Taxonomy and Biogeography of Late Cretaceous Gastropoda

Dissertation

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Steffen Kiel

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und Prof. Dr. Christian Spaeth

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Prof. Dr. U. Bismayer
Dekan
des Fachbereichs Geowissenschaften

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INTRODUCTION

The Late Cretaceous was a time of changes in many respects. The old southern supercontinent Gondwana was falling apart; South America, Africa, India, Australia and Antarctica were developing into their present shapes. Between the drifting continents, the Atlantic and Indian Oceans were forming. The Late Cretaceous also experienced one of the major transgressions in earth history, and large parts of the continents were flooded. The Tethys Ocean between the northern and southern continents with its reefs and rudist-biostromes is considered to represented the tropical realm. Due to circum-equatorial currents, it yielded a fairly uniform fauna, distinct from that of the temperate provinces north and south of the Tethys.

The new oceans and the large epicontinental seas with their new migration-routes and changing currents provided the evolutionary breeding grounds for many new marine organisms. Among the more suspicious were the loosely and irregularly coiled heteromorph ammonites and the cup-shaped rudists which dominated tropical lagoons. The fauna on land still retained its Mesozoic character; the dinosaurs being dominant, the mammals probably did not exceed the size of a squirrel. Within the kingdom of plants, however, a major turnover was already happening. The flowering plants had appeared at the end of the Early Cretaceous and were on their way to replace the old forests of tree-ferns and gymnosperms.

The scope of this study is firstly to document two Late Cretaceous gastropod faunas. The classification is carried out with special emphasis of the protoconch morphology. Secondly, based on the results of this classification, current models of gastropod taxonomy and phylogeny are evaluated. Thirdly, these results are used to evaluate current models of gastropod biogeography during the Campanian and Maastrichtian, and to discuss possible evolutionary and paleogeographical implications.

MATERIAL

Torallola

The gastropods which are described here as being from Torallola have been collected from several places in the valley system between Torallola, Toralla and Sensui. The less steep and partly overgrown north-eastern slopes proved to be most fossil-rich and here the bulk of material has been collected. The map of the area (fig. 1) indicates the fossil localities. The nearest towns are Pobla de Segur, 2 km to the north-east and Tremp, 8 km to the south-west. The latter town provided the name for the Tremp basin and is situated about 50 km south-west of Andorra and 120 km to the north-west of Barcelona.

The material was collected during the last ten years by Klaus Bandel, Frank Riedel, Alexander Nützel, Katharina N. Hänsel, Thorsten Kowalke, Sven Nielsen, myself and many students from Hamburg University.

History

The fossils at this locality have first been recognised by Vidal (1921) with the report of several gastropod species. He was followed by Bataller (1949) who described some new species in a monograph on Spanish Cretaceous gastropods. A further contribution came from Quintero & Revilla (1966) who added new gastropods, bivalves and crinoids to the list of fossils. While these early workers considered the sediments Maastrichtian, Rosell et al. (1972) determined their age to be mid-Campanian. Further gastropods were described by Calzada (1989). The latest contribution to the fauna was a detailed description of corals by Baron-Szabo (1998) who documented members of no less than nine orders.

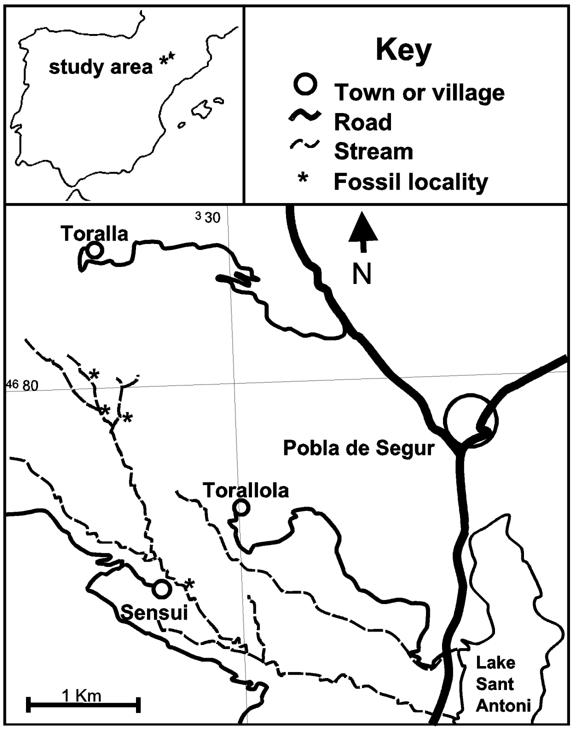


Figure 1. Map of the fossil localities around Torallola.

Geology

During most of the Mesozoic, the Pyrenean region was dominated by widespread carbonate platforms. The Iberian peninsular was rotated clockwise by 28-34° in respect to the Aquitanian plate of France. Rifting between North America and north-western Africa as well as the opening of the Ligurian Ocean between Europe and Africa began in the Jurassic. These two ocean basins formed the pan-tropical Tethys Ocean. The Pyrenean carbonate platforms were not affected by the formation of these ocean basins until the beginning of the Cretaceous, when initial rifting took place in the Bay of Biscay. This rifting continued till the end of the Campanian when the Pyrenean mountains started to form (SIMÓ 1986). This first phase of compression triggered the deposition of the Puimanyons Olisthostrome. This olisthostrom was formed by a series of events when the entire shoreline, including beaches, lagoons, cliffs, and river-estuaries became instable, slumped down the slope and carried the overrun shelf-sediments with it. The bulk of this slumped mass consists of the blue-grey to grey silts of the shelf deposits. These are mixed with sands, crystalline pebbles, carbonate blocks, blocks of pebble-beach – and numerous organisms which lived near the shore.

Several different spellings of this stratigraphic unit are found in the literature. HÄNSEL (1992) used ”Pumanous”, PUIGDFÀBREGAS & SOUQUET (1986) used ”Puimanyons”, this spelling as well as ”Pumanyons” was used by SIMÓ (1986). However, the name refers to the village of Puimanyons and a stream of the same name on which’s slopes this sequence is well exposed. Therefore, ”Puimanyons” is used herein.

Paleoenvironment

Since the fossils are buried in a slumped mass, they are not found *in situ* so that the paleoenvironment where they used to live must be inferred from the sediments, and from the habitats of living relatives of the available fossils. Gastropods are particullarly useful for such an undertaking, as they occur almost everywhere and are often closely tied to a certain environment. Among the encountered gastropods, *Melanopsis* indicates freshwater, clausilids and *Lychnus* are landsnails, living relatives of the potamidid *Echinobathra* are found mostly in brackish mangrove-environments, the abundant archaeogastropods indicate rocky shores, neogastropods and *Campanile* live near pebble beaches in the inter- to subtidal. The numerous aporrhaids probably lived on the muddy slope and were swept away with the olisthostrom. Large blocks of limestone occur in the slumped mass as well as pebbles which are of crystalline rock. Putting these data together, the paleoenvironment may be reconstructed as a pebble-beach backed by limestone-cliffs, which sometimes reached the water, incoming rivers supplied the crystalline boulders for the pebble beach and their estuaries were suitable for brackish-water organisms. Below the line of low-tide coral-stocks were living, offshore the substrate became progressively finer.

Temalac

The main locality near Temalac is registered as number 2448 in the locality catalogue of the Instituto de Geologia, Universidad National Autonoma de México. It is located in the Mexican state of Guerrero, 70 km south-east of Iguala and 125 km south of Mexico City. The outcrop is situated on the left side of the road heading north from Temalac, about 6 km out of the village (fig. 2).

The material was collected by ROBERTO CÓZATL, Mexico City, and myself during a field-trip to Latin America in 1998 funded by the DAAD.

History

The first description of 15 gastropod species from this locality has been provided by ALENCÁSTER (1980). VEGA & FELDMANN (1992) reported a new species of retroplumid crab. Molluscs, stratigraphy and age of the locality were studied by PERRILLIAT & VEGA (1996) and PERRILLIAT et al. (2000), and the age of the sediments was determined to be early Maastrichtian.

Geology

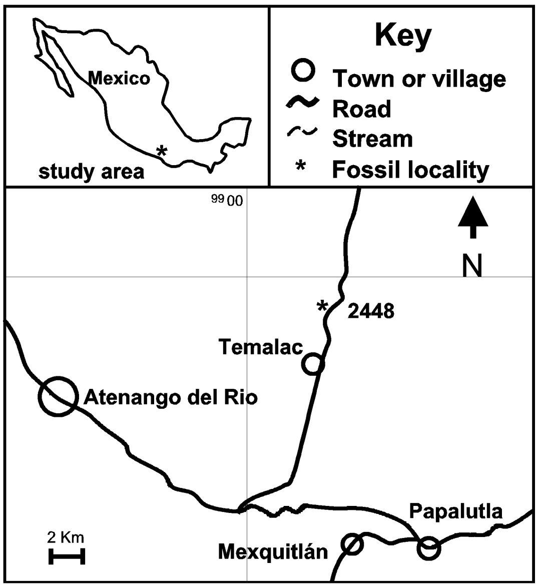


Figure 2. Map of the fossil locality near Temalac.

During the Late Cretaceous, large parts of Mexico were flooded with epicontinental seas. To the east and north-east of Temalac, around the Gulf of Mexico, this resulted in the development of large carbonate platforms (ALENCÁSTER 1980, LEHMANN et al. 1999). North of Temalac, the Cardenas Formation represents shallow-water, possibly intertidal sediments with oysters and *Trochactaeon* being the most common molluscs (BÖSE 1923, own obs.). Further north, in the Difunta Group, delta-related sediments yielded a mollusc assemblage resembling that of the northern Gulf Coast (WOLLEBEN 1977). The western margin of Cretaceous Mexico was dominated by volcanic activity driven by the subduction of oceanic crust. This volcanic arc progressed southward during the late Mesozoic and Cenozoic and separated Gulf Coast and Californian waters during the Campanian/Maastrichtian (ALENCÁSTER 1984, ANDERSON & SCHMIDT 1983, SCOTT 1984).

In the considered locality 2448, lower Maastrichtian strata of the Mexcala Formation crop out. These sediments consist of alternating coarse and fine grained clastics (FRIES 1960) and overlay the Zicapa Formation (Aptian-Albian), the Morelos Formation (Albian-Cenomanian) and the Cuautla Formation (Cenomanian-Coniacian). These older Formations consist mainly of limestone (PERRILLIAT et al. 2000) and were connected to the carbonate platform of Yukatan (SCOTT 1984). The Mexcala Formation becomes sandier towards the top and is disconformably overlaid by the lower Tertiary Balsas Formation. The arrival of clastic sediments in this area may be connected to the rise of the southern Sierra Madre as a result of the volcanism along the Mexican westcoast.

Paleoenvironment

The fossils occur in unconsolidated, sandy to silty sediments. The majority of the gastropods, especially the numerous strombids and cerithids preferred this kind of substrate. The abundant individuals of *Dontostoma* and *Otostoma* most probably inhabited the intertidal. In many cases, fragile parts of gastropod shells are broken off. This may either indicate a high-energy environment or postmortal transport. In sum, the gastropods probably lived on clastic substrate from the intertidal to the shallow subtidal.

Additional material

Two species of the Campanilidae are described from Čerević stream in the Fruška Gora Mountains in Serbia. This material was collected by NENAD BANJAC, Belgrade, and myself in spring 1998. The locality was described in detail by PETHÖ (1906) and is considered Maastrichtian.

RIEDEL's (1932) type-material from the Mungo Cretaceous of Cameroon was made available by the Staatliches Museum für Naturkunde Stuttgart. RIEDEL (1932) and REYMENT (1954) regarded the age of these deposits as Coniacian.

Specimens from the Quiriquina Formation in Central Chile were loaned from the collection of the University of Concepción, additional material was collected by K. BANDEL. The sediments represent a rocky shore environment and the ammonites indicate Maastrichtian age (STINNESBECK 1986).

The gastropod fauna of the Ammonite-Hills in western Egypt was collected by K.W. BARTHEL and W. HERRMANN-DEGEN during their work for the SFB 69 in Berlin. They also dated the sediments as Maastrichtian (BARTHEL & HERRMANN-DEGEN 1981).

From the Coon Creek tongue of the Ripley Formation in Tennessee, USA, material was collected by K. BANDEL and D.T. DOCKERY. The fossils are of late Campanian age (DOCKERY, 1993).

Material from the Umzamba Formation in South Africa was collected by K. BANDEL and myself in 1995, additional material was loaned from the South African Museum in Cape Town. We discovered most of the species described by WOODS (1906) and RENNIE (1930), and some new ones. The age of these deposits was determined by KLINGER & KENNEDY (1980) to be middle to late Santonian and early Campanian.

Some species from the probably Maastrichtian fauna of the Paita peninsular in northern Peru described by OLSSON (1944) were availlable for comparison. They were extracted by myself from the hard rocks of that outcrop in 1998.

On Baja California in north-western Mexico, Late Cretaceous fossil were collected at three localities by myself in spring 2000. Those of the Rosario Formation from Punta Banda and Punta San Isidro are of late Campanian or early Maastrichtian age (SQUIRES 1993), the gastropods from the Alisitos Formation lived at Albian time (ALLISON 1955).

METHODS

The fossils were cleaned from attached sediment using water and brushes, a subsonic device, a collection of needles, and REWOQUAD®. This is a tenside-alcohol-solution in which the fossil is drowned for one or two days to dissolve the attached fine silts and clays. After this treatment, the fossil was washed several times with alcohol and water.

The sediment samples were dissolved in a basin with a H_2O_2-solution of about 5%. After fractionating the processed samples, using sieves of 2 mm, 1 mm, 0.5 mm and 0.2 mm mesh-size, they were dried and the microfossils were extracted from the sediment under a binocular. They were then cleaned using the same methods as described for the macrofossils. Those specimens which seemed interesting were mounted on stubs, sputtered with gold and photographed with a scanning electron microscope.

For identification, classification and paleobiogeographic reconstructions, photos and fossils were compared with pictures, drawings and descriptions from the literature, with pictures and specimens of K. BANDEL's large collection, with specimens loaned from museums and with specimens collected by myself.

TAXONOMY

According to the rules of the International Code of Zoological Nomenclature (ICZN) all type material and all figured specimens must be deposited in an institution open to the public. When a new taxon is introduced, type locality and type strata should always be cited for each taxon. To avoid endless repetitions, deposition, type locality and strata are named once for each locality below.

Temalac

Deposition: The material will be deposited in the paleontological collection of the Instituto de Geologia (IGM), Universidad National Autonoma de Mexico (UNAM).

Type locality: Locality 2448 of the locality catalogue of the IGM, about 6 km north of Temalac, in the Mexican state of Guerrero.

Type strata: The marly Maastrichtian of the Mexcala Formation.

Torallola

Deposition: The material from Torallola will be deposited in the type collection of the Geologisches- paläontologisches Institut (GPI), Universität Hamburg.

Type locality: The valley system between Torallola, Toralla and Sensui in the Tremp basin of the southern Pyrenees.

Type strata: The Campanian Puymanions Olisthostrom of the Vallcarga Formation.

Additional material

All additional material is deposited in the type collection of the Geologisches-paläontologisches Institut, Universität Hamburg.

Class Gastropoda CUVIER, 1797

Subclass Archaeogastropoda THIELE, 1925

Members of the subclass Archaeogastropoda differ from those of all other subclasses in shell-structure and in the formation of the protoconch. They build their shells - or at least parts of it - of nacre (mother-of-pearl). This shell structure is not used by any other gastropod subclass. Archaeogastropod larvae do not feed on plankton but on yolk which they carry with them. The resulting larval shell consists of about half a whorl and has a very characteristic shape (see pl. 4, fig. 10). Larvae of all other subclasses feed on plankton and their shells consist of two or more whorls.

Slit-bearing (selenimorph) groups

Among the living slit-bearing archaeogastropods, five families can be recognised. Three of them, the Pleurotomariidae SWAINSON, 1840, the Haliotidae RAFINESQUE, 1815, and the Seguenziidae VERRILL, 1884 have a predominantly nacreous shell (BANDEL 1979), while the Fissurellidae FLEMMING, 1822 and the Scissurellidae GRAY, 1847 construct their shell mainly of aragonitic crossed lamella structure (BANDEL 1998). Members of the five families are well distinguishable by their radula (TROSCHEL 1856, THIELE 1929-35, HICKMAN 1981, MARSHALL 1993) and by shell characters. Relationships between and within these families are still a matter of debate. They have all been raised to superfamilies by various authors, HASZPRUNAR (1988) even regarded the Seguenziidae as an independent archaeogastropod suborder. BATTEN (1975) considered the Scissurellidae to represent neotenously derived fissurellids, and MCLEAN (1984a) suggested a derivation of the Fissurellidae directly from the Bellerophontidae M'COY, 1851. Both suggestions could not be verified by the fossil record (BANDEL 1998).

Most of these families have already existed during the Late Cretaceous (HOLZAPFEL 1888, SOHL 1992). In the case of the Seguenziidae, members have been recognized in the Late Triassic (BANDEL 1991b) and again from the Eocene to modern time (MARSHALL 1988), with no record from the Jurassic or Cretaceous. The Pleurotomariidae can be traced to the Triassic and with some probability into the Paleozoic, where selenimorph species with nacreous shell are known for example from the Carboniferous and Devonian (BATTEN 1972, BANDEL & GELDMACHER 1996). Pleurotomariids could well be among those groups that lived during the early days of gastropod existence in the lower Ordovician. Among the Haliotidae, the oldest characteristic *Haliotis*-like species are known from the Late Cretaceous (ANDERSON 1902, DURHAM 1979, SOHL 1992, GEIGER & GROVES 1999). However, there is a gap in the fossil record from Paleocene through Oligocene (SOHL 1992). It was suggested that the Haliotidae relate to the Temnotropidae (LAUBE 1869, KOKEN 1897) which used to have their latest known representatives in the Late Triassic (KITTL 1891, BANDEL 1991b). The most ancient representative of the Scissurellidae apparently lived in the Late Triassic, and rather "normal" scissurellids are known from the early Jurassic onwards (BANDEL 1991b, 1998). The Fissurellidae originated at about the same time; *Emarginula* LAMARCK, 1801 for example was already quite differentiated in the Late Triassic (ZARDINI 1978, BANDEL 1998).

Going back in the fossil record, it usually becomes more and more difficult to connect the species of selenimorph archaeogastropods with living ones. Several selenimorph species from the Triassic can be regarded as possible stem-group representatives of the Recent families. Others were interpreted as independent, now extinct groups with Paleozoic character (BANDEL 1991b). The selenimorph archaeogastropods had their heydays in the Paleozoic; WENZ (1938-44) and KNIGHT et al. (1960) listed no less than fifteen Paleozoic pleurotomarioid subfamilies. Unfortunately, many of these taxa can neither be related to any modern group, nor can they be placed in a well defined taxon of extinct species (BANDEL & FRÝDA 1996).

Family Pleurotomariidae SWAINSON, 1840

Genus *Perotrochus* FISCHER, 1885

Type species: *Perotrochus quoyana* FISCHER & BERNARDI, 1885 which lives on deep reef slopes in the Caribbean Sea and the Gulf of Mexico (ABBOTT 1974: fig. 1).

Description: The moderate to low-spired, conical shell has whorls which may be shouldered and are sculptured with fine spiral and axial lines. The slit is situated in about the centre of the whorl, its base is umbilicate, and the aperture is of rhomboid shape.

Remarks: *Perotrochus* differs from *Pleurotomaria* SOWERBY, 1821 by having convex or angular whorls, whereas they are straight or concave in the later. *Stuorella* KITTL, 1891 differs by having a small, straight-sided shell with indistinct sutures.

***Perotrochus* cf. *distincta* (GOLDFUSS, 1841)**

Plate 1, Figures 1-2

1841 *Pleurotomaria distincta* GOLDFUSS: 71, pl. 187, fig. 6.
1888 *Pleurotomaria distincta* GOLDFUSS – HOLZAPFEL: 176, pl. 20, fig. 6.

Material: Seven specimens from the Campanian of Torallola, Spain.
Description: The protoconch is globular and smooth, and measures about 0.4 mm across. The first two to two and a half volutions of the teleoconch are smooth and well rounded, afterwards an ornamentation of fine transverse cords and spiral cords begins as well as the slit. The teleoconch is large and trochiform, consists of six angular whorls with the slit at the periphery. The base is ornamented with spiral lirae that continue into the deep and large umbilicus. The largest specimen is 25 mm high and 43 mm wide.

Genus *Stuorella* KITTL, 1891

Type species: *Trochus subconcava* MÜNSTER, 1841 from the Middle Triassic of the St. Cassian Formation (BANDEL 1991b: pl. 9, figs. 7, 8; pl. 10, figs. 1-5, 7).
Description: The small, conical shell has straight sides and indistinct sutures. The slit is situated in the lower half of the whorl, the aperture trapezoid and the base concave (BANDEL 1991b: 25).

***Stuorella cretacea* n. sp.**

Plate 1, Figures 3-4

Holotype: GPI 3962, pl. 1, figs. 3-4.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: This is the first species of *Stuorella* from the Cretaceous.
Diagnosis: A small *Stuorella* with backward sloping lirae on the upper half and lower quarter of the whorls and a trapezoid aperture.
Description: The small, conical shell consists of seven to eight volutions. Its whorls are sculptured with fine, backward sloping lirae on the upper half and on the lower quarter, the slit is situated between these. The base is concave and sculptured with fine spiral lirae. The aperture is of trapezoid shape. The shell is 7 mm high and 8 mm wide.
Remarks: *Stuorella costalaricensis* ZARDINI, 1978 from the Triassic of the St. Cassian Formation has a very similar shell that differs only marginally in having straighter sides (BANDEL 1991b).

Discussion: The selenimorph group *Stuorella* consists of the Late Triassic genera *Stuorella* and *Codinella* KITTL, 1899 as well as the Permian *Lamellospira* BATTEN, 1972 and the Carboniferous *Glyptotomaria* KNIGHT, 1945 (BANDEL & GELDMACHER 1996). A relation to Jurassic Pleurotomariidae has been suggested (KITTL 1891, WENZ 1938-44, KNIGHT et al. 1960, BANDEL 1991b, TRACEY et al. 1993), which is now further supported by a surviving representative in the Campanian. Modern pleurotomariids like the here redescribed *Perotrochus* cf. *distincta* lived alongside with *Stuorella cretacea*.

Family Temnotropidae COX, 1960

Genus *Temnotropis* LAUBE, 1870

Type species: *T. carinata* (MÜNSTER, 1841) from the St. Cassian Triassic of the Italian Alps.
Description: The low, ear-shaped shells consist of few, fast-growing volutions. The slit is situated at the upper flank, the base is concave and the aperture oblique.

Temnotropis frýdai n. sp.

Plate 1, Figures 5-7

Holotype: GPI 3964, pl. 1, figs. 6-7.
Paratype: GPI 3963, pl. 1, fig. 5.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of the Czech paleontologist JIŘÍ FRÝDA and his contribution to our knowledge of Paleozoic gastropods.
Diagnosis: This *Temnotropis* has rounded early whorls, an umbilicus and a narrow, lenticular aperture.
Description: The low conical shell has flat but convex whorls which increase fast in size. The first one and a half whorls are convex and smooth and without slit. Afterwards, the whorl's upper side is sculptured with 15 spirals and the slit appears near the outer margin. The base is concave, umbilicate and shows four spirals on the outer side; the aperture is flatly lenticular. The shell's largest diameter measures 3.3 mm.
Remarks: This new species is distinct from the Triassic type by its narrower aperture, its lower-lying slit and the presence of an umbilicus. In shape, it very closely resembles *Haliotis antillesensis* SOHL, 1992 from the Maastrichtian of Puerto Rico.

Discussion: The earlier proposal that Recent Haliotidae have their ancestors in the Temnotropidae (LAUBE 1869, KOKEN 1897, BANDEL 1991b) can be supported. The latest representative of *Temnotropis* has hitherto been known only from the Late Triassic (KITTL 1891, BANDEL 1991b). However, the discovery of *Temnotropis frýdai* n. sp. in the Spanish Campanian shows that *Temnotropis* still lived when *Haliotis* LINNÉ, 1758 first appeared.

Family Scissurellidae GRAY, 1847

Genus *Scissurella* D'ORBIGNY, 1823

Type species: *Scissurella costata* D'ORBIGNY, 1823 living in the Mediterranean (WENZ 1938-44: fig. 269).
Description: The shell is low-turbiniform, the slit is situated above the peripheral margin and the apex is flattened.
Remarks: According to BANDEL (1998) *Anatoma* WOODWARD, 1859 differs by its higher spire, and *Maxwellella* BANDEL, 1998 is planispirally coiled and its whorl cross-section increases slower than in the case of *Scissurella*.

Scissurella hispanica n. sp.

Plate 1, Figures 8-9

Holotype: GPI 3965, pl. 1, figs. 8-9.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after Spain, the country of its occurrence.
Diagnosis: This low spired *Scissurella* has strong but short axial ribs. The slit starts after 1.25 teleoconch whorls.
Description: The nearly disc-shaped scissurellid shell has its protoconch and the first quarter volution imbedded in the following whorl. Sculpture consists of four opisthocline ribs on the last quarter volution before the onset of the slit. Afterwards, they are restricted to the inner half of the upper whorl-side. The slit starts after 1.25 teleoconch-whorls and is in prove with the high marginal rim. About half of the height of the whorl's outer side is occupied by a smooth constriction below the slit, the lower half is ornamented with strong transverse ribs. The aperture is oval and almost twice as wide as high. The shell is 0.6 mm high and 1 mm wide.
Remarks: This new species is distinct from *Scissurella lleidania* n. sp. by its low shape and strong ribs, which are finer and more numerous on the former. Similar ornament can be seen on *Scissurella peyrerensis* LOZOUET, 1986 from the French Oligocene (BANDEL 1998: pl. 4, fig. 8; pl. 5, figs. 1-3) but that species is higher and the slit starts about half a volutions later than on *Scissurella hispanica* n. sp.

Scisurella lleidania n. sp.

Plate 1, Figures 10-11

Holotype: GPI 3966, pl. 1, fig. 10.
Paratype: GPI 3967, pl. 1, fig. 11.
Material: Three specimens from the Campanian of Torallola, Spain.
Derivation of name: After the province of Lleida, to which the locality of Torallola belongs.
Diagnosis: The first volution including the protoconch is imbedded in the following whorl. The shell is sculptured with transverse ribs and the aperture shows a straight inner and a concave outer side.
Description: This scissurellid shell has a small and low spire and a large last whorl. Its protoconch and the first quarter volution of the teleoconch are imbedded in the succeeding whorl. The slit starts after 1.25 volutions of the teleoconch and is situated at the periphery. Below the slit is a smooth constriction followed by the convex outer side of the whorl that is sculptured with numerous axial to transverse ribs. The umbilicus is widely open, axially ribbed inside and shows two spiral cords. The large aperture shows a straight columellar lip and a broadly convex outer lip. The shell is 1 mm high and 1.5 mm wide.
Remarks: Very closely related and distinct only by its convex columellar lip is *Scissurella marchmontensis* SOHL, 1992 from the Caribbean Maastrichtian. *Scissurella hispanica* n. sp. described below is flatter, and possesses less but stronger axial ornament. Similar Recent shells include *Scissurella hoernesi* SEMPER, 1965, *Scissurella reticulata* PHILIPPI, 1853, and *Scissurella koeneni* SEMPER, 1865 (see BANDEL 1998) but they possess spiral ornament also, absent from *Scissurella lleidania* n. sp.

Discussion: Only one Cretaceous species of *Scissurella* has hitherto been known, two are added here. One differs only marginally from the one described by SOHL

(1992) from the Jamaican Maastrichtian, while the other shows affinities to European species from the Paleogene.

Family Fissurellidae FLEMMING, 1822

Genus *Emarginula* LAMARCK, 1801

Type species: *Patella fissura* LINNÉ, 1758, Recent, from the North Sea (WENZ 1938-44: fig. 276).
Description: The patelliform shell has the elongated and narrow slit at its anterior margin between two radial ribs.

Emarginula radiocostata n. sp.

Plate 1, Figures 12-14

Holotype: GPI 3968, pl. 1, figs. 12-14.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: This species shows radial costae only.
Diagnosis: This *Emarginula* is a little wider than high, possesses a downward-pointing, slightly twisted apex, and strong radial sculpture.
Description: The slightly twisted, limpet-like shell has a downward-pointing apex and is sculptured with 14 radial ridges and fine lines in between. The aperture is rounded rectangular and the slit is situated on the dorsal side between the two strongest ribs. The aperture is 7 mm long, 4.5 mm wide, and the shell is 5 mm high.
Remarks: SOHL (1992) described three species of *Emarginula* from the Upper Cretaceous of the Caribbean, but they all show strong concentric sculpture in addition to the radial ribs. The same applies to the numerous species of *Emarginula* described by KAUNHOWEN (1897) from Maastricht.

Discussion: The Fissurellidae are known since the Triassic (BANDEL 1991b) and the newly described *Emarginula* does not provide new insights to the history of the family. However, it is quite unique with its slightly twisted shell.

Superfamily Trochoidea RAFINESQUE, 1815

The Trochoidea have been evaluated extensively by HICKMAN & MCLEAN (1990) and according to their diagnosis they can be characterised as having a shell without slit or foramen. The shape of the shell is conispiral with diameter of whorls increasing slowly, with exception of some derived genera. An umbilicus is present or not and the aperture is commonly of rounded shape with free anterior margin and commonly inclined position in regard to the shell axis. The operculum is organic or calcified. Other features charactizing this taxon regard the ctenidium, appendages to the foot, sensory cilia of the head tentacles and the rhipidoglossate radula. Modern groups (families and subfamilies) are usually recognised by features of the soft body; regarding the shell there are numerous convergencies among these units. Due to such convergence the assignment of fossils to Recent groups bears a certain amount of insecurity, especially when these fossils are about 80 million years old.
HICKMAN & MCLEAN (1990) distinguished three families within the Trochoidea, but their shell shapes are not very distinctive from each other. In their key they noted that usually unpigmented and maximally 5 mm large shells are found within the Skeneidae CLARK, 1851, usually pigmented and commonly larger than 5 mm large shells compose the Turbinidae RAFINESQUE, 1815 and Trochidae. The difference between Turbinidae and Trochidae may regard the growth edge of the

operculum which is commonly long in Turbinidae and short in Trochidae. This later family comprises conical shells that show a very oblique aperture without thickening and usually have a nacreous interior and apparently they never calcify their operculum. Distinctive characters to the Turbinidae are few, as pointed out by HICKMAN & MCLEAN (1990), and not even all of these calcify their operculum.

Family Turbinidae RAFINESQUE, 1815

The family diagnosis presented by HICKMAN & MCLEAN (1990) is based mainly on radula characters and is therefore of little use in the fossil record. These authors as well as WENZ (1938-44) described members of the Turbininae as high-conical to disc-shaped, with an interior nacreous layer and a radial to oblique aperture. Although they live in all latitudes, diversity is highest in tropical environments (HICKMAN & MCLEAN 1990).

Subfamily Liotiinae ADAMS & ADAMS, 1854

Typical shell characters include a nearly radial aperture with an uninterrupted peristome and lamella-like axial ribs on the teleoconch (HICKMAN & MCLEAN 1990). The same authors noted a nearly world-wide distribution of the Recent species, exclusive the north-eastern Atlantic and the Mediterranean.

Genus *Pseudoliotina* COSSMANN, 1925

Type species: *Liotia sensuyi* VIDAL, 1921 from the Campanian of Torallola, Spain.
Description: The genus includes planispiral shells with angular whorls. Ornament consists of several keels and fine axial lamella. The aperture is circular, thickened and has radial grooves corresponding with the keels of the whorls in fully grown individuals.
Remarks: The Recent *Cyclostrema* MARRYAT, 1854 is similar but has an oblique aperture which lacks the radial grooves of *Pseudoliotina*. *Liotia* GRAY, 1847 is trochiform rather than planispirally coiled. ABBOTT (1974) considered *Pseudoliotina* and *Mundita* FINLEY, 1926 as synonymous, HICKMAN & MCLEAN (1990) regarded *Pseudoliotina* as a valid genus. COSSMANN's (1925) and HICKMAN & MCLEAN's (1990) opinion is followed here due to the above mentioned diagnostic differences.

Pseudoliotina sensuyi (VIDAL, 1921)

Plate 2, Figures 1-2

1921 *Liotia sensuyi* VIDAL: 99, pl. 6, figs. 2-3.
1925 *Pseudoliotina sensuyi* (VIDAL) – COSSMANN: 286.
1949 *Liotia sensuyi* VIDAL – BATALLER: 16.

Material: One specimen from the Campanian of Torallola, Spain (figured: GPI 3969).
Description: The medium sized, planispiral shell has at least three volutions. Its sculpture consists of two jagged spiral cords on the upper side, three on the outer side and two on the base, the second of which is very weak. Growthlines are strong, the aperture is round and the shell is 3 mm high and 11 mm wide.
Remarks: This species is distinct from *Pseudoliotina mcleani* n. sp. by its three jagged cords on the outer side.

Pseudoliotina stinnesbecki n. sp.

Plate 2, Figures 3-5

Holotype: The specimen illustrated in pl. 1, figs. 3-5 (GPI 3970).
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: In honour of WOLFGANG STINNESBECK, Karlsruhe, who is working with Cretaceous molluscs.
Diagnosis: The planispiral shell has two jagged spirals on the upper side and two on the lower side.
Description: The planispiral shell is made of three volutions and shows strong growthlines. Its sculpture consists of three jagged spiral cords on the upper side and two on the lower side. The upper side is little convex, the lower side flat and the outer side is inclined. The aperture is round and reinforced with a flaring margin that has grooves corresponding with the spiral keels on the shell. The shell is 7 mm high and 18 mm wide.
Remarks: The Puerto Rican *Pseudoliotina mcleani* SOHL, 1998 shows strong axial ribs instead of lamellae as does the type species, it has an oblique aperture unlike *Pseudoliotina sensuyi* and also in size it resembles *Cyclostrema* more closely than *Pseudoliotina*.

Genus *Arene* ADAMS & ADAMS, 1853

Type species: *Arene radiata* (KIENER) according to WENZ (1938-44: fig. 792), and *Arene cruantata* (MÜHLFELD) according to ABBOTT (1974).
Description: The small and thick, depressed turbinate shell has a rimmed and thickened round aperture. The sculpture consists of spiny spiral cords.

Arene mcleani n. sp.

Plate 2, Figures 6-7

Holotype: The specimen illustrated in pl. 1, figs. 6-7 (GPI 3971).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of JAMES MCLEAN, who contributed greatly to the classification of Archaeogastropoda.
Diagnosis: The low spired shell has an angular body whorl and is sculptured with beaded spiral cords. The aperture has small denticles on its base.
Description: The small shell consists of four volutions, its protoconch and first whorl are smooth and planispirally coiled, the body whorl is angular, has seven beaded spiral cords and fine axial lamella. The base is sculptured with three spirals, the umbilical slit is bordered by a beaded ridge. The aperture is round with denticles on the basal side. The shell is 2.1 mm wide and 2.6 mm high.
Remarks: SOHL (1998) described a related species as *A. truncatospaera* SOHL, 1998 from the Jamaican Maastrichtian. It has only four spirals on the last whorl but these are stronger than in *A. mcleani*. A similar Recent species is *Arene bairdii* DALL (in: ABBOTT 1974: 55) from the North American east coast. It shows almost identical sculpture but no apertural denticles and is about three times larger.

Discussion: HICKMAN & MCLEAN (1990) considered several Triassic and Jurassic genera as possible members of the Liotiinae, and also included *Pseudoliotina* from the Cretaceous. The two species of *Pseudoliotina* documented here are comparable with the Triassic *Woehrmannia* BÖHM, 1895, as well as modern *Cyclostrema*. This group of planispiral liotiids apparently exists since the Triassic. *Arene* exists according to WENZ (1938-44) since the Miocene, and SOHL (1998) described a species from the Maastrichtian. Thus, the new species described here represent the oldest member of this genus.

Subfamily Colloniinae COSSMANN, 1916

Recent members of this turbinid subfamily live world-wide on gravel and hard substrates from intertidal to bathyal depth (HICKMAN & MCLEAN 1990). Comparing anatomical characters, HICKMAN & MCLEAN (1990) considered the Colloniinae to intermediate between the primitive Liotiinae and Angariinae on one side and more advanced turbinids on the other.

Genus *Homalopoma* CARPENTER, 1864

Type species: *Turbo sanguineaum* LINNÉ, 1758 living in the Mediterranean (WENZ 1938-44: fig. 798).
Description: This genus comprises small, low spired shells with convex volutions, a narrow or closed umbilicus and a roundish aperture.
Remarks: *Collonia* GRAY, 1850 shows according to WENZ (1938-44) an open umbilicus with beaded margin. According to HICKMAN & MCLEAN (1990), *Collonia* is rather smooth while *Homalopoma* clearly shows spiral sculpture. But whether these rather minor differences are consistent enough to justify generic separation remains an open question.

Homalopoma minimum (QUINTERO & REVILLA, 1966)

Plate 2, Figure 11

1966 *Turbo minimum* QUINTERO & REVILLA: 48, pl. 7, fig. 7.

Material: One specimen from the Campanian of Torallola, Spain (figured: GPI 3972).
Description: The small, relatively high spired turbiform shell has whorls with numerous spiral cords. The whorl-sides are straight until the strong fifth cord, below which it is more convex. It has a round aperture and an umbilicate, concave base with spiral cords. The shell is 4 mm high and wide.
Remarks: *Homalopoma schroederi* n. sp. has a larger last whorl and a flat-topped spire, *Collonia wollemanni* SCHRÖDER, 1995 from the Aptian/Albian of northern Germany shows a much lower spire, a wider umbilicus and its whorls are more rounded.

Homalopoma schroederi n. sp.

Plate 2, Figure 8

Holotype: The specimen illustrated in pl. 1, fig. 8 (GPI 3973).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for MICHAEL SCHRÖDER, Hamburg, who worked on Jurassic and Cretaceous gastropods.
Diagnosis: This nearly flat-topped species of *Homalopoma* has well rounded whorls and two denticles in the aperture.
Description: The small, roundish shell with four convex volutions and deep sutures is sculptured with fine spiral lirae. The first two whorls are almost flat-topped. The rounded base is spirally sculptured and has a narrow umbilical slit. The circular aperture shows two denticles. The shell is 5 mm high and wide.
Remarks: An almost identical Recent species is *Homalopoma baculum* (CARPENTER) from California (HICKMAN & MCLEAN 1990: fig. 17 B).

Homalopoma chica n. sp.

Plate 10, Figures 1-2

Holotype: The specimen illustrated at pl. 10, figs. 1-2.
Material: One specimen from the Maastrichtian of Temalac, Mexico.
Derivation of name: From the Spanish word “chica”, for small.
Diagnosis: The small turbiniform shell is ornamented with spiral cords on its rounded whorl surface, and the smooth base has a small umbilicus.
Description: The protoconch measures 0.15 mm across, the teleoconch is low turbiniform, consists of three volutions and the aperture is higher than the spire. On the first whorl of the teleoconch five spiral ribs are present, while the next whorl shows 6. The body whorl has twelve such spirals, which near the periphery appear beaded. Its whorls are convex and sculptured with spiral ridges. The base is smooth, shows a small umbilicus that is accompanied by a spiral rib, and the aperture is roundish. The holotype is 1.5 mm high and 1.8 mm wide.
Remarks: *Collonia wollemanni* from the Aptian/Albian of northern Germany is quite similar but possesses spiral cords on the base (SCHRÖDER 1995: pl. 1, figs. 17-21) which contrasts to the smooth base of *Homalopoma chica.*

Discussion: The three species of *Homalopoma* described here resemble Recent as well as mid-Cretaceous species. Although the origin of this group is still unclear, these gastropods seem to have not changed very much in the last 100 m.a. of their history.

Subfamily Turbininae RAFINESQUE, 1815

The shells can be relatively large, are cone-shaped and the apertural inclination is highly variable (WENZ 1938-44, HICKMAN & MCLEAN 1990). The latter authors proposed that a bicarinate early shell is an apomorphic character of this subfamily. Members of the Turbininae today live in all tropical and subtropical seas from the intertidal to bathyal depth.

Genus *Barbotella* COSSMANN, 1918

Type species: *Turbo hoernesi* BARBOT, from the Russian Miocene (WENZ 1938-44: fig. 834).
Description: Shells are of moderate size, their volutions are convex with deep sutures and sculptured with strong, irregular axial ribs.

Barbotella maestrichtiensis (QUINTERO & REVILLA, 1966)

Plate 2, Figures 9-10

1966 *Delphinula maestrichtiensis* QUINTERO & REVILLA: 48, pl. 7, fig. 6.
1992 *Delphinula maestrichtiensis* QUINTERO & REVILLA – HÄNSEL: 81, pl. 4, fig. 22.

Material: Three specimens from the Campanian of Torallola, Spain (figured: GPI 3974).
Description: A relatively high spired turbiform shell with at least seven convex volutions and deep sutures. The early whorls show fine spiral lirae, later they are ornamented with irregularly deformed axial to transversal ribs which are crossed by spiral cords. The aperture is round, its inner lip is a little reinforced and there is no umbilicus. The shell is 40 mm high and 33 mm wide. Nacre is still demonstrable in its original aragonitic state in some specimen (HÄNSEL 1992).

