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Earliest known (Campanian) members of the Vermetidae, Provannidae and Litiopidae (Cerithioidea, Gastropoda), and a discussion of their possible relationships

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With 7 Figures

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Abstract

The newly discovered Campanian species *Vermetus nielseni* n. sp., *Desbruyeresia antiqua* n. sp. and *Litiopella schoeningi* n. gen. n. sp. are described and the taxonomy of these gastropod groups is reassessed. Based on their protoconch morphology and radula characters, the Dendropominae, Provannidae, Litiopidae and *Sculptifer* are considered as related taxa within the Cerithioidea. They are interpreted to have arisen from a common ancestor that lived during the Cretaceous, apparently parallel to the radiation of the Vermetidae.

Zusammenfassung

Die neuen campanischen Arten *Vermetus nielseni* n. sp., *Desbruyeresia antiqua* n. sp. und *Litiopella schoeningi* n. gen., n. sp. werden beschrieben und die Taxonomie dieser Gastropoden-

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Gruppen neu bewertet. Basierend auf der Morphologie ihrer Protoconche und Radulae werden die Dendropominae, Provannidae, Litiopidae und *Sculptifer* als verwandte Taxa innerhalb der Cerithioidea angesehen, die sich wahrscheinlich aus einem gemeinsamen kretazischen Vorfahren entwickelten. Die Entwicklung dieser Gruppe verlief offensichtlich parallel zur Radiation der Vermetidae, deren Vertreter jedoch eine andere Protoconchmorphologie zeigen.

I. Introduction

Vermetids are sessile marine gastropods with a tubular shell that is irregularly coiled and totally or partly cemented to hard substrates. Sessile gastropods with vermiform shells were placed all together in the family Vermetidae RAFINESQUE, 1815 as MÖRCH (1862) had suggested and was adopted by THIELE (1931) and WENZ (1939). These authors placed the Vermetidae into the superfamily Cerithioidea FÉRRUSAC, 1819. WENZ (1938) included into the taxon Vermetidae genera like *Vermetus* DAUDIN, 1800, *Petalococonchus* LEA, 1843, *Stephopoma* MÖRCH, 1860, *Vermicularia* LAMARCK, 1799, *Laxispira* GABB, 1877, *Tenagodus* GUETTARD, 1770, and *Pyxipoma* MÖRCH, 1860.

MORTON (1953, 1965) realized, that not all of these are closely related to each other but that they rather form two independent groups. He distinguished the Vermetidae s.s. from *Vermicularia* and found the later to be more closely related to *Turritella* LAMARCK, 1799. HOUBRICK (1988) supported this suggestion by finding anatomical differences to exist between Vermetidae and Turritellidae GRAY, 1840. MORTON (1951b, 1955, 1965), in addition, suggested that also the Siliquariidae ANTON, 1838 with *Tenagodus* and relation are rather more related to the Turritellidae than to the Vermetidae. This suggestion was mainly based on the structure of the operculum which bears bristles in siliquariids as are found in some members of *Turritella*. Such a bristle rimmed operculum was the evidence by which Keen (1961) placed *Stephopoma* within the Turritellidae, Vermiculariinae, FAUSTINO, 1928.

HEALY (1988) recognized that vermiform caenogastropods belong into two quite separate groups regarding their sperm morphology. PONDER & WARÉN (1988) and WELLS (1998), thus, regarded the Vermetidae to represent their own superfamily Vermetoidea with genera like *Vermetus* and *Dendropoma* and being related to the Xenophoridae TROSCHEL, 1852 and Cypraeidae RAFINESQUE, 1815 rather than the Cerithioidea. HEALY (1988) even suggested a closer relation of the Vermetidae to Stromboidea RAFINESQUE, 1815 and Calyptraeidea LAMARCK, 1809 than to the Cerithioidea, while he regarded Turritellidae and Siliquariidae as representatives of the superfamily Cerithioidea. HOUBRICK (1988) in contrast included the Vermetidae in the Cerithioidea.

