</i> Klein in Schumacher, 1817
Sherborniidae Iredale, 1917	<i>Typhis</i> de Montfort, 1810
<i>Sigapatella</i> Lesson, 1830	<i>Urceolabrum</i> Wade, 1916
Skeneidae Clark, 1851	Vanikoridae Gray, 1840
<i>Solariorbis clara</i> (Sohl, 1960)	<i>Verania</i> Koken, 1897
<i>Solariorbis</i> Conrad, 1865	Vermetidae Rafinesque, 1815
Soleniscidae Wenz, 1938	Vermetoidea Rafinesque, 1815
<i>Soleniscus</i> Meek & Worthen, 1861	<i>Vermetus</i> Daudin, 1800
<i>Spirocyclus eucyclus</i> (Laube, 1869)	<i>Vermicularia</i> de Lamarck, 1799
<i>Stantonella</i> Wade, 1926	<i>Vermicularia spirata</i> (Philippi, 1836)
<i>Stegocoelia</i> Donald, 1889	Vitrinellidae Bush, 1897

Table 1 (continued)

<i>Viviparidae</i> Gray, 1847	<i>Xenophoridae</i> Troschel, 1852
<i>Viviparus arkelli</i> Huckriede, 1967	<i>Zardinistylus</i> Bandel, 1991
<i>Viviparus</i> de Montfort, 1810	<i>Zebinostoma</i> Conti & Fischer, 1983
<i>Volutidae</i> Rafinesque, 1815	<i>Zemelanopsis</i> Finlay, 1927
<i>Volutoderma</i> Gabb, 1877	<i>Zittelia</i> Gemmelaro, 1870
<i>Volutomorpha</i> Gabb, 1877	<i>Zygopleura</i> cf. <i>haueri</i> (Klippstein, 1841)
<i>Weeksia</i> cf. <i>amplificata</i> (Wade, 1926)	<i>Zygopleura</i> Koken, 1892
<i>Weeksia</i> Sohl, 1960	<i>Zygopleuridae</i> Wenz, 1938
<i>Xenophora</i> Fischer von Waldheim, 1807	<i>Zygopleuroidea</i> Bandel, 1991
<i>Xenophora</i> sp.	

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