Remarks: This species is higher spired and a little stronger ornamented than the type species. Similar ornament is found on the Jurassic *Turbo crispicans* LORIOL, 1886-1888.

Genus *Marmorostoma* SWAINSON, 1829

Type species: *Turbo crysostomus* LINNÉ, 1758, living around the Philippines (WENZ 1938-44: fig. 822).
Description: The large, conical shells have rounded to angular whorls with denticulate or spiny spiral cords and deep sutures.

Marmorostoma sensuyi (VIDAL, 1924)

Plate 3, Figures 1-3

1924 *Delphinula sensui* VIDAL, in: CAZURRO et al.: 42.
1949 *Delphinula sensui* VIDAL – BATALLER: 16.
1992 *Delphinula sensui* VIDAL – HÄNSEL: 77, pl. 4, fig. 20.

Material: 21 specimens from the Campanian of Torallola, Spain (figured: GPI 3975).
Description: The embryonic part measures 0.21 mm across, is smooth and separated from the teleoconch by a weak varix. The first teleoconch whorl is almost planispirally, ornamentation starts with two ridges on the outer side of the whorl and one close to the inner suture. After one volution, three minor ridges appear between the strong inner and outer ones. The adult shell is turbiform with four to five convex volutions and the sculpture turns into numerous jagged spiral cords. The peaks of the first three cords are of equal size, those of the fourth are quite large, those of the fifth resemble them of the first three, are slightly larger on the sixth cord and then again of similar size as the first three from the seventh cord onwards. The aperture is round and reinforced and the umbilicus small with a beaded margin. The shell is 35 mm high and 39 mm wide. Nacre is still demonstrable in its original aragonitic state in some specimen (HÄNSEL 1992).
Remarks: The Eocene *Delphinula lima* LAMARCK (see COSSMANN 1915: pl. 9, figs. 13-14) is similar but its whorls are more angular. The same applies to the Jurassic *Turbo bonjouri* ÉTALLON (see LORIOL 1886-1888: pl. 19, figs. 1-4). Similar species from the Late Cretaceous include *Turbo goupilianus* D'ORBIGNY, 1842, *Solarium kirsteni* GEINITZ, 1874, and *Turbo leonhardi* GEINITZ, 1871 from the Cenomanian or Turonian of Saxony in Germany (GEINITZ 1871-75).
Similar species were described by SOHL (1998) from the Caribbean Campanian-Maastrichtian. He assigned them to *Metriomphalus* Cossmann, 1916 which he considered to represent Colloniinae. The type species of *Metriomphalus* is of mid-Jurassic age, that of *Marmorostoma* is recent. Thus, both are about 80 million years away from the Campanian species concerned here.

Genus *Callopoma* GRAY, 1850

Type species: *Turbo (Callopoma) fluctuosus* (WOOD) living off California in the Pacific Ocean (WENZ 1938-44: fig. 833).
Description: The moderate to large shells have more or less angular whorls with spiral sculpture and a round aperture.

Callopoma iredalei n. sp.

Plate 3, Figures 7-9

Holotype: The specimen illustrated in pl. 2, figs. 7-9 (GPI 3976).
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: In honour of T. IREDALE who contributed to our knowledge of Australian gastropods.
Diagnosis: This *Callopoma* has strongly shouldered whorls and strong spines.
Description: A low spired shell with at least three volutions which are strongly shouldered to almost rectangular. Sculpture consists of two nodular cords on the upper side and spines on the periphery, and the outer side shows nodular cords of increasing number towards later whorls. On the body whorl appear fine axial lirae and the spines are very strong. The spiral cords continue on the bottom. The shell is 13 mm high and 17 mm wide.
Remarks: *Delphinula pelossei* ROMAN & MAZERAN, 1913 from the French Turonian shows very similarly angulated whorls.

Genus *Astraea* RÖDING, 1798

Type species: *Astraea helitropium* MARTYN, Recent, New Zealand (WENZ 1938-44: fig. 837)
Description: Recent members of this genus have a low conical shell, whorls with denticulate or spiny keels, and a wide or callus-covered umbilicus.

Astraea batalleria n. sp.

Plate 3, Figures 4-6

1992 *Delphinula guerini* BATALLER – HÄNSEL: 79, pl. 4, fig. 21.

Holotype: The specimen figured in pl. 3, figs. 4-6 (GPI 3977).
Material: 13 specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of J.R. BATALLER who was working on Spanish Cretaceous gastropods.
Diagnosis: The low spired shell with four to five volutions has rather deep sutures and whorls that are jagged at the sutures. The peaks above the suture develop into enormous spines on the body whorl. The shell is otherwise ornamented with spiral cords which continue down into the umbilicus. The last whorls are often loosely coiled. This species shows a broad variability in the height of its spire. Its aperture is round and radial, the shell is 16 mm high and 25 mm wide. Nacre is still demonstrable in its original aragonitic state in some specimen (HÄNSEL 1992).
Remarks: *Astraea (Delphinula) guerini* BATALLER, 1945 has a much larger umbilicus and a simpler aperture. The Jurassic species *Delphinula stellata* BURIGNIER (In: LORIOL 1893) shows deep sutures and a smooth surface. *Astraea hickmanae* n. sp. lacks the strong spiral sculpture on the spire. A very similarly ornamented species occurs in the Trichinopoli formation in southern India (BANDEL 2000) but has a more rounded base. Similar although with less but larger spines is the Anisian (Middle Triassic) *Asperilla mayfensis* COSSMANN, 1915.

Astraea hickmanae sp.

Plate 3, Figures 10-11

Holotype: The specimen illustrated in pl. 2, figs. 10-11 (GPI 3978).
Material: Nine specimens from the Campanian of Torallola, Spain.

Derivation of name: In honour of CAROLE S. HICKMAN.
Diagnosis: A low spired shell with four whorls that are denticulate at the upper suture and develop broad spines on the periphery of the body whorl. The aperture is round with a little notch in the outer lip, formed by the broad spines. The umbilical margin is broadly dented. The shell is 9 mm high and 15 mm wide.

Astraea sp.

Plate 3, Figures 12-14

Material: One specimen from the Campanian of Torallola, Spain (figured: GPI 3979).
Description: The medium sized, almost flat shell has more than three volutions. The initial two are smooth and convex, later whorls are ornamented with strong axial ribs. The base is convex and the umbilicus has a dented margin. The shell is 7 mm high and 17 mm wide.

Discussion: Shells resembling those of Recent *Angaria, Astraea* and *Turbo* can be traced through the fossil record back to Triassic time or to even older strata (BANDEL 1993a, YIN & YOCHELSON 1983). For example, *Gizhouia* YIN & YOCHELSON, 1983 from the Chinese Triassic is strikingly similar to modern *Astraea*. Also BANDEL (1993a) connected the Triassic *Coelocentrus* ZITTL, 1882 with Recent forms. If the variability in shell shape documented by BEU & PONDER (1979) for the genus *Bolma* RISSO, 1826 is considered, it appears rather impossible to distinguish these groups in the fossil record. Exceptions may be some direct ancestors of living species in Neogene sediments. The species in question are here assigned to existing genera and discuss related forms known from the literature. However, due to the rarely good preservation of gastropods that lived on a rocky shore, the fossil record of these groups is too patchy for a truly consistent treatment.

Family Trochidae RAFINESQUE, 1815

Subfamily Tegulinae KURODA, HABE & OYAMA, 1971

Tegulinae represent one of the twelve subfamilies of the Trochidae distinguished by HICKMAN & MCLEAN (1990). The subfamily is interpreted to contain only the genus *Tegula* including five subgenera which are noted only since late Tertiary. Most Neogene and recent representatives of this subfamily live in the temperate North Pacific except *Tegula* (*Agathistoma*) OLLSON & HARBISON, 1953 from the tropical seas around Central America. Their preferred habitat are brown algae and rocks in the intertidal to shallow sublittoral (HICKMAN & MCLEAN 1990).

Genus *Tegula* LESSON, 1832

Type species: *Tegula pellisserpertis* (WOOD, 1828) living in the shallow sea of the Central American Pacific.
Description: The turbinate shell has solid flattish whorls with or without umbilicus. The ornament consists of spiral lirae or striae. The columella is thickened or toothed and the aperture is oblique.

Tegula? *simplex* (QUINTERO & REVILLA, 1966)

Plate 4, Figure 1

1966 *Trochus simplex* QUINTERO & REVILLA: 49, pl. 8, fig. 3.

1989 *Clanculus simplex* (QUINTERO & REVILLA) – CALZADA: 31, pl. 2, figs. 1a, b.

Material: Seven specimens from the Campanian of Torallola, Spain (figured: GPI 3908).

Description: The small trochiform shell with six weakly convex volutions is ornamented with fine spiral lirae that are continuing on the bottom. The aperture is oblique, round to slightly oval, denticulate and callused on its parietal lip. The base is weakly convex and there is no umbilicus. The shell is 8 mm high, 8 mm wide, and has an apical angle of about 60°.

Remarks: This species resembles the type species of *Tegula* as figured by WENZ (1938-44: fig. 681) and HICKMAN & MCLEAN (1990: Fig 35 D) although it is much smaller and the columellar denticle is less well developed. CALZADA (1989) assigned this species to *Clanculus*. Recent species of that genus all have a wide umbilicus. *T.*? *simplex* lacks an umbilicus and thus its placement with *Clanculus* appears unlikely.

A related species may be ”*Jujubinus*” *botijasensis* SOHL, 1998 from the Puerto Rican Campanian, which has a lower apical angle. Generally similar but with a lower spire and a less elongate aperture than *T.*? *simplex* is a shell described as *Ataphrus* cf. *dosori* (PICTET & CAMPICHE) by KASE (1984: pl. 6, figs. 6-7) from the Aptian/Albian of Japan. Also related might be *Trochus virdunensis* BURIGNIER (in: LORIOL & PELLAT 1874) from the Upper Jurassic of Northern France, but that species seems to lack a columellar denticle.

Discussion: According to WENZ (1938-44) and HICKMAN & MCLEAN (1990) the Tegulinae appeared as late as Miocene. While the latter found the Miocene members restricted to Japan and North America, the former stated a broader distribution of North and South Pacific. Due to the similarity of the species described here with the type species of *Tegula*, a Cretaceous origin for *Tegula* is suggested with some reservations. BANDEL (1993a) indicated possible relations even to Jurassic genera such as *Tylotrochus* KOKEN, 1896.

Subfamily Eucyclinae KOKEN, 1897

The members of this subfamily are united by the presence of axial ribs on the first whorls of the teleoconch.

HICKMAN & MCLEAN (1990) introduced a new tribe, the Calliotropini, to include several thin shelled Recent genera restricted to the clastic, outer shelf to deep water facies. The Eucyclini are defined by HICKMAN & MCLEAN (1990) by the ontogenetic change from an interrupted peristome in the juvenile stage to a closed one in the adult. However, such a change can also be observed in other groups of the Trochoidea. The example of such a case given by HICKMAN & MCLEAN (1990) showed a member of *Amberleya* MORRIS & LYCETT, 1851. But the systematic position of this genus is still doubtful (BANDEL 1993a). On the other hand, the Calliotropini are defined as thin shelled, whereas the included *Cidarina* DALL, 1909 and *Calliomphalus* COSSMANN, 1888 represent rather thick shelled gastropods. Also the here presented members of the name-giving genus *Calliotropis* SEQUENZA, 1903 is thick shelled. The definition of the Calliotropini, thus, is not very useful and only the Eucyclini and Chilodontini with *Calliotropis* and *Cidarina* included in the latter tribe are recognized here.

Tribe Eucyclini KOKEN, 1897

Recent Eucyclini occur world wide mainly in depth greater than 200 m and live on fine, unconsolidated sediment. An exception is *Cidarina* which lives in shallower waters on coarse grained substrates (HICKMAN & MCLEAN 1990).

Genus *Eucyclomphalus* AMMON, 1892

Type species: *Eucyclomphalus cupido* D'ORBIGNY from the Lower Jurassic of Charmouth, Département Calvados, France (WENZ 1938-44: fig. 369).
Remarks: The genus *Eucyclomphalus* was treated by WENZ (1938-44) as a member of the Cirridae COSSMANN, 1916 but in a recent evaluation of this family BANDEL (1993b) redefined this group as sinistrally coiled archaeogastropods without slit and with a dextrally coiled protoconch. HICKMAN & MCLEAN (1990) included *Eucyclomphalus* in the Eucyclinae.

Eucyclomphalus reminescencius n. sp.

Plate 4, Figure 3

1992 *Trochus carinatus*? QUINTERO & REVILLA – HÄNSEL: 74, pl. 4, fig. 17.

Holotype: The specimen illustrated in pl. 4, fig. 3 (GPI 3946).
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: This Late Cretaceous species is a reminiscence of the numerous early Mesozoic members of this genus.
Diagnosis: This *Eucyclomphalus* shows a strong and spiny keel and a strongly beaded subsutural cord.
Description: The high conical shell with about eight angular and keeled whorls is sculptured with a beaded subsutural cord. The strong keel shows semitubular spines. The shell is 15 mm high and the early whorls have an apical angle of about 50°; later whorls are flattened and measurements would be inaccurate. Nacre is still preserved in its original aragonitic state in some specimen (HÄNSEL 1992).
Remarks: Although quite similar to the lower Jurassic type species, the beaded subsutural cord is more strongly developed in *Eucyclomphalus reminiscencius*.

Genus *Calliotropis* SEQUENZA, 1903

Type species: *Calliotropis ottoi* (PHILIPPI, 1844) living on the shelf of the eastern Atlantic Ocean near New England, USA.
Description: The conical shell has flattened whorl sides and an open umbilicus. Ornament consists of small spirally arranged beads, and the aperture is oblique and angular.

Calliotropis torallolensis n. sp.

Plate 4, Figure 7

Holotype: The specimen illustrated in pl. 1, fig. 7 (GPI 3909).
Material: 14 specimens from the Campanian of Torallola, Spain.
Diagnosis: The higher than wide *Calliotropis* has three, in the last whorl four rows of pointed, delicate tubercules. The base is smooth with a small umbilicus that is surrounded by denticles.
Description: The medium sized, trochiform shell consists of seven whorls with straight sides and deep sutures. It is sculptured with four spiral rows of pin-like tubercles, the third being the strongest and the fourth covered by the succeeding whorl. The umbilicus is small with denticulate margin and the base is convex with weak spiral lines on its outer margin, otherwise smooth. The aperture is rounded. The shell is 13 mm high, 9 mm wide and has an apical angle of about 65°.
Remarks: The beaded umbilical margin and more strongly transverse growth lines distinguishes *Calliotropis torallolensis* from the otherwise very similar Recent type

species. *Calliotropis nilssoni* (MÜNSTER) described by MÜLLER (1847-51) from the Vaals Greensands is very similar in shape but has stronger tubercles.

Calliotropis seguris n. sp.

Plate 4, Figures 4-5

Holotype: The specimen illustrated in pl. 1, figs. 4-5 (GPI 3911).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after the town of Pobla de Segur near the locality of Torallola.
Diagnosis: The 10 mm high and slightly less wide, conical shell has flattened flanks with two tuberculate ridges on the early whorls and three on the body whorl. The base is ornamented by many spiral lirae and is pierced by an umbilicus with a dented margin.
Description: The small to medium sized shell consists of seven whorls with flattened sides. Two tuberculate ridges are present on each volution except the last where a third row appears. Growth lines are well developed, the umbilicate bottom shows many tuberculate spiral lines, margin of umbilicus denticulate. The shell is 10 mm high, 9 mm wide and has an apical angle of about 70°.
Remarks: *Calliotropis torrallolensis* has small spines, which are unknown from *Calliotropis seguris*.

Calliotropis sp.

Plate 4, Figure 2

Material: Three specimens from the Campanian of Torallola, Spain (figured: GPI 3910).
Description: The small, conical shell has five to six volutions separated from each other by deep sutures. The whorls are straight-sided and bear three spiral cords with strong tubercules. The basal margin is rounded, the base flat and umbilicate and sculptured with three weak tuberculate spiral cords. The shell is 8 mm high and 8 mm wide and has an apical angle of about 60°.
Remarks: The three equally sized cords distinguish this new species from *Calliotropis seguris* n. sp. with its two cords.

Genus *Ilerdus* CALZADA, 1989

Type species: *Trochus melgari* BATALLER, 1949, described below.
Diagnosis: The conical shell is higher than wide, shows axial and spiral sculpture, and has incised sutures. The apertural margin is in one plane and the columella has an abapical denticle (translated Spanish diagnosis of CALZADA 1989).
Remarks: *Basilissa* WATSON, 1879 and its subgenera build similar shells but differ in having an umbilicus and by showing an adapical columellar denticle rather than an abapical one like *Ilerdus*. *Pseudoclanculus* COSSMANN, 1918 is distinct with its columellar fold rather than a tooth. Also *Cidarina* DALL, 1909 appears closely related but has a convex base rather than a flat one as *Ilerdus*.

Ilerdus melgari (BATALLER, 1949)

Plate 4, Figures 6, 10, 13

1949 *Trochus Melgari* BATALLER: 20.
1989 *Ilerdus melgari* (BATALLER) – CALZADA: 27, pl. 2, figs. 7a, b.
1992 *Trochus maestrichtiensis* VIDAL – HÄNSEL: 61, pl. 2, fig. 9.

Material: About 90 specimens from the Campanian of Torallola, Spain (figured: GPI 3912, 3913).
Description: The large protoconch measures 0.4 mm across. The first teleoconch whorls are axially ribbed. These ribs develop strong tubercles on their upper and lower ends on the second whorl. Two more tubercles appear on later whorls and thus generate the carinate ornament of the adult whorls consisting of four nodular spiral cords. The adult shell is of high conical shape with a flat and smooth base and no umbilicus. The aperture is of trapezoid outline. The shell with eight whorls is 16 mm high, 13 mm wide and has an apical angle of about 40°. According to HÄNSEL (1992) a central layer of nacre is present and in some shells it is still preserved in its original aragonitic composition.
Remarks: CALZADA (1989) described the protoconch of this species to consist of two smooth whorls. This is superficially the case on worn adult shells. However, as shown in pl. 4, fig. 6, the protoconch is clearly of the archaeogastropod type. *Trochus ilerdensis* QUINTERO & REVILLA, 1966 was included in the synonymy of *Ilerdus melgari* by CALZADA (1989). This is doubted here because that species (QUINTERO & REVILLA, 1966: pl. 7, figs. 8-9) shows five or more spirals per whorl, while *Ilerdus melgari* has strictly four. These four spiral also distinguish *Ilerdus melgari* from *Ilerdus pyrenaeus* which has an ornamented base and the numbers of spirals increase on latter whorls up to eight.

Ilerdus pyrenaeus n. sp.

Plate 4, Figures 8-9, 11-12

Holotype: The specimen illustrated in pl. 1, fig. 8-9 (GPI 3914).
Paratype: The specimen illustrated in pl. 1, fig. 11-12 (GPI 3915).
Material: Nine specimens from the Campanian of Torallola, Spain.
Diagnosis: The high spired *Ilerdus* is sculptured with beaded spiral cords which increase in number during growth from three to 8. There are four such cords on the base.
Description: The protoconch measures about 0.23 mm across. The small and relatively high spired trochiform adult shell consists of at least five whorls with flattened sides. The earliest whorls are ornamented with axial ribs which later turn into string-of-pearls-like cords. Their number increases from three to eight towards the body whorl. The base is ornamented with four similar cords. The shell is 10 mm high, 8 mm wide and has an apical angle of about 55°.
Remarks: These specimen resemble *Trochus cirrus* WHITE, 1887 from the Maastrichtian of north-eastern Brazil.

Genus *Eucycloscala* COSSMANN, 1895

Type species: *Eucycloscala binodosa* (MÜNSTER, 1841) from the late Triassic of the Italian Alps, Dolomites (BANDEL 1993a, pl. 10, figs. 2-3).
Description: The high-conical shell has a nacreous internal wall composition. The archaeogastropod-type protoconch is succeeded by rounded axially ornamented juvenile teleoconch whorls. In addition there are fine spiral lirae which also ornament the base which may be umbilicate.

Eucycloscala cretacea n. sp.

Plate 4, Figures 14-15

Holotype: The specimen illustrated in pl. 1, figs. 14-15 (GPI 3916).

Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: This is a Cretaceous representative of its genus.
Diagnosis: In this *Eucycloscala* the protoconch deviates only slightly from the axis of coiling, the whorls are angular and are sculptured with two spiral cords which form tubercles at the intersections with the axial ornament.
Description: The preserved conical shell consists of only two and a half volutions. The protoconch measures about 0.2 mm across and its coiling axis forms a small angle with that of the teleoconch. Early whorls are convex with axial ribs, later they are angulated by two spiral keels, and the intersections with the axials are tuberculate. The base is sculptured with axial ribs only. The shell is about 1.2 mm high, slightly wider and has an apical angle of about 75°.
Remarks: The small shell illustrated here most probably represents a juvenile specimen, and fully grown individuals have not been found. The Triassic *Eucycloscala elegans* (MÜNSTER, 1841 in BANDEL 1993a) which also shows two spiral ridges and only a minor deviation of the coiling axis of the protoconch appears closely related. A similar species but with spirals on the base was reported by ANDERSON (1975) as *Eucycloscala basistriata* from the Paleocene of western Germany.

Discussion: Within the Eucyclinae KOKEN, 1897, HICKMAN & MCLEAN (1990) unified three tribes: the Chilodontini and Calliotropini with fossil and living genera, and the extinct Eucyclini with Mesozoic members only, although their definition of the Eucyclinae was solely based on radula characters. The diagnostic differences proposed by HICKMAN & MCLEAN (1990) to distinguish Calliotropini and Eucyclini regarding shell-thickness and apertural features are inconsistent with the data presented here. Therefore, the Calliotropini are not recognised, but included in the Eucyclini. It is proposed to include Chilodontini and Eucyclini within the Eucyclinae, united by the presence of axial ribs on the earliest teleoconch whorl. Both tribes can be distinguished by the presence or absence of apertural denticles respectively. *Microdonta* MEEK & WORTHEN, 1866 may represent a Palaeozoic ancestor of the Eucyclinae as was indicated by BANDEL (1993a). According to WENZ (1938-44) *Microdonta* shows axial ribs on the early ontogenetic whorls. When further evidence from the fossil record confirms this suggestion, these groups may be united in their own family.

Tribe Chilodontini WENZ, 1938

This group is characterised by apertural thickenings or apertural denticles and the shells mostly possess a carinate ornament. Recent Chilodontini live on hard substrate in shallow tropical seas.
The Chilodontini have been treated as an exclusively Mesozoic group by WENZ (1938-44), but MCLEAN (1984b) presented a living member that he related to the Early Cretaceous genus *Agathodonta* COSSMANN, 1918. Due to this discovery as well as several shell and anatomical characters, HICKMAN & MCLEAN (1990) united all members of the Chilodontidae and several recent genera to the tribe Chilodontini. Additionally, the strong similarities between Cretaceous and Eocene species of *Chilodonta* support the connection of Mesozoic and Recent Chilodontini.

Genus *Hudledonta* n. nom.

Type species: *Chilodontoidea ooliticia* HUDLESTON, 1896 from the Bajocian of Dorsetshire, UK (WENZ 1938-44: fig. 649).

Description: The small pupoid shell has a high spire and well developed sutures. The ornament consists of spiral and axial ribs forming a reticulate pattern. The body whorl is a little less expanded than former whorls, with rounded aperture that is lowly funnelled on its upper edge and bears a thickened continuous callus margin in the fully grown individuals. The columellar lip has an upper denticle and may be thickened.

Remarks: According to the rules of the ICZN, the ending –oidea is reserved for superfamilies. *Chilodonta* is already a valid name (see below), so the new name *Hudledonta* is introduced here, honouring W.H. HUDLESTON who introduced the genus *Chilodontoidea* HUDLESTON, 1896.

According to statements of WENZ (1938-44) and SOHL (1987) the Jurassic *Chilodontoidea* (now *Hudledonta*) and *Wilsoniconcha* WENZ, 1938 as well as the predominantly Cretaceous *Chilodonta* ÉTALLON, 1859, *Calliomphalus* and *Planolateralus* SOHL, 1960 compose the largest portion of the Mesozoic Trochidae. Also according to these authors they mostly became extinct during the transition from the Cretaceous to the Tertiary. These ideas appear to be erroneous in the light of the new data presented here.

Hudledonta nicolae n. sp.

Plate 5, Figures 1-2

Holotype: The specimen illustrated in pl. 5, figs. 1-2 (GPI 3917).

Material: Four specimens from the Campanian of Torallola, Spain.

Derivation of name: Named for KATHARINA NICOLA HÄNSEL who worked on the shell structure of the gastropods of Torallola.

Diagnosis: This *Hudledonta* has concave whorl-sides and is sculptured with five beaded spirals per whorl, there is no axial ornamentation.

Description: The small to medium sized trochiform shell consists of seven whorls. The early whorls have flattened sides and the body whorl is a little concave with a strong cord marking its largest diameter. Ornament consists of five string-of-pearl-like spiral cords, nine of them are found on the base. There is no axial sculpture. The aperture is round with one denticle at the base of the columella. The shell is 9 mm high, 7 mm wide, and exhibits allometric growth with the early whorls forming an apical angle of about 70° which lowers to about 40° on the last one.

Remarks: *Hudledonta nicolae* is distinguished from the type species by its more tuberculate base and a tuberculate sutural cord. A species with a similarly constricted last whorl but a more rounded basal margin is described as *Trochus retectus* WHITE, 1887 from north-eastern Brazil.

Genus *Chilodonta* ÉTALLON, 1859

Type species: *Chilodonta clathrata* ÉTALLON, 1859 from the late Jurassic of France (WENZ 1938-44: fig. 651).

Description: The rounded conical shell is higher than wide with narrow whorls separated by deep sutures and large body whorl occupying 60% of shell height. Ornament consists of a reticulate pattern formed by vertical axial ribs and spiral ribs. The base is rounded and the aperture is denticulate on the inner and outer lip that forms a varix.

Chilodonta ilerdensis (VIDAL, 1921)

Plate 5, Figures 5-8

1921 *Clanculus ilerdensis* VIDAL: 101, pl. 5, figs. 5-7.

1949 *Clanculus ilerdensis* VIDAL – BATALLER: 26.
1966 *Trochus pseudoclanculosus* QUINTERO & REVILLA: 50, pl. 8, fig. 4.
1989 *Chilodonta ilerdnesis* (VIDAL) – CALZADA: 25, pl. 2, figs. 4-5.
1992 *Clanculus ilerdensis* VIDAL - - HÄNSEL: 43, pl. 1, fig. 1.

Material: 19 specimens from the Campanian of Torallola, Spain (illustrated: GPI 3918, 3920).

Description: The embryonic shell measures about 0.3 mm across. The first teleoconch whorl shows axial ribs which are continuous from one suture to the other. The fully grown shell consists of six volutions and is ornamented with equally strong spiral and axial cords. The number of spiral cords increases with age. The aperture is large and on its outer and basal lip has six equally strong denticles, on its inner lip with four denticles and columella with a strong plate. The base shows only spiral cords. The shell is 10 mm high, 6 mm wide and has an apical angle of about 60°.

Remarks: For differences to other Cretaceous members of *Chilodonta* see the remarks on *Chilodonta crespelli* below. *Monodonta ozennei* CROSSE from the Eocene of the Paris Basin has very similar columellar and parietal denticles, but a lower spire and the volutions are strongly convex.

Chilodonta crespelli BATALLER, 1959

Plate 5, Figures 3-4

1959 *Chilodonta crespelli* BATALLER: 59.
1989 *Chilodonta crespelli* BATALLER – CALZADA: 26, pl. 2, figs. 2a, b.

Material: Six specimens from the Campanian of Torallola, Spain (figured: GPI 3919).

Description: The small conical shell consists of four volutions with a carinate ornament of axial ribs crossed by five weaker spiral lines. The margin is keeled and the base is ornamented with spiral lines. The large aperture has the inner lip broadly callus covered. The columella is provided with two small, closely spaced denticles, and the outer margin carries four equally strong and equally spaced denticles. The shell is 6.5 mm high, 6.5 mm wide and has an apical angle of about 70°.

Remarks: A very similar species was described from Puerto Rico as *Chilodonta obliqua* SOHL, 1998. It differs from *Chilodonta crespelli* by the presence of wrinkles and tubercles on the callus of the inner lip. *Chilodonta jamaicaensis* SOHL, 1998 with its higher spire appears more closely related to *Chilodonta ilerdensis* described above, although the latter species has less rounded whorl-sides. The aperture of *Chilodonta marçaisi* D'ORBIGNY, 1842 from the Turonian of the Uchaux basin is smaller and the columellar lip shows only one denticle (ROMAN & MAZERAN 1913). *Chilodonta rudis* BINKHORST, 1861 from the Maastrichtian has also only four columellar denticles and shows finer carinate ornament (KAUNHOWEN 1897). *Chilodonta geslini* D'ARCHIAC as figured by WEINZETTL (1910: pl. 2, figs. 16-19) from the Upper Cretaceous of the Czech Republic is a very similar species but possesses more spiral cords. Much larger and ornamented with numerous nodular spiral cords is *Chilodonta ovallei* (PHILIPPI, 1887) from the Maastrichtian of Quiriquina, Central Chile.

Genus *Danilia* BRUSINA, 1865

Type species: *Monodonta tinei* CALZADA, 1839, Recent, from the Mediterranean (HICKMAN & MCLEAN 1990: fig. 40 H).

Description: The conical shell is higher than wide and sculptured by spirals and scurfy growthlines. The base is rounded, the aperture circular, thickened and the columella shows a strong denticle.

Danilia kosslerae n. sp.

Plate 5, Figures 9-11

Holotype: The specimen illustrated in pl. 5, figs. 9-10 (GPI 3932).
Material: Three specimens from the Campanian of Torallola, Spain (figured: GPI 3921, 3932).
Derivation of name: Named after ANNETTE KOSSLER, Hamburg, who is working on Tertiary gastropods.
Diagnosis: This high-conical *Danilia* has a large last whorl and is sculptured with rows of gutter-like spines. The columella bears one strong and one minor denticle, and there is no umbilicus.
Description: This conical shell with a pointed spire and more or less straight sides is sculptured with four spirals with strong, scurfy growthlines. The base is rounded and similarly sculptured, and there is no umbilicus. The aperture is thickened and the columella bears one strong and at least one weak denticle. The shell is 10 mm high, 8 mm wide and its last three whorls have an apical angle of about 60°.
Remarks: This species resembles modern chilodont genera like *Turcica* ADAMS, 1854, *Herpetopoma* PILSBRY, 1889, or *Euchelus*, PHILIPPI, 1847 rather than the typical Mesozoic chilodonts described above. It represents the oldest *Danilia* known to date.

Discussion: The Chilodontini made their first appearance in the Triassic with *Pseudoclanculus* (HICKMAN & MCLEAN 1990), but remained a minor group until the Cretaceous when they followed the post-Jurassic expansion of the "coraline facies" (SOHL 1987). Although members of the Chilodontini are widely distributed within the "coraline facies" and abundant in the tropical Tethyan environment of Torallola, several species are known from the cooler waters around South Africa and Chile (RENNIE 1930, PHILIPPI 1887). SOHL (1998) considered *Denticulabrum* SOHL, 1998 a member of the Trochinae, based on the presence of a basal plate similar to that of *Discotectus*. However, his figure of the earliest whorls of *Denticulabrum laevigatum* (SOHL 1998: pl. 15, fig. 1) shows axial ribs which are characteristic for the Eucyclinae. Thus, this genus may belong to the Chilodontini rather than to the Trochinae, as also indicated by the constricted aperture.

Subfamily Margaritinae STOLICZKA, 1868

According to HICKMAN & MCLEAN (1990) their Recent habitat is disjunct. Some members are found in high latitudes in cool shallow waters, others in tropical deep waters. Shell characters of the Margaritinae include smooth to predominantly spiral ornament, shells of about equal height and width, a roundish and oblique aperture and an interrupted peristome. The umbilicus may be open or closed.

Genus *Margarites* GRAY, 1847

Type species: *Margarites margarita* (MONTAGU, 1815) living off the shore of England in the eastern Atlantic Ocean (WENZ 1938-44: fig. 557).
Description: The small turbiform shell with rounded whorls and well developed sutures is smooth or has weak spiral ornament. The aperture is simple, large and rounded.

Margarites kasei n. sp.

Plate 5, Figures 16-17

Holotype: The specimen illustrated in pl. 5, figs. 16-17 (GPI 3922).
Material: Four specimens from the Campanian of Torallola, Spain.
Derivation of name: In honour of TOMOKI KASE, Tokyo, who is and has been working on Cretaceous gastropods.
Diagnosis: This *Margarites* is 10 mm wide, slightly higher and weakly sculptured by indistinct spiral lirae.
Description: The medium sized, turbiform shell has at least four convex volutions which are smooth or have weak spiral lirae. The base is covered by weak spiral lirae and the aperture is roundish. The shell is 11 mm high, 10 mm wide and has an apical angle of about 80°.
Remarks: *Margarites kowalkei* n. sp. and *Margarites nielseni* n. sp. have a lower spire as is present in *Margarites kasei*. With this feature it is also distinguished from the type species.

Margarites nielseni n. sp.

Plate 5, Figures 12-13

Holotype: The specimen illustrated in pl. 2, figs. 12-13 (GPI 3923).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after SVEN NIELSEN, Hamburg, who helped to collect this material.
Diagnosis: This *Margarites* is wider than high and sculptured with five to six weak spiral cords posteriorly and three stronger cords anteriorly on adult whorls.
Description: The medium sized, low spired, turbiform shell has three convex volutions. The first two whorls are smooth, while the body whorl is ornamented with five to six weak cords situated close to the upper suture and three stronger cords present on the outer side. The base is smooth and convex, the aperture round. The shell is 10 mm high, 12 mm wide and has an apical angle of about 110°.
Remarks: *Margarites nielseni* is distinct from *Margarites kowalkei* n. sp. by the broad spiral cords of its ornament.

Margarites kowalkei n. sp.

Plate 5, Figures 14-15

Holotype: The specimen illustrated in pl. 2, figs. 14-15 (GPI 3924).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for THORSTEN KOWALKE, Pinneberg, who helped collecting in Torallola.
Diagnosis: A *Margarites* with convex volutions, fine spiral ornamentation and deep sutures.
Description: This small, low spired conical shell consists of five convex volutions, separated by deep sutures. Its ornament consists of spiral lines that are interrupted by fine transverse grooves, which are strongest near the upper suture. The base is convex, sculptured with similar spiral lines as the spire and umbilicate. The aperture is subcircular in outline and has a heavily callused inner lip. The shell is 6 mm high, 9 mm wide and has an apical angle of about 120°.
Remarks: *Margarites kowalkei* is distinct from *Margarites nielseni* n. sp. by its fine spiral ornament. *Margarita radiulata* FORBES as figured by HOLZAPFEL

(1888: pl. 17, figs. 7-9) shows a beaded umbilical margin and, according to HICKMAN & MCLEAN (1990), is therefore better placed in *Solariella* WOOD, 1842.

Discussion: The Upper Cretaceous to Eocene genus *Periaulax* COSSMANN, 1888 was excluded from the Margaritinae by HICKMAN & MCLEAN (1990) due to its beaded umbilical margin and a late Eocene origin of the group proposed. Judging from their figures of margaritinids (HICKMAN & MCLEAN 1990 figs. 48 A-G) this margin may be smooth or spirally ornamented. The three species discovered in the Campanian of Torallola have a non-beaded umbilical margin and show a wide morphologic diversity. WENZ (1938-44) also indicated an Upper Cretaceous origin of this group with *Atira* STEWARD, 1927.

Subfamily Trochinae RAFINESQUE, 1815

Tribe Trochini RAFINESQUE, 1815

Recent Trochini live in the intertidal to shallow sublittoral, under rocks, associated with coral reefs or on algae (HICKMAN & MCLEAN 1990, HERBERT 1993). They prefer tropical or subtropical climate except for a clade that occurs in New Zealand. Apomorphic characters are an incomplete peristome due to the lack of a parietal lip and a columella extending into a pseudoumbilicus (HICKMAN & MCLEAN 1990).

Genus *Tectus* MONTFORT, 1810

Type species: *Tectus mauritianus* (GMELIN) living in the shallow Indian Ocean.
Description: The shell is conical or convex conical with whorls flattened on their sides or a little convex. The ornament consists of spiral grooves and transverse ribs. The body whorl has a rounded margin and the base is flat or slightly convex with spiral ornament. The columellar lip of the aperture is short and folded.

Tectus carinatus (QUINTERO & REVILLA, 1966)

Plate 6, Figures 1, 4

1966 *Trochus carinatus* QUINTERO & REVILLA: 49, pl. 8, fig. 2.
1989 *Tectus carinatus* (QUINTERO & REVILLA) – CALZADA: 31, pl. 1, fig. 5.
1992 *Trochus sensuyi* VIDAL – HÄNSEL: 53, pl. 1, fig. 5.

Material: Eleven specimens from the Campanian of Torallola, Spain (figured: GPI 3925).
Description: The medium sized trochiform shell has seven to eight volutions. The initial whorls are convex, later whorls are flattened on their sides, with spiral lines and transverse axial ribs in the lower half. The base is weakly convex and ornamented by spiral lines. The aperture is of lenticular shape. The shell is 15 mm high, 17 mm wide and has an apical angle of about 55°. The nacreous structure of the shell walls is still evident in some specimen when they are prepared by peel technique but the shell material is recrystallized into Fe-Calcite (HÄNSEL 1992).
Remarks: A steeper apical angle and a more rounded margin distinguishes *Tectus sensuyi* from *Tectus carinatus*. *Calliostoma sohli* CALZADA, 1988 has a lower spire but very similar ornament. This species from the Spanish Aptian is found only 150 km south-west of the Tremp basin (CALZADA 1988) and lived about 35 Million years earlier, perhaps representing a stem group representative to *Tectus carinatus.* A specimen named *Trochus bundei* D'ARCHIAC, 1847 and figured by WEINZETTL (1910: pl. 2, fig. 3) from the Czech Cenomanian appears to be closely related as well.

Tectus convallii (VIDAL, 1874)

Plate 6, Figure 14

1874 *Trochus convallii* VIDAL: 31, pl. 5, figs. 28, 28a.
1949 *Trochus convallii* VIDAL – BATALLER: 18.

Material: Two specimens from the Campanian of Torallola, Spain (figured: GPI 3926).

Description: The small trochiform shell has whorls that are ornamented with four nodular spiral cords and a fifth smooth one just above the suture. The base is concave and smooth and sutures are deep. The shell is 7 mm high, 9 mm wide and has an apical angle of about 60°.

Remarks: Similarly sculptured is *Tectus kauffmani* SOHL, 1998 from the Jamaican Maastrichtian, but that species has a higher spire. *Tectus carinatus* possesses denticulate spirals in contrast to the smooth spirals present on *Tectus convallii.*

Tectus sensuyi (VIDAL, 1921)

Plate 6, Figures 2, 5

1921 *Trochus sensuyi* VIDAL: 100, pl. 6, figs. 19-20.
1949 *Trochus sensuyi* VIDAL – BATALLER: 24.
1989 *Tectus sensuyi* (VIDAL) – CALZADA: 32, pl. 1, fig. 3.

Material: Five specimens from the Campanian of Torallola, Spain (figured: GPI 3927).

Description: The slender, trochiform shell consists of eight or more whorls. Volutions are ornamented by short, transverse ribs in the lower part of the whorl. The base is smooth and convex with a rounded edge with the whorl flanks. There is no umbilicus. The shell is 16 mm high, 13 mm wide and has an apical angle of about 52°.

Remarks: *Tectus carinatus* has a similar ornament but in contrast to *Tectus sensuyi* a sharp basal edge. A related Eocene species may be *Trochus novoatus* DESHAYES, 1866 (pl. 59, figs. 5-6) from the Paris Basin, but this species has fewer ribs per whorl.

Tectus revillai (BATALLER, 1959)

Plate 6, Figures 3, 6

1959 *Trochus revillai* BATALLER: 57.
1989 *Tectus revillai* (BATALLER) – CALZADA: 32, pl. 1, fig. 5.
1992 *Trochus revillai* BATALLER – HÄNSEL: 51, pl. 1, fig. 4.

Material: 19 specimens from the Campanian of Torallola, Spain (figured: GPI 3928).

Description: This moderate to large trochiform shell consists of at least eight volutions, is sculptured with three nodular cords and the sutures are marked by a sharp ridge. The base is flat to concave, shows spiral lirae and growthlines, and the basal edge is very sharp. Its aperture is narrow and lenticular and the shell is 30 mm high, 33 mm wide and has an apical angle of about 60°. Nacreous shell-structure is still evident in some specimen but is recrystallised to Fe-Calcite (HÄNSEL 1992).

Tectus almelai BATALLER, 1959

Plate 6, Figures 7, 10

1959 *Trochus almelai* BATALLER: 58.
1989 *Sensuitrochus almelai* (BATALLER) – CALZADA: 30, pl. 1, fig. 6.
1992 sp.indet. HÄNSEL: 55, pl. 1, fig. 6.

Material: Nine specimens from the Campanian of Torallola, Spain (figured: GPI 3929).

Description: The medium to large sized trochiform shell consists of six volutions. The whorls are flattened at their sides and bear a sharp edge above the suture. Ornament consists of four nodular spiral cords, the first covering the suture, and the third weaker than the others. Transverse growth lines are visible on the spire and base. The base is weakly convex and smooth. The shell is 18 mm high, 26 mm wide and has an apical angle of about 80°. Nacre may be preserved in its original aragonitic composition in some specimen (HÄNSEL 1992).