BANDEL & KOWALKE (1997) evaluated protoconch morphology and ornament of fossil and Recent vermetoid gastropods. They confirmed that *Tenagodus* and *Vermicularia* are closely related to the Turritellidae and introduced the Stephopominae BANDEL & KOWALKE, 1997 for siliquariids with a planispiral protoconch. Within the Vermetidae, they recognized two clearly distinct protoconch types, that of *Vermetus* on one side and *Dendropoma* with axial to cancellate sculpture on the other.

A similar *Dendropoma*-type protoconch is found for example among members of the Provannidae WARÉN & PONDER, 1991 and Litiopidae FISCHER, 1885. These two families inhabit quite different as well as unusual habitats. The Provannidae have adapted to the deep sea hydrothermal vent environment and grow chemotrophic symbiotic bacteria in their gills (OKUTANI & OHTA 1988; WARÉN & PONDER 1991; BECK 1991; WARÉN & BOUCHET 1993). The

name giving *Provanna* DALL, 1918 was assigned to the Trichotropidae GRAY, 1850 by WENZ (1938) and to the Cerithioidea by WARÉN & BOUCHET (1986). WARÉN & PONDER (1991) erected the family Provannidae which was considered to belong to the Loxonematoidea KOKEN, 1889 by WARÉN & BOUCHET (1993).

Recent Litiopidae live in shallow-water seagrass environments in the case of *Alaba* H. & A. ADAMS, 1860 or on floating *Sargassum*-banks in the case of *Litiopa* RANG, 1829 (BEESLEY et al. 1998). In a substantial work on these two genera, HOUBRICK (1987) pointed out that they were formerly assigned to the Cerithiopsoidae H & A ADAMS, 1853, Planaxidae GRAY, 1850, Diastomidae COSSMANN, 1895 and various subfamilies of the Cerithiidae. He considered the Litiopidae an independent family within the Cerithioidea.

Based on the description of three new species and one re-evaluated species from the Campanian sediments near Torallola, the history of vermetid gastropods is herein reassessed and possible relationships are discussed.

II. Material and methods

The material of this study originates from the Pumanous Olistostrom of Torallola near Pobra de Segur in the Basin of Tresp in north-eastern Spain. These sediments consist of grey, unconsolidated marls of several slump masses that have been deposited in the Campanian (ROSSELL et al. 1972). The gastropods found in this basinal sediment had their origin in the shore and near-shore environment. Fossils and sediment samples have been collected by the authors and students from the University of Hamburg during several field trips since 1989. The sediment samples were treated with diluted H₂O₂, washed, dried, the fossil content extracted under a binocular microscope. They were then mounted on stubs and photographed with a scanning electronic microscope. All figured specimens are deposited in the type collection of the Geologisch-Paläontologisches Institut und Museum, University of Hamburg (labeled SGPIHno. 3956-3959).

III. Systematics

Superfamily Cerithioidea FÉRRUSAC, 1819

Family Vermetidae RAFINESQUE, 1815

Remarks: In the strict sense as the Vermetidae are seen here, there are three protoconch types found among them, one like that of *Vermetus nielsenii* n. sp. with a helicoform shape, and another one like *Petalococonchus* with a barrel-like shape (BANDEL & KOWALKE 1997, Pl.1, fig.7). The third type is present on the Late Cretaceous *Laxispira* with ornament of rows of granulae as documented by SOHL (1960), DOCKERY (1993), and BANDEL & KOWALKE (1997).

Genus *Vermetus* DAUDIN, 1800

Description: The protoconch is conical or barrel-shaped with smooth rounded whorls. After metamorphosis the animal attaches to hard substrate cementing its shell to it. The teleoconch is ornamented by more or less regular growth lines and more or less regular longitudinal ribs. The type is *Vermetus adansoni* DAUDIN, 1800 from the equatorial eastern Atlantic (WENZ 1939).

Vermetus nielseni n. sp.

