

# 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 Neritimorpha 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 planktotrophic 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 Rissooidea, which seem to merge into one and the same stock during the Mesozoic. The Subulitoidea, 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 Rissooidea 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; Houbbrick, 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 *Plesiotrochus* (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 Dialidae, 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 *Stegocoelia*, 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

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## 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.

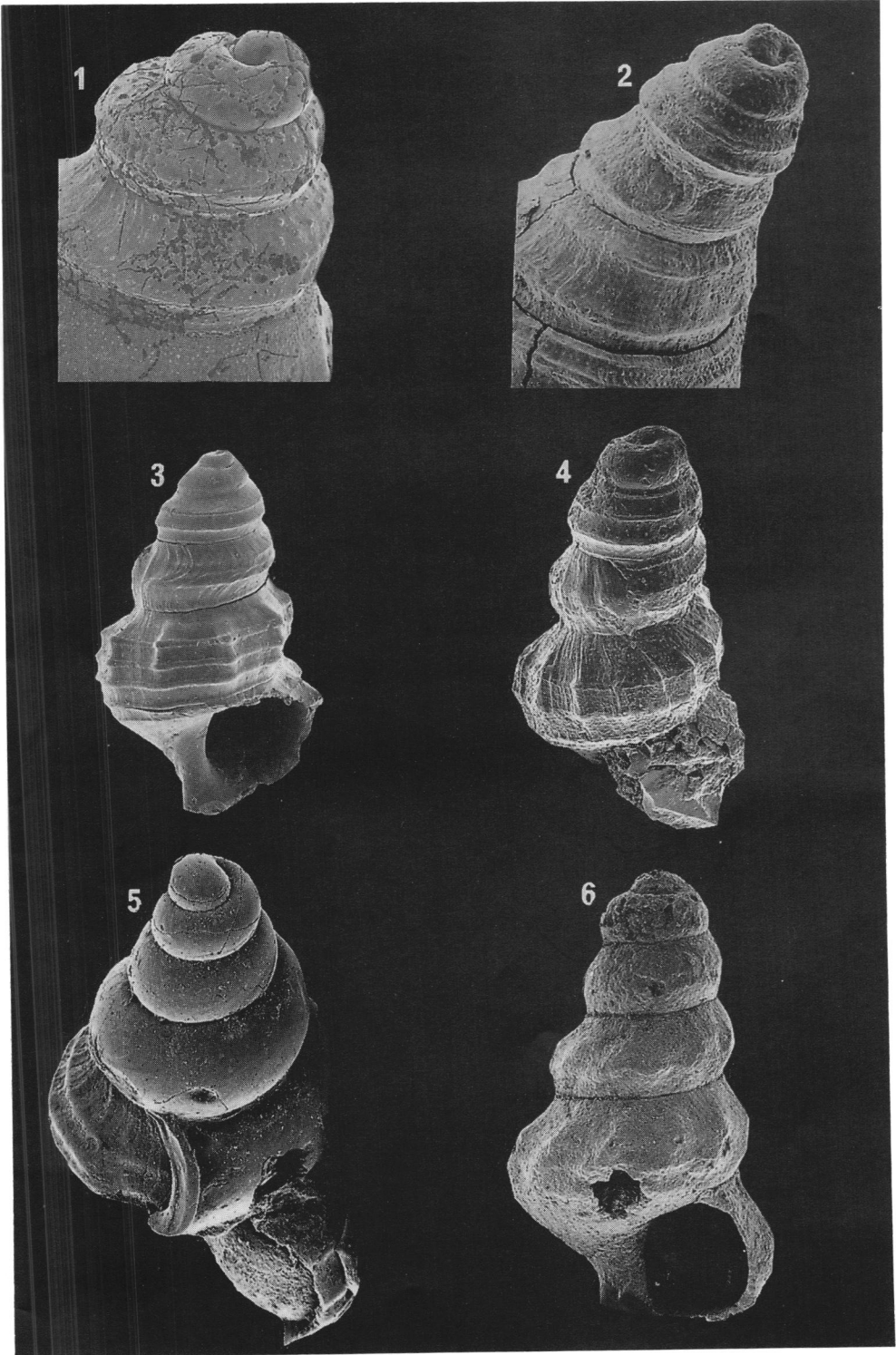


Plate 1

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 Nakhil (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 rissooideans as found among the Pomatiasidae, 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

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## 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.