Remarks: This species was considered by CALZADA (1989) as a member of *Sensuitrochus*, a genus introduced by QUINTERO & REVILLA (1966) for a sinistrally coiled archaeogastropod from the same locality. There are two objections on this treatment: (1) *Sensuitrochus* was introduced for sinistrally coiled shells, *Tectus almelai* is dextrally coiled, and (2) *Sensuitrochus* is considered synonymous with *Hamusina* GEMMELLARO, 1878 (see below).

Tectus quinteroi n. sp.

Plate 6, Figures 8, 11

Holotype: The specimen illustrated in pl. 6, figs. 8, 11 (GPI 3930).

Material: Four specimens from the Campanian of Torallola, Spain.

Derivation of name: In honour of INDALECIO QUINTERO, who described several molluscs from Torallola in 1966.

Diagnosis: This *Tectus* has early whorls with a smaller apical angle than present in later whorls and the flattened flanks have indistinct sutures and fine spiral liration.

Description: The medium sized trochiform shell consists of six whorls with flattened sides. The flanks are steeper on the early volutions than on later ones and the sutures are almost invisible. Ornament consists of fine spiral lirae. The base is flat with fine spiral lines. The aperture is of lenticular shape with angular outline. There is no umbilicus. One specimen shows remains of colour patterns consisting of dark brown elongate spots which appear on the last one and a half volutions close to the lower margin. They are about 1-2 mm long and have a distance of 2-4 mm from each other. The shell is 11 mm high, 16 mm wide and has an apical angle of about 80°.

Remarks: The smooth shell of *Tectus quinteroi* distinguishes this species clearly from the other members of *Tectus* described here which have sculptured whorls.

Genus *Discotectus* FAVRE, 1913

Type species: *Discotectus massolongoi* (GEMMELLARO, 1911) from the Upper Jurassic of France (WENZ 1938-44: fig. 686).

Description. The shell is composed of many whorls of little height, is conical in shape with the early whorls forming a concave flank while the later whorls have straight sides. The base is flat and the basal margin sharp, and there is no umbilicus. The aperture is angular, wider than high, and bears a basal disc or plate.

Remarks: The geologic range of this genus was given as Middle Jurassic to Lower Cretaceous by WENZ (1938-44) and HICKMAN & MCLEAN (1990). The latter authors characterised the genus as "an abundant element in some Mesozoic Tethyan carbonate-platform fauna" (HICKMAN & MCLEAN 1990: 95).

Discotectus pallarsensis (QUINTERO & REVILLA, 1966)

Plate 6, Figure 13

1966 *Trochus pallarsensis* QUINTERO & REVILLA: 49, pl. 7, fig. 10.
1989 *Discotectus pallarsensis* (QUINTERO & REVILLA) – CALZADA: 24, pl. 2, figs. 8a, b.
1992 *Trochus pallarsensis* QUINTERO & REVILLA – HÄNSEL: 66, pl. 2, fig. 12.

Material: 22 specimens from the Campanian of Torallola, Spain (figured: GPI 3933, 3936).

Description: The protoconch measures about 0.27 mm across. The small trochiform adult shell consists of about six volutions which are ornamented with four tuberculate spiral cords. The base is flat and smooth. A thick tongue of callus extends from the base of the columella forming a basal plate. The aperture is strongly oblique with about 50-55° inclination to the coiling axis. The early whorls increase in diameter more rapidly than later whorls which results in a change of the apical angle. Some specimen were demonstrated by HÄNSEL (1992) to have nacre in original composition in their shell walls. One specimen shows grey colour pattern on the last two whorls. They are formed by about 1mm wide transverse stripes that cover the entire height of the whorl. The shell is 8 mm high, 9 mm wide and the earlier whorls have an apical angle of about 60°; the last whorl increases only little in width, compared to the penultimate whorl.

Remarks: This species resembles the Jurassic type species but shows nodular spiral cords instead of smooth ones and it has fewer whorls. *Discotectus pallarsensis* shows convex sides in contrast to the straight ones of *Discotectus gavalai* described below. Its closest relative appears to be the Jurassic *Discotectus crassoplicatus* ÉTALLON (in: LORIOL 1886, pl. 22, figs. 1-3). None of the species of *Discotectus* described by SOHL (1998) from the Caribbean seems to have closer relations to *Discotectus pallarsensis*, they all exhibit finer spiral sculpture compared to the coarsely beaded cords of *Discotectus pallarsensis*.

Discotectus gavalai (BATALLER, 1949)

Plate 6, Figures 9, 12, 15

1949 *Trochus gavalai* BATALLER: 20.
1992 *Trochus gavalai* BATALLER – HÄNSEL: 57, pl. 2, fig. 7.

Material: About 100 specimens from the Campanian of Torallola, Spain (figured: GPI 3934 with colour patterns, and GPI 3935).

Description: The small to medium sized trochiform shell consists of six volutions. Whorls are flattened and ornamented with three nodular ridges and a strong, smooth and sharp ridge just above the suture. This suture is sometimes marked by a tuberculate cord. The base is flat, smooth and bulging near the aperture. The outer lip of the aperture is oblique, attached to the penultimate whorl for a quarter of a volution. Some specimen still show colour-patterns of dark brown axial stripes of about 2-3 mm width which are separated from each other by 1-2 mm wide colourless zones. The shell is 13 mm high, 16 mm wide and has an apical angle of about 65°. In some specimens, nacre was demonstrable in its original aragonitic state (HÄNSEL 1992).

Remarks: *Discotectus gavalai* is distinct from *Discotectus pallarsensis* by its lower conical spire and sharp sutural ridge. *Discotectus scotti* SOHL, 1998 from the Puerto Rico Campanian/Maastrichtian shows a very similar ornamentation but has a higher spire and the basal keel in not as strongly developed as in *Discotectus gavalai*. *Discotectus buneli* (D'ARCHIAC) figured by WEINZETTL (1910: pl. 2, fig. 1) from the Czech Cretaceous is similar in shape but the lower sutural keel is beaded and the base spirally ornamented.

Genus *Thoristella* IREDALE, 1915

Type species: *Trochus (Thoristella) chathamensis* HUTTON, 1873 which lives near the Chatham Islands, New Zealand.
Description: The small conical shell has whorls which are convex to concave, and shouldered. The basal margin is keeled, the base is umbilicate and little convex and sculptured with fine spirals.
Remarks: *Thoristella* is distinct from *Trochus* by larger cephalic dentacles and the lack of umbilical spiral cords (MARSHALL 1998). This author also indicated the earliest fossil record of this genus as Miocene.

Thoristella marshalli n. sp.

Plate 7, Figures 1-3

Holotype: The specimen illustrated in pl. 7, figs. 1-3 (GPI 3937).
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of BRUCE MARSHALL, who contributed to our knowledge of Recent gastropods from Australia and New Zealand.
Diagnosis: The trochiform shell is a little wider than high and has straight to slightly concave sides. A carinate pattern forms the ornament.
Description: The small trochiform shell consists of six whorls with straight to concave sides and a fine carinate pattern. The aperture is almost rectangular. The base is convex, with fine spiral lirae and with an open umbilicus. The shell is 7 mm high, 9 mm wide and has an apical angle of about 80°.
Remarks: The type species differs by a smaller umbilicus but otherwise closely resembles *Thoristella marshalli*. Even though *Thoristella* belongs to a New Zealandian cool-water clade which is regarded as generally distinct by HICKMAN & MCLEAN (1990), it could well be related to the species described above.
The Recent *Astele* (*Callistele*) COTTON & GODFREY, 1935 of the Calliostominae THIELE, 1924 from Australia also produces similar shells but it has a protoconch with a honeycomb-pattern that has not been found in sediment samples from the Puimanyons Olisthostrom.

Discussion: The Trochinae are abundant in the fauna of Torallola with eight species assigned to *Tectus* and two to *Discotectus*. But the species discussed here are difficult to connect with younger species, except in the case of *Thoristella marshalli* n. sp. which is similar to members of a rather independent clade from around New Zealand (HICKMAN & MCLEAN 1990, MARSHALL 1998). *Jujubinus* has often been cited to have Recent as well as late Cretaceous members. This assumption is only based on COSSMANN's (1918: 291) assignment of a single Turonian species from India which he described as sinistral. However, the placement of a sinistral species within *Jujubinus* is highly inappropriate. Leaving out this questionable species, *Jujubinus* can be traced back in time only to the Eocene.

Tribe Gibbulini STOLICZKA, 1868

Genus *Amphigibbula* n. gen.

Type species: *Amphigibbula vidali* (COSSMANN, 1915) from the Campanian of Torallola, Spain.

Diagnosis: The shells are initially high-conical and keeled, later they develop a wider apical angel, become more sturdy and are sculptured with beaded spirals. The umbilicus is bordered by a beaded margin and the aperture is roundish.

Derivation of name: A combination of *Amphitrochus* and *Gibbula*, two similar genera.

Remarks: *Amphigibbula vidali* (COSSMANN, 1915) was originally placed by COSSMANN (1915: 155-157) to his new genus *Semisolarium*. He assigned this genus among *Straparollus* MONTFORT, 1810, *Pseudomalaxis* FISCHER, 1883, and *Discohelix* DUNKER, 1848 to the Euomphalidae DE KONINCK, 1881. This family was evaluated by BANDEL (1988) and BANDEL & FRÝDA (1998) and represents a polyphyletic group with members of several gastropod subclasses. WENZ (1938-44) tentatively placed *Semisolarium* in the Omalaxidae within the Cerithioidea FÉRUSSAC, 1819. However, the protoconch type places this species within the Archaeogastropoda. Its early shell resembles that of *Amphitrochus*, a genus which was assigned to the Angariinae by KNIGHT et al. (1960) and HICKMAN & MCLEAN (1990). But *Amphigibbula vidali* lacks the broad spines of Recent *Angaria* and its sturdy, later whorls are more similar to *Gibbula* RISSO, 1826.

Amphigibbula vidali (COSSMANN, 1915)

Plate 7, Figures 4-7

1915 *Semisolarium vidali* COSSMANN: 157, pl. 6, figs. 26-27.
1921 *Semisolarium vidali* COSSMANN - VIDAL: 102, pl. 1, figs. 12-16.
1949 *Semisolarium vidali* COSSMANN - BATALLER: 35.
1992 *Semisolarium vidali* COSSMANN – HÄNSEL: 83-86, fig. 24.

Material: 80 specimens from the Campanian of Torallola, Spain (figured: GPI 3941, 3947).

Description: The protoconch measures 0.35 mm across, the first teleoconch whorl shows two ridges of which the second is obscured by the next whorl. The first ridge becomes tuberculate after about one volution. The adult shell is conical; the first four and a half whorls are straight-sided with a nodular keel close to the lower suture. On later whorls this ornamentation merges into three tuberculate spiral cords, the third one is jagged on the body whorl. The bottom shows growthlines and spiral lines and a large umbilicus with denticulate margin. The aperture is round and the shell is 11 mm high and 14 mm wide. Aragonite was still evident in a thin section (HÄNSEL 1992) but in a peel, no nacreous structure was found.

Subfamily Solariellinae POWELL, 1951

Shells are usually smaller than 10 mm, have rounded whorls with impressed sutures, the umbilicus is usually open and has a beaded margin (HICKMAN & MCLEAN 1990). Their distribution in the Paleogene is described as low-latitude but extra-Tethyan by HICKMAN & MCLEAN (1990). These authors noted that recent members of this genus usually live offshore on unconsolidated sediment and feed on detritus.

Genus *Solariella* WOOD, 1842

Type species: *Solariella maculata* WOOD, 1842 from the Pliocene of Suffolk, England (WENZ 1938-44: fig. 579).

Description: This genus contains small shells with more or less convex volutions, groove-like sutures, spiral cords and transverse growthlines. The last whorl is large, the base convex or keeled, the aperture is circular and the peristome is uninterrupted.

Solariella montsecana (VIDAL, 1921)

Plate 7, Figures 8-10

1921 *Margarita montsecana* VIDAL: 100, pl. 6, figs. 12-14.
1925 *Margarita montsecana* VIDAL – COSSMANN: 289
1949 *Margarita montsecana* VIDAL - BATALLER: 26.
1992 *Margarita montsecana* VIDAL – HÄNSEL: 59, pl. 2, fig. 8.

Material: 80 specimens from the Campanian of Torallola, Spain (figured: GPI 3938, 3939).

Description: The embryonic shell measures 0.4 mm across. The teleoconch-ornament starts with three spiral cords, the first turns into a tuberculate shoulder after about one whorl, while the two lower ones disappear. The adult shell is small, turbiniform and consists of eight convex volutions separated by deep sutures. The spiral cords become more nodular or smooth on the last whorls. The base is convex, shows strong growth lines and an umbilicus with denticulate margin. The aperture is round with an inclination of about 20° to the coiling axis. The fully grown shell is 12 mm high, 11 mm wide and has an apical angle of about 70°. Nacre is still preserved in its original aragonitic state in some specimen (HÄNSEL 1992).

Remarks: The Mexican *Solariella mexcalensis* described below shows a very similar early ornamentation, but *Solariella montsecana* differs by having deeper sutures, less numerous spirals and a base sculptured only with few spirals, while in *Solariella mexcalensis* the base is wholly covered with beaded spirals.Very similar adult shells are present in *Calliomphalus* and its subgenus *Planolateralus* but the two species figured by DOCKERY (1993) show that their teleoconch ornament starts with axial ribs in contrast to the spiral cords of *Solariella montsecana.* Similar adult shells are described from central Europe with *Turbo retifer* BÖHM, 1885, *Turbo zekelii* BINKHORST, 1861 and *Turbo rimosus* BINKHORST, 1861 (see HOLZAPFEL 1888 and KAUNHOWEN 1897). Their early ornament is unknown and thus their taxonomic position remains unknown.

Solariella cossmanni VIDAL, 1921

Plate 8, Figure 1

1921 *Solariella cossmanni* VIDAL: 100, pl. 6, fig. 17-18.
1949 *Solariella cossmanni* VIDAL – BATALLER: 27.

Material: Four specimens from the Campanian of Torallola, Spain (figured: GPI 3940).

Description: The small turbiniform shell consists of four to five volutions. Sutures are weakly impressed and ornament consists of fine spiral lirae which is also present on the base. The umbilicus is small and accompanied by a denticulate margin. The aperture is round and 45° inclined. The shell is 10 mm high, 8 mm wide and has an apical angle of about 60°.

Remarks: This species of *Solariella* possesses an exceptionally high spire for the genus.

Solariella mexcalensis (PERRILLIAT, VEGA & CORONA, 2000)

Plate 10, Figures 3-4

2000 *Calliomphalus (Planolateralus) mexcalensis* PERRILLIAT, VEGA & CORONA: 8, figs. 5.7-5.11.

Material: More than 40 specimens from the Maastrichtian of Temalac, Mexico.

Description: The embryonic part is smooth and measures about 0.23 mm across. The teleoconch ornament starts with six spiral cords and intimations of axial ribs. After one and half volutions the axial ribs are more dominant than the spiral cords and the first, fourth and sixth spiral cords are strongest. On later whorls the ornament turns into a nodular pattern. The sutures are deep, the base is concave and shows dense, nodular spiral cords and an umbilicus with a beaded margin. The aperture subcircular. The figured shell is 6 mm high and 6 mm wide.

Subgenus *Suavotrochus* DALL, 1924

Type species: *Suavotrochus lubrica* (DALL, 1881) that lives in the Atlantic Ocean off the Florida Keys (ABBOTT 1974: fig. 290).

Description: The small and conical shells have a smooth surface except for a carinate subsutural belt. This carina may spread over the entire last whorl.

Remarks: *Suavotrochus* shows a radula typical for the Solariellinae (HICKMAN & MCLEAN 1990). These authors also recognised a shift in the distribution of *Solariella* from low-latitude but extra-Tethyan in the Paleogene to higher latitudes in the Neogene. Recent *Suavotrochus* lives in deep waters (360-1500 m according to ABBOTT 1974) in the Gulf of Mexico.

Suavotrochus ponsi n. sp.

Plate 8, Figures 2-3

Holotype: The specimen illustrated in pl. 5, fig. 3 (GPI 3942).

Paratype: The specimen illustrated in pl. 5, fig. 2 (GPI 3943).

Material: Ten specimens from the Campanian of Torallola, Spain.

Derivation of name: In honour of the Spanish paleontologist JOSE MARIA PONS, Barcelona.

Diagnosis: This *Suavotrochus* has smooth early whorls with a subsutural belt of cancellate sculpture. This belt becomes wider during growth and the cancellate pattern covers the whole last whorl.

Description: The embryonic shell measures 0.3 mm across. The early whorls of the teleoconch have a smooth and strong keel that becomes nodular after 1.5 volutions. The adult shell is small, trochiform, composed of seven convex volutions with a carinate belt in their upper portion and the remainder of the whorl smooth. A carinate pattern appears on the last whorl and continues all over the base. The shells are up to 8 mm high, 6 mm wide and its sides are slightly convex; the last whorl has an apical angle of about 60°.

Remarks: This species is distinct from the type species by its carinate body whorl. A similar beaded subsutural belt is also present in *Turbo scrobiculatus* REUSS, 1845 from the Late Cretaceous of Kutschlin, Bohemia. But this species is, in addition, ornamented with a carina on early whorls (REUSS 1845-46), which in *Suavotrochus ponsi* is only present on the last whorl.

Discussion: *Periaulax* and *Solariella* are considered to represent Late Cretaceous members of the Solariellinae (HICKMAN & MCLEAN 1990), also a species of *Suavotrochus* is reported here. Late Cretaceous shells of *Solariella*, *Calliomphalus* and *Planolateralus* are difficult to distinguish based on their adult shell alone. Members of *Calliomphalus* and *Planolateralus* possess axial ribs on the first teleoconch whorl (DOCKERY 1993) and are therefore regarded as Calliotropini (HICKMAN & MCLEAN 1990, BANDEL 1993a). Species belonging to *Solariella,* in contrast, show spiral cords as initial teleoconch sculpture which later merge into a carinate pattern (see HERBERT 1987, WARÉN 1993). Although such an ontogenetic change of ornament can also be observed on Recent *Thoristella* (MARSHALL 1998), this transition is not as well timed and recognizable as in the case of *Solariella*, where it appears after the first whorl. Recent members of the Solariellinae and Calliotropini are both known to live on soft sediment in deeper waters (HERBERT 1987, HICKMAN & MCLEAN 1990). HICKMAN & MCLEAN (1990) postulated that the appearance and radiation of both groups has taken place parallel to each other in clastic facies outside the tropical Tethyan carbonate belt. This new data indicates that *Solariella* was also present in the Cretaceous tropics. The earliest known shells of the *Calliomphalus*-*Solariella* type are *Calliomphalus aptiensis* KASE, 1984 from the Aptian of Japan and *Trochus vivaplane* (NICKLÉS) from the Spanish Aptian/Albian (BATALLER 1949).

Subfamily Umboniinae ADAMS & ADAMS, 1854

Tribe Monileini HICKMAN & MCLEAN, 1990

Genus *Ethalia* ADAMS & ADAMS, 1854

Type species: *Ethalia guamensis* (QUOY & GAIMARD, 1834) that lives in the Indian Ocean around the Philippines (HICKMAN & MCLEAN 1990: pl. 82, fig. B).
Description: The thick, low spired shells have minor spiral ornamentation or a smooth surface. Whorls are little convex, the basal margin and the base are rounded and the umbilicus is partly or totally covered with callus.
Remarks: HERBERT (1993) described Recent South African *Ethalia* as semi-infaunal, burrowing gastropods that are deposit-feeders.

Ethalia vinxae n. sp.

Plate 8, Figures 4, 6, 8

Holotype: The specimen illustrated in pl. 8, figs. 4, 6, 8 (GPI 3944).
Material: Four specimens from the Campanian of Torallola, Spain.
Derivation of name: For EVA VINX who helped to photograph some of the species described here in a very good way.
Diagnosis: A smooth *Ethalia* which is twice as wide as high and has a moderate umbilical denticle.
Description: The medium sized, low spired shell consists of five rounded volutions sculptured only with growth lines. The aperture is roundish with 50° inclination, and its parietal side is callus covered. The umbilicus is deep and bears a strong denticle on its apertural side. The shell is 7 mm high, 15 mm wide and has an apical angle of about 125°.
Remarks: *Ethalia vinxae* is distinct from the type species that has been figured by WENZ (1938-44: fig. 727) and HICKMAN & MCLEAN (1990) by its broader apical angle, flatter base and the lack of a parietal callus that extends across the umbilicus.

Tribe Umboniini ADAMS & ADAMS, 1854

Remarks: Recent *Umbonium* LINK, 1807 lives as a filter-feeders on soft bottom in shallow, commonly intertidal water (HERBERT 1992).

Genus *Protorotella* MAKIYAMA, 1925

Type species: *Protorotella yuantaniensis* MAKIYAMA, 1925 from the Miocene of the Yuyanotani Province, Yamashiro/Japan (WENZ 1938-44: fig. 729).
Description: The low conical shells have straight sides, a sharp basal margin and a rounded base. There is no umbilicus but the umbilical region is callus covered.

Protorotella herberti n. sp.

Plate 8, Figures 5, 7, 9

1992 sp. indet. HÄNSEL: 47, pl. 1, fig. 3.

Holotype: The specimen illustrated in pl. 5, fig. 5, 7, 9 (GPI 3945).
Material: Five specimens from the Campanian of Torallola, Spain.
Derivation of name: In honour of DAVID HERBERT, Pietermaritzburg, who contributed to the knowledge of Recent South African gastropods, among them species similar to the one described here.
Diagnosis: This *Protorotella* is about twice as wide as high, the initial whorls having steeper sides than later ones, and there is no umbilicus.
Description: The small to medium sized, low spired, trochiform shell consists of five whorls with flattened and smooth sides. The initial whorls are steeper than the later ones. The aperture is lenticular and angular. There is no umbilicus. The shell is 9 mm, 18 mm wide and has an apical angle of about 110°. Nacre is still preserved in its original aragonitic composition forming the bulk of the shell wall in some specimen (HÄNSEL 1992).

Discussion: HERBERT (1992) suggested little callus-deposit in the umbilicus to be a primitive state, whereas large callus-masses in the umbilical region were more derived. This coincides with the meagre callus-deposit of *Ethalia vinxae* n. sp. which is formed by an umbilical denticle. Although HICKMAN & MCLEAN (1990) mentioned a Late Cretaceous *Umbonium* from Oman, they only recognised the Oligocene *Conominolia* FINLEY, 1927 as earliest Umboniinae. SOHL (1998) considered *Camitia* (*Micatia*) SOHL, 1998 from the Jamaican Maastrichtian an umboniid and suggested a Cretaceous derivation of the group. However, this treatment is doubtful due to the basal plate in its aperture, which is quite unusual for Umboniinae. BANDEL (1993a) connected the Umboniinae with Paleozoic and Triassic Anomphalidae WENZ, 1938 which WENZ (1938-44: 249) characterized as *Umbonium*-like. Based on this assumption, the quantity of umbilical callus deposits does not indicate the state of development, since callus deposits are widespread in these earlier forms.

Family Skeneidae CLARK, 1851

Numerous small shelled Archaeogastropoda living today are unified in this family. FRETTER & GRAHAM (1977) indicated that the Skeneidae are detrivours.

Genus *Skenea* FLEMING, 1825

Type species: *Skenea serpuloides* (MONTAGU), living off England (WENZ 1938-44: fig. 745).

Description: The small, low conical shells with convex volutions show deep sutures, a wide umbilicus and a round aperture.

Skenea wareni n. sp.

Plate 3, Figure 15

Holotype: The specimen illustrated in pl. 2, fig. 15 (GPI 3980).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: In honour of Anders Warén.
Diagnosis: The shell is about as wide as high, its body whorl large and the umbilicus bordered by a smooth ridge.
Description: The embryonic part measures 0.2 mm across, the shell is composed of three smooth volutions, has a round and reinforced aperture. The umbilicus is small and its margin is marked by a ridge. The shell is 1.7 mm high.
Remarks: This species is distinct from *Skenea sutura* n. sp. by a lower spire, the reinforced aperture, and its keeled umbilicus, the umbilicus of *Skenea sutura* has a beaded margin. A similar Recent species is *Skenea trochoides* (Friele see Warén 1991: fig. 3G).

Skenea sutura n. sp.

Plate 3, Figure 16

Holotype: The specimen illustrated in pl. 3, fig. 16 (GPI 3981).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after its subsutural groove.
Diagnosis: A *Skenea* which is higher than wide and shows a subsutural rim.
Description: The embryonic part measures 0.25 mm across, the teleoconch is made of four smooth and convex volutions with a subsutural groove, have a round aperture and a small umbilicus with a beaded margin. The shell is 1.8 mm wide and 2.2 mm high.

Skenea torallensis n. sp.

Plate 9, Figures 1

Holotype: The specimen illustrated in pl. 9, fig. 1 (GPI 3982).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after the village of Toralla, to the North of the outcrops where this new species was found.
Diagnosis: This *Skenea* has rimmed sutures and an oblique aperture.
Description: The small, low spired and umbilical shell consists of two and a half smooth volutions. The sutures are little incised and show a weak rim below. The aperture is roundish, oblique and a little reinforced. The embryonic shell measures 0.2 mm across, the whole shell is 2.1 mm wide and 1.5 mm high.
Remarks: Very similar in shape is *Skenea buitronae* n. sp. described below but it differs by lacking an umbilicus.

Skenea buitronae n. sp.

Plate 10, Figure 5

Holotype: The specimen illustrated in pl. 10, fig. 5.
Material: One specimen from the Maastrichtian of Temalac, Mexico.

Derivation of name: Named after BLANCA BUITRON, Mexico City, who is also working on Cretaceous molluscs.
Diagnosis: This small *Skenea* has a low spire and a reflected inner lip.
Description: The protoconch measures about 0.21 mm across and the adult shell is about 2.5 mm wide and 1.7 mm high. The spire is low, the volutions smooth and little convex and separated by low sutures. The fully grown shell consists of three whorls. The aperture is ovate and has a reflected inner lip.

Discussion: The four small and smooth species resembling modern skeneids are assigned to *Skenea*, although this taxonomic treatment is far from being save. The modern Skeneidae are not well known and probably represent a polyphyletic group. MARSHALL (1988) described several distinct radulae among the members of this family. WARÉN (1993) indicated anatomical characters diagnostic for *Skenea* to be absent from other skeneid genera. In their revision of Trochoidean gastropods HICKMAN & MCLEAN (1990) summarised problems concerning skeneid classification and considered also their own treatment to be 'highly provisional'. They traced the fossil record of this group back only to the lower Miocene. BANDEL (1993a) illustrated similar shells from the Triassic which would be placed within the Skeneidae if they had lived today.

Family uncertain

Genus *Torallochus* n. gen.

Type species: *Torallochus torallochus* n. gen. n. sp. from the Campanian of Torallola, Spain.
Diagnosis: Small, pupoid shell with flat, discoidal early whorls which are sculptured with strong axial ribs, thickened at the periphery. Later whorls are angular and keeled.
Derivation of name: A *Trochus*-like shell from Torallola, Spain.

Torallochus torallochus n. sp.

Plate 9, Figures 4-6

Holotype: The specimen illustrated in pl. 9, figs. 4-6 (GPI 3983).
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: This species represents the type of its genus.
Diagnosis: As for the genus.
Description: The protoconch measures about 0.25 mm across and is made of about three quarters of a whorl. The teleoconch consists of six whorls which are initially planispiral, but the last three whorls are turriform; the last whorls has, if at all, a very slow increase in diameter. The first teleoconch whorl has about ten spiny ribs on the periphery, later whorls are angular and have a spiny, median keel and a subsutural row of tubercles. The base is rounded and smooth and the shell is about 5 mm high and 4 mm wide.

Torallochus pupiformis n. sp.

Plate 9, Figures 7-8

Holotype: The specimen illustrated in pl. 9, figs. 7-8 (GPI 3984).
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for its pupiform shell.

Diagnosis: This *Torallochus* has strong axial ribs which are subsuturally constricted.

Description: Four whorls of the pupiform shell are preserved. They are sculptured with strong axial ribs which are spiny when they cross the median keel and are subsuturally constricted to a row of tubercles. The shell is 1.7 mm high and 1.2 mm wide.

Remarks: This species is smaller than the type and also has stronger axial ribs.

Torallochus discus n. sp.

Plate 9, Figures 2-3, 11

Holotype: The specimen illustrated in pl. 9, figs. 2-3, 11 (GPI 3985).

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: Of the three species of *Torallochus* described here, this is the most disk-shaped one.

Diagnosis: The discoidal shell has 16 radial ribs on the first teleoconch-whorl and the whorl's flanks are convex and smooth.

Description: the protoconch is made of ¾ of a whorl and measures 0.2 mm across. The teleoconch-whorls are flat and smooth on top, have radial ribs on the periphery and are smooth and convex on the outer flank. Only the last whorl shows turriform coiling. The shell has a diameter of 2.4 mm.

Remarks: A discoidal shell with similar sculpture and a protoconch of similar shape was described as *Discohelix* sp. by SCHRÖDER (1995).

Discussion: The new genus *Torallochus* holds Archaeogastropoda of quite unique, pupoid shape. I am not aware of any similar Recent taxa. A shell resembling *Torallochus*' flat, early whorls was illustrated by SCHRÖDER (1995: pl. 1, figs. 5-8) from the Callovian of Poland, and assigned to *Discohelix*. Due to its rounded base, this classification is doubted here, although no better alternative can be offered.

Superfamily Cirroidea COSSMANN, 1916

The Cirroidea are a group of archaeogastropods with sinistrally coiled shells which have a dextrally coiled embryonic shell and also the first whorl may be dextrally coiled. This group can be traced back into the Paleozoic (BANDEL 1993b).

Family Cirridae COSSMANN, 1916

Subfamily Hesperocirrinae HAAS, 1953

Genus *Hamusina* GEMMELLARO, 1878

Type species: *Turbo bertheloti* ORBIGNY, 1850 from the Upper Liassic of France.

Description: The high conical shell has flattened whorl flanks and a sharp basal margin. Ornamentation consists of nodes and spiral threads connected to oblique growthlines. The base is almost flat or weakly rounded and has no open umbilicus.

Remarks: *Sensuitrochus* QUINTERO & REVILLA, 1966 was introduced for the sinistrally coiled species described below, and sinistral coiling was the major diagnostic difference which led QUINTERO & REVILLA (1966) to introduced this genus. However, CALZADA (1989) modified the diagnosis to include a dextrally coiled species from Torallola. This treatment is not accepted here. The additional species of CALZADA (1989) is considered a member of *Tectus* MONTFORT, 1810 and *Sensuitrochus* is synonymised with *Hamusina* because *H. ferreri* (QUINTERO & REVILLA, 1966), the type species of *Sensuitrochus*, fits well into the diagnosis of

Hamusina. Also *Shikamacirrus* KASE, 1984 is synonymised with *Hamusina* because the type species *Shikamacirrus nipponicus* KASE, 1984 fits into the diagnosis of *Hamusina*.

Hamusina ferreri **(QUINTERO & REVILLA, 1966)**

Plate 9, Figures 9-10

1966 *Sensuitrochus ferreri* QUINTERO & REVILLA: 51, pl. 8, figs. 6-7.
1989 *Sensuitrochus ferreri* QUINTERO & REVILLA – CALZADA: 29, pl. 1, fig. 2.
1992 *Sensuitrochus ferreri* QUINTERO & REVILLA – HÄNSEL: 63, pl. 2, fig. 10.
1993 *Sensuitrochus ferreri* QUINTERO & REVILLA – BANDEL: 62.

Material: Ten specimen from the Campanian of Torallola, Spain (figured: GPI 3986).
Description: This sinistrally coiled, trochiform shell is made of eight or more whorls. Its ornament consists of six strong, string-of-pearl-like cords and three weak cords above between and below the two strong cords in the middle. The two lowermost cords are a little elevated and form a clear lower margin for the whorl. The aperture is rhomboid, the base is sculptured with numerous weak spiral lines and there is no umbilicus. The shell is 15 mm high and 16 mm wide. Nacre is still demonstrable in its original aragonitic state in some specimen (HÄNSEL 1992).
Remarks: *Hamusina radovesnicensis* (WEINZETTL 1910: pl. 2, figs. 31-32) is a very closely related species that possesses only four small tuberculate cords, and the thick collar above the lower suture is not as strongly developed as in *Hamusina ferreri*. Another similar species is *Hamusina nipponicus*, but it has coarser spirals on spire and base. *Hamusina kahrsi* BANDEL, 1993 from the Kassenberg Cenomanian of Germany has deeper sutures and its whorls are angular at its base.

Discussion: The here redescribed *Hamusina ferreri* represents according to BANDEL (1993b) the youngest species of the Cirroidea. The same species was also found in presumably Maastrichtian strata near St. Engracia about 5 km south-west of Torallola (own obs.). Thus the Cirroidea apparently reached the end of the Mesozoic era.

Subclass Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Marine Neritimorpha usually provide their shell with a thick calcitic outer layer. Where a plankton-feeding larva is developed, its shell has a very characteristic shape: most of the preceding whorl is covered by the next, so that only very little can be seen of the spire. Additionally, the larval shell shows growthlines.

Superfamily Neritopsoidea RAFINESQUE, 1815

Within the Neritimopha, members of the superfamily Neritopsoidea do not resorb their inner shell walls (COSSMANN 1925, WENZ 1938-44). Cretaceous to modern species belong to only one family, the Neritopsidae GRAY, 1847. Their globular shell has a protruding spire with large last whorl. The inner lip of the aperture is broad and smooth. Their characteristic calcareous operculum is angular with two attachment scars of the retractor muscle on their inside.
Neritopsoidea had quite a number of genera in the late Paleozoic and the early Mesozoic (KNIGHT et al. 1960), but since then they declined steadily. Only two known living species of *Neritopsis* GRATELOUP, 1832 have been reported. According to BATTEN (1984) this genus can be derived from the Permian *Trachydomia*, and according to WENZ (1938-44) and KNIGHT et al. (1960), it exists

since Jurassic times. Also COSSMANN (1925) noted Triassic representatives. With begin of the Tertiary only representatives of *Neritopsis* have survived in the family.

Family Neritopsidae RAFINESQUE, 1815

Genus *Neritopsis* GRATELOUP, 1832

Type species: *Neritopsis moniliformis* GRATELOUP, 1832 from the Miocene of the Aquitaine, according to KNIGHT et al. (1960), and *N. radula* LINNÉ, 1757 according to COSSMANN (1925) and WENZ (1938-44).
Description: The medium sized shell with upright spire has a globular last whorl with evenly convex flanks. Sculpture consists of thick granulated spiral cords that may be intersected by axial ribs and form reticulate ornament. The orbicular aperture has a moderately thickened concave inner lip that has a quadrangular depression at is middle into which the operculum is fitted that is trapezoid and with quadrangular projection at its adaxial side.
Remarks: The genus *Hayamia* KASE, 1980 with the type *Hayamia rex* KASE, 1980 from the Aptian of Japan (KASE & MAEDA 1980) differs from *Neritopsis* by having an elliptical operculum and no groove at its inner lip.
Neritopsis radula from the Indo-Pacific and *N. atlantica* SARASUA, 1973 from the Caribbean Sea have been considered "living fossils" by BATTEN (1984). According to HAYAMI & KASE (1993) *N. radula* occurs commonly in sublittoral caves in southern Japan.

Neritopsis ilerdensis VIDAL, 1921

Plate 11, Figures 1-3

1921 *Neritopsis ilerdensis* VIDAL:101, pl. 6, figs. 1-2.

Material: ten specimens from the Campanian of Torallola, Spain.
Description: The about 14 mm high and 14 mm wide shell has a low but erect spire with two whorls of the teleoconch separated by deep sutures and rapid increase in whorl width. Its last whorl is globular with evenly convex flanks. The aperture has an evenly rounded outer lip and also a convex inner lip and columella. The inner lip is moderately thickened forming a concave callus band and has a quadrangular depression at the middle of its columellar edge. Sculpture consists of about 30 spiral cords that are intersected by fine collabral growth increments. The umbilicus is closed up to a narrow slit. Five shells are from Torallola, some of which have been worn on the beach prior to their emplacement.
Remarks: The Recent *Neritopsis radula* is larger (about 20 mm high), has fewer spiral ribs and a less developed inner lip-callus. *Neritopsis tanohatensis* KASE, 1984 differs by being larger, perhaps also broader. Otherwise both species are very similar in their ornament of about 30 spiral ribs and features of the inner lip of the aperture. *Neritopsis ornata* D'ORBIGNY, 1842 from the mid-Cretaceous of Europe is also similar and may even be the same species.
According to KASE (1984) there are the Mesozoic species *Neritopsis sulcosa* D'ARCHIAC, 1843 from the Bathonian of England and France, *Neritopsis semiplicata* BRÖSAMLEN, 1902 from the late Jurassic of southern Germany, *Neritopsis renauxiana* D'ORBIGNY, 1842, *Neritopsis delphinula* D'ORBIGNY, 1842 from the early Cretaceous of France, *Neritopsis ornata* D'ORBIGNY, 1842 from the Cenomanian of France, *Neritopsis costulata* (RÖMER, 1841) from the Turonian of Germany. He added to these the species *Neritopsis tanohatensis* KASE, 1984 and *Neritopsis japonica* KASE, 1984 from the early Cretaceous of Japan.

Superfamily Neritoidea RAFINESQUE, 1815

Family Neritidae RAFINESQUE, 1815

Genus *Dontostoma* KLEIN, 1753, in HERRMANNSEN, 1845

Type species: *Nerita polita* LINNÉ, 1758 from the tropical Indo-Pacific.
Description: The shell has a low spire and no spiral sculpture but rather a collabral sculpture consisting of closely spaced wrinkle-like ribs which are slightly reflected away from the outer lip. The outer lip is weakly dented within or smooth and the columellar lip bears three to five teeth in its central part which is slightly concave. The callus of the inner lip is smooth or weakly transversely wrinkled. The outside of the operculum is smooth and has a raised ridged or granulated rim.
Remarks: Spiral ornament is present in *Nerita* and absent in *Dontostoma*. What is considered as *Nerita (Linnerita)* VERMEIJ, 1984 had already been distinguished from *Nerita (Nerita)* as *Dontostoma* KLEIN, 1753, in HERRMANNSEN, 1845. Also *Neodesmieria* based on *Nerita sanctistephani* COSSMANN & PEYROT, 1917 from the Oligocene of the Aquitaine could represent a species of *Dontostoma* since it has only axial ornament.

Dontostoma bergadana (VIDAL, 1921)

Plate 11, Figures 4-6

1921 *Nerita bergadana* VIDAL: pl. 6, figs. 15-16.

Material: Two specimens from the Campanian of Torallola, Spain
Description: The rounded shell of about 9 mm in height and 13 mm in width has a low spire and consists of about one and a half whorls of the teleoconch. Ornament consists of fine growth lines and irregular large dots. The inner lip is callus covered, slightly tuberculated and has five teeth on its convex columellar margin. The umbilical side of the aperture is smooth and rounded. On the inner side of the outer lip there are about seven denticles.
Remarks: The Recent type species *Dontostoma polita* differs from *Dontostoma bergadana* by its few, small denticles which are of different size and are concentrated in the centre of the inner lip.

Dontostoma? sp.

Plate 10, Figures 6-7

Material: More than ten specimens from the Maastrichtian of Temalac, Mexico.
Description: The shell is small, low spired and smooth and has a large last whorl with a semicircular aperture bearing four plications on the inner lip callus. The largest specimen is 5 mm wide and has an aperture that is 4 mm high.

Genus *Otostoma* D'ARCHIAC, 1859

Type species: According to KASE (1984) and KNIGHT et al (1960) the type is *Otostoma rugosa* (HOENINGHAUS, 1865) from the European Maastrichtian (=*O. rugosa* (ROEMER, 1841)), but according to WENZ (1938-44: fig. 1020) the genotype is *Otostoma ponticus* ARCHIAC, 1859 from Anatolia with an evenly dented inner lip. This later species is very badly illustrated and documented.
Description: The globular shell has a depressed spire and rapidly expanding, more or less unicarinate whorls. The characteristic ornament consists of folded axial ribs which are connected to a peripheral spiral ridge and fine spiral lirae. The

semilunular aperture is provided with an expanded and thickened inner lip which on its columellar edge bears strong subequal denticles.

Remarks: *Nerita* has spiral ribs only, and *Dontostoma* is smooth, while *Otostoma* has an ornamental pattern of axial ribs crossed by spiral elements. WENZ (1938-44) regarded *Lyosoma* WHITE, 1830 and *Damesia* HOLZAPFEL, 1888 as subgenera of *Otostoma*. In the latter case this choice was not correct since *Damesia* represents a *Nerita*-shaped allogastropod and thus belongs to the subclass Heterostropha and not to the Neritimorpha. This was demonstrated by DOCKERY (1993) who illustrated the sinistrally coiled protoconch of *Damesia*.

According to CUSHING WOODS & SAUL (1986), *Otostoma* occurs from the Aptian to the Paleocene. But the Paleocene species considered by these authors actually differ from *Otostoma* in ornament and in inner lip dentition. Also the small *Otostoma* sp. from the Paleocene of Greenland (KOLLMANN & PEEL 1983: fig. 40) is problematic as its axial ornament is merely more than growthlines, while Cretaceous *Otostoma* developed strong sculpture right from the beginning of the teleoconch.