(figs. 1-3)

Holotype: SGPIHno. 3956, illustrated in figs. 1, 2.

Paratype: SGPIHno. 3957, illustrated in figs. 3.

Derivatio nominis: Named after Sven NIELSEN, Hamburg, who accompanied the field work.

Diagnosis: The smooth, trochospiral protoconch consists of about three volutions. The uncoiled teleoconch has strongly developed, irregular growthlines and a keel-like ridge.

Description: The shell is attached right from the end of the protoconch onward. The protoconch is of rounded helicoid shape with about 0.1 mm wide first whorl which probably represents the embryonic shell. It is succeeded by about two larval whorls that end in a wide apertural projection. The whole protoconch measures about 0.35 mm in height and in width. Ornament consists only of fine growth lines. In the freshly attached first teleoconch the apertural anterior sinus is closed and following whorls are free on one side and attached to substrate with the flattened opposite side. The protoconch may project from the early teleoconch as is the case in one of the specimen or it may be partly covered by the teleoconch as is the case in the other specimen. The teleoconch is ornamented by growth increments and some spiral ribs one of which forms an outer keel-like ridge. Ornament is rather irregular.

Remark: The shape of the protoconch of *Vermetus nielseni* resembles the larval shell of a vermetid from the Eocene as illustrated by KOWALKE (1998, Pl. 8, fig. 3).

Discussion: With the presence of a member of the genus *Vermetus* in Campanian time, *Laxispira* can no longer be regarded a stem group representative of the Vermetidae as suggested by BANDEL & KOWALKE (1997), because both genera existed next to each other at the same time.

Family Provannidae WARÉN & PONDER, 1991

Remarks: This family comprises the genera *Alviniconcha* OKUTANI & OHTA, 1988, *Desbruyeresia* WARÉN & BOUCHET, 1993, *Ifremeria* WARÉN & PONDER, 1991 and *Provanna* each of which has a quite differently shaped teleoconch. WARÉN & BOUCHET (1993) documented a slender protoconch with cancellate sculpture for their new genus *Desbruyeresia*. *Alviniconcha* with much blunter teleoconch has an almost identical protoconch (WARÉN & BOUCHET 1993, Fig.44C) and that of *Provanna* has relicts of that ornament but is of a more lecithotrophic, and thus simplified type (WARÉN & BOUCHET 1993: Fig. 57A,B).

Genus *Desbruyeresia* WARÉN & BOUCHET, 1993

Description: The medium sized (around 12 mm high) melanoid, turritiform shell is tall and slender with an anterior siphonal notch at the aperture. The protoconch has a larval shell with cancellate ornament of strong axial ribs crossed by finer spiral ribs. The type species is *Desbruyeresia spinosa* WARÉN & BOUCHET, 1993 which lives in the North Fiji Basin (WARÉN & BOUCHET (1993).

Desbruyeresia antiqua n. sp.

(figs. 4, 5)

Holotyp: SGPIHno. 3958, illustrated in figs. 4, 5.

Derivatio nominis: This new species represents the most antique species of its genus.

Diagnosis: The multiwhorl protoconch has collabral ribs, the teleoconch is sculptured with few strongly tuberculate axial ribs.

Description: Only the early teleoconch is known with the protoconch fully preserved. The embryonic whorl measures about 0.3 mm in diameter and appears to have been smooth. The larval portion of the protoconch consists of a little more than two whorls added to the embryonic whorl,

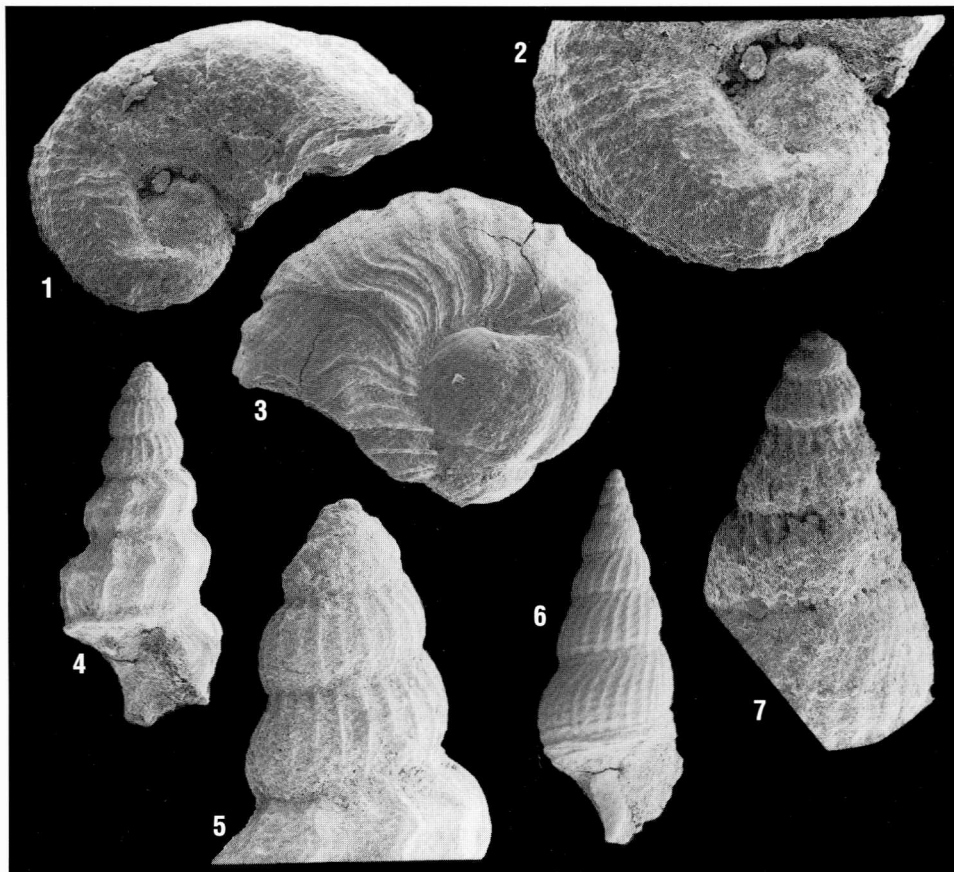


Fig. 1: *Vermetus nielseni* n. sp., holotype, x 50. Fig. 2: Same specimen as fig. 1 with the protoconch enlarged, x 70. Fig. 3: *Vermetus nielseni* n. sp., paratype, x 50. Fig. 4: *Desbruyeresia antiqua* n. sp., holotype, x 32. Fig. 5: Same specimen as fig. 4 with the protoconch enlarged, x 100. Fig. 6: *Litiopella schoeningi* n. gen. n. sp., holotype, x 15. Fig. 7: Same specimen as fig. 6 with the protoconch enlarged, x 62.

with the protoconch consisting of a little more than three whorls, about 0.5 mm in height and 0.3 mm in width of the last whorl. Ornament of the larval whorls consists of simple collabral axial ribs and a fine pattern of spiral ribs between them. About 18 of these ribs ornament the last whorl of the protoconch. The transition to the teleoconch is abrupt. The first two whorls of the teleoconch are preserved. Their ornament is dominated by a spiral rib that is crossed by few axial ribs forming tubercles with each other. There is another spiral rib at the corner to the flattened base, which lies in the suture when the next whorl is attached.

Remarks: *Desbruyeresia cancellata* WARÉN & BOUCHET, 1993 as illustrated by WARÉN & BOUCHET (1993: Fig. 44 E) is very similar in size and ornament of the larval shell as well as the first whorl of the teleoconch. The differences are minute and regard the position of the central keel on the first whorl of the teleoconch which is more central in position with both flanks apically and posteriorly a little more flattened than is the case in *Desbruyeresia antiqua*.