Otostoma vidali n. sp.

Plate 11, Figures 7-9

Holotype: The specimen illustrated in pl. 11, figs. 7-9.

Material: 15 specimens from the Campanian of Torallola, Spain.

Derivation of name: In honour of LUIS MARIANO VIDAL who described many gastropods from the Cretaceous of Catalonia.

Diagnosis: The up to 20 mm wide neritiform shell has a flattened base and almost round outline seen from the apical side. It has a strongly noted peripheral angulation and a change from fine radial ribs in early teleoconch whorls to coarser ribs in later teleoconch whorls. The callus of the inner lip has a straight dented columellar margin with about eight denticles decreasing in size from posterior to anterior direction.

Description: The thick-walled shell is as wide as high and consists of about four whorls of the teleoconch. Two and a half of these are ornamented by fine axial ribs and succeeding whorls develop spiral ribs that form tubercles with the axial ribs. The peripheral spiral rib produces high tubercles with the axial ribs forming a peripheral tuberculate edge that varies somewhat in different individuals. Some also form a low depression above and below that peripheral edge, other do not. Below the periphery the body whorl is regularly rounded and ornamented by several tuberculated and regularly spaced spiral cords. The begin in the second whorl. The callus of the inner lip is flat and slightly concave toward its anterior portion. The denticles on the columellar edge are relatively large and may differ in number from seven to nine. They are inclined and decrease in size, with the second or third posterior one usually the largest.

Remarks: *Otostoma japonicum* (NAGAO, 1934) is similar to *O. vidali* but differs by having a denticle in the outer lip and by a convex columellar edge of the inner lip. *Otostoma trempense* n. sp. differs by ornament, teeth on the columellar edge and rounded periphery also in the adult stage. Both species have lived close to each other in the same shore environment.

Otostoma trempense n. sp.

Plate 11, Figures 10-12

Holotype: The specimen illustrated in pl. 11, figs. 10-12.

Material: 30 specimens from the Campanian of Torallola, Spain.
Derivation of name: An *Otostoma* from the Tremp Basin.
Diagnosis: The up to 20 mm wide neritiform shell with flattened base and almost round outline seen from the apical side has a rounded periphery and a similar pattern of radial ribs on early and late teleoconch whorls. The callus of the inner lip has a straight dented columellar margin with about seven denticles with central ones the largest.
Description: The thick-walled shell is as wide as high and consists of about three whorls of the teleoconch reaching a size of about 24 mm in height and width. Ornamented is by fine axial ribs which increase in size with shell growth and in the late whorl have fine collabral ribs between the larger ones. Spiral ribs are present only at the base and form fine and rounded tubercules with the axial ribs. The periphery as well as the sides are rounded. The callus of the inner lip is flat and slightly concave toward its anterior portion covering much of the flatted base. The denticles on the straight or slightly convex columellar edge are relatively large and may differ in number from seven to ten. They are upright and decrease in size from the centre to the margins.
Remarks: In contrast to *Otostoma japonicum* (NAGAO, 1934) the dentition of the inner lip is stronger. The outer tubercle is not developed and the peripheral angulation is less expressed. *Otostoma marcouana* from the Albian of Texas is quite similar with *O. trempense* but seems to have more basal spiral ribs. It has weak axial ribs as are found in *O. coralina* (STOLICZKA, 1868) from India (BANDEL, in press, pl. 1, fig. 6), while *Semineritina apparata* (CRAGIN, 1893) from the same strata in Texas may be very similar to *O. trempense* but details of the inner lip of the aperture and of the ornament of the base appear to be missing (AKERS & AKERS 1996, fig. 31). This is also the case with a species called *Semineritina apparata* by ALLISON (1955) from the Mid-Cretaceous of Baja California, Mexico.

***Otostoma* sp.**

Plate 10, Figures 8-10; Plate 11, Figures 13-15

2000 *Nerita* cf. *divaricata* D'ORBIGNY – PERRILLIAT, VEGA & CORONA: 9, figs. 5.15, 5.16.

Material: Five specimens from the Maastrichtian of Temalac, Mexico.
Description: A *Nerita*-like shell with strong ribs that are transverse on the upper side and crenulated at the flanks. The inner lip is heavily callused, straight and bears five denticles of about equal strength. The outer lip is convex. The largest shell is 3 mm high and about 4 mm wide.
Remarks: The studied individuals represent juvenile shells. In order to compare them with species of *Otostoma* from other localities, fully grown shells would have to be found.

Genus *Neritoplica* OPPENHEIM, 1892

Type species: *Neritoplica uniplicata* (SOWERBY) (=*Neritoplica globulus* (DESHAYES)) from the upper Paleocene of the Paris Basin (WENZ 1938-44: fig. 1031).
Description: The smooth neritinid shell has an oblique, semicircular aperture that has a strong fold on the posterior columellar edge of the inner lip which continues into the shell's interior. Some weak denticles may be present below.
Remarks: OPPENHEIM (1892: 774) noted that Recent neritinids never show a strong columellar fold like *Neritoplica*. He regarded this feature as primitive and

considered *Neritoplica* as a link between Recent *Nerita*, the Neritininae and Cretaceous *Deianira*.

Neritoplica torallolensis n. sp.

Plate 12, Figures 1-3

Holotype: The specimen illustrated in pl. 12, figs. 1-3
Material: ten specimens from the Campanian of Torallola, Spain.
Derivation of name: Named according to its type locality Torallola.
Diagnosis: This *Neritoplica* has one strong denticle on the otherwise smooth inner lip, and it is keeled at the periphery.
Description: The shell consists of the protoconch and about three whorls of the teleoconch which increase in width quite rapidly. The spherical shell is about 15 mm wide and high. Ornament consists only of fine growth lines and a colour pattern of dark and light dots and lines of zigzagged stripes. The apical portion of the shell is usually corroded as if the nine individuals studied had lived in the intertidal zone exposed to the activity of corrosive endolithic algae. The spire is low and the oblique aperture consists of a broad, flattened inner lip callus with a columellar edge bearing one large plication in its posterior portion.

Neritoplica trochispira n. sp.

Plate 12, Figure 4

Holotype: The specimen illustrated in pl. 12, fig. 4.
Material: The holotype from the Campanian of Torallola, Spain.
Derivation of name: Named according to its trochiform spire.
Diagnosis: This *Neritoplica* has one major tooth and two minor ones below it on the concave inner lip of the aperture, and the spire is relatively high.
Description: The teleoconch consists of about three volutions which increase rapidly in size. The spire is low, trochiform and the body whorl is sculptured with fine, transverse growthlines. The inner lip callus is smooth and possesses a strong denticle on its posterior side. The shell is 7 mm high.
Remarks: This new species is distinct from *Neritoplica torallolensis* by its trochiform spire and the lack of a peripheral ridge.

Genus *Neritoptyx* OPPENHEIM, 1892

Type species: *Nerita goldfussii* KEFERSTEIN, 1829 (non ZEKELI, 1852) (OPPENHEIM 1892: 773, pl. 36, fig. 5).
Description: The teleoconch is ornamented by spiral ribs crossed by collabral growth elements in a regular way and the aperture has one columellar fold on the upper part of the inner lip.
Remarks: While the inner lip of the aperture has a columellar fold as is also the case in *Neritoplica*, the teleoconch bears an ornament of spiral ribs crossed by collabral ones as may be found in *Nerita*. Probably due to its granulated spiral ribs WENZ (1938-44) who had followed COSSMANN (1925) in this regard, assumed that *Neritoplica goldfussii* is a member of *Neritopsis* which is not the case as pointed out by KOWALKE & BANDEL (1996). They documented that *Neritoptyx* dissolves its internal wall and is, therefore, a member of the Neritidae.

Neritoptyx reticulirata (DOCKERY, 1993)

Plate 12, Figures 5-6

1993 *Nerita reticulirata* DOCKERY: 43, pl. 1, figs. 18-20; pl. 2, figs. 1-2.

Material: ten specimens from the Coffee Sand member of the Ripley Formation, USA.

Description: The shells have a smooth protoconch and a strongly lirate teleoconch with a single denticle on the upper part of the inner lip. The smooth protoconch of spherical shape consists of several whorls overlapping onto each other strongly and measures about 0.15 mm in diameter. The early teleoconch in contrast to the later shell is almost smooth with fine, closely spaced growth laminations. A first spiral lira is present here but is covered by the succeeding whorl. Spiral lirae appear abruptly on the teleoconch after two basically smooth whorls of early teleoconch. These lirae number 20 or more in the adult and form a reticulate pattern with fine simple growth laminae crossing them. The aperture is semicircular and the inner lip septum is bordered by a denticle at the terminus of an internal lira at the base of the inner lip. On the specimen studied here another smaller and lower denticle is seen further up on the inner lip. The shell is up to 4 mm high.

Remarks: This American species resembles the type but differs with its lacking juvenile sculpture and the presence of an additional denticle in the aperture.

Family Pileolidae, n. fam.

Diagnosis: The Pileolidae contain limpet shells with a protoconch like that of Recent *Nerita*. Ornamentation consists of dominant radial ribs and the aperture is semilunular to sickle-shaped and may be dented.

Remarks: Other neritimorph limpets like the species of the Phenacolepadidae have the inner lip totally reduced. In the *Septaria*-relation of the Neritinidae the shell is usually smooth and the aperture is wider. Members of both these groups are only known from the Neogene to recent, while those of the Pileolidae are not known from Jurassic and Cretaceous strata. The Triassic Pseudorthonychiidae have a more horn-like shape and also a wider aperture without the walls of the inner lip preserved.

Limpet-like shells have repeatedly formed among the Neritimorpha within different lineages (BANDEL 1997, BANDEL & FRÝDA 1999, FRÝDA & BANDEL 1997). *Pileolus* arose in the Jurassic and apparently disappeared latest during the Cretaceous/Tertiary mass extinction (WENZ 1938-44, SOHL 1987). *Pileolus* and relation derived from *Nerita*-like ancestors in fully marine development of reef and beach environment (MUSTAFA & BANDEL 1992).

Constituting genera: The family contains *Pileolus* SOWERBY, 1823 and its subgenus *Salihia* MUSTAFA & BANDEL, 1992. WENZ (1938-44) included in *Pileolus* the subgenera *Pileolus*, *Gargania* GUISCARD, 1856, *Velatella* WHITE, 1879, and *Tomostoma* DESHAYES, 1823 which have not been investigated.

Genus *Pileolus* SOWERBY, 1823

Type species: *Pileolus plicatus* SOWERBY, 1823 from the Bathonian of England (WENZ 1938-44: fig. 1011).

Description: A limpet shell with subcentral apex and concave base. The aperture is half-moon shaped. The outer lip is closed around the margin of the base. The inner lip protrudes as a broad septum with a smooth or dentate margin and reduces the aperture to a lunate slit. The outer shell layer is calcitic, the inner one consists of aragonitic crossed lamellar structure. In the subgenus *Pileolus (Pileolus)* the

patelliform shell is wider than high, has a broadly oval basis which is entirely formed by the outer lip that is closed around the margin. The apex lies in acentric position. The inner lip forms a broad septum and the aperture is slit-shaped and simple. The entire interior of the shell is taken up by a single cavity in which all former walls except for the outer ones have been dissolved.
Remarks: The type of the subgenus *Pileolus (Salihia)* MUSTAFA & BANDEL, 1992 represents a large, up to 50 mm wide and 40 mm high patelliform shell that is broader than high and has a slightly convex outline, a broadly oval basis. From the central apex strong ribs radiate and are crossed by concentric growth lines. The aperture is crescent shaped and constricted by two massive swellings on the inner side of the outer lip.

Pileolus cozatli n. sp.

Plate 10, Figures 11-13; Plate 12, Figures 10-11

Holotype: The specimen figured at pl. 10, fig. 12.
Material: Three specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named after R. CÓZATL, for the pleasant time during the field work.
Diagnosis: A *Pileolus* with radial ribs and a narrow aperture with denticulate margin.
Description: The protoconch is smooth, roundish, 0.75 mm long, 0.55 mm wide and 0.45 mm high. The adult shell is patelliform, small, and is ornamented by 33 radial ribs and fine growthlines. In the roundish base, the aperture is sickle shaped with a convex inner lip. Its outer side is bordered by two beaded ridges and a small, round hole at the front. The inner side shows a denticulate margin. A semi-circular beaded ridge is situated opposite the aperture, bordering the flattened shelf of the inner lip callus. The largest specimen is 3 mm long, 2.5 mm wide, and 1.5 mm high.
Remarks: This new species is distinct from the type by its dented apertural margin. Similar apertures but also with non-dented outer margins are present in two species from the Cenomanian of Saxony, Germany, *Pileolus koninckianus* DE RYCKHOLT, 1874 and *Pileolus orbignyi* GEINITZ, 1871 (GEINITZ 1871-75). A new species of *Pileolus* was reported by SOHL (1987: fig. 3) from the Maastrichtian of Puerto Rico, which lacks the small apertural hole of *Pileolus cozatli*.

Pileolus ponsi n. sp.

Plate 12, Figures 7-9

Holotype: The specimen illustrated in pl. 12, figs. 7-9.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for JOSE MARIA PONS, Barcelona.
Diagnosis: The small *Pileolus* has a ridge and groove pattern on the shelf formed by the inner lip. The aperture is narrow and crescentic and bordered by the inner lip with denticles. The juvenile shell is smooth and only later radial ribs appear. The shell has a diameter of 6 mm.

Discussion: Cretaceous neritimorphs of the marine and brackish environment have in part a clearly distinct fashion, in part they represent the lineages which appear to be ancestral to the Tertiary and modern species. Among those with a strictly Mesozoic touch the Pileolidae and the *Otostoma*-group can be named, exclusively Cretaceous are apparently the rotelliform Deianiridae. Within the Neritidae, Cretaceous representatives of the modern *Dontostoma* can be documented, *Neritoptyx* and *Neritoplica* are seen as intermediating or ancestral to the Neritinidae.

Subclass Caenogastropoda COX, 1960

The shells built by caenogastropod larvae are coiled in the same direction as the adult shell, their shape ranges from almost flat via conical to turriform. Often, but not always, it terminates in a larval hook.

Order Cerithiimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Campaniloidea DOUVILLÉ, 1904

Tracing the history of the largest snail that ever creeped on earth has kept scientists engaged for more than a century. Early workers classified *Campanile* FISCHER, 1884 as cerithiid (LAMARCK 1804, COSSMANN, 1906, WENZ 1938-44) due to similarities of shell ornament and shape. WENZ (1938-44) united *Campanile* and *Plesiotrochus* FISCHER, 1878 among a few other doubtful genera in the subfamily Campanilinae DOUVILLÉ, 1904 within the Cerithiidae FÉRRUSAC, 1819. DELPEY (1941) presented the first consistent phylogenetic treatment of this group. *Diatinostoma* COSSMANN, 1905, *Ditretus* PIETTE, 1874, and *Pyrazus* MONTFORT, 1810 were discussed as ancestral or related genera. DELPEY, however, considered *Campanile* to be a descendant of *Nerinea* DESHAYES, 1827 because of the occurrence of columellar plates. For a comprehensive outline of earlier works on *Campanile* see HOUBRICK (1981).

Modern biological studies on the spermatozoa (HEALY 1986b), its anatomy (HOUBRICK 1981, 1989) and the ultrastructure of the osphradium (HASZPRUNAR 1992) revealed that Recent *Campanile symbolicum* IREDALE, 1917 is quite unique among the Caenogastropoda. It has been placed in its own superfamily, the Campaniloidea (HOUBRICK 1989). But there has always been some doubt about this treatment. The Eocene type species *Campanile giganteum* LAMARCK, 1804 possesses two columellar plates (JUNG 1987, pl. 3, fig. 2) while the Recent species shows a smooth columella (HOUBRICK 1981, fig. 2f, g). Although BOUSSAC (1912), WRIGLEY (1940), DELPEY (1941) and HOUBRICK (1981) discussed this matter and concluded that columellar plates alone do not allow generic separation of the Recent and the type species, satisfactory evidence is still lacking.

Plesiotrochus is anatomically so distinct from other Cerithioidea that HOUBRICK (1990) erected an own family, the Plesiotrochidae HOUBRICK, 1990. This family has later been transferred to the Campaniloidea by HEALY (1993) according to similarities he found in their spermatozoans, confirming the earlier placement of WENZ (1938-44). However, PONDER & LINDBERG (1997) doubted this treatment, and BANDEL (1991c) noted that the larval shell of *Plesiotrochus* resembles that of *Bittium* LEACH, 1847 which represents an undoubted cerithioidean.

HOUBRICK (1989) raised the Campanilidae to superfamily rank in order to exclude them from the Cerithioideans by reason of anatomical differences. However, HOUBRICK did not present a diagnosis of this superfamily. Since HEALY (1993) included the Plesiotrochidae with small and rather conical shells, the protoconch as seen on *Campanile houbricki* n. sp. is proposed here to be the unifying shell-character. However, this character can only be used in species with a planktotrophic larva but not in cases of lecithotrophic development.

Family Campanilidae DOUVILLÉ, 1904

The shell is elongate and turreted, has straight-sided or slightly convex whorls and moderately incised sutures. The growth lines are sinuous and sculpture consists of sutural cords and nodes that are frequently absent or weak on later whorls. Its body whorl is truncate, the aperture narrow and fusiform, possesses an anterior canal of moderate length, and the columella is smooth or plaited. The larval shell (if developed) is smooth and globular, consists of two to two and a half volutions, is 0.3 to 0.4 mm high and wide, and terminates in a strong varix.

Genus *Campanile* FISCHER, 1884

Type species: *Campanile giganteum* LAMARCK, 1804 from the Eocene of the Paris Basin.

Description: The turriform shell has numerous low volutions. The whorls are sculptured with a broad, tuberculate subsutural collar, spiral cords which may be beaded, and a cover of fine incised striae. Columellar and parietal plates may occur and the ornament may change on the last whorls.

Remarks: Members of the Potamididae ADAMS & ADAMS, 1854 are known to produce similar shells. An example is ”*Tympanotonus*” *hungaricus* ZITTEL (see SZÖTS 1953, pl. 3, figs. 9-18) from the Eocene of Gant, Hungary. However, most Potamididae are restricted to intertidal, often brackish or hypersaline environments (HOUBRICK 1991), whereas Recent *Campanile symbolicum* lives in the subtidal (HOUBRICK 1989). According to DONOVAN & BLISSETT (1998) also the Eocene *Campanile* lived in a fully marine subtidal environment. The protoconch of potamidids with a planktotrophic larva have an ornament characterised by two spiral cords (KOWALKE 1998, BANDEL & KOWALKE 1999) which contrasts with the smooth protoconch of the Campaniloidea.

Campanile houbricki n. sp.

Plate 13, Figures 1-5

Holotype: IGM 7806, pl. 13, fig. 4.

Paratype: IGM 7807, pl. 13, fig. 3; IGM 7808, pl. 13, fig. 5.

Material: Several specimens from the Maastrichtian of Temalac, Mexico (IGM 7806-7810).

Derivation of name: In honour of RICHARD S. HOUBRICK who worked on the biology of the Recent *Campanile*.

Diagnosis: This small and slender *Campanile* shows one plate low on the columella which is dissolved further inside the shell. The ornament bears two minor spirals below the broad, subsutural belt.

Description: The protoconch is smooth and round, consists of two convex volutions, and terminates with a strong varix that is flaring in its lower half. The embryonic part composing half a whorl measures about 0.14 mm across. The entire protoconch is 0.33 mm high and 0.35 mm wide with one and a half whorls formed by the larva. The early teleoconch is sculptured with two finely beaded spiral keels. The adult shell is straight-sided, shows a broad, beaded subsutural belt and two minor spirals below. The base is smooth and one plication is present low on the columella. This plate is dissolved in the interior of the shell. The size of a fully grown shell may have been about 60 mm in height, and the largest fragment has a diameter of 11 mm.

Remarks: Although many workers regard *Campanile* as a predominantly Tertiary genus (HOUBRICK 1981, HASZPRUNAR 1992), palaeontologists have described numerous Late Cretaceous species. Distinction between these species is based mainly on the number of minor spiral cords below the subsutural belt, and the number of columellar plates. The oldest species known is probably represented by *Campanile bircki* (GEINITZ, 1875) from the Cenomanian or Turonian of Saxony in Germany. It has two columellar plates in its aperture and three minor and relatively broad spirals in its ornament. *Campanile cossmanni* VIDAL, 1917 as described below appears to be closely related to this species. It is characterised by two equally strong and beaded minor spirals in its ornament, and two columellar plates and two parietal plates in its aperture. Also *Campanile inauguratum* (STOLICZKA, 1868) is closely related. It has minor spirals that are variable in number and strength and two columellar plates. The newly collected specimen from Serbia shows one parietal plate. Within this relation but somewhat doubtful may be *Campanile hispidium* (ZEKELI, 1852) with only one minor spiral as ornament. While ZEKELI (1852) did not mention columellar plates in his original description, DELPEY (1941) mentioned two to be present in this species. *Campanile houbricki* n. sp. has a sculpture that resembles that of *Campanile inauguratum* but it differs from the latter by its smooth interior. *C. houbricki* is also exceptionally small for the genus.

Campanile? *carezi* VIDAL, 1917 and *Campanile*? *regens* PETHÖ, 1906 show a distinct sculpture of a broad, axially ribbed belt in the upper half of the whorl, as well as columellar and parietal plates. They resemble *Campanile* in general shape and in size but the specimens are not well enough preserved to decide whether they belong to *Campanile* or even the Campanilidae or represent members of another taxon. However, due to their general similarity they are here tentatively placed within *Campanile*.

WHITE (1887) described some species named *Nerinaea buarquiana* WHITE, 1887, *Nerinaea inaugurata* STOLICZKA, 1868 and *Nerinaea sagrittana* WHITE, 1887 from the late Cretaceous of Brazil of which WRIGLEY (1940) suggested that they rather represent members of *Campanile* and actually lived in the Eocene.

Campanile cossmanni VIDAL, 1917

Plate 13, Figures 10-11

1917 *Campanile cossmanni* VIDAL: 6, pl. 3, figs. 2-4.
1949 *Campanile cossmanni* VIDAL – BATALLER: 110.

Material: Eight specimens from the Campanian of Torallola, Spain (GPI 3948).

Description: There are two columellar plates in the aperture of which the upper one is much weaker than the second, and two parietal plates of which the outer one is sometimes interrupted. Both the parietal and the weak columellar plates disappear about half a volution before they reach the aperture. The whorls are ornamented with a strongly tuberculate, subsutural collar, two beaded cords below it, and a third smooth ridge that is often obscured by the following whorls. The diameter of the largest specimen is 38 mm.

Campanile inauguratum (STOLICZKA, 1868)

Plate 13, Figure 7

1868 *Cerithium inauguratum* STOLICZKA: 193, pl. 15, figs.19-20.
1902 *Cerithium* sp. cf. *inauguratum* STOLICZKA – QUAAS: 262, pl. 26, figs. 27a, b.
1922 *Campanile inauguratum* (STOLICZKA) – COTTREAU: 61, pl. 8, figs. 3-5.

Material: One specimen from Čerević stream in the Serbian Fruška Gora mountains (GPI 3949).

Description: The large, high spired shell has low whorls and is ornamented with a tuberculate, subsutural belt with fine incised striae and four spiral cords of different strength below. In a cross section, two columellar and one parietal plate are visible. Its largest diameter is 45 mm.

Campanile? *regens* PETHÖ, 1906

Plate 13, Figure 6

1906 *Campanile regens* – PETHÖ: 161, pl. 10, fig. 12.

Material: One specimen from Čerević stream in the Serbian Fruška Gora mountains (GPI 3950).

Description: The large, high spired shell consists of more than twelve low volutions and is sculptured with axial ribs that are strongest near the upper suture. The columella bears two plates and the aperture ends in a basal canal. The figured specimen is 140 mm high and 60 mm in diameter.

Remarks: *Campanile*? *carezi* is distinct by its three parietal plates while *Campanile*? *regens* shows only one.

Campanile? *carezi* VIDAL, 1917

Plate 13, Figures 8-9

1917 *Campanile carezi* VIDAL: 7, pl. 3, fig. 6.
1949 *Campanile carezi* VIDAL – BATALLER: 109-110.

Material: One specimen from the Campanian of Torallola, Spain (GPI 3951).

Description: The large, high spired shell consists of numerous low volutions which are sculptured with axial ribs that thin out on the lower half of the whorl. The columella shows three parietal plates, the first at the outer margin of the whorl, the second and strongest in the centre and a last weak one near the columella. All three plates disappear at least half a volution before they reach the aperture. The damaged specimen is 74 mm high and 54 mm wide.

Genus *Metacerithium* COSSMANN, 1906

Type species: *Cerithium trimonile* MICHELIN, 1838 from the Aptian/Albian of France.

Description: The small to medium sized, high spired shell has volutions with three beaded spiral cords, of which the central one may be weak. Its base is a little rounded and the anterior canal is straight (WENZ 1938-44).

Remarks: ABBASS (1973, p. 133, pl. 4, figs. 2, 3, 7, 8, 10) described and illustrated well preserved specimens of the type species. Accordingly, opisthocline axial ribs are present on the earliest whorl and a subsutural band appears from the fourth whorl onwards. The ornament then gradually becomes tuberculate. This coincides with the development of ornamentation observed on the new species described below. The new species has the protoconch preserved, while its shape and ornament is not known from the type. Due to these similarities of the teleoconchs and the *Campanile*-like protoconch of the new species, *Metacerithium* is herein regarded to belong to the Campanilidae. *Metacerithium* is distinct from *Campanile* by its strong, beaded spiral ridge near the base of the volutions.

Metacerithium ponsi n. sp.

Plate 14, Figures 1-4

Holotype: GPI 3953, pl. 14, figs. 1, 3.
Paratype: GPI 3952, pl. 14, fig. 4.
Material. Three specimens from the Campanian of Torallola, Spain (GPI 3952-3954).
Derivation of name: Named after JOSÉ MARIA PONS, Barcelona, for his introduction to the geology of the Tremp Basin and the locality of Torallola.
Diagnosis: This *Metacerithium* has two tuberculate spiral cords and a smooth base.
Description: The protoconch is smooth and roundish, is made of two and a half volutions and terminates at a varix. It is 0.25 mm high and 0.33 mm wide. The teleoconch is slender turriform. The first eight whorls have a subsutural row of tubercles and a strong, beaded spiral ridge near the base. The aperture has a straight columella without plates and its anterior siphonal canal is constricted and short. The holotype is 6.4 mm high and the paratype is 9 mm high.
Remarks: *Metacerithium ponsi* has more denticles per whorl on the basal keel than are present in the type species *Metacerithium trimonile*.

Discussion: DELPEY (1941) suggested *Diatinostoma* and *Ditretus* (see COSSMANN 1906, pl. 5, figs. 1-10) to represent possible ancestors of *Campanile*. The former possesses axial ribs which are strongest near the upper suture and fine spiral lines below; this may be regarded as similarities to *Campanile*. The latter shows a strong, nodular spiral cord near the base of the whorls resembling those of young *Metacerithium*. However, the protoconch morphology of *Diatinostoma* and *Ditretus* are still unknown, and thus their relations to the Campanilidae remain in doubt. DELPEY (1941) also discussed a possible relation of *Pyrazus* to *Campanile*. However, *Pyrazus* is based on a Recent Australian species which belongs to the Batillariidae HOUBRICK, 1991 (BEESLY et al. 1998).
Nerineans possess columellar and parietal plates but often also show labral plates, unknown from *Campanile*. Since several nerinean species have been documented with a heterostrophic, sinistrally coiled protoconch (BIGOT 1896, BANDEL 1993c, KOWALKE & BANDEL 1996), this family is regarded to belong to the Allogastropoda (Heterostropha). However, their adult shells can be quite similar to those of the Campanilidae.
Another problematic genus often assigned to the Campanilidae is *Diozoptyxis* COSSMANN, 1896. As VAUGHAN (1988) pointed out, COSSMANN (1896) and D'ORBIGNY (1843) independently named two different species as *Nerinea monilifera*. COSSMANN's species, which he defined as the type species of *Diozoptyxis,* bears three internal plates and an open umbilicus, whereas D'ORBIGNY's only shows one plate and no umbilicus. VAUGHAN (1988) suggested to assign COSSMANNs *Nerinea monilifera* to a new species *Diotoptyxis monilifera*. According to this treatment, *Diozoptyxis* contains umbilicate shells with three internal plates. It is therefore well distinguished from *Campanile* and could very well represent a member of the Nerineidae ZITTEL, 1873.
HOUBRICK (1989) included *Dirocerithium* WOODRING & STENZEL, 1959 from the Panamese Eocene in the Campanilidae based on WOODRING's (1959) comments on similarities of *Dirocerithium* and *Campanile gomphoceras* BAYAN, 1870. In fact, WOODRING never mentioned *Campanile* in this context but included "*Campanile" gomphoceras* in *Bellatara* STRAND, 1928 and both genera *Dirocerithium* and *Bellatara* are placed within the Cerithiidae. The early ornament of *Dirocerithium wechesense* STENZEL (in WOODRING 1959, pl. 24, fig. 14) consists of axial ribs

crossed by three to four spiral cords and resembles that of *Cerithium* rather than *Campanile*.

The new species of *Metacerithium* possesses a protoconch similar to that of *Campanile houbricki*. Its teleoconch sculpture resembles that of the early shell of *Metacerithium trimonile* which was well described and figured by ABBASS (1973) from the English Aptian, and represents the type species of this genus. Because of its protoconchmorphology, *Metacerithium* is transferred to the Campanilidae.

This raises the question whether the other genera constituting the Metacerithiinae also belong to the Campanilidae. *Microschiza belgica* D'ARCHIAC, 1841 was defined by COSSMANN (1906) as the type species of *Cimolithium* COSSMANN, 1906 which is thought to be a member of the Metacerithiinae (WENZ 1938-44). The same species was considered by DELPEY (1941) as a possible early *Campanile*. Upper Cretaceous species of *Teretrina* COSSMANN, 1912, members of the Mathildidae DALL, 1889 (Heterostropha) resemble *Bathraspira* COSSMANN, 1906, another member of the Metacerithiinae. A specimen of *Bathraspira* sp. with heterostrophic protoconch and two teleoconch whorls was illustrated by KOLLMANN (1982, pl. 8, figs. 3-5). But KOLLMANN was not sure whether his assignment was correct due to some apertural features of *Bathraspira*. His data also indicate that this genus may not belong to the *Metacerithium*-relation. However, neither the protoconchs of the type species of *Cimolithium* or *Bathraspira* are known, nor those of any further metacerithiinid, therefore their placement remains uncertain.

Only a few Neogene fossils of *Plesiotrochus* are known (LADD 1972). However, comparing the early teleoconch sculpture of *Metacerithium* and *Plesiotrochus* (pl. 14, figs. 5, 6), *Metacerithium* may be considered as possible stem group representative of the Plesiotrochidae.

Protoconchs similar to those of *Campanile houbricki* can be found in the Triassic *Settsassia* BANDEL, 1992 (BANDEL 1992, pl. 11, fig. 4) and *Angularia* KOKEN, 1892 (BANDEL 1993c, pl. 14, fig. 4), on the upper Carboniferous *Palaeostylus* MANSAY, 1914 and *Orthonema* MEEK & WORTHEN, 1861 (NÜTZEL 1998, pls. 32-33), and *Stegocoelia* (YOO 1988, figs. 71, 79; 1994, pl. 15). But relations of these genera to *Campanile* and *Metacerithium* are still open.

Superfamily Cerithioidea FÉRRUSAC, 1819

Family Vermetidae RAFINESQUE, 1815

Vermetids are sessile marine gastropods with a tubular shell that is irregularly coiled and totally or partly cemented to hard substrates. In the strict sense as the Vermetidae are seen here, there are three protoconch types found among them, one like that of *Vermetus nielseni* n. sp. with a helicoform shape, and another one like *Petaloconchus* with a barrel-like shape (BANDEL & KOWALKE 1997, pl. 1, fig. 7). The third type is present on the Late Cretaceous *Laxispira* with a pitted surface. It has been documented by SOHL (1960), DOCKERY (1993), and BANDEL & KOWALKE (1997).

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 (1938-44). These authors placed the Vermetidae into the superfamily Cerithioidea. WENZ (1938-44) included into the taxon Vermetidae genera like *Vermetus* DAUDIN, 1800, *Petaloconchus* LEA, 1843, *Stephopoma* MÖRCH, 1860, *Vermicularia* LAMARCK, 1799, *Laxispira* GABB, 1877, *Tenagodus* GUETTARD, 1770, and *Pyxipoma* MÖRCH,1860.

MORTON (1965) realised 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 (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) recognised that vermiform caenogastropods belong into two quite separate groups regarding their sperm morphology. PONDER & WARÉN (1988) and BEESLEY et al. (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 Calyptraeoidea 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 Vermitidae, they recognised two clearly distinct protoconch types, that of *Vermetus* on one side and *Dendropoma* with axial to cancellate sculpture on the other.

Genus *Vermetus* DAUDIN, 1800

Type species: The Recent *Vermetus adansoni* DAUDIN, 1800 from the equatorial eastern Atlantic (WENZ 1938-44).

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.

Vermetus nielseni n. sp.

Plate 15, Figures 1-3

Holotype: GPI 3956, illustrated in pl. 15, figs. 1-2.

Paratype: GPI 3957, illustrated in pl. 15, fig. 3.

Material: Two specimens from the Campanian of Torallola, Spain.

Derivation of name: Named in honour of 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.

Remarks: 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). With the presence of a true *Vermetus* in Campanian time, *Laxispira* can no longer be regarded a stem group representative of the Vermitidae as suggested by BANDEL & KOWALKE (1997).

Discussion: From the Vermitidae sensu WENZ (1938-44), the Vermiculariinae and the Siliquariidae are long considered independent and rather closely related to the Turritellidae (MORTON 1965, KEEN 1961, HEALY, 1988, HOUBRICK 1988). BANDEL & KOWALKE (1997) distinguished within the Vermitidae the Vermitinae and the Dendropominae BANDEL & KOWALKE, 1997. As shown above, *Vermetus* s. str. was already present in the Campanian 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.

Family Litiopidae FISCHER, 1885

The 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* RANG, 1829 and *Alaba* H. & A. ADAMS, 1860, and considered *Fenella xanthacme* MELVILL, 1904 as another possible member.

Recent Litiopidae live in shallow-water seagrass environments in the case of *Alaba* or on floating *Sargassum*-banks in the case of *Litiopa* (BEESLEY et al. 1998). In a substantial work on these two genera, HOUBRICK (1987) pointed out that they were formerly assigned to the Cerithiopsoidea 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.

Genus *Litiopella* n. gen.

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

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.

Derivation of name: Derived from *Litiopa*.

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 axials and the lack of the strong spiral keels on the protoconch.

Litiopella schoeningi n. sp.

Plate 15, Figures 6-7

Holotype: GPI 3959, illustrated in pl. 15, figs. 6-7.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after MEIKE SCHÖNING, Hamburg, who collected in Torallola in spring 1999.
Diagnosis: As for the genus.
Description: Only a juvenile shell with four whorls of the teleoconch is present. The 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. The 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.
Remarks: 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.

Discussion: The larval shells of the Litiopidae differ only slightly from the protoconchs the Provannidae, Dendropomidae and *Sculptifer*: it shows one or two fine but distinct spiral keels on its whorls (HOUBRICK 1987: figs. 8, 10). 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).

Family Provannidae WARÉN & PONDER, 1991

The family comprises the genera *Alviniconcha* OKUTANI & OHTA, 1988, *Desbruyeresia* WARÉN & BOUCHET, 1993, *Ifremeria* WARÉN & PONDER, 1991 and *Provanna* with quite differently shaped teleoconchs. 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).
The Provannidae have adopted to the deep sea hydrothermal vent environment and grow chemotrophic symbiontic 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 (1938-44) 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).

Genus *Desbruyeresia* WARÉN & BOUCHET, 1993

Type species: *Desbryueresia spinosa* WARÉN & BOUCHET, 1993 which lives in the North Fiji Basin (WARÉN & BOUCHET 1993).
Description: The medium sized (around 12 mm high) melanoid, turriform 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.

Desbruyeresia antiqua n. sp.

Plate 15, Figures 4-5

Holotype: GPI 3958, illustrated in pl. 15, figs. 6-7.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: 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, 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 difference is minute and regards 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*.
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.

Discussion: 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, Cerithiopsoidea and Triphoroidea GRAY, 1847 (BANDEL 1991a, 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. For these unusual species FRÝDA & BANDEL (1997) created the order Stylogastropoda, to encompass high spired archaeogastropods that are convergent in shell shape with caenogastropods that occur from Carboniferous onwards (BANDEL 1993c, 1997, NÜTZEL 1998). Most probably *Loxonema* belongs here, is thus a member of the Archaeogastropoda and, therefore, not available for models 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. of *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* (LINNÉ, 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 & CAMPELL 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.

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

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, but indicates that this species is a direct developer and, thus, no larval shell has been built. 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 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.

It can be concluded that Provannidae, Dendropominae, Litiopidae, and *Sculptifer* 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, they are considered related taxa within the Cerithioidea. A Cretaceous origin of this group can be assumed as *Desbruyeresia antigua* and *Litiopella schoeningi* were already present in the Campanian. The independence of the Vermitidae from that group at Campanian time is evident from the presence of *Vermetus nielseni* in the same sediments as *Desbruyeresia antigua* and *Litiopella schoeningi*.

Order Ptenoglossa GRAY, 1853

The composition of the Ptenoglossa has undergone considerable changes since they were introduced by GRAY (1853). The name is derived from the shape of the radula of an epitoniid with numerous small, needle-like teeth in a row with the central tooth missing. TROSCHEL (1856-63) and THIELE (1928) considered Epitoniidae and Janthinidae as Ptenoglossa and WENZ (1938-44) united these two families as Scalacea. The same author treated the Cerithiopsidae and the Triphoridae as families within the Cerithioidea.

The first who doubted this classical treatment was RISBEC (1955). He investigated radula and digestive organs of some triphorids and observed similarities with those of the neogastropod family Columbellidae. Consequently, the Triphoridae were removed from the Cerithioidea. KOSUNGE (1964, 1966) agreed with this treatment and established a new superfamily Triphoroidea and placed it together with the Epitoniidae, Mathildidae and Architectonicidae in the new suborder Heterogastropoda. But also this new treatment did not last long. HASZPRUNAR (1985) introduced the new taxon Allogastropoda to include Mathildidae, Architectonicidae and other gastropod groups with heterostrophic protoconch and several anatomical similarities. Triphoroidea, Cerithiopsoidea and Janthinioidea were left as Caenogastropoda with uncertain affinities. HEALY (1986a, 1988) and HASZPRUNAR (1988) showed that these superfamilies are related to each other but are distinct from the Cerithioidea and the Eulimidae. BANDEL (1991a) compared larval shells of Triassic ”Loxonematoidea” with those of living Ptenoglossa and grouped them into the superfamilies Zygopleuroidea, Triphoroidea and Janthinoidea. In a throughout investigation of the fossil record, NÜTZEL (1998) distinguished several evolutionary lineages and traced their history back to the very beginning of caenogastropod evolution. He considered the Zygopleuridae ancestral to the Janthinoidea and the Protorculidae ancestral to the Cerithiopsoidea, from which later the Triphoroidea evolved.

Ptenoglossa live in marine environments only. While Triphoroidea and Cerithiopsoidea usually feed on sponges, coelenterates are known to be the primary diet of Epitoniidae (KOSUNGE 1966, BANDEL & WEDLER 1987, NÜTZEL 1998).

Superfamily Cerithopsoidea GOLIKOV & STAROBOGATOV, 1975

Shells of the Cerithiopsoidea are turriform to pupoid with reticulate or mainly spiral ornament. The protoconch is smooth or with non-collabral ribs in the case of the Cerithiopsidae, and is provided with strongly developed collabral, axial ribs in the case of the Eumetulidae.

Family Cerithiopsidae ADAMS & ADAMS, 1854

Genus *Cerithiopsis* FORBES & HANLEY, 1849

Type species: The Recent *Cerithium tubercularis* (MONTAGU, 1803) from the coast of England.
Description: The slender Cerithiopsidae have a reticulate teleoconch ornamented and a smooth or non-collabrally ribbed protoconch.

Cerithiopsis seguris n. sp.

Plate 16, Figure 1

Holotype: The specimen illustrated in pl. 16, fig. 1.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after the town of Pobla de Segur near the type locality.
Diagnosis: A small *Cerithiopis* with a smooth and turriform protoconch made of five and a half volutions and a teleoconch with two beaded spirals.
Description: The protoconch is turriform, made of five and a half smooth volutions, and is 0.6 mm high and 0.28 mm wide. The teleoconch is ornamented with axial ribs and two spiral cords with nodular intersections. The aperture ends anteriorly in a canal. The shell is 1 mm high.
Remarks: *Ceritiopsis* cf. *rosenkranzi* from the Danish Paleocene described by NÜTZEL (1998) is similar in shape but the protoconch has one more whorl and is about 50% larger than the one figured here.