Discussion: Even though the mode of life of *D. antiqua* must have been a quite different one as that of its so similar modern counterpart *D. cancellata* from the Lau Basin off Fiji from about 2000 m depth, both are very similar regarding protoconch and early teleoconch.

WARÉN & BOUCHET (1993) suggested to place the Provannidae in the Loxonematoidea. This treatment was based on similarities in larval shell sculpture with Carboniferous Pseudozygopleuridae KNIGHT, 1930 figured by HOARE & STURGEON (1985). The latter authors assigned the Pseudozygopleuridae within the Loxonematoidea following the classification of KNIGHT et al. (1960). However, more recent studies of Paleozoic and early Mesozoic gastropods showed that this classical treatment can no longer be accepted.

The Pseudozygopleuridae are now included in the Zygopleuroidea WENZ, 1938 which are seen in an evolutionary lineage leading to the modern Janthinioidea LAMARCK, 1810, Cerithiopsoida and Triphoroidea GRAY, 1847 (BANDEL 1991; NÜTZEL 1998). The genus *Loxonema* PHILLIPS, 1842 is highly problematic because its type species is of Silurian age and is only badly known. In case of *Stylonema* PERNER, 1907, FRÝDA & BANDEL (1997) described the protoconch of a species that is close to *Loxonema* and lived in the early Devonian. While the teleoconch of *Stylonema* closely resembles that of *Loxonema*, *Stylonema parvula* FRÝDA & BANDEL, 1997 has an archaeogastropod-type protoconch. FRÝDA & BANDEL (1997) created for these unusual species the order Stylogastropoda, to encompass high spired archaeogastropods that are convergent in shell shape with caenogastropods. The later are proven to occur from Upper Carboniferous onwards (BANDEL 1993, 1997; NÜTZEL 1998). Most probably *Loxonema* is, thus, a member of the Archaeogastropoda and, therefore, not available for models in the reconstruction of caenogastropod relations. The radulae of three species of *Desbruyeresia* were illustrated by WARÉN & BOUCHET (1993: Figs. 55A, B; 56C) and proved to be very similar to that of *Angiola lineata* (DA COSTA, 1778) from the pebble beach of the Caribbean Sea (BANDEL 1984: Pl. 2, fig. 5). This similarity regards the feature of all teeth in the radula ribbon. The radula of *Provanna buccinoides* WARÉN & BOUCHET, 1993 (WARÉN & BOUCHET 1993: Fig. 56A) in turn closely resembles that of the mud flat potamidid *Cerithidea costata* (DA COSTA, 1778) (BANDEL 1984: Pl. 3, fig. 6). BECK (1991: Pl. 4, figs. 1-5) illustrated the radulae of his *Olgaconcha* (syn. to *Ifremeria* that was published a few months earlier by WARÉN & PONDER 1991) and that of *Alviniconcha* demonstrating that they are quite similar to each other. They closely resemble the radula of *Modulus modulus* (LINNEUS, 1758) (BANDEL 1984: Pl. 3, figs 3, 4) that lives on the lower beach of the Caribbean Sea. BECK (1991) suggested contrary to OKUTANI & OHTA (1988) that *Ifremeria* and *Alviniconcha* are Cerithiimorpha.

Sediments and fossils which are considered to represent ancient cold-seep, chemosynthetic communities have been reported from numerous localities (see GOEDERT & CAMPBELL 1995 for a review) but most gastropods are badly preserved. SQUIRES (1995) even reported a new Oligocene species of *Provanna*, however, without the knowledge of its protoconch morphology, this classification remains doubtful.

Family Litiopidae FISCHER, 1885

Remarks: This family holds small, thin-shelled cerithioideans having a weak, shallow anterior canal and a protoconch sculptured with numerous axial riblets and subsutural plaits (HOUBRICK 1987). This author included *Litiopa* and *Alaba*, and considered *Fenella xanthacme* MELVILL, 1904 as another possible member.

Genus *Litiopella* n. gen.

Type species: *Litiopella schoeningi* n. sp. described below.

Derivatio nominis: Derived from *Litiopa*.

Diagnosis: The small, high spired shells have rounded whorls and well developed sutures. Ornamentation of the early teleoconch whorls consists of inclined and curving axial ribs. The protoconch is conical and made of several whorls which have axial ribs and fine spirals.

Remarks: The Recent *Litiopa* is either smooth or shows mainly spiral sculpture, although it develops considerable axial growthlines, and the columella has one small tooth (see HOUBRICK 1987: Figs 8, 9). *Alaba* possesses a teleoconch similar to that of *Litiopa* but with a smooth columella, and its

protoconch lacks fine spirals. *Litiopella* differs from both Recent genera by its curved axial ribs on the teleoconch.

Litiopella schoeningi n. sp.

(figs. 6, 7)

Holotype: SGPIHno. 3959, illustrated in figs. 6, 7.

Derivatio nominis: After Meike SCHÖNING (Hamburg) who collected with us in Torallola in spring 1999.

Diagnosis: As for the genus.

Description: Only a juvenile shell with four whorls of the teleoconch is present. Its apical angle is about 30°. The protoconch consists of about 4.3 whorls with the first whorl measuring less than 0.1 mm in width. The following larval whorls are ornamented by about 20 straight axial ribs on each whorl. These are crossed by fine spiral lirae. The whole protoconch is about 0.6 mm high. Transition into the teleoconch is documented by a change of ornament, which is now formed by inclined and curving axial/collabral ribs, again about 20 on each whorl. The whorls of the protoconch as well as the teleoconch are evenly rounded on their sides and sutures are well developed. The aperture is anteriorly notched with columella curving sideways. The shell is 3.6 mm high.

Discussion: The new species described here does not show the distinct spirals on the protoconch as can be seen on Recent *Litiopa* and *Alaba*. But considering its age and its overall shape, it could well be seen as an ancestral representative of the Litiopidae. This model implies that the axial to cancellate protoconch sculpture without keels is a primitive character and, therefore, the Litiopidae may be seen in the relation of the Provannidae and Dendropominae with similar protoconchs. Also the radula of the Litiopidae supports this model. On the other hand, Houbrick (1987) listed several anatomical characters which the Litiopidae share with *Bittium* GRAY, 1847, *Cerithium* BRUGIÈRE, 1789, *Rhinoclavis* SWAINSON, 1840, *Batillaria* BENSON, 1842 and *Cerithidea* SWAINSON, 1840 as well as with the Modulidae FISCHER, 1884 and Thiaridae TROSCHEL, 1857.

IV. Discussion

From the Vermetidae sensu WENZ (1938), the Vermiculariinae and the Siliquariidae have long been considered independent and rather closely related to the Turritellidae (MORTON 1965, KEEN 1961, HEALY 1988, HOUBRICK 1988). BANDEL & KOWALKE (1997) distinguished within the Vermetidae the Vermetinae and the Dendropominae BANDEL & KOWALKE, 1997. As shown above, *Vermetus* s.str. was already present at Campanian time along with *Laxispira*. The Dendropominae, on the other hand, are now considered independent from the Vermetidae and relations to the Provannidae and allied taxa are supposed. Its protoconch resembles that of *Desbruyeresia* and *Laeviphitus* in every respect. Also the radula of *Dendropoma lamellosa* as figured by BEESLEY et al. (1998: Fig. 15.129 I) does not differ fundamentally from those of the two latter genera.

The cancellate protoconch appears to be a rather uniform feature within the Provannidae despite their highly derived anatomy and their differently shaped adult shells (WARÈN & BOUCHET 1993). Concerning the radula, the type present in *Desbruyeresia* is found among numerous other cerithioid families. The shell of *Desbruyeresia* has apparently not changed significantly since the Late Cretaceous.