Family Eumetulidae GOLIKOV & STAROBOGATOV, 1975

Genus *Vatopsis* GRÜNDEL, 1980

Type species: *Cerithium bimoniliferum* Sandberg, 1858 from the Oligocene of Germany.
Description: A Cerithiopsidoidea with reticulate teleoconch ornamented. A planktotrophic protoconch possesses one or two spiral keels in the lower half of the whorls and collabral ribs above.
Remarks: Similar larval shells can be traced back into the Jurassic (NÜTZEL 1998: 110) and are also found on the Triassic *Protorcula marshalli* NÜTZEL, 1998. The *Vatopsis*-type protoconch is considered by NÜTZEL (1998) a very basic one within the Cerithiopsoidea.

Vatopsis nodoliratium (WADE, 1926)

Plate 16, Figure 2

1926 *Cerithium nodoliratum* WADE: 155, pl. 54, figs. 4-5.
1960 *Cerithium nodoliratum* WADE - SOHL: 82-83, pl. 9, figs. 15-16, 24.
1993 *Cerithiella nodoliratum* WADE - DOCKERY: 79, pl. 23, figs. 3-5; pl. 24, figs. 3-4; pl. 40, fig. 4.
1998 *Vatopsis nodoliratum* WADE - NÜTZEL: 112, pl. 17, figs. W-Z.

Material: Several specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch is high spired and made of about six volutions. The initial part measures almost 0.1 mm across, the entire protoconch is 0.75 mm high, 0.5 mm wide, and ornament consists of axial ribs that start at the upper suture and end at a spiral keel in the lower quarter. There are two and a half teleoconch whorls

preserved which are sculptured with axial ribs and four spiral cords, the fourth obscured by the next whorl. The shell is 1.7 mm high.

Genus *Variseila* DOCKERY, 1993

Type species: *Cerithiopsis meeki* WADE 1926 from the Maastrichtian Ripley Formation of the USA.

Description: The axially ribbed protoconch is high-spired, the teleoconch is very slender, flat sided and spirally ribbed, the anterior canal is twisted.

Remarks: NÜTZEL (1998) considered the *Seila*-like teleoconch to have evolved twice within the Cerithiopsoidea. In the case of *Seila* it is connected with a smooth, *Cerithiopsis*-like protoconch, while it is of the collabrally ribbed, *Eumetula*-type in the case of *Variseila* and *Tembrockia*. NÜTZEL (1998) supposed that the *Seila*-type of ornament is easily generated by the subpression of the axial ribs, a process observable in the ontogeny of the Recent *Specula styliformis* SUTER, 1908 (see NÜTZEL 1998: pl. 3, figs. I-K). The teleoconch whorls of *Variseila catalania* n. sp. described below also show an ontogenetic transition from a relatively strong axial ornament on the earliest whorl to a more spirally dominated sculpture on the later whorls, supporting NÜTZEL's (1998) hypothesis.

Variseila catalania n. sp.

Plate 16, Figure 3

Holotype: The specimen illustrated in pl. 16, fig. 3.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: For the Spanish province of Catalania, where the type locality of Torallola is found.

Diagnosis: A species with collabrally ribbed protoconch and a teleoconch with three spirals and fine axial in between.

Description: The protoconch shows collabral ribs, no larval hook and is 0.3 mm wide. The ornamentation of the teleoconch starts with three equally strong spiral ridges and axial ribs. The first spiral ridge soon becomes the strongest, while the axial ornament weakens. The shell is about 1 mm high.

Genus *Ataxocerithium* TATE, 1894

Type species: The Recent *Cerithium serotinum* ADAMS, 1855 from southern Australia.

Description: The slender, high spired shell is ornamented with five or more spiral ridges and axial ribs. A planktotrophic larval shell is high spired and sculptured with collabral axial ribs.

Remarks: *Ataxocerithium* is distinct from *Eumetula* by its five or more spiral cords, while *Eumetula* has four or less.

Ataxocerithium heliclina (DOCKERY 1993)

Plate 16, Figure 4

1993 *Eccliseogyra heliclina* DOCKERY: 82, pl. 25, figs. 1-5; pl. 26, figs. 15-16.
1998 *Eccliseogyra heliclina* DOCKERY - NÜTZEL: 130, pl. 18, figs. V-W.

Material: One specimen from the Maastrichtian of Temalac, Mexico.

Description: The conical protoconch consists of four and a half volutions with little oblique axial ribs, is 0.65 mm high and 0.53 mm wide. The teleoconch consists of convex whorls with five spiral cords and weak axial ribs. The shell is 2.2 mm high.

Remarks: DOCKERY (1993) described this species from the Campanian of the Coffee Sand Formation and placed it within *Eccliseogyra* DALL, 1892 because of its well developed larval hook. But NÜTZEL (1998) doubted this placement since BOUCHET & WARÉN (1986) described *Eccliseogyra* having undulating axial lamella, absent from the Campanian species. The species described herein from the Maastrichtian of Mexico is placed within *Ataxocerithium* due to its five spiral cords and the axially ribbed protoconch.

Genus *Eumetula* THIELE, 1912

Type species: The Recent *Eumetula dilecta* THIELE, 1912 from the shores of Antarctica.
Description: The protoconch is axially ribbed, the teleoconch whorls have axial ribs and two to four spiral cords. The base is relatively flat and the aperture egg-shaped.

Eumetula monospiralia n. sp.

Plate 16, Figures 5-6

Holotype: The specimen illustrated in pl. 16, figs. 5-6.
Material: Several specimen from the Campanian of Torallola, Spain.
Derivation of name: Named according to its single spiral cord on the teleoconch.
Diagnosis: The teleoconch of this new species shows straight to transverse axials and one spiral cord in the lower half of the whorl.
Description: The protoconch consists of three and a half volutions with simple collabral ribs and a weakly developed larval hook. It is 0.3 mm high and 0.25 mm wide. The teleoconch is made of at least two volutions with transverse to axial ribs, a more or less well developed spiral ridge in the lower half and ultra fine spiral lamella. The apertural base shows a siphonal canal. The entire shell is 0.62 mm high.

Eumetula risbeci n. sp.

Plate 16, Figures 7-8

Holotype: The specimen illustrated in pl. 16, figs. 7-8.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of J. RISBEC for his work on Recent cerithiopsids and triphorids.
Diagnosis: An *Eumetula* with a lecithotrophic protoconch and a slender teleoconch with one spiral cord and fine spiral lamella.
Description: The protoconch is blunt and smooth, is made of two volutions, and is 0.23 mm high and 0.3 mm wide. The teleoconch whorls are slender and sculptured with more or less curved axial ribs, fine spiral lamella and one spiral ridge in the lower third. The shell is about 1 mm high.
Remarks: This species is more slender than *Eumetula monospiralia* and has a protoconch-shape reflecting a lecithotrophic ontogeny. Similar protoconchs of Recent and Cretaceous cerithiopsoids are figured by NÜTZEL (1998: pl. 3, figs. C, H; pl. 17, fig. C).

Eumetula marshalli n. sp.

Plate 16, Figure 9

Holotype: The specimen illustrated in pl.16, fig. 9.
Material: Two specimens from the Campanian of Torallola, Spain.

Derivation of name: Named in honour of BRUCE MARSHALL, for his work on Recent Ptenoglossa.

Diagnosis: An *Eumetula* with lecithotrophic protoconch and a teleoconch with one spiral cord in the lower third.

Description: The protoconch is blunt and smooth, and is made of almost two volutions which are 0.2 mm high and 0.3 mm wide. The teleoconch is sculptured with curved axial ribs, fine spiral lamella and a spiral ridge in the lower half, the shell is 1.8 mm high.

Remarks: The teleoconch whorls are indistinguishable from those of *Eumetula monospiralia* but its protoconch is of the lecitotrophic type.

Subgenus *Marshallaskeya* GRÜNDEL, 1980

Type species: The Recent *Altispecula elegantula* POWELL, 1930 from New Zealand.

Description: An Eumetulid with axially ribbed teleoconch and a collabrally ribbed larval shell.

Remarks: *Marshallaskeya* was introduced by GRÜNDEL (1980) as a subgenus of *Laskeya*. Since the radula of the type species is yet unknown, a synonymy with *Eumetula* or *Laskeya* is still possible (NÜTZEL 1998). Therefore, *Marshallaskeya* is treated here as a subgenus of *Eumetula*.

Marshallaskeya nuetzela n. sp.

Plate 16, Figure 10

Holotype: The specimen illustrated in pl. 16, fig. 10.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: Named after ALEXANDER NÜTZEL, who evaluated the fossil history of the Ptenoglossa.

Diagnosis: This new species shows a collabrally ribbed protoconch with a well developed larval hook and the teleoconch is sculptured with axial ribs only.

Description: The planktotrophic protoconch is made of three volutions sculptured with numerous collabral ribs. It is about 0.38 mm high and 0.3 mm wide. The transition to the teleoconch is marked by a well developed, sinuous larval hook. Of the teleoconch two whorls are preserved which have rather straight axial ribs and no spiral sculpture. The columella bears one fold. The shell is about 4 mm high.

Subgenus *Cerithina* HOLZAPFEL, 1888

Type species: *Cerithina vaalsensis* HOLZAPFEL, 1888 from the Campanian of western Europe.

Description: The slender turriform protoconch is made of numerous axially ribbed whorls. The teleoconch is turriform, the whorls are more or less straight sided and have strong axial and spiral ornament. The interspaces between the axials are about as wide or little wider than the ribs. There are three to four spiral cords, the base is more or less flat and the columella may bear one plate.

Remarks: The genus *Uchauxia* COSSMANN, 1906 of uncertain taxonomic position has a similar shell but the base is rounded and the columella does not show plates. *Eumetula* may have convexer volutions with less spiral cords, *Ataxocerithium* possesses convexer whorls with finer and more spiral cords. Apart from the type, the following species are included: *Cerithina dockerya* n. sp. from the Maastrichtian of

Mexico; *Cerithium simpsonese* STEPHENSON, 1941 from the Maastrichtian of Texas, and *Cerithina granulata* HOLZAPFEL, 1888 from the Campanian of Germany.

Eumetula (*Cerithina*) *vaalsensis* HOLZAPFEL, 1888

Plate 16, Figures 11-12

1888 *Cerithina vaalsensis* HOLZAPFEL: 143, pl. 21, fig. 14.

Material: Three specimens from the Campanian of Torallola, Spain.
Description: The protoconch is slender, consists of six and a half volutions with deep sutures, and is sculptured with axial ribs that are constricted near the sutures. The teleoconch is slender and flat sided with numerous volutions, and ornamentation consists of four tuberculate spiral cords with the tubercles axially arranged. The base is flat and smooth, the inner lip is reflected and the columella bears one plate.
Remarks: A similar species but with a wider apical angle is described from the Maastrichtian of Texas as *Cerithium simpsonese* STEPHENSON, 1941. It may be have closer relations to *Cerithina granulata* HOLZAPFEL, 1888 from the Vaals greensands, Germany.

Eumetula (Cerithina) dockerya n. sp.

Plate 17, Figure 1

1993 *Cerithiella* sp. DOCKERY: 80, pl. 23, figs. 1-2.

Holotype: The specimen illustrated in pl. 17, fig. 1.
Material: One specimen from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for DAVID T. DOCKERY III who described this species in open nomenclature from the Coffee Sand in Mississippi and Tennessee, USA.
Diagnosis: A *Cerithina* with a slender, multiwhorl protoconch and a teleoconch with four beaded spiral cords and axial ribs which are in a vertical order.
Description: The embryonic shell is smooth and globular, measures about 0.1 mm across. The larval shell is high spired, made of four and a half collabrally ribbed volutions. It is 0.7 mm high and 0.4 mm wide. The first teleoconch whorls have three spiral lines, equally strong axial ribs and weak sutures. The adult shell is made of numerous straight volutions which are ornamented with axial ribs crossed by four spiral cords, intersections are nodular. The first two spirals are a bit closer to each other than the others. The basal margin has two strong keels, the base is concave. The aperture is roundish, has a reflected inner lip and the rostrum is short and straight. The shell is 1.6 mm high.
Remarks: The specimen on DOCKERY's (1993) figure shows a columellar plate. *E.(C.) vaalsensis* shows four spiral cords and is also is distinct by its constricted ribs on the protoconch, those of *E.(C.) dockerya* run from suture to suture. NÜTZEL (1998: pl. 15) figured two unnamed species from the Eocene of Gan, France, of which *Retilaskeya*. sp. 1 has more transverse ribs on the protoconch and a teleoconch with deeper sutures, whereas *Retilaskeya*. sp. 2 has only two spiral cords on the teleoconch and the last protoconch whorl is smaller than the preceding one.

Discussion: Among the Cerithiopsoidea, the Eumetulidae are considered the older and more primitive family of the Cerithiopsidae and Eumetulidae (NÜTZEL 1998). They can be traced back into the Jurassic, and also in the two Late Cretaceous fossil localities investigated here, members of the Eumetulidae far outnumber the only cerithiopsid specimen. However, *Cerithiopsis seguris* n. sp. is the oldest and only Cretaceous cerithiopsid with the typical smooth protoconch preserved.

Superfamily Triphoroidea GRAY 1847

Family Triphoridae GRAY 1847

This family includes sinistrally coiled shells with predominantly reticulate sculpture. The aperture has a posterior siphonal canal that may be canal- or tube-like, the anterior canal is usually tube-like.

Genus *Trempinella* n.gen.

Type species: *Bithium sensuyi* VIDAL, 1921 from the Campanian of Torallola, Spain.
Diagnosis: This new genus includes slender, sinistrally coiled shells of moderate size. Its sculpture consists of numerous spiral cords which are finely beaded. The larval shell is bicarinate and the columella may bear a fold.
Derivation of name: A combination of Tremp - a town near the type locality, and *Inella* BAYLE, 1878 – a presumably related triphorid genus.
Remarks: Beaded spirals are an unusual ornament for triphorids and distinguish this new genus well. The Recent *Inella* possesses one or two spirals on the larval shell (MARSHALL 1983) and may therefore be a related genus.

Trempinella sensuyi (VIDAL 1921)

Plate 17, Figures 2-3

1921 *Bithium sensuyi* VIDAL: 102, pl. 6, fig. 4.
1949 *Bithium sensuyi* VIDAL – BATALLER: 112.

Material: Six specimens from the Campanian of Torallola, Spain.
Description: The protoconch consists of four and a quarter sinistrally coiled volutions and ornamented with two equally strong spiral keels. It is 0.66 mm high and 0.3 mm wide. Teleoconch large for the family, slender, high spired, early ornament consists of three smooth spiral cords, the first two attached to each other, the third below an irregular constriction. On later whorls the spirals show fine axial ribbing and their number increases to up to eight on the largest fragment found. The columella shows a strong plate at its base.
Remarks: Proto- and teleoconch are considered to belong to the same species, even no actual transition was observed. No other sinistrally coiled, triphoroid-like shells have been found in Torallola.

Triphorid larval shell

Plate 17, Figure 4

Description: The embryonic part measures almost 0.1 mm across, the larval shell is conical and consist of three and three quarters of a volutions that show subsutural denticles and two spiral ridges. The whole larval shell is 0.58 mm high.
Remarks: Only larval shells but no teleoconchs were discovered at the locality near Temalac, but the larval shells are quite abundant among the small shells extracted from the sediment. They resemble the protoconch of *Epetrium? cretacea* (RAVN, 1933) as figured by NÜTZEL (1998: pl. 18, figs. K-N) in every aspect.
Material: Several specimens from the Maastrichtian of Temalac, Mexico.

Discussion: Sinistrally coiled triphorid larval shells are documented for the first time from the Late Cretaceous. Their dominant sculptural feature are two spiral ridges which are also known from Paleocene species (NÜTZEL 1998). Recent Australian species of *Inella* evaluated by MARSHALL (1983) all have a more or less reticulate teleoconch ornament, but protoconchs which show one or two spiral keels and no axial sculpture. *Inella* is regarded by MARSHALL (1983) as a primitive member of the Triphoriae. Here biological and paleontological data agree on the point that the bicarinate larval shell is the basal type within the Triphoridae.

In his discussion on the origin of the Triphoroidea, NÜTZEL (1998) pointed out that the oldest triphorid larval shells resemble those of the dextrally coiled Procerithiidae COSSMANN, 1906 rather than the predominantly axially ribbed protoconchs of the Zygopleuridae and Protorculidae. But since relations of the Ptenoglossa with the Cerithioidea were rejected by HASZPRUNAR (1988) and HEALY (1986a, 1988), NÜTZEL (1998) suggested the following scenario: The Triphoroidea split from the Cerithiopsoidea by developing the posterior siphonal canal. In a second evolutionary step the bicarinate, sinistrally coiled larval shell evolved. He pointed out that *Triforis* DESHAYES, 1834 shows characters which he would expect from intermediate forms between Ceritiopsoidea and Triphoroidea (e.g. collabrally ribbed protoconch and a posterior siphonal canal). Whether the posterior siphonal canal or sinistral coiling evolved first cannot be tested yet, no aperture of *Trempinella sensuyi* is preserved. The posterior siphonal canal, regarded by NÜTZEL as uniting apomorphy of the Triphoridae and Triforidae is also known from the presumably cerithioid genus *Sherbornia* IREDALE, 1917 (CHERNOHORSKY 1981, PONDER & WARÉN 1988) and may be a product of convergence.

A protoconch-type ancestral to the bicarinate, triphorid larval shell may be found on *Vatopsis* and *Protorcula*. This type with axial ribs and spirals near the base can be traced back into the mid-Jurassic, *Vatopsis* is known from the Late Cretaceous and survived until the Miocene (GRÜNDEL 1980, DOCKERY 1993, NÜTZEL 1998, herein). Already NÜTZEL (1998) derived the *Vatopsis*-like protoconch from the Triassic *Protorcula marshalli* (NÜTZEL 1998: pl. 27, fig. F-J) and concluded it to be the most basal one within the Cerithiopsoidea.

It is proposed here that the bicarinate protoconch of the early triphorids evolved from a *Vatopsis*-like larval shell in a single step by the reduction of the axial ribs and the inversion of the coiling axis. Sinistral coiling, the bicarinate larval shell and the posterior siphonal canal are regarded as apomorphies. The dextrally coiled Triforidae may represent an independent clade which evolved later from the Eumetulidae. This is in accordance with MARSHALL's (1980) study of *Triforis'* radula.

Superfamily Janthinoidea LAMARCK, 1810

Family Epitoniidae BERRY, 1810

The Epitoniidae include high spired or loosely coiled shells with axial ribs or lamella that may be crossed by fine spiral cords. The distinguishing character to the Nystiellidae is their smooth protoconch.

WENZ (1938-44) listed about 100 genera and subgenera under the family Scalidae, many of them monotypic and based on minute differences, most without description or figure of the protoconch. Since the shape of the protoconch is the only character to distinguish epitoniids and nystiellids, only genera with known protoconch morphology are considered here.

Genus *Cylindriscala* BOURY, 1909

Type species: The Recent *Cylindriscala acus* (WATSON) from the northern Atlantic. Its smooth protoconch has been figured by WENZ (1938-44: fig. 2326).

Description: Epitoniidae with a slender teleoconch with broad, non-lamellar, varix-like axial ribs, fine spiral sculpture may occur.

Remarks: *Aciculiscala* SOHL, 1963 was introduced for small, slender epitoniids and SOHL repeatedly pointed out that the protoconch shows a carinate pattern (SOHL 1963: 748, 1964: 321). However, DOCKERY (1993) diagnosed the protoconch as smooth and described a new species, *Aciculiscala coffea* with a smooth protoconch. This species is regarded by NÜTZEL (1998) as oldest Epitoniid known to date with the typical smooth protoconch. He also pointed out that a carinate protoconch ornament is ”highly unusual” for the Epitoniidae. *Aciculiscala coffea* should be transferred to *Cylindriscala* and *Aciculiscala* should not be used until the uncertainties concerning its type species *Aciculiscala acuta* SOHL, 1963 are clarified.

Cylindriscala mexcalia n. sp.

Plate 17, Figure 5

Holotype: The specimen illustrated in pl. 17, fig. 5.
Material: One specimen from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named according to the Mexcala formation, where this species comes from.
Diagnosis: A small epitoniid with transverse axial ribs and fine spiral lirae.
Description: The protoconch is smooth and egg-shaped, is made of two and a half volutions and is about 0.5 mm wide and 0.6 mm high. The teleoconch is high spired and made of at least four volutions. The whorls are convex, have deep sutures and are sculptured with transverse axial ribs and fine spiral striae. The shell is 3.2 mm high.
Remarks: *Aciculiscala coffea* DOCKERY 1993 has straight axial ribs, no spiral ornament and deeper sutures (e.g. more convex whorls).

Family Nystiellidae CLENCH & TURNER 1952

Genus *Opaliopsis* THIELE, 1928

Type species: The Recent *Opaliopsis elatum* THIELE, 1928 from the shores of South Africa.
Description: *Opaliopsis* is used herein in the broad sense of NÜTZEL (1998) for high spired Nystiellidae with non-lamellar teleoconch ribs and occasional spiral cords.
Remarks: *Proscala* is distinct by its subsuturally constricted whorls. The distinguishing character to *Confusiscala* is the absence of a basal plate from the teleoconch whorls of *Opaliopsis.*

Opaliopsis punctata n. sp.

Plate 17, Figure 6

Holotype: The specimen illustrated in pl. 17, fig. 6.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for the fine punctation on the teleoconch whorls.
Diagnosis: A nystiellid with transverse ribs on the protoconch and a teleoconch sculptured with axial ribs and spiral rows of fine tubercles.
Description: The protoconch is 0.28 mm high and 0.2 mm wide, consists of three volutions with curved, transverse ribs, the third whorl is about as large as the second. The teleoconch consists of three volutions, shows axial ribs and spiral rows of very fine tubercles. The shell is about 1.0 mm high and 0.4 mm wide.
Remarks: The North American *Opaliopsis faearium* (DOCKERY, 1993) has more numerous and broader protoconch whorls, the same applies for the newly described *Opaliopsis temalacia* from Mexico (see below).

Opaliopsis temalacia n. sp.

Plate 17, Figure 7

Holotype: The specimen illustrated in pl. 17, fig. 7.
Material: One specimen from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for the village of Temalac, six kilometres south of the fossil bearing outcrop.
Diagnosis: An *Opaliopsis* with oblique ribs on the protoconch and a teleoconch with varix-like ribs and fine spiral lines.
Description: The embryonic part is smooth, measures about 0.15 mm across, the larval shell is high spired, convex-conical, and made of three and a half volutions with strongly oblique axial ribs. The first teleoconch whorl is convex with about ten curved axial ribs, crossed by numerous fine spiral lines. Later whorls have about 13 widely spaced axial ribs overridden by fine spiral lirae. The sutures are deep and sometimes show a basal plate. The shell is about 1.2 mm high.
Remarks: PERRILLIAT et al. (2000) illustrated four slightly differently ribbed *Epitonium*-like teleoconchs from the Mexcala formation, all with fine spiral liration.

Genus *Proscala* COSSMANN, 1912

Type species: *Proscala albensis* (D'ORBIGNY, 1842) from the Hauterivian (Early Cretaceous) of France.
Description: The high spired shell has little convex volutions with varix-like axial ribs and fine spiral striae. Sutures are constricted and show a basal plate.
Remarks: Although the protoconch of the type species remains unknown, *Proscala* is tentatively placed within the Nystiellidae due to the axially ribbed larval shell of *Proscala campaniana* n. sp. described below.

Proscala campaniana n. sp.

Plate 17, Figures 8-9

Holotype: The shell figured at pl. 17. fig. 8.
Material: Six specimens from the Campanian of Torallola, Spain.
Derivation of name: The type species is named according the Albian stage, this new species is named for its Campanian age.
Diagnosis: The protoconch is slender and has collabral ribs, the teleoconch axial ribs and constricted sutures; there are about two varices per whorl.
Description: The protoconch is made of four axially ribbed volutions and is 0.58 mm high and 0.33 mm high. The teleoconch is high spired with nine or more little convex volutions. The sutures are marked by a constriction that generates a tuberculate collar. The axial ribs are numerous and curved, and there are usually two varices per volution.
Remarks: The type species *Proscala albensis* shows a similar sutural constriction but is more slender.

Discussion: While the protoconch of the Nystiellidae is sculptured with strong collabral ribs, the Epitoniidae are characterised by a smooth or very finely axially ribbed protoconch of conical or rounded outline. The finely axially ribbed type does not occur prior to the Oligocene (NÜTZEL 1998), all epitoniid protoconchs from the Late Cretaceous known so far are of rounded conical shape. Numerous epitoniform genera are known from the Late Cretaceous with a broad variety of teleoconch characters (SOHL 1964, CLEEVELY 1980, DOCKERY 1993). But unfortunately protoconch-morphology is unknown from most of these genera. All Late Cretaceous Epitoniidae with preserved protoconch discovered to date possess small, slender shells with varix-like ribs only.

Superfamily Zygopleuroidea WENZ, 1939

Family Protorculidae BANDEL 1991

This family includes slender, high spired gastropods. The volutions are smooth or develop beaded sutural ridges giving the whorls a concave appearance. Their larval shell are also slender and high spired and are collabrally ribbed or show spiral ridges and axial ribs.

Genus *Atorcula* NÜTZEL, 1998

Type species: The Triassic *Melania canalifera* Münster 1841 from the St.Cassian Formation.
Description: A Protorculidae with a more or less smooth teleoconch and an axially ribbed protoconch.

Atorcula americana n. sp.

Plate 17, Figure 10

Holotype: The specimen illustrated in pl. 17, fig. 10.
Material: One specimen from the Maastrichtian of Temalac, Mexico.
Derivation of name: While *Atorcula* was previously only known from Europe, this is the first report from the North American continent.
Diagnosis: The pProtoconch shows axially ribbed volutions and measures 0.5 mm in diameter. Adult whorls are smooth, little convex, and have shallow sutures. The shell is 1.4 mm high.
Remarks and discussion: NÜTZEL (1998) described several species of *Atorcula* from the Italian St.Cassian Triassic. *Atorcula anoptychopsis* NÜTZEL (1998) is distinct by its straight to concave volutions, *Atorcula canalifera* MÜNSTER 1841 shows sinus-like growth lines, *Atorcula apicostata* NÜTZEL (1998) possesses irregularly shaped volutions. The same author assigned *Cimolithium* cf. *ascheri* WOLLEMANN, 1908 figured by ABBASS (1973: pl. 2, fig. 7) from the Barremian of the UK to *Protorcula* and proposed that the Protorculidae ranges from the Triassic to the lower Cretaceous. The new finding indicates that this family may have reached the end of the Cretaceous.

Order Strombimorpha BANDEL, 1991

Superfamily Stromboidea RAFINESQUE, 1815

Family Aporrhaidae MÖRCH, 1852

Aporrhaids are easily recognised by their finger- or spine-like extensions of the outer lip. They have a moderate to high spire and are variously sculptured with axial and spiral ornament. Their larval shells are very large, usually between 0.6 and 2.0 mm in diameter. They are smooth and conical in shape, and the transition to the teleoconch is gradual.
Attempts to trace the Aporrhaidae back even into the Palaeozoic have been undertaken by BANDEL (1991a, 1993c). He suggested that the Triassic *Cassianozyga* BANDEL, 1991 and Carboniferous *Hemizyga* GIRTY, 1915 possibly were early members of a lineage leading to the Stromboidea, but these connections

are still quite hypothetical. The first undoubted Aporrhaids are known from Jurassic times with numerous genera. Also larval shells similar to those produced by Recent *Aporrhais pespelicani* LINNÉ, 1758 (see RICHTER & THORSON 1975) are known since then (SCHRÖDER 1995, GRÜNDEL 1998b). However, their generic names are used in a confusing manner and a revision is needed to clarify the early history of this gastropod group.

Genus *Anchura* CONRAD, 1860

Type species: *Anchura abrupta* CONRAD, 1860 from the Upper Cretaceous of Tippah County, Mississippi, USA.
Description: The high spired aporrhaid shows tuberculate spiral sculpture on the last whorl. The first spiral often extents into an posterior spine which may be attached to the spire or may be loose. The third or fourth spiral often turns into a keel and extents onto the dagger-like wing of the outer lip.

Anchura denticulata n. sp.

Plate 19, Figures 4-5

Holotype: IGM 7787, figured at pl. 19, figs. 4-5.
Material: Two fragments with the last two whorls preserved from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for the two heavy reinforced ribs next to the inner lip of the aperture.
Diagnosis: Medium sized *Anchura* with a short adapical spur and two enlarged axial ribs next to the aperture.
Description: The smooth and conical protoconch is 1.2 mm wide and high, comprises five volutions, the embryonic part measures 0.15 mm across. The teleoconch whorls are convex with axial or slightly transverse ribs crossed by five to six fine spiral lines. Two strong ribs develop on the last whorl next to the inner lip, after that the fourth spiral line evolves into a strong keel. The adapical spur is about one and a half whorls high; the inner lip is heavy callused. The diameter of the last whorl of the holotype is about 11 mm wide.
Remarks: The two strong ribs near the inner lip are a quite unique feature for an *Anchura* and make this species easily distinguishable even when its outer lip is not known.

Anchura sp.

Plate 20, Figure 2

Material: One fragment with the two last whorls preserved from the Maastrichtian of Temalac, Mexico (IGM 7789).
Description: Whorls convex with a carinate ornament of axial ribs crossed by seven spiral cords, the fourth being the strongest; it develops into a keel on the last whorl. The diameter of the last whorl is about 20 mm.

Genus *Lispodesthes* WHITE, 1876

Type species: *Anchura nuptialis* WHITE, 1874 from the Cenomanian-Turonian of the Colorado Formation, Pajuate in New Mexico, USA.
Description: Rather low spired aporrhaid which covers the shell with callus in the adult. The outer lip shows one posterior wing and a peg below.

Lispodesthes lilipus n. sp.

Plate 20, Figures 3-5

Holotype: IGM 7791, figured at pl. 20, figs. 3-5.
Material: Two juvenile and one adult specimen and several fragments of the outer lip from the Maastrichtian of Temalac, Mexico.
Derivation of name: This species is unusually small for the genus.
Diagnosis: Pugnellid shell, small for the genus, entire shell callus covered, no ornament visible except a strong single rib adjacent to the aperture.
Description: The adult shell consists of six volutions with the last whorl being twice as high as the spire. Spire and last whorl of a juvenile specimen without callus-cover show no axial or spiral ornament. The aperture is long, narrow and concave, shoulder and margin of the outer lip are thickened with callus. A little peg is present halfway between the adapical extension and the abapical canal; a strong transverse rib is present adjacent to the aperture. The holotype is 21 mm high and 14 mm wide including the wing.
Remarks: *Lispodesthes amplus* DOCKERY, 1993 from the Coffee Sand of Mississippi is very similar except it has no rib on the dorsal side, it also is much larger.

Genus *Pterocerella* MEEK, 1864

Type species: *Harpago tippanus* CONRAD, 1858 from the Upper Cretaceous Owl Creek Formation, Mississippi, USA.
Description: The shell is of moderate height with either smooth whorls or with an ornament of spiral ridges. The aperture has lenticular shape and is inclined to the axis of coiling. The outer lip expands greatly with six thin digitations which are connected with variable amounts of shell webbing.

Pterocerella sp.

Plate 20, Figure 6

Material: One specimen from the Maastrichtian of Temalac, Mexico (IGM 7792).
Description: Medium to large shell with at least seven volutions. The whorls are little convex and show a smooth keel in the lower third. Its wing is attached to about half of the height of the penultimate whorl. The figured shell is 26 mm high and 15 mm wide.
Remarks: Only one poorly preserved specimen is available for study. Its wing is not preserved so it cannnot with certainty be assigned to a known species but the attached beginning of the wing on the penultimate whorl suggests that it does not belong to any of the species from the Gulf Coastal Plain of Mississippi, Tennessee and Texas. DOCKERY (1993) figured the protoconch of *Pterocerella maryea* DOCKERY 1993 which is quite similar to that of modern *Aporrhais*.

Genus *Mexopus* n. gen.

Type species: *Mexopus mexicanus* n. sp. from the upper Maastrichtian of the Mexcala Formation, Guerrero, southern Mexico.
Diagnosis: High spired aporrhaid shell with irregular, weak and slightly curved axial ribs. They may be crossed by fine spiral lines in the upper half of the whorl. A band of callus extends from the inner lip onto the spire and may cover the apex.
Derivation of name: Derived from Mexico, its country of origin, and *Chenopus*, a synonym of *Aporrhais*.

Remarks: *Latiala* SOHL, 1960 appears to be a close relative of *Mexopus* n. gen. but possesses stronger and well-formed ribs. *Tibiaporrhais* ELDER, 1990 is similar in having only spiral lirae and growthlines on the spire, but its wing is not attached to the penultimate whorls and it also has a higher spire. Juvenile specimens of *Mexopus* quite resemble species of *Nudivagus* WADE, 1917 but the last whorls of *Nudivagus* can be constricted and have sharper basal margins.

Mexopus mexicanus n. sp.

Plate 21, Figures 1-3

Holotype: IGM 7793, figured at pl. 21, figs. 1-3.
Material: Ten specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: For its occurrence in Mexico.
Diagnosis: Small aporrhaid gastropod with weak axial and spiral ornament and two strong ribs behind the aperture.
Description: The egg-shaped protoconch is about as wide as high and made of four well-rounded volutions, sutures marked by a thin spiral cord. The whorls of the high spired teleoconch are a little convex with faint axial ornament or growthlines, crossed by weak spiral lines that are strongest near the upper suture. The last whorl is bulging, with two strong ribs behind the aperture. The wing is attached to the penultimate whorl; a lobe of callus starting from the inner lip extends above the wing; the inner lip only little callused. The holotype is 20 mm high and the last whorl without wing is 9 mm in diameter.

Mexopus robustus n. sp.

Plate 21, Figures 4-5

Holotype: IGM 7795, figured at pl. 21, figs. 4-5.
Material: 13 specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: This species looks quite robust compared with the fragile *Mexopus mexicanus* n. sp.
Diagnosis: Aporrhaid gastropod with almost straight sided whorls and deep sutures; upper margin of the whorls keeled, whorls with weak axial and spiral ornament.
Description: Medium to large shell with nine or more volutions. Whorls straight or little convex with weak axial ribs or growthlines, keeled at the upper suture where are also some spiral lines. The sutures are deep and varices occasionally occur. The wing is attached some two to four whorls high on the spire, with a thick tongue of callus on the inner side. The axial ribs of the last whorl bend forward when reaching the base that shows only spiral lines. The holotype is 32 mm high and 14 mm in diameter.
Remarks: Distinguished from *Mexopus mexicanus* n. sp. by its deep sutures and more straight-sided whorls.

Discussion: Among the aporrhaids reported herein, *Pterocerella* apparently is restricted to Campanian and Maastrichtian strata of the North Atlantic, while *Anchura* is known from the Albian to the Paleocene (ALLISON 1955, ELDER & SAUL 1996) and reached a cosmopolitan distribution in the temperate to tropical realm. On the other hand, members of the newly introduced genus *Mexopus* appear to be restricted to their type locality, despite their large larval shell. The uncertainties concerning *Lispodesthes*' placement in the Pugnellidae or

Aporrhaidae have been discussed by KIEL & BANDEL (1999), and the new species does not help to solve this problem.

Family Strombidae RAFINESQUE, 1815

Strombids are almost indistinguishable from aporrhaids by means of shell-shape alone (and thus in the fossil record). Living individuals differ in the mode of locomotion, strombids use the operculum to pull themselves forward, aporrhaids don't.

Genus *Rimella* AGASSIZ, 1840

Type species: *Rostellaria fissurella* (LINNÉ) from the Eocene of the Paris Basin, France.
Description: The moderately sized, high spired shells has convex whorls and may show varices. The outer lip is smooth and only slightly expanded. A canal extents from the aperture up to the apex where it bents downwards.
Remarks: *Hippocrenes* MONTFORT, 1810 from the Maastrichtian of the Netherlands (KAUNHOWEN 1897), Yugoslavia (PETHÖ 1906) and Egypt (own data) seems to be closely related to *Rimella*. *Hippocrenes* distribution during the Upper Cretaceous is restricted to the European Tethys whereas *Calyptraphorus* occurred on the southern shores of the Tethys between America and India (PERRILLIAT & VEGA 1997). *Rimella* seems restricted to the western Tethys Realm. Their relation to the Turonian *Rostellaria monopleurophila* ROEMER, 1889 from Texas remains obscure.

Rimella mexcala n. sp.

Plate 18, Figures 1-3

1980 *Drepanochilus texanus* STEPHENSON – ALENCASTER: 40, fig. 5.
2000 *Calyptraphorus*? sp. - PERRILLIAT, VEGA & CORONA: 13, pl. 5, fig. 30; pl. 6, fig. 1.

Holotype: IGM 7783, figured at pl. 18, fig. 2.
Paratype: IGM 7782 figured at pl. 18, figs. 1, 3.
Material: 14 specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named after its occurrence in the Mexcala formation, Mexico.
Diagnosis: Medium sized shell with strong axial ornament and spiral grooves near the upper sutures.
Description: The conical protoconch consists of four convex whorls with a weak ridge in the lower fourth. It is 1.5 mm high and a little wider. The teleoconch is high spired and formed of seven volutions with strong axial ribs. Two spiral grooves cross the ribs near the upper suture; spiral lirae can also be present and are strongest near the lower suture. The sutures are deep. Two varices per volution are common. A strong varix occurs opposite the aperture. Spiral lines become the dominant ornament on the base of the last whorl. The aperture continues adapically into a canal that is attached to the spire. This canal almost reaches the apex and bents downward at the end. The holotype is 17 mm high and its last whorl has a diameter of 9 mm.
Remarks: The adapical canal that curves down near the apex assigns this species to *Rimella* and distinguishes it from *Alarimella* SAUL, 1998. Also its axial ribs are generally opisthocline rather then prosocline as it is the case with *Alarimella*. A figure of *Aporrhais saharica* QUAAS, 1902 shows no varix opposite the aperture and may be a juvenile specimen of *Hippocrenes*. The Eocene species of *Rimella*

figured by GARDNER (1945, pl. 17, figs. 7-9) differ in having much weaker sutures. The type species *Rimella fisurella* (LINNÉ, 1758) from the Paris Basin shows finer ribs, weaker sutures and no subsutural spiral cords. STEPHENSON (1941) described three specimens as "*Drepanocheilus*" *corbetensis* STEPHENSON, 1941 from the Navarro Group of Texas. They may represent juvenile specimens of *Rimella*.

Genus *Calyptraphorus* CONRAD, 1857

Type species: *Rostellaria velata* CONRAD, 1833, by subsequent designation (COSSMANN 1904), from the Eocene of Claiborne, Alabama, USA.
Description: The moderately sized, high spired shell has straight to convex whorls which may be axially sculptured or smooth. A canal extents from the aperture up to the apex where it bents downwards. In fully grown adults, callus may cover the entire shell and a lobe of callus might be attached to the spire.

Calyptraphorus binodiferus PERRILLIAT & VEGA, 1997

Plate 18, Figures 4-5; Plate 19, Figures 1-3

1997 *Calyptraphorus binodiferus* PERRILLIAT & VEGA: 121, pl. 1, figs. 1-8; pl. 2, figs. 1-8.

Material: 123 specimen in all stages of ontogeny from the Maastrichtian of Temalac, Mexico.
Description: The conical protoconch has four convex whorls, embryonic part about 0.13 mm across, the larval shell is 2 mm high and 1.5 mm wide. The teleoconch is formed of six whorls with a decreasing number of ribs towards the later whorls. The last whorl shows no ornament except for two strong tubercles behind the aperture. A large grooved callus develops from the aperture up the spire and curves downwards just before reaching the apex, leaving two or three initial whorls free of callus; the grooved callus continues down the spire and ends on the last whorl just behind the two strong tubercles. A large lobe of callus develops on the abaxial side on the spire. The largest specimen is 30 mm high and 18 mm wide.
Remarks: Evolution and relationships of this species have been extensively discussed by PERRILLIAT & VEGA (1997).

Discussion: The early history of the Strombidae has long been a matter of debate. Their adult shells are often very similar, and also the protoconch of Recent *Strombus* LINNÉ, 1758 is quite variable in shape (see BANDEL et al. 1997) and cannot be distinguished without doubt from those of the aporrhaids figured herein. Members of the Pugnellidae, once considered the earliest strombids (WENZ 1938-1944, SOHL 1960) have been united to form their own family. They may have relationships to certain Struthiulariidae rather than the Strombidae (KIEL & BANDEL 1999).
Two genera from the Late Cretaceous of California were considered to intermediate between the Aporrhaidae and the Strombidae (ELDER 1990, SAUL 1998). The latter found the juvenile ornament of *Calyptraphorus binodiferus* similar to that of *Alarimella veta* (PACKARD, 1922). This observation cannot be confirmed. *Calyptraphorus* has a wider apical angle, much weaker but more numerous ribs which are more curved than those of *Alarimella veta*. Also, there are no spiral lirae on the base of *Calyptraphorus*. Based on some poorly preserved specimens, ELDER (1990) proposed *Tibiaporrhais* ELDER, 1990 to connect *Tibia* RÖDING, 1798 with aporrhaids.
Calyptraphorus, Rimella and *Hippocrenes* MONTFORT, 1810 are supposed to represent members of the Strombidae, are most common in the Paleogene, but were also present in the Late Cretaceous. They all have one character in common: A

canal which extends from the aperture almost to the apex, where it then bends downwards. JUNG & ABBOTT (1967) presumed a similar canal seen on *Terebellum terebellum*, would support a mantle-appendage which informs the animal whether it is buried or not. SAVAZZI (1991) concluded that such a canal indicates an infaunal mode of life. This character is considered here the unifying apomorphy of the early strombids, whereas the ”stromboid notch” is apparently not yet developed.

Family Pugnellidae KIEL & BANDEL, 1999

Species of the Pugnellidae are characterised by a low spire, an enlarged and reinforced outer lip, often with horn-like extensions, and a callus-coated inner lip. The callus is commonly spread out to cover large parts of the shell. Except for a small group which may have survived into the Paleogene of the cool-temperate Weddellian Province, the Pugnellidae were an cosmopolitan, exclusively Late Cretaceous group (KIEL & BANDEL, 1999).

Genus *Torgnellus* OLLSON, 1944

Type species: *Torgnellus peruvianus* OLLSON, 1944 from the Maastrichtian of Paita in northern Peru.
Description: The medium-sized, pugnellid shell has a short spire and adult shells are completely covered with callus. The aperture is long with parallel sides. The rostrum is straight and the outer margin of the outer lip is thickened.

Torgnellus sp.

Plate 22, Figures 1-2

Material: One specimen from the Maastrichtian of Temalac, Mexico (IGM 7796).
Description: Pugnellid shell with heavy callus cover and no ornament; aperture long, narrow and little concave. The callus that covers the spire is a little bent to the right side in apertural view. The shell is 25 mm high and the last whorl without wing is 13 mm in diameter.
Remarks and discussion: This species is assigned to *Torgnellus* due to the absence of ornament and its strong resemblance to *Torgnellus peruvianus* from the Maastrichtian of the Paita Peninsula, northern Peru. The occurrence of *Torgnellus* was previously restricted to this Peruvian locality. If the new species is correctly assigned to this genus, the geographic range *Torgnellus* extends north across the equator.

Family Xenophoridae TROSCHEL, 1852

The low, trochiform shells often have foreign objects like gastropod or bivalve shells, or rocks attached to it.

Genus *Aacanthoxenophora* PERRILLIAT & VEGA, 2000

Type species: *Acanthoxenophora sinuosa* PERRILLIAT & VEGA, 2000, described below.
Description: The shell is small and conical, foreign objects are attached to the first three teleoconch whorls, or the imprints of these can be seen. From the fourth whorl onwards, attachment of objects ceases and the development of spines begins.

Acanthoxenophora sinuosa PERRILLIAT & VEGA, 2000

Plate 22, Figures 3-5

2000 *Acanthoxenophora sinuosa* PERRILLIAT & VEGA, figs. 3-12.

Material: About 25 specimens from the Maastrichtian of Temalac, Mexico.
Description: The smooth, low conical protoconch consists of three and a half volutions, is 1.5 mm wide, 0.7 mm high and the embryonic part measures 0.1 mm across. The first whorl is almost planispiral, then increasing fast in size. The first two to three whorls of the teleoconch show moulds where foreign shells had been attached. One specimen shows remains of a *Turritella* (pl. 22, fig. 3). The moulds disappear when the first spines develop. The first two or three spines are pointing forward and little downward and appear as single spines in the lower half of the whorl. Later there are usually two of three spines above each other; the upper ones usually pointing forward, the lower one sometimes backwards. The spiny whorls show very oblique growthlines. The largest specimen is 18 mm high and 13 mm in diameter without spines.
Remarks: The embryonic shell is smaller and the larval shell larger than of Recent species. Protoconch and the non-spiny early teleoconch whorls resemble *Xenophora leprosa* (MORTON, 1834) from the Coffee Sand of Mississippi as figured by DOCKERY (1993, pl. 20, figs. 1-4). Those figured by SOHL (1960, pl. 10, figs. 19, 23-27) have a much lower spire.

Discussion: The Jurassic genera *Jurassiphorus* COSSMANN, 1915 and *Lamelliphorus* COSSMANN, 1915 have often been discussed as earliest Xenophoridae (COSSMANN 1915, WENZ 1938-44, PONDER 1983) although they do not show any evidence for agglutinated particles. In the case of *Jurassiphorus*, GRÜNDEL (1997a) showed that the protoconch of the type species *Jurassiphorus cailliaudanum* D'ORBIGNY, 1853 is of the archaeogastropod-type. GRÜNDEL (1997a) also re-evaluated *Lamelliphorus ornatissimus* D'ORBIGNY, 1850, type species of *Lamelliphorus*. Its protoconch was too badly preserved for speculations on the taxonomic position of that genus. The earliest typical *Xenophora* according to PONDER (1983) is a specimen described but not figured by STEPHENSON (1952) from the Cenomanian of Texas. It yields moulds that may have been caused by agglutinated shell fragments (STEPHENSON 1952: 152). The protoconch is described as low, smooth, trochiform and made of about one and a half volutions. A typical xenophorid protoconch today is multispiral, but smaller protoconchs can be produced by a lecitotroph early ontogeny (BANDEL 1982).
WENZ (1938-44) placed the Xenophoridae in the superfamily Stromboidea without explanation. Based on adult shell characters alone, MORTON (1958) considered *Xenophora* and *Calyptraea* as related to each other and withdrew the Xenophoridae from the Stromboidea. Numerous workers followed this suggestion (TAYLOR & SOHL 1962, BEESLEY et al. 1998). But MORTON (1958) also acknowledged wide disparity in life-habit between the Xenophoridae and Calyptraeidae LAMARCK, 1809. BERG (1974) studied locomotion and shell-righting behaviour among other habits of strombid gastropods and considered *Xenophora* closely related to the Strombidae. Protoconch morphology is also inconsistent with a separation of xenophorids and stromboideans. *Xenophora* possesses a low, trochiform protoconch with typically three to four volutions and a diameter of 0.9-1.2 mm. The embryonic shell measures 0.08-0.11 mm across (BANDEL 1993c, herein). A calyptraeid protoconch consist of 1.5 to 1.7 volutions, is smooth and rather planispiral and has an embryonic part measuring about 0.18 mm across (BANDEL

& RIEDEL 1994). With their protoconch morphology, habits and anatomy taken into account, the Xenophoridae are here considered members of the Stromboidea.

Order Neomesogastropoda BANDEL, 1991

Family Naticidae FORBES, 1838

This family comprises globular and umbilicate shells with a semicircular aperture. The umbilicus may be covered with callus. Naticidae today are found from the tropics to the coolest polar regions (POWELL 1951, ABBOTT 1974) and their activities are easily recognised by drillholes in mollusc shells.

Subfamily Gyrodinae WENZ, 1938

Genus *Gyrodes* CONRAD, 1860

Subgenus *Gyrodes* (*Gyrodes*) CONRAD, 1860

Type species: *Gyrodes supraplicata* CONRAD, 1858
Description: The subglobose, low spired shell has a deep umbilicus with crenulate and sharp umbilical margin and is crenulated near the suture. Growthlines near the suture may be notched. The aperture is oval in outline and inclined.

Gyrodes supraplicatus (CONRAD, 1858)

Plate 23, Figures 1-2

2000 *Gyrodes supraplicata* CONRAD - PERRILLIAT, VEGA & CORONA: 14, fig. 6.8

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The gyrodiform shell consists of six volutions. The early whorls are smooth and well-rounded, the later develop a weak, beaded sutural ridge, a shallow subsutural groove with curved growthlines, a strongly beaded shoulder and strong transverse growthlines. The umbilicus is wide, rimmed by a strong funicle and shows a second, weaker funicle inside. The incomplete shell is 9 mm high and 10 mm wide.
Remarks: This species is widely distributed in Campanian and Maastrichtian sediments on the Gulf coast plains (PERRILLIAT et al. 2000). Its closest relative in California seems to be *Gyrodes* (*G.*) *dowelli* WHITE, 1889 of Turonian age (POPENOE et al. 1987) but this species has smooth whorl sides. A similar species from Europe is *Natica cretacea* GOLDFUSS, 1841 as figured by KAUNHOWEN (1897: pl. 5, fig. 8a).

Subgenus *Gyrodes* (*Dockeryella*) BANDEL, 1999

Type species: *Gyrodes (Dockeryella) major* WADE, 1926 from the Ripley Formation, Tennessee, USA.
Description: This subgenus is distinct from *Gyrodes* s.s. by the lack of a subsutural groove and a non-crenulated umbilical margin (BANDEL 1999).

Gyrodes (*Dockeryella*) cf. *major* (WADE, 1926)

Plate 23, Figures 3-4

2000 *Gyrodes major* WADE - PERRILLIAT, VEGA & CORONA: 13, fig. 6.7

Material: Three specimens from the Maastrichtian of Temalac, Mexico.
Description: This gyrodiform shell has six or more volutions and a very low spire. The low subsutural ramp is crenulated with slightly curved growthlines. The

umbilicus is wide and bordered with a smooth funicle and a reflected inner lip. A second, crenulated funicle is present inside the umbilicus and corresponds with a notch on the inner lip. The body whorl shows weak transverse growthlines. The shell is 10 mm high and 11 mm wide.

Subfamily Naticinae FORBES, 1838

Genus *Natica* SCOPOLI, 1777

Type species: *Nerita vitellus* LINNÉ, 1758, Recent from the Indo-Pacific.
Description: The smooth and globular shell has an umbilicus of moderate size which may be covered with a plug of callus. The aperture is semicircular.

Natica cf. *perspecta* WHITFIELD, 1865

Plate 23, Figures 5-6

1945 *Natica perspecta* WHITFIELD – GARDNER: 171, pl. 14, fig. 11.

Material: One specimen from the Maastrichtian of Temalac, Mexico.
Description: The moderately sized, naticiform shell has five smooth and well-rounded volutions, very shallow sutures, and a weak subsutural constriction. Growthlines are transverse, the umbilicus is deep with a well-rounded margin, and the inner lip is lightly callused. The shell is 11 mm high and 12 mm high.
Remarks: This species is quite unique among Upper Cretaceous Naticidae. All Californian species assigned to *Natica* by POPENOE et al. (1987) have a funicled umbilical margin, and a more angular whorl outline. *Natica perspecta* from the Paleocene of the Midway Formation of north-eastern Mexico (see GARDNER 1916) is strikingly similar, even in size.

Discussion: Three species of the Naticidae and also naticid larval shells were discovered in the fauna of Temalac. Surprisingly, drillholes like those caused by these predatory gastropods today, are almost absent in the molluscs of Temalac. Also in Torallola, *Gyrodes*-like shells occur and drillholes are few. Undoubted naticid drillholes are known from the Albian of England (TAYLOR et al. 1983) and the first typical naticid protoconch is known from the Santonian (BANDEL 1993c). SOHL (1969) and TAYLOR (1981) presumed that earlier Naticidae had different modes of feeding. It has recently been revealed that one or two gastropod groups with naticoid shells – which also occurred in the Late Cretaceous – apparently do not belong to the Naticoidea. Preliminary investigations of the soft body of *Globularia fluctuata* indicated characteristics of the Architaenioglossa (KASE 1990). *Pseudamaura* yields a protoconch different from Naticidae and is now considered a cerithioidean with uncertain affinities (KOWALKE & BANDEL 1996, BANDEL 1999). As a result, many Late Cretaceous ”naticids” may in fact belong to other groups, which could partly explain the absence of drillholes at sites where those ”naticids” are found.

Family Cypraeidae RAFINESQUE, 1815

Genus *Cypraea* LINNÉ, 1758

Type species: *Cypraea tigris* LINNÉ, 1758 living in the Indopacific.
Description: Adult shells are convolute, shiny and smooth, and the aperture occupies the entire length of the shell and is bordered with denticles.

Cypraea s.l. sp.

Plate 24, Figures 1-2

Material: Two specimens from the Campanian of Torallola, Spain.
Description: The spire is elevated and consists of convex whorls with two spiral ridges near the sutures and fine axial lines. Only the last whorl becomes convolute and encloses the spire. The last whorl is smooth, the aperture narrow with dented margins, and the inner lip is flat and callused. The posterior end of the aperture bents to the left above the apex. The shell is 1.0 mm high.
Remarks and discussion: With its elongate apertural ends it resembles *Bernaya* (*Protocypraea*) *mississippiensis* GROVES, 1990 from the Campanian of the Coffee Sand, Mississippi. The Cypraeidae apparently have not changed much since their first appearance in the Cenomanian (ANDERSON 1958).

Family Trichotropidae GRAY, 1850

Genus *Trichotropis* BRODERIP & SOWERBY, 1829

Type species: *Trichotropis bicarinata* (SOWERBY), Recent, from the Japanese Coast (WENZ 1938-44: fig. 2618).
Description: The turbiform shell has angular whorls and an umbilical slit. It is sculptured with two keels and shows fine growthlines. The larval shell usually exceeds 1 mm in diameter, is smooth and its top is flat.

Trichotropis konincki (MÜLLER, 1851)

Plate 24, Figure 7

1888 *Turbo konincki* MÜLLER - HOLZAPFEL: 149, pl. 15, figs. 6-9.

Material: Three specimens from the Campanian of Torallola, Spain.
Description: The small, biconical shell has four angular volutions. The later whorls are marked by two strong beaded keels, of which the lower one is obscured by the succeeding whorl. The shell is covered by a carinate sculpture of closely spaced axial and spiral cords. The basal slope is straight, the aperture is lenticular and the inner lip callused. The umbilical slit is more or less well developed. The shell is 1.5 mm wide and 2.5 mm high.
Remarks: Although the specimens figured by HOLZAPFEL (1888) show strong axials below the first keel, they are all bigger but show no axials on their earliest whorls. The specimens illustrated here probably represent juveniles of *Trichotropis koninckii*. The South African *Lysis capensis* RENNIE, 1930 shows three spiral keels and has no axial ornament except growhtlines. *Trichotropis squamosa* (GABB, 1876) figured by DOCKERY (1993: pl. 17, figs. 11-12) intermediates between the South African and Spanish species. It shows two keels and an umbilical fasciole like the Spanish and no axial sculpture but only growthlines like the South African one.

Superfamily Cassoidea LATREILLE, 1825

The Cassoidea have developed a larval pallial tentacle which allows the veliger to secrete, form fix and dissolve periostracal sculptural elements (RIEDEL 1995). This feature is considered the only synapomorphy of the Cassoidea by RIEDEL (1995), while BEU (in RIEDEL 1995) suggested episodic growth of the teleoconch as another. Cassoid larval shells are the largest of all gastropods with diameters from 1 to 5.4 mm (RIEDEL, 1995). They are smooth or sculptured with a cancellate pattern. The adult shells are fusiform, often show varices and in a few cases the columella has a fold, otherwise it is smooth.

Family Ranellidae GRAY, 1854

Genus *Gyrineum* LINK, 1807

Type species: *Murex gyrinum* LINNÉ, 1758
Description: The fusiform to turbinate shell has angular whorls and two opposing rows of channelled varices. The aperture is channelled at both ends with a short, rather straight columella and anterior canal. Sculpture consists of crenulated spiral threads.

Gyrineum gwinae DOCKERY, 1993

Plate 24, Figure 3

1993 *Gyrineum gwinae* DOCKERY: 77, pl. 21, figs. 6, 7, 9; pl. 22 figs. 1-5.

Material: One specimen from the Campanian of Torallola, Spain.
Description: The moderately sized shell has at least six volutions with two varices per whorl. The axial and spiral cords form a nodular pattern. The axial ribs disappear below the sixth spiral cord on the body whorl where undisturbed spiral cords follow, and there are three to four fine spiral lirae between all spiral cords visible. The aperture is lenticular and the inner lip lightly callused but body ornamentation shines through. The shell is 28 mm high and 16 mm wide.
Remarks: The protoconch of the one specimen available is not preserved, but the adult shell is about four times larger than the biggest one figured by DOCKERY (1993).

Genus *Sassia* BELLARDI, 1872

Type species: *Triton appeninicum* SASSI, 1827
Description: The fusiform shell has rounded whorls and beaded spiral ornament. The whorls may be slightly distorted and have a varix every 270°.

Sassia praegranosum (COTTREAU, 1922)

Plate 24, Figures 4-6

1922 *Euthriofusus* (*Sassia*) *praegranosum* COTTREAU: pl. 9, figs. 4-7.

Material: Four specimens from the Campanian of Torallola, Spain.
Description: The protoconch consists of at least three convex whorls with a fine and dense cancellate sculpture, and is 1.2 mm wide and about 1 mm high. The teleoconch is fusiform, made of six convex, little distorted volutions and shows varices about every 240°. Sculpture consists of three strong spiral cords, numerous fine spirals in between and axial ribs that form tubercles when crossing the spirals. The parietal lip is callused and with four denticles of which the outer one is the strongest. The shell is 21 mm high and 12 mm wide.
Remarks: The specimens from Madagascar figured by COTTREAU (1922) are badly corroded and about two times larger than those reported here, but the sculpture appears fairly similar. The large larval shell of this Spanish species indicates that it could well have travelled from Spain to Madagascar or vice versa. Today's cassoid larvae may stay up to one year in the plankton (RIEDEL 1995 and references therein).

Genus *Anomalofusus* WADE, 1926

Type species: *Anomalofusus substriatus* WADE, 1926 from the Ripley formation, USA.

Description: The globular, multiwhorl protoconch has a diameter of at least 1 mm and is smooth. The teleoconch is fusiform, sculptured by sinuous axial ribs which are crossed by fine spiral lirae. The columella is smooth and the outer lip is dented within.

Anomalofusus alani n. sp.

Plate 23, Figures 7-9

Holotype: The specimen figured at pl. 23, fig. 8.

Material: Six specimens from the Maastrichtian of Temalac, Mexico.

Derivation of name: Named in honour of ALAN G. BEU, who contributed to our knowledge of Cassoidean evolution.

Diagnosis:. A small *Anomalofusus* with spire and last whorl of equal height and a decreasing number of axial ribs from early to later whorls.

Description: The large, globular protoconch consists of two and a half smooth volutions and is 1.7 mm high and 1.3 mm wide. The teleoconch consists of three and a half convex volutions with the spire making half of the entire shell height. It is sculptured with strongly prosocline axial ribs, their number decreases with increasing whorl size, there are eleven on the body whorl. They are crossed by six spiral cords and fine lirae on the later whorls. Axial ribs fade towards the base where spiral cords dominate. The aperture is drop shaped, ends anteriorly in a twisted canal and the inner lip is lightly callused but underlying ornament shines through. The holotype is 14 mm high.

Remarks: *Anomalofusus subnodosus* SOHL, 1964 appears to be the closest relative of this new species. *A. subnodosus* possesses a very similar ornament but the shell is more slender.

Genus *Cantharulus* MEEK, 1876

Type species: *Fusus vaughani* MEEK & HAYDEN from the Campanian of the Fox Hill group, North Dakota, USA (according to WENZ 1938-44).

Description: The fusiform shell has angular whorls formed by a subsutural ramp (but no constriction) and a rounded base. The aperture is elongate egg-shaped and the columella has no folds.

Remarks: *Anomalofusus* lacks the subsutural ramp of *Cantharulus* and consequently its whorls are more rounded, additionally, *Anomalofusus* appears to have a higher spire.

C*antharulus* sp.

Plate 23, Figure 10

Material: One specimen from the Maastrichtian of Temalac, Mexico.

Description: The fusiform shell has six volutions, earlier whorls are convex with straight axial ribs and four spiral cords which are made of two parallel lines, the first cord is weaker than the following three. Later whorls are more angular, ribs are curved to sinuous, the basal slope is moderately constricted and forms a siphonal canal. The figured shell is 19 mm high and 11 mm wide.

Remarks: The curved to sinuous ribs are unusual for the genus. A similar species was described as *Clinura anassa* MURPHY & RODDA, 1960 from the Albian of California and was considered as the oldest turrid. This appears doubtful.

Neomesogastropod larval shell type 1

Plate 23, Figure 11

Material: One specimen from the Maastrichtian of Temalac, Mexico.
Description: The embryonic part measures about 0.15 mm across, the larval shell consists of three and a half volutions and is sculptured with two fine spiral cords and equally strong axial stripes; the base has four spirals. The specimen is about 0.8 mm high and wide.
Remarks: This type of larval shell is found mainly on Cassoideans (see RIEDEL, 1995).

Neomesogastropod larval shell type 2

Plate 23, Figures 12-14

Material: Numerous specimens from the Maastrichtian of Temalac, Mexico.
Description: The initial portion measures 0.12 mm across, the larval shell is about 0.8 mm wide and 0.6 mm high, made of three volutions and sculptured with a cancellate pattern which continues on the rounded and umbilicate base.
Remarks: A similar larval shell from the Claiborne Eocene was figured by BANDEL (1993c: pl. 12, fig. 4) and considered as ”protoconch of an unknown Caenogastropod”.

Discussion: Three groups of Late Cretaceous cassoid gastropods where protoconch morphology is known occur in Torallola and Temalac.
Charonia/Sassia-like shells with distorted teleoconch and a cancellate protoconch. A single species belongs to this group: *Eutritonium* (*Sassia*) *praegranosum*, reported by COTTREAU (1922) from the Campanian of Madagascar, and herein from the Campanian of Torallola. Although BEU (1988: 89) considered this species as the earliest undoubted *Distorsio*, its grade of distortion does not exceed that of Recent *Sassia*, *Charonia* or *Cymatium*. The aperture of the specimen from Torallola shows fine columellar and parietal denticles but not the heavy dentition of *Distorsio*. Its protoconch shows cancellate sculpture and resembles that of *Gyrineum gwinae* (see below).
G*yrineum gwinae* from Torallola is a species with undistorted whorls and a varix every 180°. Its protoconch with cancellate sculpture was documented by DOCKERY (1993: pls. 21, 22) from the Coffee Sand Campanian (USA).
Of the widespread *Anomalofusus/Cantharulus*-clade, *Anomalofusus alani* n. sp. from Temalac is a typical representative and shows a smooth and large protoconch like Recent *Sassia* or *Distorsio* (compare RIEDEL 1995: figs. 7, 9, 12, 35). Its teleoconch has undistorted whorls, is without or with only very weakly developed varices, and is sculptured with double-lined spirals characteristic for many ranellids.
The earliest cassoid species is TONNA.1, a specimen figured by SCHRÖDER (1995: pl. 7, figs. 3, 4) from Aptian/Albian-boundary layers in Germany. It has a large, cancellate protoconch and only half a teleoconch-whorl preserved, so distortion or varices are indeterminable and an assignment to *Charonia*/*Sassia* or *Gyrineum* are impossible.
These data support the earlier suggestion of BEU (1988) and RIEDEL (1995) that the *Sassia-Charonia*-clade of the Ranellidae represents the oldest lineage within the

Cassoidea. The grade of distortion of the teleoconch among the Late Cretaceous cassoids does not exceed that of living *Charonia*, *Cymatium* or *Sassia*. Contrary to the assumptions of BEU (1988) and RIEDEL (1995, 2000), there is no evidence for a Cretaceous origin of *Distorsio*. Also *Plesiotriton* (Cancellariidae) shows distorted whorls (BEU & MAXWELL 1987: pl. 25), so this feature alone appears insufficient for identifying *Distorsio* in the fossil record.

The *Anomalofusus/Cantharulus*-clade is here assigned to the Ranellidae. They may represent a distinct Late Cretaceous group where protoconch-sculpture and varices were apparently reduced early in their evolutionary history – assuming these features are the plesiomorphic condition in cassoidean gastropods. A possible Paleocene descendant of this group may be *Pseudofax* FINLAY & MARWICK, 1932 from New Zealand and Patagonia (GRIFFIN & HÜNICKEN, 1994). The oldest species which may belong to this clade is *Clinura anassa* MURPHY & RODDA, 1960 from the Albian of California. The description and the figure provided by MURPHY & RODDA (1960) agree well with *Cantharulus* sp. 2 from Temalac, especially regarding the shape of the growthlines, the three primary spirals below the angulation and ornament in general. This species was previously considered the oldest turrid (MURPHY & RODDA 1960, POWELL 1964), however, the protoconch of this questionable species is unknown, so a more reliable classification is not yet possible.

The presence of the same species of *Sassia* in Spain and Madagascar in the Campanian, the fairly wide distribution of *Cantharulus* and *Anomalufusus*, and their large larval shells indicate that cassoideans attained their extreme teleplanktic larval-phase very early in their evolutionary history.

Order, superfamily and family uncertain

Genus *Lamelligyra* n. gen.

Type species: *Lamelligyra lamellaris* n. sp. n. gen. from the Campanian of Torallola, Spain described below.

Diagnosis: The fusiform shell is sculptured with several spiral ridges which may be regularly interrupted by spiny projections, and fine axial lamellae between the ridges. Varices occur every 120°. The inner lip bears two columellar folds, and also parietal folds or denticles.

Derivation of name: A *Gyrineum*-like shell sculptured with lamellae.

Remarks: The protoconch of the new genus *Lamelligyra* remains unknown, but its teleoconch shares characters of the Ranellidae (varices), the Plesiotritoninae (varices and columellar folds) and the Trichotropidae (ornament of spiral keels and axial lamellae).

Lamelligyra lamellaris n. sp.

Plate 24, Figures 8-9

Holotype: The specimen illustrated in pl. 24, figs. 8-9.

Material: Two specimens from the Campanian of Torallola, Spain.

Derivation of name: Named for its lamellar sculpture.

Diagnosis: As for the genus.

Description: Protoconch unknown. The teleoconch is fusiform and consists of six or more whorls. Sculpture consists of two keels which forms a hexagonal spiral when viewed apically, the corners may develop spines. The upper keel is the stronger one and the body whorl shows two more such keels. Varices occur every 120°, e.g. every second corner; and axially there are fine lamellae. The columella bears two folds, there is one parietal fold and the parietal part of the aperture shows fine denticles. The holotype is 23 mm high.

Genus *Morea* CONRAD, 1860

Type species: *Morea cancellaria* CONRAD, 1860.
Description: The low-spired shell is egg-shaped, sculptured with a cancellate pattern and has an umbilical slit. The columella is smooth.

Morea sp.

Plate 29, Figures 4-5

Material: Two specimens from the Campanian of Torallola, Spain.
Description: The small, conical spire has rather straight whorl-sides. The body whorl is large, convex and sculptured with a cancellate pattern. The protoconch is bulbous, consists of one and a half whorls and the transition to the teleoconch is indistinct. The shell is 11 mm high and 8 mm wide.

Discussion: SOHL (1964: 175) discussed the controversial familiar assignments of *Morea*. Accordingly, it was placed within the Cancellariidae (TRYON 1883), the Purpuridae (COSSMANN 1925, WADE 1926), the Drupinae of the Muricidae (WENZ 1941) and the Moreidae (STEPHENSON 1941), a family which was then considered as subfamily of the Muricidae by SOHL himself. More recently, BANDEL (1993c: 38) on one hand pointed out that *Morea*'s protoconch is like that of *Schizobasis*, *Weeksia* and *Sargana*, which are similar to that of *Trichotropois*. On the other hand, BANDEL (1993c: 39) considered *Morea* a possible neogastropod. However, the protoconch of *Morea* has not yet been figured and the one of the species described below is of the lecithotrophic type, so it does not help to the solve the problem.

Genus *Maturifusus* SZABO, 1983

Type species: *Maturifusus densicostatus* SZABO, 1983 from the Bajocian (Middle Jurassic) of Hungary.
Description: The fusiform shells are sculptured with axial and spiral ornament. The protoconch is large, consists of several whorls and is sculptured with two spirals.
Remarks: Due to its bucciniform adult shell, SZABO (1983: 44) considered his new genus *Maturifusus* as an early member of the Buccinidae. Unfortunately, the protoconch of the type species is not preserved. SCHRÖDER (1995: pl. 4, figs. 17-20) described a new species, *Maturifusus szaboi* SCHRÖDER, 1995 from the Aalenian (early Middle Jurassic) and figured its protoconch. It is large, conical and resembles that of the Pyrifusidae, except for its two fine spiral cords. Another new species, figured by GRÜNDEL (1998b: pl. 7, figs. 5-8) from the Oxfordian shows a similar protoconch with the two spirals well developed. Both SCHRÖDER (1995) and GRÜNDEL (1998b) doubted its placement within the Buccinidae, however, considered it as a member of the Neogastropoda. Also RIEDEL (2000: 116) discussed *Maturifusus* as a possible ancestor of the "higher Caeongastropoda" exclusive Naticoidea, Cypraeoidea and Lamellaroidea. Spirals on the larval shell are today known from the Nassariidae IREDALE, 1916 (BANDEL et al. 1997), however, according to RIEDEL (2000: 185f) this group is known only since the Eocene.

Maturifusus? sp.

Plate 25, Figure 1

Material: Two specimens from the Campanian of Torallola, Spain
Description: The conical protoconch is about 1 mm high and wide, has convex whorls with deep sutures and two spiral cords per whorl. Only one teleoconch whorl is preserved and shows about 20 axial ribs on the periphery, crossed by about nine fine spirals. The entire shell is 2.2 mm high.
Remarks: Compared with the Jurassic members of *Maturifusus*, where spiral and axial sculpture on the teleoconch are of about equal strength, the spirals are much finer on the species figured here.

Discussion: *Maturifusus* is herein first reported from the Late Cretaceous. This species, like those figured by SCHRÖDER (1995) and GRÜNDEL (1998b), has two spirals on its otherwise *Pyrifusus*-like protoconch. Therefore, it appears more likely that *Maturifusus* represents a Mesozoic side-branch of the neogastropod-stem group rather than a direct ancestor.

Order Neogastropoda THIELE, 1928

Family Cancellariidae GRAY, 1853

The fusiform shells have a cancellate sculpture, the inner lip of the aperture shows columellar and parietal folds, the protoconch is truncate-conical to flat-topped. Cancellariids have modified their radula into a long, hollow sting which is used to suck liquids like blood or yolk.

Genus *Cancellaria* LAMARCK, 1799

Type species: *Cancellaria reticulata* LINNÉ, 1758.
Description: As for the family.

Cancellaria puimanyonsia n. sp.

Plate 25, Figures 2-3

Holotype: The specimen illustrated in pl. 25, figs. 2-3.
Material: Four specimens from the Campanian of Torallola, Spain.
Derivation of name: Named after the Puimanyons Olisthostrom in Spain.
Diagnosis: The protoconch consists of two and a half volutions with the initial half whorl measuring about 0.3 mm across. The entire protoconch is about 1 mm high and wide and the transition into the teleoconch is gradual. The large initial portion and the gradual transition into the teleoconch indicate lecithotrophic development. The adult shell has four convex volutions and is sculptured with three spiral cords and axial ribs of increasing number. The inner lip is callused, and possesses one parietal fold and two columellar folds. The shell is 6.5 mm high.

Cancellaria nissenae n. sp.

Plate 30, Figures 1-4

Holotype: The specimen figured at pl. 30, fig. 3.
Material: Six specimens from the Maastrichtian of Temalac, Mexico.

Derivation of name: Named after SILKE NISSEN, Hamburg, who patiently helps with linguistic matters.
Diagnosis: A *Cancellaria* with two columellar and two parietal folds, a relatively high spire and a large aperture with the inner lip strongly callused.
Description: The protoconch is globular, about 1.5 mm wide, smooth, and made of three and a half volutions. The initial whorl is almost planispirally coiled and the transition to teleoconch is oblique. The teleoconch consists of three volutions, the spire is little lower than the aperture, whorls are convex, have numerous axial ribblets that are bent forward near the upper suture, and about ten spiral cords. The aperture is large, lenticular, with a broadly callused inner lip. The columella has two plates, and the parietal lip has a few ridges. The figured shell is 10 mm high and 5 mm wide.
Remarks: This new species is distinct from *Cancellaria macnairyensis* SOHL, 1964 from the Ripley formation by its longer and narrower aperture.

Discussion: The Cancellariidae have been placed within the Toxoglossa by TROSCHEL (1856-63) WADE (1926), and STEPHENSON (1941); in the Volutacea by WENZ (1938-44), SOHL (1964), and ABBOTT (1974), and within its own order Nematoglossa by OLSSON (1970). The most widely used classification today is that of PONDER (1973) who considered the Cancellarioidea to represent a distinct superfamily within the Neogastropoda. Lately, ROSENBERG et al. (1994) indicated a that *Cancellaria* may share a more recent common ancestor with Muricidae than with Buccinidae based on RNA sequences, while RIEDEL (2000) recognised similarities of anatomy and adult shell with the Mitridae. However, from the biological point of view there was never any doubt on *Cancellaria*'s position within the Neogastropoda.
The protoconch of *Cancellaria nissenae* n. sp. documented here from Temalac is large and the initial whorl is sunken into the following whorls. It resembles that of the neomesogastropod *Trichotropis* rather than that of any neogastropod. The similarity of *Trichotropis*' larval shell and that of *Cancellaria* was already noted by BANDEL & RIEDEL (1994). But these authors pointed out that the embryonic shell of *Cancellaria* has a pattern of tubercles, while the embryonic shell of *Trichotropis* is smooth. On the other hand, tubercles on the embryonic shell are not a unique feature of neogastropods, but occur also in the neomesogastropod *Natica* (see BANDEL 1999: pl. 2, figs. 1, 4, 5). The teleoconch of *Cancellaria* can be recognized since the Albian (MARLIÈRE 1939) and a flat-topped protoconch is reported herein from the Maastrichtian.
STEPHENSON (1952) described a flat-topped protoconch for *Paladmete* from the Cenomanian. The taxonomic position of this genus, however, has always been a matter of doubt. Its type species bears the ambiguous name *Trichotropis cancellaria* CONRAD, 1858 and – nomen est omen – was moved back and forth between the two groups (see SOHL 1964: 271 for directions). This is understandable as the protoconch is similar in both groups and its adult shell resembles that of *Cerithioderma* (Trichotropidae) just as well as that of *Admete* (Cancellariidae). Flat-topped protoconchs also occurs in other Cretaceous gastropods of doubtful taxonomic position, like *Sargana*, *Weeksia*, *Morea* and "*Ecphora*" *proquadricostata* (BANDEL 1993c).
The larval shells of modern cancellariids and trichotropids, however, only superficially resemble each other. Not only have the embryonic shells of the two groups different morphologies (BANDEL & RIEDEL 1994), also concerning the larval shell there is a marked difference. Trichotropid larvae develop a scaphoconch or echinospira, a periostracal cover around the inner, weakly calcified shell. No scaphoconchs are developed by cancellariids (or any other known

neogastropod). The similarities in the morphology of the larval shell might therefore be regarded as a matter of convergence.

Regardless of the probability of any of these scenarios, *Cancellaria* had already developed its typical protoconch-type at a time when most if not all other neogastropods (Toxoglossa and Rachiglossa) still possessed the conical and smooth type. The antiquity of this protoconch-type indicates that *Cancellaria* split earlier from the neogastropod stem-group than toxoglossa and rachiglossa, and supports a placement within its own superfamily.

Family Turridae SWAINSON, 1840

Turrid shells are slender, high-spired to biconical, the growthline shows are well-developed sinus subsuturally or peripherially. The radula of many Turridae has been modified to a poisonous arrow which is used to hunt prey.

Genus *Koenenia* HOLZAPFEL, 1888

Type species: *Koenenia speciosa* HOLZAPFEL, 1888 from the Vaals Greensands, Germany.

Description: Moderately sized, fusiform shells,the whorls have a subsutural ramp or collar on which the anal sinus is located. Sculpture consists of axial ribs crossed by spiral lines. There are no columellar folds. The multiwhorled protoconch is rounded conical, smooth and measures 0.6-0.8 mm in diameter.

Remarks: *Koenenia* was introduced by HOLZAPFEL (1888) for a Campanian species from the Vaals Greensands of Germany and assigned to the Pleurotomidae (=Turridae). Later, WENZ (1938-44) referred to this genus as *Beisselia* and placed it within the Pholidotominae (Volutidae). PILSBRY & OLLSON (1954) and SAUL & POPENOE (1993) doubted this position within the volutids. Holzapfel's original assignment is followed here due to the presence of a well-developed anal sinus and the lack of columellar plates.

Koenenia kilburni n. sp.

Plate 30, Figures 5-6

Holotype: The specimen illustrated in pl. 30, figs. 5-6.

Material: One specimen from the Maastrichtian of Temalac, Mexico

Derivation of name: Named after R. N. KILBURN, Pietermaritzburg, who worked on southern African turrids.

Diagnosis: The fusiform shell has a large subsutural ramp and strongly shouldered axial ribs.

Description: The high spired, fusiform teleoconch consists of six or more volutions. The whorls are anteriorly constricted to a ramp where the anal sinus is located, have 8-9 axial ribs crossed by four spiral cords, and a base with alternating strong and weak spiral lines. The aperture is subovate and the inner lip callused. The figured shell is 33 mm high and 17 mm wide.

Remarks: This new species differs from the very similar type species by its longer an straight siphonal canal. *K. octocostata* n. sp. is distinct in having a subsutural collar rather than a ramp, *K. kirsteni* n. sp. has finer and more numerous growthlines and the posterior constriction of the whorls is not as strong as in the previously discussed species. Also *K. multispirata* n. sp. has more numerous (seven to eight) and finer spirals than *K. kilburni*. Additionally, the maximum of the anal sinus of *K. multispirata* is situated at the transition from the subsutural constriction to the ribbed periphery of the whorl, while in the previously discussed species, the anal sinus is always on the subsutural ramp.

Koenenia octacostata **n. sp.**

Plate 30, Figure 7

Holotype: The specimen illustrated in pl. 30, fig. 7.
Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named after the eight axial ribs on each whorl.
Diagnosis: A *Koenenia* having convex volutions which are posteriorly constricted to a collar, and sculptured with eight axial ribs per whorl.
Description: Medium sized, elongate fusiform shell with turrid growthline, whorls sculptured by seven to eight axial ribs and three to four spiral cords, posteriorly constricted to a collar with remnants of a posterior canal. The holotype is 23 mm high and 11 mm wide.

Koenenia kirsteni **n. sp.**

Plate 30, Figures 9-10

Holotype: The specimen illustrated in pl. 30, figs. 9-10.
Material: 13 specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named after KIRSTEN SCHROETER, for her support in Hamburg.
Diagnosis: Spire and last whorl of about equal size, whorls convex and posteriorly constricted.
Description: Protoconch smooth, globular, made of two and a quarter volutions. Teleoconch slender fusiform, seven to eight volutions, whorls posteriorly constricted to a subsutural collar, nine axial ribs per volution, crossed by four spiral cords. Aperture lenticular, elongate with a long anterior canal, columella smooth. The figured shell is 16 mm high and 6 mm wide, the largest 24 mm high and 9 mm wide.

Koenenia multispirata **n. sp.**

Plate 30, Figures 11-12

Holotype: The specimen illustrated in pl. 30, fig. 11.
Material: Five specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for its numerous fine spiral lirations.
Diagnosis: A *Koenenia* with posteriorly constricted whorls covered with numerous fine spiral lirations and axial ribs, the anal sinus is situated at the transition from the subsutural constriction to the ribbed periphery.
Description: The protoconch is smooth, low conical, made of three volutions, 0.8 mm high and 0.7 mm wide. The slender, high spired fusiform teleoconch has seven volutions which are posteriorly constricted to a narrow collar. There are eight axial ribs per volution crossed by seven to eight fine spiral cords; the basal slope shows spiral cords only. The aperture is elongate, the transition from the parietal to the columellar lip is strongly constricted. The largest shell is 14 mm high and 5 mm wide.

Koenenia cf. *octocostata* n. sp.

Plate 25, Figures 5-6

Material: Two specimens from the Campanian of Torallola, Spain
Description: The high spired shell is of moderate size, has eight strong axial ribs per volution, crossed by three spiral lines. The anal sinus form a broad subsutural collar. The figured shell is 1.5 mm high.
Remarks: The specimens of *Koenenia octocostata* from Temalac show beaded spirals, which cannot be observed on the Spanish specimens. But this may be a matter of corrosion rather than a distinctive feature. The older (Santonian) species *Koenenia kaffraria* (RENNIE, 1930) from the Umzamba Formation in South Africa has a similar ornamentation, but its shell is more slender.

Koenenia sp. 1

Plate 25, Figure 4

Material: One specimen from the Campanian of Torallola, Spain.
Description: The relatively large, high spired shell has six, subsuturally constricted whorls which are sculptured with nine axial ribs per whorl, crossed by six to seven spiral cords and fine spiral lirae. The anal sinus is only weakly developed. The aperture is lenticular to roundish and the inner lip callused. The shell is 38 mm high and 16 mm wide.

Koenenia sp. 2

Plate 25, Figure 5

Material: One specimen from the Campanian of Torallola, Spain.
Description: A large, high spired shell with convex, subsuturally constricted whorls. Sculpture consists of twelve axial ribs per whorl which are crossed by four to six spirals and fine spiral lirae. The only available fragment consists of three and a half volutions and 42 mm high and 21 mm wide.

Subgenus *Koenenillia* n. subgen.

Type species: *Koenenillia typica* n. sp. described below.
Diagnosis: The slender fusiform shell has a spire that is higher than the aperture; the sculpture consists of numerous fine spirals and well-developed axials; the anal sinus is situated subsuturally, but there is no constriction; the aperture is narrow and elongate lenticular with a smooth, callused inner lip. The protoconch is conical and consists of convex and smooth whorls; there are fine axial ribs on the last half volution.
Derivation of name: Derived from *Koenenia*.
Remarks: *Koenenillia typica* n. sp. appears to be a continuation of the evolutionary lineage from *Koenenia kilburni* via *Koenenia kirsteni* to *Koenenia multispirata* regarding the successive reduction of the subsutural ramp or collar; in *Koenenillia typica* this collar is completely reduced. As this subsutural collar is a diagnostic character of *Koenenia*, the introduction of a distinct subgenus is necessary. This subgenus superficially resembles *Pleurofusia* GREGORIO, 1890, but the species of that genus has a more complexly sculptured protoconch (MACNEIL & DOCKERY 1984).