Larval shells resembling those of the Provannidae are known from several gastropod families, previously considered as unrelated. *Laeviphitus japonicus* OKUTANI, FUJIKURA & SASAKI, 1993 dredged from the Kaikata Seamount in a depth of 440 m with a rather featureless,

Hydrobia-like teleoconch possesses a protoconch made of two whorls and cancellate pattern. Its radula resembles that of *Dresbruyeresia cancellata* (see OKUTANI, FUJIKURA & SASAKI, 1993: Figs. 37-43) and the species was considered to belong to the Elachisinidae PONDER, 1985. However, the protoconch of *Elachisina floridiana* figured by PONDER (1985: Fig. 6G) is smooth and low. It indicates that this species has a direct development with much yolk involved and, thus, no larval shell has been build. Otherwise, teleoconch and radula agree well with *Laeviphitus japonicus*. Based on the results of his anatomical examination of *Elachisina floridiana*, PONDER (1985) erected the family Elachisinidae and considered it related to the Hydrobiidae TROSCHEL, 1857 and Iravadiidae THIELE, 1928.

Another little-known species with almost identical larval shell is *Sculptifer neozelanica* (DELL, 1956) figured by BEU & CLIMO (1974: Figs. 17-20). Unfortunately, that species lacks a radula. BEU & CLIMO (1974) suggested that it lives ectoparasitic on ophiuroids but found it "strikingly little modified" for this mode of life, compared with other ectoparasitic gastropods. They introduced the new genus *Sculptifer* BEU & CLIMO, 1974 and tentatively placed it within the Fossaridae TROSCHEL, 1861.

Slightly different from the protoconchs discussed so far is that of the Litiopidae FISCHER, 1885. Apart from its overall similarity concerning shape, size and sculpture, it shows one or two fine but distinct spiral keels (HOUBRICK 1987: Figs 8, 10). However, also the radulae are similar to those of *Desbruyeresia* and *Laeviphitus* (see HOUBRICK 1987: Figs. 13, 14, 18-20). They differ only by a smaller central tooth in the case of *Litiopa melanostoma* RANG, 1829 and by simplified marginal teeth in *Alaba incerta* (ORBIGNY, 1842).

Among modern gastropods, there are some more groups which have a cancellate protoconch sculpture and should be discussed here. These include the Cypraeidae and the neogastropod families Turridae SWAINSON, 1840 and Muricidae RAFINESQUE, 1815 (see BANDEL et al. 1997), but their larval shells are generally larger. Also their adult shells are well distinguishable and their anatomy and radulae are distinct, so there should be no confusion. Of similar size and sculpture are the larval shells of the Eumetulidae GOLIOKOV & STAROBOGATOV, 1975 within the Cerithioptoidea, and the Nystiellidae CLENCH & TURNER, 1952 among the Janthinioidea (NÜTZEL 1998). Recent representatives of these families are distinguishable from cerithioids with cancellate protoconch by radulae and anatomy. Eumetulid adult shells are small (usually not exceeding 10 mm) and have a characteristic reticulate ornament. The *Epitonium*-like nystiellids are also well distinguishable.

It can be concluded that Provannidae, Dendropominae and Litiopidae represent a group of gastropods which are not yet well known, and only few species of each taxon have been studied to date. Based on the similarities which are recognizable among the protoconch sculpture and the radulae of these groups, we consider them to be related taxa within the Cerithioidea. A Cretaceous origin of this group can be assumed as *Desbruyeresia antiqua* and *Litiopella schoeningi* were already present in the Campanian. The independence of the Vermetidae from that group at Campanian time is evident from the presence of *Vermetus nielsenii* in the same sediments as *Desbruyeresia antiqua* and *Litiopella schoeningi*.

OKUTANI et al. (1993) were struck by the disjunct distribution of *Laeviphitus* VAN AARTSEN, BOGI & GIUSTI, 1989. They dredged it from a West Pacific seamount while WARÉN et al. (1990) reported it from the slope of the Mediterranean shelf, based on empty shells. However, if our assumption of a Cretaceous origin of this group is correct, these gastropods had enough time to spread through the entire Tethys realm, making the present distribution well explainable.

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