Koenenillia typica n. sp.

Plate 30, Figures 13-14

Holotype: The specimen illustrated in pl. 30, fig. 14.
Paratype: The specimen illustrated in pl. 30, fig. 13.
Material: Three specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: This is the type species of the new genus *Koenenillia*.
Diagnosis: As for the genus.
Description: The protoconch is made of three volutions, is 0.8 mm wide, 0.7 mm high and the initial part measures 0.24 mm across. Fine axial ribs are visible on its last whorl. The elongate teleoconch consist of six volutions with 7-9 strong transverse ribs and numerous nodular spiral cords; the spire is about one quarter higher than the body whorl. The aperture is narrow, ends anteriorly in a straight canal of moderate length, and has a callused inner lip. The holotype is 14 mm high and 4 mm wide.

Subgenus *Beretra* STEPHENSON, 1941

Type species: *Beretra firma* STEPHENSON, 1941 from the Maastrichtian Navarro Group of Texas, USA.
Description: *Beretra* differs from *Koenenia* by its straight-sided whorls and the mostly smooth subsutural collar.
Remarks: STEPHENSON (1941) diagnosed straight-sided whorls with weak spiral sculpture for *Beretra*. With *B. ornatula*, however, he included a species with quite well developed spirals. As *Beretra* differs only marginally from *Koenenia*, it is herein treated as a subgenus of the latter. Members of *Beretra* have previously been reported form the Ripley Formation in Mississippi and Tennessee (SOHL 1964) and the Navarro Group of Texas (STEPHENSON 1941). This report from Mexico extends its range remarkably to the South. However, it is not yet known from outside the Gulf Coast area.

Beretra ornatula STEPHENSON, 1941

Plate 30, Figure 8

1941 *Beretra ornatula* STEPHENSON: 377, pl. 72, figs. 9-10.

Material: Four specimens from the Maastrichtian of Temalac, Mexico.
Description: Teleoconch high spired, with five volutions. Subsutural constriction forming a broad collar; whorls shouldered numerous axial ribs crossed by five spiral cords. The figured shell is 17 mm high and 7 mm wide.

Genus *Eopleurotoma* COSSMANN, 1889

Type species: *Pleurotoma multicostata* (DESHAYES) from the Eocene of the Paris basin.
Description: The highspired, spindle-shaped shell has little convex whorls and a short anterior canal. Its sculpture consists of sinuous axial ribs which are interrupted by the anal-sinus and become knob-like below it. The anal-sinus located at the periphery.
Remarks: *Eopleurotoma* is, in contrast to all other turrid genera considered in this study, not restricted to the Late Cretaceous, but in fact based on an Eocene species. COSSMANN (1889) considered it to range stratigraphically from Paleocene to

Oligocene. However, the new species described below fits well into COSSMANN's generic description and therewith represents its oldest member.

Eupleurotoma formosa (BINKHORST, 1861)

Plate 25, Figures 8-9; Plate 26, Figures 1-2

1861 *Fusus formosus* BINKHORST: 70, pl. 5, figs. 7a-c.
1897 *Pleurotoma* (*Surcola*) *formosa* BINKHORST – KAUNHOWEN: 106, pl. 13, fig. 8.

Material: Three specimens from the Campanian of Torallola, Spain.
Description: Protoconch conical, smooth, made of three and a half little convex volutions, about 0.9 mm high and 0.75 mm wide. Teleoconch with about six volutions, early whorls sculptured with little transverse and shouldered axial ribs, crossed by four beaded spiral cords, whorls posteriorly constricted forming a subsutural collar. On later whorls the ribs fade and turn into a ridge. The shell is 20 mm high and 7 mm wide.

Discussion: Members of the Turridae are recognisable by their anal sinus (POWELL 1964, MCLEAN 1971, RIEDEL 2000). Although there are numerous different teleoconch-types present in the examined Late Cretaceous localities of Torallola and Temalac (*Koenenia*, *Koenenillia*, *Eupleurotoma*, and *Beretra*), their protoconchs are simple and – apart from a few ribs near the aperture – smooth. Cenozoic and Recent turrid protoconchs exhibit a broad variety of ornamentation which may be useful to distinguish subfamilies (MCLEAN 1971, BOUCHET 1990, RIEDEL 2000). The latter author pointed out that genera with more or less smooth larval shells today occur exclusively in the Drilliinae, and considered this smooth type as a ”reduction-type”. However, with all Cretaceous turrids possessing the smooth type, it more probably represents the basic type from which all sculptured ones derived. Therefore, no attempt is made here to assign the genera in question to any turrid subfamily. Additionally, since conids and terebrids only appear as late as Eocene (see RIEDEL 2000 for references), their ancestors are probably found among these genera as well.

Family Volutodermidae PILSBRY & OLLSON, 1954

The shells are fusiform, have a straight basal slope, are subsuturally constricted, and show cancellate sculpture which may turn into spiral sculpture on the body whorl. The columella shows one or more plates.

Genus *Volutoderma* GABB, 1877

Type species: *Volutoderma averillii* GABB, 1866 from the Cretaceous of California.
Description: The fusiform shell has spiral and axial ornament, spirals may dominate on the last whorl. The whorls are subsuturally constricted to a collar. The columella shows strong folds.
Remarks: DALL (1907) proposed a number of subgenera of *Volutoderma,* including *Rostellaca* with the here redescribed *Volutoderma zitteliana* as type species. This species is characterized by a well-developed subsutural constriction rather than a ramp as in *Volutoderma averillii*. However, compared with the variability of this feature in *Koenenia* (Turridae, see above), it appears of doubtful value in generic separation. STEPHENSON (1941) introduced the subgenus *Longoconcha* for large and slender members of *Volutoderma*. But whether the slenderness of the shell is a clearly distinctive feature separating the two subgenera is highly questionable.

Although all these subgenera were subsequently raised to generic rank by PILSBRY & OLLSON (1954) and SOHL (1964), they are doubted here.

Volutomoderma cf. *zitteliana* HOLZAPFEL, 1888

Plate 26, Figures 5-6

1888 *Volutoderma Zitteliana* HOLZAPFEL: 90, pl. 8, figs. 4a-c.

Material: One specimen from the Campanian of Torallola, Spain.
Description: High spired shell, volutions, constricted posteriorly forming a subsutural collar, with shouldered axial ribs and three visible spiral cords. Inner lip light callused with the underlying ornamentation shining through; four columellar ridges. The shell is 17 mm high and 11 mm wide.
Remarks: HOLZAPFEL (1888) described this species as rare in the Aachen greensands, his specimen are about twice as big as the one reported here.

Volutoderma? sp.

Plate 31, Figures 10-12

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The almost biconical teleoconch has few but strong axial ribs on the last whorl, their number increases on the earlier whorls. The last volution is covered with carinate axial and spiral lines, the earlier ones only with spiral lines. The largest shell is 34 mm high and 20 mm wide.
Remarks: This shell strongly resembles species of *Volutoderma* or *Longoconcha* but does not show any traces of columellar folds, which are characteristic for these genera.

Discussion: PILSBRY & OLSSON (1954) introduced the Volutoderminae for a group of Late Cretaceous volutiform shells. Although they provided an extensive diagnosis, they neither reasoned why the group was actually placed within the Volutidae, nor did they point out characteristic differences to other groups. In their diagnosis of the subfamily, they emphasised the cancellate to spiral sculpture of the adult shell, the straight basal slope and the plicate columella. Spiral sculpture is very uncommon in modern volutids (although not absent, see *Fulgoraria rupestris* (GMELIN) in ABBOTT & DANCE, 1983). All three features are developed today within the Mitridae, which, however, usually have a spire higher than the aperture. PILSBRY & OLSSON (1954) considered *Volutomorpha* GABB, 1877 as synonymous with *Volutoderma*. SOHL (1964) did not agree with this opinion but treated *Volutomorpha* as an independent genus which he placed – following PILSBRY & OLSSON - within the Volutoderminae. However, the genus possesses a constricted basal slope and develops a callus-glaze in the adult, two features which contradict the diagnosis of Volutoderminae and rather place the genus within the Athletinae. In fact, some specimens described by SOHL (1964) - *Volutomorpha retifera*, juvenile *V. mutabilis* - strongly resemble the athletid *Volutocorbis*. With *Volutomorpha* excluded, the Volutoderminae from a well-tied group of Late Cretaceous neogastropods. As they resemble volutids as much as they resemble mitrids, they are herein raised to family rank. They could either represent the stem-group of athletids, volutids and mitrids, or their sister-group.

Family Athletidae PILSBRY & OLLSON, 1954

The shells are at first subfusiform with a high spire and strong cancellate sculpture, sometimes becoming *Cassis*-like or strombiform in the adult, with or without a callus-glaze on the shell. The anterior canal is straight and the columella has one or more strong plates.

Genus *Liopeplum* DALL, 1890

Type species: *Volutilithes* (*Athleta*) *lioderma* CONRAD, 1860.
Description: The shell is strombiform, has axial sculpture on the early whorls, while the latter are usually smooth and may be callus-covered. The aperture is long and narrow and the columella shows several folds.
Remarks: With its elegant strombiform and glazing shells, *Liopeplum* is a conspicuous element of Late Cretaceous gastropod faunas. Based on a species originally assigned to *Volutilithes*, the genus was placed among the Volutidae by the early workers (CONRAD 1860, STEPHENSON 1941, WADE 1926, WENZ 1938-44) until PILSBRY & OLLSON (1954) included *Liopeplum* in their Athletinae. Perhaps due to SOHL's (1964) statement *Liopeplum* would primarily be a Gulf Coastal Plain genus, SAUL & POPENOE (1993) introduced *Varens* for some Californian species, however, their diagnosis of *Varens* is identical with that of *Liopeplum* in every detail, including a thin callus-glaze. *Varens* is herein synonymized with *Liopeplum*. The same authors established *Konistra* SAUL & POPENOE, 1993 with a lower spire than *Liopeplum* and without callus-glaze, a genus which might intermediate between *Carota* and *Liopeplum*. SAUL & POPENOE (1993) assigned *Varens* and *Konistra* to the Volutoderminae.

Liopeplum pyrenaeum n. sp.

Plate 26, Figures 3-4

Holotype: The specimen illustrated in pl. 26, figs. 3-4.
Material: Three specimens from the Campanian of Torallola, Spain.
Derivation of name: Named after the Pyrenean mountains.
Diagnosis: In the elongate strombiform shell, spire and last whorl are of about equal height. The whorls are more or less shouldered, subsuturally constricted, and sculptured with numerous fine axial ribblets. The basal slope is little concave and the columella bears four plates. The shell is up to 36 mm high and 16 mm wide.
Remarks: Among the slender strombiform members of *Liopeplum*, *L. capensis* from the Umzamba formation of South Africa has an almost indistinguishable teleoconch, however, its protoconch reflects lecithotrophic development. It can therefore hardly be conspecific with the new species from northern Spain, although the protoconch of the new species is unknown. *L. cretaceum* from Tennessee, USA, has weaker developed and less columellar folds.

Liopeplum cretaceum (CONRAD, 1858)

Plate 31, Figures 1-2

2000 *Liopeplum cretaceum* CONRAD - PERRILLIAT, VEGA & CORONA: 17, figs. 7.4-7.5.

Material: One specimen from the Maastrichtian of Temalac, Mexico.
Description: The teleoconch is made of six volutions, the first three and half show strong and closely spaced axial ribs, later whorls have only growthlines and are somehow constricted near the suture. The columella bears five weak plates. The figured shell is 27 mm high and 13 mm wide.

Liopeplum costatum n. sp.

Plate 31, Figures 3-6

2000 *Pugnellus densatus* CONRAD - PERRILLIAT, VEGA & CORONA (partly): 13, fig. 6.3.

Holotype: The specimen illustrated in pl. 31, figs. 3-4.
Paratype: The specimen illustrated in pl. 31, figs. 5-6.
Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for its strong costae.
Diagnosis: A *Liopeplum* with large and elongate axial ribs on the adult shell.
Description: The fusiform to spindle shaped teleoconch has an aperture which is higher than the spire. On the early whorls, the axial ribs are straight and numerous and crossed by fine spiral lirae. On the latter whorls, ribs stronger and transverse; the sutures are very weak. The aperture is lenticular, the inner lip is smooth, and the columella has two plates. The largest shell is 46 mm high and 24 mm wide.
Remarks: PERRILLIAT et al. (2000) figured two specimens as *Pugnellus densatus*. The first (PERRILLIAT et al. 2000: fig. 6.2) may belong to that species, the other, however, shows the fine striae on the upper part of the whorls, characteristic for *Liopeplum costatum* n. sp. This new species is distinct from *Liopeplum cretaceum* and *Liopeplum nodosum* SOHL, 1964 by its well developed, elongate axial ribs. The figured holotype is, apart from a questionable *Trochactaeon*, the largest gastropod from the Temalac fauna.

Discussion: *Liopeplum* fits well into the diagnosis of the Athletinae provided by PILSBRY & OLSSON (1954), and also SOHL (1964) pointed out that certain Eocene athletids resemble *Liopeplum*. However, there are no Paleocene shells similar to those of *Liopeplum*. The genus can be traced back into the Turonian of California where *Varens* occurs (SAUL & POPENOE 1993), a genus herein considered synonymous with *Liopeplum*. Also from the Turonian, ROMAN & MAZERAN (1913) described *Boncavailia requieniana* (D'ORBIGNY, 1842), a species which appears to intermediate between *Liopeplum*, *Caricella* and *Volutifusus*. Separation of Volutidae, Athletidae and Volutodermidae might therefore have taken place as early as Turonian. RIEDEL (2000) raised the Athletinae to family rank based on their triserial radula and the lack of an operculum. Although the latter character is only a weak one – most Volutidae s. str. also lack an operculum – the antiquity of the Athletidae supports its independent family status. Apart from *Liopeplum*, the other Late Cretaceous genera tentatively assigned to this family by PILSBRY & OLSSON (1954) are highly doubtful and discussed under the Pyrifusidae.

Family Volutidae RAFINESQUE, 1815

The shells are ovate to strombiform and have a high or low spire. Sculpture consists principally of axial riblets often forming strong nodes or sharp spines on the shoulder, sometimes wholly smooth. The columellar folds are usually strong and are generally long and slender. The siphonal notch is deep and the outer lip is thickened in the adult. All known volutids today have a lecithotrophic ontogeny resulting in very large protoconchs which are often irregularly formed.

Genus *Volutifusus* CONRAD, 1863

Type species: *Volutifusus mutabilis* CONRAD, 1834 from the Miocene.
Description: The fusiform, glossy shell is sculptured with weak axials and has a constricted base. Adults have no columellar folds.

Volutifusus olssoni n. sp.

Plate 26, Figures 7-10

Holotype: The specimen illustrated in pl.26, fig. 7.
Paratype: The specimen illustrated in pl. 26, figs. 9-10.
Material: Three specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of the malacologist and paleontologist A. A. OLSSON.
Diagnosis: Protoconch large, initial part spiny, whorls smooth and convex, height 8.5 mm, width 5 mm, transition to the teleoconch indistinct. Teleoconch fusiform, sculptured with curved axial ribs, 13 on the first, eleven on the second whorl, and fine spiral lines. Basal slope well rounded, siphonal canal little twisted, smooth. The holotype is 16 mm high, the paratype is 25 mm high.

Genus *Lyria* GRAY, 1847

Type species: *Lyria nucleus* (LAMARCK) living around northern Australia.
Description: The shell is elongate egg-shaped with a conical spire. Whorls are little convex and sculptured with strong axial ribs. The outer lip is thickened and the columella has numerous plates.

Lyria? sp.

Plate 31, Figures 7-9

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The slender, fusiform shell has convex volutions with elongate, S-shaped axial ribs and growthlines, and spiral lines that fade away on the body whorl. The subsutural constrictions forms a nodular collar. On young specimens, the columella bears two plates; on adult shells this number increased to four, of which the two outer ones are weaker than the two middle ones. The largest shell is 15 mm high and 8 mm wide.
Remarks: A related species from the Ripley Formation may be *Latirus keownvillensis* SOHL, 1964. But it is distinct by its more sinuous ribs and stronger ribs.

Discussion: Volutids today are known to possess the largest protoconchs of all gastropods, with diameters up to 25 mm (see RIEDEL 2000 for references). They arise from embryos which are supplied with – and consume – large amounts of yolk, or in a few cases, nurse eggs (PONDER 1973, RIEDEL 2000). But also small multispiral protoconchs occur (PILSBRY & OLSSON 1954, DARRAGH 1988, RIEDEL 2000). Planktotrophic development is unknown from any living volutid.
Volutifusus olssoni n. sp. bears a huge "soft ice"-protoconch which was previously only known from Cenozoic and Recent members of the Volutidae. It represents the oldest member of this family with this characteristic protoconch known to date. BANDEL (1993c) figured a large and globular protoconch reflecting a lecithotrophic ontogeny from the Maastrichtian of Egypt. The connected teleoconch resembles that of *Caricella* and is thus of very different shape than that of *Volutifusus*. Whether this strongly lecithotrophic mode of development evolved twice within the Volutidae from two precursors with planktotrophic development, or only once, remains unknown.

Family Pseudolividae FISCHER, 1884

The ovate to fusiform shels are usually spirally sculptured and have a groove onthe basal half of the last whorl. The last whorl comprises more than 60% of the total shell height

Pseudolivid?

Plate 30, figs. 15-17

Material: Several specimens from the Maastrichtian of Temalac, Mexico.
Description: The embryonic portion of the protoconch measures about 0.1 mm across, the larval shell is smooth, made of 2.5-3 volutions, is 0.6 mm wide and 0.5 mm high. The teleoconch is sculptured with a cancellate pattern of equally strong axial and spiral ribs. On the periphery it shows only weak spirals. The basal margin is little rounded and has a small spiral groove. The aperture has a short posterior canal, the anterior canal is broad but short; and there seems to be a very transverse fold low on the columella. The largest specimen is 4.5 mm high.
Remarks: VERMEIJ (1998) considered the spiral groove on the lower part of the last whorl the most characteristic feature of the Pseudolividae. This groove is only weakly developed in the species described here. It is not very similar to *Sulcobuccinum* D'ORBIGNY, 1850 which is considered the only Cretaceous pseudolivid by VERMEIJ (1998). The species described here shows some resemblance to *Buccinopsis* regarding general shape but lacks the subsutural and the basal constriction of that genus, it is somehow similar to *Pyropsis* and *Pyrifusus* but has a higher spire and less sculpture than the former and lacks the subsutural constriction of the latter. A comparably small neogastropod was described as *Cryptoconus mcnairyensis* (WADE, 1917) from the Ripley formation but that species is characterised by angular whorls and a smooth columella. In addition, the species described here does not show any traces of a sinuous growthline, characteristic for *Cryptoconus* KOENEN, 1867.

Family Pyrifusidae BANDEL & STINNESBECK, 2000

This family contains shells which are fusiform in the broadest sense, from slender to broad, from high to low spired, sculpture consists of axials and spirals, and the columella may be smooth or has one to numerous plates. The larval shell is smooth, conical, consists of several whorls and measures between 0.6 and 1.0 mm in diameter.

Genus *Drilluta* WADE, 1916

Type species: *Drilluta communis* WADE, 1916 from the Ripley Formation in Tennessee and Mississippi, USA.
Description: The slender fusiform shell has axial and spiral sculpture, the whorls are subsuturally constricted and the columella is smooth.
Remarks: *Drilluta* was introduced for some high spired, fusiform Late Cretaceous gastropods with dominantly axial sculpture, a posterior constriction, one well-developed columellar fold and commonly two minor folds. The species constituting this genus had previously been assigned to *Drillia* GRAY, 1838 (Turridae), *Voluta*, *Fasciolaria* and *Fusus* (WADE 1926: 116). Considering this list alone, including representatives of three of the major neogastropod families, attempts to classify this genus may be controversial. Subsequently, STEPHENSON (1941) followed WADE's treatment, PILSBRY & OLLSON (1954) tentatively assigned *Drilluta* to their new volutid subfamily Athletinae, and WENZ (1938-44), without explanation, hesitantly

placed it within the turrid subfamily Brachytominae. SOHL (1964) considered the spire of *Drilluta* as ”rather high for these families” and transferred it to the Fasciolariidae. SAUL & POPENOE (1993) and PERRILLIAT et al. (2000) followed SOHL’s assignment without further discussion.

However, no anal sinus is known from any species of *Drilluta*, therefore, a placement within the Turridae can be rejected. But a similarly high spire is also present among undoubted living volutids like *Teramachia* KURODA, 1931 and *Neptunopsis* SOWERBY, 1898. However, *Fasciolaria* indeed produces similar shells, although lacking the posterior constriction. Summing up, the assignment of *Drilluta* to either the Fasciolariidae or the Volutidae appears arbitrary rather than based on verifiable shell characters.

Drilluta gloriae PERRILLIAT, VEGA and CORONA, 2000

Plate 32, Figures 1-4

2000 *Drilluta gloriae* PERRILLIAT - VEGA & CORONA: 17, pl. 6, figs. 22-25.

Material: 20 specimens from the Maastrichtian of Temalac, Mexico.

Description: The fusiform teleoconch is made of six and a half volutions, the spire is about as high as the last whorl. The subsutural collar is rough, the volutions are shouldered and sculptured with 11-12 axial ribs and three spiral lines. The narrow aperture has a posterior short notch, and an anterior canal; the columella has three plates, last one weak. The figured shell is 16 mm high and 6 mm wide, the largest 22 mm high and 10 mm wide.

Drilluta cf. *communis* WADE, 1916

Plate 31, Figure 13

Material: One specimen from the Maastrichtian of Temalac, Mexico.

Description: The protoconch is rounded-conical, smooth and made of three volutions. The teleoconch consists of five or more volutions which are shouldered and have a deep subsutural constriction that forms a nodular collar; the axial ribs are straight on the early whorls and become more transverse on the later whorls; there is no spiral ornament on the spire, and the columella shows three plates. The figured shell is 16 mm high and 7 mm wide.

Remarks: The specimen is too badly preserved for a safe determination.

Drilluta sp.

Plate 27, Figure1

Material: One specimen from the Campanian of Torallola, Spain.

Description: This small specimen consists of about four, axially ribbed, subsuturally constricted and little convex whorls. The columella bears at least three folds. It is 10 mm high and 5 mm wide.

Genus *Graphidula* STEPHENSON, 1941

Type species: *Graphidula terebreformis* STEPHENSON, 1941 from the Navarro group of Texas, USA.

Description: The slender fusiform shell has a spire higher than the aperture. Sculpture consists of transverse ribs and/or spiral lirae. The siphonal canal is long and straight and the columella bears no to two plates.

Remarks: Less winding than the history of *Drilluta*, but just as unsatisfying are the attempts to classify *Graphidula*. It was designed for species resembling *Drilluta* but lacking the posterior constriction. STEPHENSON (1941: 345) introduced the Graphidulidae for *Graphidula*, *Lomirosa* and *Piestochilus*, but did neither diagnose nor discuss this family. However, it was placed within the Rachiglossa, between the Fusidae and the Volutidae, reminiscent to *Drilluta'*s controversial position. Not surprisingly, SOHL (1964: 211) also transferred *Graphidula* to the Fasciolariidae, without explanation, except that "separate familial designation for *Graphidula* does not appear necessary". ERICKSON (1974: 192) followed SOHL's treatment but noted that *Graphidula* and *Piestochilus* are "yet poorly understood groupings". This statement can only be supported and the taxonomic conclusions made here regarding *Drilluta* also apply to *Graphidula*. Even its own validity may be doubted, as *Graphidula maastrichtiensis* (KAUNHOWEN, 1897) described below, shows indications of a posterior constriction of the whorls, obliterating the only distinguishing character from *Drilluta*. With the variability of *Graphidula maastrichtiensis'* columellar plication considered, ranging from none to two, there is also a transition into *Remera*.

Graphidula maestrichtiensis (KAUNHOWEN, 1897)

Plate 27, Figures 2-5

1897 *Fusus maestrichtiensis* KAUNHOWEN: 84, pl. 10, fig. 9.

Material: 35 specimens from the Campanian of Torallola, Spain

Description: The moderately sized, high spired shell is made of about eight volutions, and its spire is little higher than the body whorl. The dominant axial ribs range from suture to suture, and are in some cases slightly constricted subsuturally. Fine spirals may cover the whole shell or are restricted to the base. The columella usually bears one strong plate, which is sometimes absent (in seven specimens) and sometimes supported by a weaker fold above it (in five specimens). The number of columellar plates is neither correlated with the subsutural constriction of the whorls, nor with the degree to which the fine spirals cover the shell. These characters appear quite variable within this species. The shell is 25 mm high and 8 mm wide.

Genus *Paleopsephaea* WADE, 1926

Type species: *Paleopsephaea mutabilis* WADE, 1926 from the Ripley Formation, USA, Maastrichtian.

Description: The slender fusiform shell has convex volutions with predominantly axial sculpture. The whorls are not subsuturally constricted and the columella bears one or more plates.

Remarks: Just like the previously discussed genus *Drilluta*, *Paleopsephaea* was introduced by WADE (1926) as a member of the Volutidae, and later transferred to the Fascoilariidae by SOHL (1964). STEPHENSON (1941, 1952), as usual, adopted WADE's assignment. WENZ (1938-44) treated *Paleopsephaea* as a subgenus of *Volutilithes*, PILSBRY & OLSSEN (1954) tentatively included the genus in their Athletinae, rejecting WENZ' placement. Although WADE (1926: 123) considered the genus as "well characterized by high fusiform, strongly axial, costate, volutid shells", distinction of its species is not always easy. In the cases of *Drilluta* and *Bellifusus*, the lacking subsutural constriction appears the only distinguishing character. However, analogously to the case of *Drilluta* and *Graphidula*, this constriction is relatively weak in *Bellifusus angulicostata* SOHL 1964 (pl. 25, figs. 15, 18-20, 25-26) and *Drilluta distans* (SOHL 1964: pl. 27, figs. 27-28 for example), and indications of such a constriction are visible on *Paleopsephaea tenulirata* (see SOHL 1964: pl. 28, figs. 7, 8). Considering the number of columellar plates, WADE (1926: 129) diagnosed ”about three oblique folds”. In his description of the type species *Paleopsephaea mutabilis* he mentioned three to four plates, SOHL (1964: pl. 28, fig. 6) even figured a specimen with six. Like in the cases of *Drilluta* and *Graphidula*, there are no clear-cut characters which would allow to assign *Paleopsephaea* to either the Fasciolariidae or the Volutidae with an acceptable degree of certainty.

***Paleopsephaea octacostata* n. sp.**

Plate 27, Figures 6-7

Holotype: The specimen illustrated in pl. 27, figs. 6-7.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: Named according to its eight axial ribs per whorl.
Diagnosis: This *Paleopsephaea* has a slightly convex spire and is characterised by its eight strong axial ribs which are crossed by eight moderately strong spiral cords.
Description: The high spired shell has seven volutions and the spire is about as high as the body whorl. There are eight strong axial ribs per volution crossed by eight spiral cords. The inner lip is covered with little callus and the columella bears two folds. The shell is 31 mm high and 12 mm wide.
Remarks: Similarly sculptured is *Paleopsephaea tenuilirata* SOHL, 1964 from the Ripley Formation but its spire appears slightly concave in outline while that of *Paleopsephaea octacostata* is slightly convex. *Paleopsephaea stephensoni* has ten instead of eight ribs per whorl and the spirals are stronger developed. *Paleopsephaea orbignyana* (MÜLLER, 1851) from the Vaals greensands of Germany has according to HOLZAPFEL (1888: 97) 16 to 20 axial ribs but also two equally strong columellar folds.

***Paleoplephaea stephensoni* n. sp.**

Plate 27, Figures 8-9

Holotype: The specimen illustrated in pl. 27, figs. 8-9.
Material: Three specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of L.W. STEPHENSON who described numerous Late Cretaceous gastropods from Texas, USA.
Diagnosis: The fusiform shell consists of at least six convex volutions with deep sutures. The strong axial ribs have equally sized interspaces, and are crossed by six to seven equally strong spiral lines. The columella bears two plates. The shell is 21 mm high and 14 mm wide.

***Paleopsephaea wadei* n. sp.**

Plate 27, Figures 10-11

Holotype: The specimen illustrated in pl. 27, figs. 10-11.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of B. WADE who described numerous Late Cretaceous gastropods from the Atlantic coast of the USA.
Diagnosis: This small *Paleopsephaea* is characterised by its strong, axially arranged, screw-like axial ribs.
Description: This small, fusiform shell has six strait volutions and the spire is about as high as the body whorl. Its axial ribs are inclined abaperturally, situated above one

another and continue down the basal slope. The columella shows two plates. The shell is 13 mm high and 5 mm wide.
Remarks: Although much smaller, this species is similar to *Paleopsephaea scalaris* RENNIE, 1930 from South Africa regarding its vertically arranged ribs.

Paleopsephaea cf. *tenulirata* SOHL, 1964

Plate 31, Figures 14-15

2000 *Paleopsephaea*? sp. PERRILLIAT, VEGA & CORONA: 17, figs. 7.1-7.2.

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The teleoconch consists of seven volutions, each whorl has seven axial ribs crossed by numerous fine spiral lines. The last whorl is constricted below the ribs, and the rostrum is sculptured with spirals only. The columella has at least one plate in anterior position. The figured shell is 30 mm high and 15 mm wide.
Remarks: *Paleopsephaea tenulirata* figured by SOHL (1964) possesses a similar ornamentation but is more elongate.

Genus *Bellifusus* STEPHENSON, 1941

Type species: *Odontofusus curvicostatus* WADE, 1926 from the Ripley Formation.
Description: The fusiform shell has a spire which takes little more than one-third of the total shell height. Whorls are posteriorly constricted to a transversely wrinkled collar and bear a sharp to well-rounded shoulder. It is sculptured with strong collabral transverse ribs that die out on the basal slope and spiral cords and liraee that cover the surface of a re restricted to the lower body slope. The columella is slightly twisted and has one strong and one weaker plate.
Remarks: SOHL (1964: 202) pointed out that *Drilluta* "is similar to *Bellifusus* […] but has much straighter transverse ribs, a distinctly higher spire and less rounded whorls". Apart from this, SOHL as well as STEPHENSON (1941: 338) both argued about the type species of *Odontofusus* WHITFIELD but neither of them discussed other related genera or its taxonomic position. It was placed, however, in the Fusinae by STEPHENSON and in the Fasciolariidae by SOHL. The presence of species intermediating between *Bellifusus* and *Paleopsephaea* was discussed in the discussion of the latter, and the uncertainties regarding its familiar placement are the same as those of *Drilluta*, *Graphidula*, *Paleopsephaea* and *Remera*.

Bellifusus curvicostatus (WADE, 1926)

Plate 31, Figures 16-17

2000 *Bellifusus curvicostatus* (WADE) - PERRILLIAT, VEGA & CORONA 16, figs. 6.18-6.19.

Material: 26 specimens from the Maastrichtian of Temalac, Mexico.
Description: The teleoconch is fusiform consists of six volutions and the spire is about as high as the body whorl. The anterior constriction of the whorls forms a spiny collar, the whorls are shouldered, have numerous axial ribs that become more transverse on later whorls; five spiral lirae covers the entire shell and becomes stronger on the basal slope. The aperture is subovate, and the columella has two plates. The figured shell is 19.5 mm high and 9 mm wide, the largest specimen reached about 40 mm in height.
Remarks: This species is quite common in the Temalac community and is very variable in size.

Bellifusus sp.

Plate 28, Figures 1-2

Material: Two specimens from the Campanian of Torallola, Spain
Description: Fusiform shell with six volutions that are posteriorly constricted to a small collar. Sculpture consists of nine straight axial ribs per whorl and numerous fine spiral lines. Basal slope constricted, columella with two folds. The shell is 25 mm high and 10 mm wide.

Genus *Mitridomus* SOHL, 1963

Type species: *Fasciolaria? ripleyana* WADE, 1926 from the Ripley Formation, Mississippi, USA, Maastrichtian.
Description: The shell is fusiform and the whorls are somewhat constricted posteriorly. Sculpture consists of low but broad collabral transverse ribs and close-spaced spiral lirae. The columella bears four plates of about equal strength and spacing.
Remarks: Since its introduction, no new species were assigned to this genus, and, thus, it has not yet been revised. SOHL (1963: 749) recognised similarities between *Mitridomus* and Recent *Vexillium,* and consequently placed his new genus within the Vexillinae (Mitridae). It is today widely accepted that the Vexillinae do not form part of the Mitridae but rather represent an independent family, the Costellariidae (KANTOR 1996). However, RIEDEL (2000: 188) pointed out that both groups are characterised by a protoconch possessing columellar folds, unknown from any other gastropod group. As long as such a protoconch is not documented for *Mitridomus*, the genus should not be placed among these two families.
The three new species described below fit well into SOHL's (1963) diagnosis of *Mitridomus*. One of them, *Mitridomus conomitriformis* n. sp. shows strong similarities with *Conomitra* CONRAD, 1865 from the Claiborne Eocene. However, also the protoconch of *Conomitra* is not yet known.

Mitridomus pseudocostellarius n. sp.

Plate 28, Figures 3-4

Holotype: The specimen illustrated in pl. 28. figs. 3-4.
Material: Three specimens from the Campanian of Torallola, Spain.
Derivation of name: This species resembles living species of *Costellaria.*
Diagnosis: The moderately sized, fusiform shell has nine volutions and the spire is about as high as the body whorl. Whorls are little angular or shouldered and are sculptured with axial ribs crossed by seven to eight spiral cords, the fourth of which is the most prominent and the one that marks the ridge on the latest whorls. The aperture is long and narrow, and the columella has four strong ribs, the last being the weakest. The shell is 40 mm high and 14 mm wide.
Remarks: This new species is distinct from the type by its nodular ribs, and from *Mitridomus conomitriformis* n. sp. by its higher spire.

Mitridomus conomitriformis n. sp.

Plate 28, Figures 5-7

Holotype: The specimen illustrated in pl. 28, figs. 5-6.
Material: 14 specimens from the Campanian of Torallola, Spain.
Derivation of name: This species resembles *Conomitra* from the Eocene.

Diagnosis: A broadly conical *Mitridomus* shouldered whorls and dominantly axial ornament.

Description: The protoconch is conical and smooth, consists of three or more little convex volutions and is about 0.8 mm wide and high. The moderately sized, fusiform teleoconch consists of about nine volutions. The first four whorls are very slender, latter ones become broader with age. The axial ribs are constricted in the upper third, forming a shoulder below and give the whorl an angular outline. These ribs crossed by fine spiral cords on later whorls. The aperture is narrow, and there are four columellar folds. The largest shell is 25 mm high and 11 mm wide.

Mitridomus varicicousus n. sp.

Plate 28, Figures 8-9

Holotype: The specimen illustrated in pl. 28, figs. 8-9.

Material: Two specimens from the Campanian of Torallola, Spain.

Derivation of name: Named according to its numerous varices.

Diagnosis: The small, spindle-shaped shell consists of about seven rather straight-sided and subsuturally constricted whorls. Ornament consists of numerous fine axials and about three varices per whorl. The inner lip is callus-covered and the columella bears four, slightly inclined folds. The shell is 17 mm high and 8 mm wide.

Remarks: This species shows a much stronger subsutural constriction than the other two newly described species here, and varices are unusual for pyrifusids in general.

Genus *Mesorhytis* MEEK, 1876

Type species: *Fasciolaria (Mesorhytis) gracilentum* MEEK, 1876 from the Campanian of the Fox Hill Group, USA (WENZ 1938-44: fig. 3665).

Description: The shell is slender fusiform, the whorls are more or less convex and have axial and spiral sculpture of equal strength. The columella has three strong plates.

Remarks: Introduced as a subgenus of *Fasciolaria*, WADE (1926) elevated it to full generic rank, and WENZ (1938-44) hesitantly placed it as a subgenus within *Vexillium* (Mitridae). SOHL (1963, 1964), following WENZ in this regard, discussed *Mesorhytis'* relationships to *Mitridomus* within the Vexillinae THIELE, 1929.

Mesorhytis eleganza n. sp.

Plate 32, Figures 5-6

Holotype: The specimen illustrated in pl. 32, fig. 6.

Material: Eight specimens from the Maastrichtian of Temalac, Mexico.

Derivation of name: For its elegant appearance.

Diagnosis: A *Mesorhytis* with convex volutions and a strongly constricted basal slope.

Description: The protoconch is made of two and a half volutions, is 0.6 mm high and wide. The teleoconch consists of seven convex volutions with 16 axial ribs and six to eight spiral cords, which are nodular at their intersections. The basal slope is constricted, the rostrum straight, the aperture is lenticular and ends anteriorly in a long canal; there are three columellar plates. The holotype is 18 mm high and 7 mm wide.

Remarks: The whorls of this new species are more convex than those of the type species, and the axial ribs are slightly sinuous in contrast to the straight ribs of *Mesorhytis gracilentum*.

Mesorhytis sp.

Plate 28, Figures 10-11

Material: One specimen from the Campanian of Torallola, Spain.
Description: Medium sized, fusiform shell, spire and last whorl of about equal height. Six convex volutions ornamented with axial and spiral cords and occasional varices. Aperture lenticular, inner lip light callused with the underlying ornamentation shining through. Basal margin gently rounded, columella with three plates. The shell is 17 mm high and 8 mm wide.

Genus *Ripleyella* HARBISON, 1945

Type species: *Ornopsis elevata* WADE, 1916 from the Ripley Formation.
Description: The elongate fusiform shell is sculptured with transverse costae which are noded at the shoulder, and numerous spiral lirae. Whorls are posteriorly constricted to a collar and anteriorly constricted to a very elongate narrow siphonal canal immediately above which, on the columella, is a narrow strong oblique plication.

Ripleyella elevata (WADE, 1916)

Plate 32, Figures 8-9

1964 *Ornopsis* (*Ripleyella*) *elevata* WADE – SOHL: 216, pl. 29, figs. 22-25.

Material: 17 specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch is conical, smooth, made of three moderately convex volutions with deep sutures, 0.5 mm high and 0.6 mm wide. The transition to the teleoconch is marked by six axial ribs that are anteriorly curved forward and of increasing strength towards the teleoconch. The elongate fusiform teleoconch consists of six volutions, the whorls are posteriorly constricted to a subsutural collar, have eight shouldered axial ribs which are crossed by five spiral lines. The basal slope is constricted and the columella is a little twisted to the left. The lenticular aperture ends anteriorly in a long canal. The figured shell is 14 mm high and 6 mm wide.

Ripleyella truncata n. sp.

Plate 32, Figure 7

Holotype: The specimen illustrated in pl. 32, fig. 7.
Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for its truncated spire, which is lower than in any other known species of *Ripleyella*
Diagnosis: A low spired *Ripleyella* with a thick inner lip callus and vertically arranged ribs.
Description: The broad fusiform teleoconch has six posteriorly constricted volutions with seven axial ribs per whorl; their strength increasing with whorl size and they are vertically arranged above each other. The ribs are crossed by four spiral cords, the first is very weak or obscured by the subsutural constriction on earlier whorls. The rostrum shows jagged spiral cords only; the aperture is of equal

height or larger than the spire, lenticular, has a narrow posterior canal and a long anterior canal; the inner lip is callused. The largest specimen is 27 mm high and 18 mm wide.
Remarks: This new species is distinct from *Ripleyella elevata* by its truncate spire.

Genus *Buccinopsis* CONRAD, 1857

Type species: *Buccinopsis perryi* CONRAD, 1857.
Description: The globular low-spired shells with well-rounded to well-shouldered whorls which are constricted posteriorly to a subsutural collar and anteriorly to a twisted short pillar. The pillar is bounded above by a deep sulcus that terminates in a tooth on the outer lip. The siphonal notch is deep and the fasciole corrugated. Sculpture is variable, of both transverse and spiral elements.
Remarks: As its name suggests, *Buccinopsis* was classified as a buccid by previous workers, and *Seminola* WADE, 1917 was considered a synonym by SOHL (1964). WENZ (1938-44) did not accept the genus and listed it as synonyms of the Recent buccinids *Truncaria* ADAMS & REEVE, 1848 and *Liomesus* STIMPSON, 1865 probably because CONRAD's type species is an internal mould. Although there are many Recent buccinid genera which indeed resemble *Buccinopsis*, the muricid genera *Trophon* MONTFORT, 1810, or *Cronia* H. & A. ADAMS, 1853 of the *Drupa*-relation also produce similar shells. Additionally, WADE (1926: 144) considered *Pseudoliva* SWAINSON, 1840 a related buccinid. Today there is little doubt that *Pseudoliva* belongs to the Olividae, however, despite its strong axial or cancellate sculpture, *Buccinopsis* shows a similar basal fasciole and a similar aperture.

Buccinopsis crassiaxialis n. sp.

Plate 29, Figures 1-2

Holotype: The specimen illustrated in pl. 29, figs. 1-2.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after its strong axial ribs.
Diagnosis: The small spire makes about one third of the total shell height, the whorls are straight-sided on the spire and separated by deep sutural grooves. Sculptured consists of twelve strong axial to transverse ribs on the body whorl which are apically shouldered. The basal fasciole is marked by two strong spiral ridges. The shell is 13 mm high and 7 mm wide.
Remarks: A similar European shell is *Pseudoliva amigua* KAUNHOWEN, 1897 but has more numerous axial ribs.

Genus *Pyrifusus* CONRAD, 1858

Type species: *Pyrifusus subdensatus* CONRAD, 1858 from Owl Creek, Mississippi, USA (SOHL 1964: pl. 24, figs. 1-4).
Description: The broad fusiform shell has a low spire. Whorls have a subsutural collar resulting from a short posterior canal of the aperture. Sculpture consists of strong axials and spirals, the inner lip is callused and has no plates.
Remarks: Comparing the diagnosis of *Pyrifusus* and *Deussenia* STEPHENSON, 1941, the only apparent character to distinguish the two genera is the relative height of the spire, which is ”moderate” in *Deussenia* and ”low” in *Pyrifusus*. However, comparing *Pyrifusus subdensatus* (SOHL 1964: pl. 24, figs. 1-4), *Pyrifusus ejundicus* (SOHL 1964: pl. 24, figs. 22, 25), and *Deussenia bellalirata* (SOHL 1964: pl. 25, figs. 3, 4, 8, 9), there appears to be a continuous transition rather than a clear distinction

between the two genera. Therefore, *Deussenia* is considered synonym with *Pyrifusus*.
When STEPHENSON (1941: 332) introduced *Deussenia*, he compared it with *Volutomorpha* and noted the lack of columellar folds in *Deussenia*. Analogously, SOHL (1964) found *Pyrifusus* similar to *Lupira* STEPHENSON, 1941 except for the presence of columellar folds on the latter. However, he placed *Pyrifusus* and *Deussenia* within the Melongenidae and *Lupira* within the Vasidae (=Xancidae).

Pyrifusus sp.

Plate 29, Figure 3

Material: ten specimens from the Campanian of Torallola, Spain.
Description: The biconical shell consists of about four to five subsuturally constricted whorls which are convex and sculptured with nine axial ribs on the last whorl. There are three to four stronger spirals and on or two weak ones above. The largest specimen is 17 mm high and 12 mm wide.
Remarks: A similar species but with 14 rather than nine axials per whorls is *Pollia fenestrata*, described by HOLZAPFEL (1888) from the Vaals greensands, Germany.

Discussion: The gastropods considered here as members of the Pyrifusidae have traditionally been classified within various families and subfamilies of the Rachiglossa (Muricoidea *sensu* PONDER 1973). They all bear a smooth and conical protoconch of about 0.6 to 0.8 mm height and width. Three statements can be made concerning this protoconch-type. Firstly, it is the most common one among Late Cretaceous neogastropods and therefore considered here the basic type. Secondly, based on this simple protoconch alone, it is impossible to assign the connected species to a certain Recent neogastropod family. Thirdly, it indicates a close relationship of the concerned genera with each other.
Among them, *Bellifusus*, *Drilluta*, *Graphidula*, and *Paleopsephaea* all show transitions into each other, raising some doubt on the validity of the younger names. They were most commonly assigned to the Fasciolariidae, Athletidae and Volutidae. *Buccinopsis* exhibits teleoconch characters which are today found in buccinids as well as (pseud-)olivids. *Pyrifusus* shows similarities to Recent buccinids and muricids (*Urosalpinx* STIMPSON, 1865 among the muricids, for example). RIEDEL (2000) considered the lack of columellar folds and the presence of ”significant varices” as apomorphies for the Muricidae. However, there are other neogastropod families which lack columellar folds, and there are numerous muricid genera lacking any varices (*Ocenebra* CARPENTER, 1864, *Nucella* RÖDING, 1798, *Acanthina* FISCHER VON WALDHEIM, 1807). It therefore appears rather impossible to distinguish muricids and buccinids among the Late Cretaceous neogastopod genera.
This problem was already noted by TAYLOR et al. (1980: 386), who pointed out that similarities are closer within the Cretaceous neogastropods than when Cretaceous and Recent ones are compared. They concluded that the assignment of Late Cretaceous genera to Recent families was rather subjective. Matters are further complicated by the fact that all genera discussed here apparently lived exclusively in the Late Cretaceous. Neither the effect of the K/T-boundary on neogastropod evolution is sufficiently examined, nor are Paleocene gastropods known well enough - especially regarding their protoconch morphology - to trace the modern lineages safely into the Late Cretaceous. Considering that Conidae and Terebridae did not appear prior to the Eocene, the same might also apply to certain rachiglossan groups. Accordingly, certain Late Cretaceous rachiglossa may turn

out to belong to distinct, intermediating, and extinct groups when critically examined.

Subclass Heterostropha FISCHER, 1885

This subclass holds gastropods with a larval shell which is coiled in the opposite direction as the adult shell.

In the traditional classification of gastropods into Prosobranchia, Opisthobranchia and Pulmonata, species with a heterostrophic protoconch were found in all three subclasses. The Pyramidellidae were considered to intermediate between Prosobranchia and Opisthobranchia. Today, most workers disagree with this old system. BANDEL (1982) divided the Gastropoda into four subclasses, Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostropha, based on the formation of the early ontogenetic shell. In this model, the Heterostropha hold the Opisthobranchia and Pulmonata, the Mathildoidea, the Architectonicoidea and the Nerineoidea of the ”Mesogastropoda” as well as the intermediating Pyramidellidae.

Regarding the Heterostropha, HASZPRUNAR (1985) came essentially to the same conclusions as BANDEL (1982), based on anatomical characters, but called them Heterobranchia. Within them, he recognised the Allogastropoda, including ”mesogastropods” with heterostrophic protoconch, and the Pyramidelloidea.

Also the classification of gastropods traditionally known as Opisthobranchia has gone through considerable changes in recent years. HASZPRUNAR (1985) divided most shelled Opisthobranchia into two groups, the Architectibranchia on one hand, holding such families as Actaeonidae, Bullinidae, Hydatinidae, Ringiculidae and Daphanidae, and on the other hand the Tectibranchia, including the Bullomorpha (=Cephalaspidea), Aplysiomorpha and Saccoglossa among others.

In a cladistic analysis, MIKKELSEN (1996) removed *Actaeon* MONTFORT, 1810 from the Opisthobranchia altogether and placed it near *Gegania* JEFFREYS, 1884 (a mathildid allogastropod) in the ”lower Heterobranchia”. *Hydatina* SCHUMACHER, 1817 and *Ringicula* DESHAYES, 1838 remained in the Architectibranchia. Within the Cephalaspidea, MIKKELSEN (1996) recognized *Bulla* LINNÉ, 1758 on one side and the Philinoidea holding *Cylichna* LOVÉN, 1846, *Retusa* BROWN, 1827, *Acteocina* GRAY, 1847 and *Scaphander* MONTFORT, 1810 etc. on the other.

Order Allogastropoda HASZPRUNAR, 1985

Family Mathildidae DALL, 1889

The small elongated shell with many whorls is sculptured by spiral carinae that may be crossed by collabral costae or growth lines. The aperture is subcircular. The protoconch is sinistral and rests on the dextral teleoconch at a right angle or an angle smaller than that. The larval shell is low conical with rounded whorls that may show some axial folds on the apical and umbilical sides. The onset of the teleoconch is always abrupt and connected with a change in sculpture.

The Mathildidae are an often described but little known group of marine gastropods. WENZ (1938-44) listed no less than 15 genera and subgenera. GRÜNDEL (1976, 1997b) and SCHRÖDER (1995) added several new genera and relied strongly on the number of spirals on the first teleoconch-whorl to distinguish them. In a survey of Recent species from New Caledonia, BIELER (1995) demonstrated a broad variety of arrangements of the initial spirals among living species. He suggested that the validity of this character in mathildid classification needs to be tested by comparison with anatomical characters. However, he minutely described the initial spirals of his species. For example, with 2+**1**+1 he described two minor, one strong and one more minor initial spiral. Since the needed anatomical studies are still wanting, BIELER's method is adopted here.

Genus *Mathilda* Semper, 1865

Type species: *Turbo quadricarinata* BROCCHI, 1814 from the Pliocene of Italy. According to SABELLI & SPADA (1978) it still lives in the sublittoral rubble down to 30 m depth in the Mediterranean Sea of southern Italy.
Description: The description of the family applies to the genus.

Mathilda campania n. sp.

Plate 33, Figure 1

Holotype: GPI 3969, figured at pl. 33, fig. 1.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named after its Campanian age.
Diagnosis: The smooth, sinistral protoconch is of lowly helicoidal shape, consists of two and a quarter whorls and rests on the dextral teleoconch at an angle of about 45°. The initial ornament includes four spiral ribs of which the second one below the suture forms a keel.
Description: The protoconch consists of two and a quarter volutions and its coiling axis forms an angle of about 45° with the coiling axis of the teleoconch. The protoconch measures 0.65 mm in diameter and ends with a varix. The teleoconch is initially ornamented by four spiral ridges arranged in a 2+**1**+1 pattern. The spirals are crossed by fine axial ribs. On the second whorl the number of spiral ridges has increased to seven. The largest specimen has a diameter of 6 mm.
Remarks: Similar are *Mathilda pentalira* DOCKERY, 1993 from the Campanian of Mississippi and *Fimbracella* sp. 1 of KOLLMANN & PEEL (1983) from the Paleocene of Greenland which both have an initial 3+**1**+1-pattern. Also several Recent species are strikingly similar to *Mathilda campania*, such as *Mathilda decorata* HEDLEY, 1903 (see BIELER 1995 figs. 19-24, 26, 27), *Mathilda salve* BARNARD, 1963 (see BIELER 1995 figs. 30, 31, 34, 35, 39) and *Mathilda sansibarica* THIELE, 1929 (see BIELER 1995 figs. 60, 63).

Mathilda mexicana n. sp.

Plate 36, Figures 1-2

Holotype: The specimen illustrated in pl. 36, fig. 1.
Material: Three specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named after Mexico, the country of its occurrence.
Diagnosis: A *Mathilda* with a sinistral protoconch forming an angle of 90° with the teleoconch. The first whorls of the teleoconch shows two weak spiral followed by two strong ridges. The later whorls are well rounded.
Description: The protoconch measures 0.5 mm in diameter. Its base bears ribs that are best developed next to the 0.1 mm wide umbilicus. Of the teleoconch six whorls are preserved, but there may have been more. Ornamentation begins with five spiral cords in a 2+**2**+1-pattern, crossed by fine axial ribs. On the last three to four volutions spiral and axial elements are of equal strength and the whorls are well-rounded. Also the base is rounded, possesses a narrow umbilical slit and a sculpture of spiral cords. The inner lip is reflected and the peristome interrupted. The adult shell is 8 mm high and 3 mm wide
Remarks: The similar *Mathilda pentalira* differs in having a 3+**1**+1-pattern on the initial teleoconch whorl. Among the Recent species described by BIELER (1995)

Mathilda houbricki BIELER, 1995, *Mathilda maculosa* BIELER, 1995, *Mathilda decorata* HEDLEY, 1903 and *Mathilda* cf. *amanda* THIELE, 1925 possess similar initial ornamentation.

Mathilda gardnerae n. sp.

Plate 36, Figure 3

Holotype: The specimen illustrated in pl. 36, fig. 3.
Material: Five specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named for the American palaeontologist JULIA F. GARDNER who also worked on Mexican fossils.
Diagnosis: A *Mathilda* with the protoconch in inclined position about 45° to the shell axis. The first teleoconch whorls bear a strong keel in the lower half, creating an angular appearance of the whorls.
Description: The protoconch measures 0.35 mm in diameter, is partly imbedded in the first teleoconch whorl and forms an angle of about 45° with the teleoconch. The teleoconch consists of eight or more angulated volutions, its ornamentation starts with spirals in a 3+2-pattern. The first of the strong spirals forms a keel. The spirals are tuberculate where they are crossed by fine axial ribs and the sutures are very deep. Later whorls are more rounded. The inner lip is reflected, the base is rounded and sculptured with spiral cords and bears a very narrow umbilical slit. The adult shell is 9.5 mm high and 4 mm wide.
Remarks: The early shell resembles *Mathilda ripleyana* WADE, 1926 from the Ripley Formation and *Fimbriatella* sp. 1 from the Paleocene of Greenland (KOLLMANN & PEEL, 1983), but the later whorls are similar to those of *Mathilda mexicana*.

Mathilda? sp.

Plate 33, Figure 2

Material: One specimen from the Campanian of Torallola, Spain.
Description: The turriform shell bears a protoconch of about 0.46 mm width. The teleoconch consists of seven to eight angular whorls sculptured with fine axials and spirals. The shell is about 5 mm high.

Genus *Gymnothilda* SCHRÖDER, 1995

Type species: *Gymnothilda levata* SCHRÖDER, 1995 from the early Cretaceous of Wonwal in Poland.
Description: The ornament of the teleoconch is by one or two spiral ribs only and without axial ribs. The protoconch is mathildoid.
Remarks: The shell is very similar to that of *Mathilda*, *Tirolthilda, Promathildia, Teretrina*, or *Tricarida*, but differs by having very little or no axial ribbing.

Gymnothilda torallolensis n. sp.

Plate 33, Figure 3

Holotype: GPI 3971, figured at pl. 33, fig. 3.
Material: One specimen.
Derivation of name: Named for its occurrence in the vicinity of Torallola, Spain.
Diagnosis: The early teleoconch bears three spiral ribs of which the anterior one becomes covered by the succeeding whorl and the posterior one is low and

subsuturally oriented. The middle one forms the peripheral keel at the end of a flattened posterior whorl side. The protoconch stands almost in a right angle to the teleoconch and measures about 0.5 mm in diameter. The specimen is about 1.2 mm high.

Genus *Carinathilda* GRÜNDEL, 1997

Type species: *Carinathilda carinata* GRÜNDEL, 1997 from the Middle Jurassic of Poland.
Description: According to GRÜNDEL (1997b), the sinistral protoconch forms an angle of up to 45° with the teleoconch, is smooth or with ribletts and forms a sharp transition to teleoconch. On the high, trochospiral adult shell, sculpture starts with two spiral keels of which the second is the strongest. The shell is covered with a fine pattern of spirals and collabral axials.

Carinathilda diminuta (PERRILLIAT, VEGA & CORONA, 2000)

Plate 36, Figure 4

1980 *Pterocerella* cf. *poinsettiformis* STEPHENSON – ALENCÁSTER: 40, fig. 7.
2000 *Nododelphinula diminuta* PERRILLIAT, VEGA & CORONA: 9, figs. 5.12-5.14.

Material: Eight specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch is imbedded in the teleoconch and measures about 0.4 mm across. The medium sized teleoconch has up to eight angular volutions with numerous fine nodular spiral cords crossed by even finer axial costae. A strong keel in the lower third marks the whorls greatest width. Its base is rounded and covered with fine spiral lirae, the umbilicus takes one third of the basal diameter and shows fine spiral lirae inside. The aperture is roundish and the upper part of the inner lip is strongly reflected. The shell is 8 mm high and 4 mm wide.
Remarks: *Carinathilda diminuta* is distinguishable from the type species by its two prominent spiral ridges on the later whorls. *Bathraspira fouadi* ABBASS, 1973 from the Albian of Folkstone, UK (ABBASS 1973), may also belong here, but shows only one strong spiral ridge and has a lower apical angle.

Genus *Tirolthilda* BANDEL, 1995

Type species: *Tirolthilda seelandica* BANDEL, 1995 from the Upper Triassic St. Cassian Formation, Italy.
Description: The high-spired, slender, turriform shell has flattened whorl flanks and a sinistral protoconch. The protoconch lies in inclined position on the dextral teleoconch, has umbilical folds and a thickened apertural margin. The first teleoconch-whorl is sculptured by two keels of equal strength and collabral axial ribs (BANDEL 1995).

Tirolthilda hispanica n. sp.

Plate 33, Figure 4

Holotype: GPI 3972, figured at pl. 33, fig. 4.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for Spain, its country of origin.
Diagnosis: A *Tirolthilda* with a regular ornament of subequal spiral and axial ribs on the first two whorls of the teleoconch.
Description: The protoconch is smooth, measures 0.25 mm in diameter and forms an angle of about 45° with the teleoconch. There are three teleoconch whorls which

are convex to angular in outline. They are ornamented by two strong spiral ridges that are crossed by equally strong axial ribs. The shell is 1.2 mm high.

Remarks: The strong axial ribs in the first two teleoconch whorls of *Tirolthilda hispanica* differ from those of *Tirolthilda seelandica* where they are weaker than the two spiral ribs.

Remarks: Protoconch and preserved early teleoconch of this species resemble those of the Triassic type species. Even though only the early teleoconch is known and the later teleoconch may be somewhat differently formed, as is the case in the type to the genus, this small shell is characteristic.

Genus *Ponsia* n. gen.

Type species: *Ponsia catalanica* n. sp.

Diagnosis: *Ponsia* has a small, dextral, conical shell with flattened flanks, the whorls are ornamented with two strongly tuberculate ridges with a weak one between them, while sutures are indistinct. The protoconch with smooth rounded whorls twist from sinistral to dextral coiling in its transition to the teleoconch.

Derivation of name: Named after JOSE MARIA PONS, Barcelona.

Remarks: *Tuba* LEA, 1833 (=*Gegania*) usually has convex whorls that are ornamented by a cancellate pattern of numerous fine spirals and axials, in contrast to the straight, approximately bicarinate whorls of *Ponsia*. Members of *Mathilda* s.l. can be distinguished by their more slender shells with narrower apical angle and convex or angular whorls. Members of the Pyramidellidae usually have a rounded base in contrast to the flat base of *Ponsia*. Higher spired shells with similar sculpture are known from *Cassiope* CONQUAND, 1865 (=*Glauconia* GIEBEL, 1852) and *Metacerithium* COSSMANN, 1906 but these have a dextrally coiled protoconch (KOWALKE 1998, see above).

Ponsia catalanica n. sp.

Plate 33, Figures 5-6

Holotype: GPI 3973, figured at pl. 33, figs. 5-6.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: Named for the Spanish province of Catalania.

Diagnosis: As for the genus.

Description: The conical shell is made of four straight-sided whorls with two strong, tuberculate spiral ridges and one weak beaded spiral cord between them. The suture is keeled and the aperture rounded rectangular with a short anterior canal. The holotype is about 2.6 mm high and 2 mm wide. The sinistral protoconch is smooth, 0.45 mm in diameter and its coiling axis forms an angle of about 45° with the coiling axis of the teleoconch.

Remarks: *Ponsia catalanica* n. sp. is quite distinct from mathildids or high spired architectonicids. *Tectus tschudi* OLSSON, 1944 representing a rare species from the Maastrichtian of the Paita peninsular in northern Peru shows some resemblance. Its apical angle is also of about 45° and it possesses two rows of strong tubercles although they seem to be somehow irregular on the earlier whorls. WEINZETTL (1910) figured two specimens as *Turbo spinifer* WEINZETTL, 1910, one of which (WEINZETTL 1910, pl. 2, fig. 22) is about 10 mm high and possesses two nodular spiral ridges. They may both belong in the relation of *Ponsia* but their protoconchs are unknown. Among the over 50 species of Archaeogastropoda within the fauna of Torallola, no trochid that is similar to *Tectus tschudi* or *Turbo spinifer* was found. A possible older relative may be represented by *Teretrina microcostata*

SCHRÖDER, 1995 from the mid-Jurassic of Poland. This species possesses two strong spiral cords, with a weak in between and also a short anterior canal.

Genus *Lemniscolittorina* SOHL, 1960

Type species: *Littorina berryi* WADE, 1926 from the Maastrichtian of the Ripley Formation, Tennessee, USA.
Description: The *Littorina*-like shell has rounded whorls and nodular spiral ornament. The protoconch is smooth and sinistrally coiled, while the teleoconch is dextral.

Lemniscolittorina elongata n. sp.

Plate 33, Figures 7-8

Holotype: GPI 3974, figured at pl. 33, figs. 7-8.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: For its elongate shape.
Diagnosis: This elongate *Lemniscolittorina* has four finely ribbed spiral cords and no umbilicus.
Description: The relatively high spired shell has at least five volutions and is sculptured with four axially ribbed spiral cords. Its base is rounded, sculptured with similar spiral cords and has no umbilicus. The roundish aperture shows a smooth columella. The shell is 22 mm high and 12 mm wide.
Remarks: *Lemniscolittorina elongata* is larger and more elongate than *L. berryi* from the Ripley Formation, USA. It differs from *L. yonkersi* DOCKERY, 1993 by having a closed umbilicus and five spirals per whorl (DOCKERY 1993, pl. 4, figs. 5-6). The protoconch of this species from the Coffee Sand Campanian (DOCKERY 1993, pl. 5, figs. 1-4) is smooth.

Discussion: Typical members of the Mathildidae can be recognised since the Triassic (BANDEL 1995) and were abundant also in the Jurassic (GRÜNDEL 1997b). The mathildids described herein can well be connected to early Cretaceous and Jurassic forms, in the case of *Tirolthilda* even to Triassic ones. On the other hand, they also closely resemble Recent species. The newly introduced genus *Ponsia* may have had relatives in Peru and Czech Republic, but this suggestion needs to be confirmed by protoconch morphology.

Family Architectonicidae GRAY, 1840

Generally, distinction between the low spired Architectonicidae and the high spired Mathildidae is obvious. However, such genera as *Heliacus* (Architectonicidae) and *Tuba* (Mathildidae) are difficult to distinguish by shell characters alone (e.g. in the fossil record). BIELER (1984) suggested the architectonicid protoconch always to be coaxial and the mathildid to have an angle of at least 45° to the coiling axial of the teleoconch. BANDEL (1995, 1996) agreed on architectonicid protoconchs to be coaxial, the mathildid, on the other hand, he found to be highly variable in its position.

Genus *Heliacus* D'ORBIGNY in SAGRA, 1842

Type species: *Helicacus heberti* (DESHAYES, 1830), Recent, Martinique.
Description: These relatively high-spired, small architectonicids with dominant spiral sculpture are umbilicate and have a field of five spiral lirae on the base (after DOCKERY 1993).

Remarks: *Heliacus* (*Heliacus)* possesses a broad umbilicus (15-40% of the basal diameter) whereas in the subgenus *Heliacus* (*Gyriscus*) TIBERI, 1867, the umbilicus is rather narrow occupying around 10% of the basal diameter (BIELER 1985).

Heliacus alencasterae n. sp.

Plate 36, Figures 5-6

2000 *Calliomphalus (Planolateralus) argenteus argenteus* WADE – PERRILLIAT, VEGA & CORONA: 7, figs. 5.1-5.2.

Holotype: The specimen illustrated in pl. 36, figs. 5-6.
Material: Three specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: Named in honour of GLORIA ALENCÁSTER, the first who described gastropods from Temalac.
Diagnosis: This straight sided *Heliacus* has four spiral cords per whorl.
Description: The almost coaxial protoconch is smooth, embedded in the early teleoconch, measures 0.7 mm in diameter. Its suture to the teleoconch is reinforced. The trochiform teleoconch is made of up to five straight whorls with four nodular spiral cords, the third being the strongest. Some weak spirals appear between the later whorls. The base is flat and sculptured with spiral and axial lirae. The umbilicus occupies about a quarter of the whorl's diameter and the aperture is roundish. The shell is 3 mm high and 2.5 mm wide.
Remarks: *Heliacus reticulatus* DOCKERY, 1993 from the Campanian Coffee Sand of Mississippi has more spiral cords which are of equal strength and the whorls appear to be more rounded. A closely related European species may be "*Eutrochus*" *quadricinctus* MÜLLER (see HOLZAPFEL 1888: pl. 19, figs. 4-6) from the Vaals greensands of Germany, which needs to be revised. PERRILLIAT et al. (2000) originally assigned this species to *Calliomphalus argenteus*, which was designated by SOHL (1960) as the type for the new subgenus *Calliomphalus* (*Planolateralus*). But the protoconch was not figured and also its description is too indistinct for determination. Therefore, it remains unclear whether *Planolateralus* belongs to *Calliomphalus*, *Solariella* or even to the *Heliacus*-relation.

Genus *Granosolarium* SACCO, 1892

Type species: *Solarium milligranus* LAMARCK, 1822, from the Tertiary of Italy.
Description: The medium-sized, discoid shells with moderately broad umbilicus are sculptured with beaded spiral elements. The umbilical margin is beaded and not separated from remainder of base by a groove; the umbilical wall bears a spiral cord between margin and suture and beaded carina is present at shell periphery (after DOCKERY 1993).
Remarks: Recent *Granosolarium* lives in deeper waters (BIELER 1985). The genus is known since the Campanian (DOCKERY 1993).

Granosolarium sp.

Plate 36, Figure 7

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch is coaxial and smooth, and measures 0.28 mm in diameter. The teleoconch consists of three volutions with incised sutures, shows two spiral ridges near the upper and two near the lower suture, transverse costae and measures almost 3 mm in diameter. The whorl sides are rounded, the spire of low conical shape and the base shows spiral cords.

Remarks: The two other Maastrichtian species known from North America, *Granosolarium coffea* SOHL, 1964 and *Granosolarium voragiformis* STEPHENSON, 1941 differ with their nodular spiral cords. A similar species from the Middle and Upper Eocene of north-eastern Mexico is *Granosolarium alveata* (CONRAD), see GARDNER 1945: 151, pl. 14, figs. 17, 20, 21, 23) which has only two spiral cords near the lower suture and transverse growthlines.

Genus *Pseudomalaxis* FISCHER, 1885

Type species: *Bifrontia zanclea* PHILLIPI, 1836 from the Pliocene of Messina in Sicily, Italy.
Description: This genus unites discoidal shells with a very wide umbilicus, a flat or low spire and whorls angulated at peripheral and umbilical margins so that the whorls have a subrectangular cross section. The protoconch is smooth and forms an angle of 180° with the teleoconch (after DOCKERY 1993).

Pseudomalaxis pateriformis STEPHENSON, 1955

Plate 36, Figures 8-9

1955 *Pseudomalaxis pateriformis* STEPHENSON: 124, pl. 21, figs. 19-21.
1960 *Pseudomalaxis pateriformis* STEPHENSON - SOHL: 67, pl. 6, figs. 35, 38.

Material: Two specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch is smooth, made of one and a half volutions and has a diameter of 0.75 mm. It forms an angle of 180° with the teleoconch, terminates in a reinforced lip and on the last quarter volution appears a ridge. The teleoconch has angular whorls, deep sutures with jagged margins and the upper whorl sides are ornamented with beaded cords. The umbilicus is very wide with transverse lirae and nodular spiral keels. The aperture is round and an incomplete shell is 10 mm wide and 4 mm high.
Remarks: The protoconch is smaller than the average Recent one and the aperture is more trapezoidal as in the Recent forms figured by BIELER (1984).

Discussion: The architectonicids described here from Mexico are similar to Recent as well as other Late Cretaceous ones.

Family Amphitomariidae BANDEL, 1996

The small, planispirally coiled architectonicoids have a sinistral protoconch and one or two angular keels on the flanks of the teleoconch. When there is no free larval stage present within the ontogeny of a species, the embryonic shell has a planispirally coiled shape like that of the teleoconch.
Architectonicidae usually have larger shells, including the protoconch, which usually shows evidence of an extended planktotrophic existence. The Amphitomariidae in contrast are mostly small sized, flatly coiled and have relatively small protoconchs. The distinction between both families is sometimes difficult and may even be arbitrary, however, characteristic representatives have existed side by side since the late Triassic (BANDEL 1996).

Genus *Amphitomaria* KOKEN, 1897

Type species: *Euomphalus cassianus* KOKEN, 1889 from the late Triassic St. Cassian formation.

Description: The small shell has planispirally coiled whorls with angular outline and keeled margins. The protoconch is sinistrally coiled with the larval shell grading into planispiral coiling before the onset of the teleoconch.

Amphitomaria dockeryana n. sp.

Plate 33, Figures 9-12

Holotype: GPI 3983, figured at pl. 33, figs. 9-12.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: The species for DAVID T. DOCKERY, Jackson, Mississippi, USA, who described a very similar species from the Campanian of the Coffee Sand Formation.
Diagnosis: This *Amphitomaria* has a protoconch made of one and a half rounded whorls. The teleoconch whorls are rhomboid and show very regular growth increments.
Description: This small, disk-shaped shell is made of about five to six whorls which have rhomboid outline in cross-section. The two lateral keels have the vertical and smooth flank between them. Growth lines are simple and straight, and whorl diameter is angular with four corners but whorl height is less on the inner side than on the outer side. The protoconch consists of one and a half sinistrally coiled, almost planispiral, rounded volutions and measures 0.36 mm across. The upper side of the teleoconch exhibits transverse growthlines, and the flanks have straight axial growthlines. The shell has a diameter of about 6 mm and is 1 mm high.
Remarks: *Amphitomaria cassiana* (KOKEN) from the late Triassic St. Cassian Formation (BANDEL 1988, pl. 1, figs. 1-5) differs by the presence of fine spiral lines and there may be an additional marginal keel. Such spiral elements are not found in *Amphitomaria dockeryana*.

Genus *Neamphitomaria* BANDEL, 1988

Type species: *Pseudomalaxis stantoni* SOHL, 1960 from the early Maastrichtian Ripley Formation in Tennessee, USA.
Description: The teleoconch is like that of *Amphitomaria* but the protoconch consists only of a large, globular embryonic shell and lacks a sinistrally coiled larval shell (BANDEL 1988).

Neamphitomaria torallolina n. sp.

Plate 33, Figures 13-14

Holotype: GPI 3984, figured at pl. 33, figs. 13-14.
Material: One specimen from the Campanian of Torallola, Spain.
Derivation of name: Named for the village of Torallola, near to the outcrop where it was found.
Diagnosis: The small discoid shell with angular whorls consists of two and a half whorls. Its protoconch measures about 0.2 mm across and is smooth and bulging. The shell's surface shows axial growthlines that produce a little tuberculate marginal keel. The shell is 1.2 mm in diameter and 0.2 mm high.
Remarks: *Neamphitomaria stantoni* (SOHL, 1960) and *N. planospira* DOCKERY, 1993 both differ in having smaller but sculptured protoconchs. *L. stantoni* additionally has a keel on the upper side of the whorls.

Discussion: The new species of *Amphitomaria* and *Neamphitomaria* are similar to their Triassic and Cretaceous relatives. The Amphitomariidae apparently have not changed much during the course of their evolution.

Family Ebalidae WARÉN, 1994

The Ebalidae were introduced by WARÉN (1994) for allogastropods with a "jaw-apparatus" rather than a radula. They have high spired shells, often with a rounded labral sinus high on the whorl and a simple oval aperture. Their ornament can consist of only growth lines or in addition spiral lirae. The protoconch is sinistrally coiled and caps the spire flatly or is deviated.

Genus *Ebala* GRAY, 1847

Type species: *Turbo nitidissimus* MONTAGU, 1803 Recent, from European *Zostera* beds (WARÉN 1994).
Description: This genus includes small, high spired shells with a sinistrally coiled protoconch and a oval aperture. The shell is smooth, shows fine growthlines and may have fine spiral liration.

Ebala gruendeli n. sp.

Plate 33, Figures 15-17

Holotype: GPI 3982, figured at pl. 33, figs. 15-17.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: Named after JOACHIM GRÜNDEL, Berlin.
Diagnosis: This *Ebala* has a drop shaped aperture. Its protoconch is lowly sinistrally coiled and its axis forms an angle of about 50° with the coiling axis of the teleoconch.
Description: The small, slender shell has a smooth protoconch that measures 0.22 mm in diameter. It consists of almost one and a half lowly and sinistrally coiled whorls. The teleoconch consists of three and a half smooth whorls that show a very regular increase in diameter, have weakly convex sides and sinuous growth-lines. The outer lip of the aperture forms a weak recess near the suture and is weakly curved creating the drop-shaped outline with the posterior end pinched. The inner lip is weakly convex and its columellar portion a little thickened. The base is evenly rounded. The shell is a little more than 1 mm high and almost 0.4 mm wide.
Remarks: *Ebala compacta* (GRÜNDEL, 1998) and *Ebala procera* (GRÜNDEL, 1998) from the Jurassic have the adapical end of the aperture more rounded and their protoconchs form an angle of almost 90° with the teleoconch. Also *Ebala bogradi* (DOCKERY, 1993) has a more rounded posterior end of the aperture.

Discussion: Introducing the Ebalidae, WARÉN (1994) included not only the modern genera *Ebala*, *Henrya* BARTSCH, 1947, and *Murchisonella* MÖRCH, 1857, but hesitantly also the Paleozoic *Donaldina* KNIGHT, 1931. BANDEL (1994a, 1996) documented that *Ebala* and *Donaldina* lived alongside already in the Triassic, and placed the latter in its own family, the Donaldinidae BANDEL, 1994, together with several Triassic genera. Recent *Ebala* and *Murchisonella*, which closely resemble *Donaldina*, both share a similar "jaw-apparatus" (WARÉN 1994), but appear to have different mantle cavities (BANDEL, pers. comm.). However, the ebalid described here is similar to its Triassic, Cretaceous as well as living relatives, identifying *Ebala* as a fairly conservative lineage.

Family Pyramidellidae GRAY, 1840

In an examination of living species, WISE (1996) showed that pyramidelloids are quite variable in shape. Their sinistral protoconch is smooth and oriented 90-150° to the dextral teleoconch. The shell's aperture is elongate to ovate and with or without columellar folds.

Genus *Syrnola* Adams, 1860

Type species: *Syrnola gracillima* ADAMS, 1860 living around Japan (WENZ 1938-44).
Description: The small, turriform shell consists of numerous more or less straight-sided smooth whorls with incised sutures. The base is rounded and the small, drop-shaped aperture has a columellar lip with a rounded, strong columellar plate.
Remarks: WENZ (1938-44) listed twelve subgenera of *Syrnola* based on differences like the depth of the sutures, the inclination of the columellar fold or the angle of the protoconch. All subgenera except *Syrnola* s.s. are described to contain only a few species or are monotypic.

Syrnola? *cretacea* (HOLZAPFEL, 1888)

Plate 34, Figures 1-2

1888 *Odostomia cretacea* HOLZAPFEL: 134, pl. 14, fig. 16; pl. 21, fig. 14.

Material: Four specimens from the Campanian of Torallola, Spain.
Description: The sinistrally coiled protoconch forms an angle of about 45° with the teleoconch. The adult shell consists of up to eight straight-sided, smooth volutions. The base is well rounded, the aperture is lenticular and ends in a short anterior canal, the inner lip shows a strong fold. The shell is about 1.8 mm high.
Remarks: Although all of HOLZAPFEL's (1888) specimens lacked the embryonic whorls, he assigned this species to the Pyramidellidae. The heterostrophic protoconch is now documented. HOLZAPFEL compared this species with the Eocene *Odostomia turbonilloides* DESHAYES, 1861 and the Oligocene *Odostomia fraternum* SEMPER, 1865.

Genus *Herewardia* IREDALE, 1955

Type species: *Rissoina kesteveni* HEDLEY, 1907, living at the coasts of Queensland, Australia.
Description: The species of *Herewardia* are egg-shaped, axially and spirally sculptured, have a smooth columella and show an umbilical slit. The protoconch is sinistrally coiled and mostly imbedded in the teleoconch.

Herewardia? sp. 1

Plate 34, Figure 3

Material: One specimen from the Campanian of Torallola, Spain.
Description: The smooth protoconch is about 0.3 mm in diameter and is partly imbedded in the first teleoconch whorl. The teleoconch ornament consists of two strong, beaded spiral ridges and a weaker ridge below them; they are crossed by transverse axial ribs. The only specimen available is 0.5 mm high and 0.6 mm wide.

Herewardia? sp. 2

Plate 36, Figures 10-11

Material: One specimen from the Maastrichtian of Temalac, Mexico.
Description: The protoconch measures only 0.2 mm in diameter, is imbedded in the early teleoconch whorls and almost coaxial, possesses a larval hook and some axial ribs near the centre of the base. There is only one teleoconch whorl which is sculptured with five strong spiral cords and axial ribs that form nodular intersections. The second spiral marks the whorls largest diameter, the last spiral forms the margin of the deep umbilicus that is axial ribbed. The aperture is round. The shell is 0.45 mm high and 0.5 mm wide.

Discussion: Ebalidae, Donaldinidae and, in some cases even from the Mathildidae, especially since WISE (1996) showed that columellar folds are not characteristic for the family. A rather typical pyramidellid is described here with *Syrnola*? *cretacea* which is similar to species from the European Tertiary.

Order uncertain

Family Misurinellidae BANDEL, 1994

BANDEL (1994b) introduced this family for the Triassic *Misurinella sinistrorsa* KITTL, 1894, a single, sinistrally coiled species with a dextrally coiled protoconch. Due to the discovery of *Haszprunariella* n. gen. with dextral and sinistral coiling within the same species, the original family diagnosis is extended to include the dextrally coiled counterparts of sinistrally coiled species. Allogastropoda of similar size and shape as found within the Misurinellidae usually have a sinistrally coiled protoconch and a dextrally coiled teleoconch, as for example found in the many species of the modern Pyramidellidae. In case of the genus *Haszprunariella* species with dextrally coiled teleoconch can only be included when a sinistrally coiled counterpart is present.

Genus *Haszprunariella* n. gen.

Type species: *Haszprunariella laevis* n. sp. from the Campanian of Torallola.
Diagnosis: This new genus holds small, slender pyramidelliform gastropods with a smooth or spirally sculptured shell without columellar plates. An inversion of the coiling axis of proto- and teleoconch occurs in each species.
Derivation of name: Named for GERHARD HASZPRUNAR, Munich, who recognised the independence of the Allogastropoda among the Heterostropha.
Remarks: The Triassic *Misurinella* BANDEL, 1994 of the Misurinellidae BANDEL, 1994 represents a sinistrally coiled, turriform shell that has a dextral protoconch. However, dextrally coiled counterparts are not known and the Triassic species is two to three times larger than those documented here.

Haszprunariella laevis n. sp.

Plate 34, Figures 4-6

Holotype: The sinistrally coiled specimen GPI 3979, figured at pl. 34, figs. 4, 6.
Paratype: The dextrally coiled specimen GPI 3978, figured at pl. 34, fig. 5.
Material: About ten specimens from the Campanian of Torallola, Spain.
Derivation of name: For its smooth shell.
Diagnosis: This *Haszprunariella* is characterised by its straight-sided, smooth whorls.

Description: The protoconch is coiled in the opposite direction as the teleoconch with which it forms an angle of about 45°. It measures 0.18 mm across and terminates in a weak varix. The teleoconch consists of up to seven little concave whorls that are separated by fine, incised sutures. The aperture is lenticular, rounded at the base and the columella is straight and smooth. The shells are up to 1.8 mm high and 0.6 mm wide.

Haszprunariella spiralis n. sp.

Plate 34, Figures 7-9

Holotype: The sinistrally coiled specimen GPI 3980, figured at pl. 34, fig. 7.
Paratype: The dextrally coiled specimen GPI 3981, figured at pl. 34, figs. 8-9.
Material: About ten specimens from the Campanian of Torallola, Spain.
Derivation of name: For its ornament of spiral keels.
Diagnosis: The whorls of this *Haszprunariella* have a spiral keel which causes a notch in the aperture.
Description: The protoconch is coiled in the opposite direction as the teleoconch with which it forms an angle of about 45°. It measures 0.13 mm across and terminates in a strong varix. The teleoconch consists of up to five straight and keeled volutions. On the first one to three volutions the main keel is situated about in the whorl's centre and it gradually shifts towards the upper suture on later whorls. Some specimens develop a second keel near the lower suture, so that the whorl gets a concave appearance. The aperture is lenticular and rounded at its base, its columella is smooth and on the outer lip an indentation corresponds with the upper spiral ridge. The shells are up to 1.2 mm high and 0.4 mm wide.
Remarks: This species is distinct form *Haszprunariella laevis* n. sp. by its keeled whorls.

Discussion: The two species assigned to this new genus have shells which generally resemble those of *Eulimella* GRAY, 1847 and *Bacteridium* THIELE, 1929 of the Pyramidellidae, but inversion of the coiling axis has not been reported from members of these genera. Nor is any other sinistrally coiled allogastropod known to date.

An analogous case of a sinistrally coiled, heterostrophic gastropod may be *Blauneria* SHUTTLEWORTH, 1854, an ellobiid (Archaeopulmonata) living on the coasts of tropical oceans (MARCUS 1965). In the case of the species *Blauneria heteroclita* (MONTAGU, 1808) from the Brazilian shore of the Atlantic the dextral protoconch changes into sinistral teleoconch. According to MARCUS & MARCUS (1965) the dextral protoconch consists of one and a quarter whorls with 0.3 to 0.4 mm width. Development is without free larva. A species of *Blauneria* from Singapore has a protoconch of almost 0.2 mm in diameter (HARBECK 1996: pl. 18, figs. 277-278) consisting of about one whorl, indicating hatching as pediveliger or crawling young, as is the case with the western Atlantic species. Based on this analogous case of a sinistrally coiled heterostrophic gastropod, BANDEL (1994b) discussed relationships of the Misurinellidae with the Pulmonata.

The two species of *Haszprunariella* do not exceed 2 mm in height and are therewith notably smaller than either *Eulimella* and *Bacteridium* or *Blauneria*. Also the Triassic *Misurinella* is at least twice as big.

The sediments from which the described species were extracted represent a slump mass. Marine, land- and freshwater gastropods are found alongside in these sediments. Therefore, it is impossible to determine the habitat in which these unusual gastropods have lived in the Campanian.

Order Opisthobranchia MILNE-EDWARDS, 1848

Family Actaeonellidae ZILCH, 1959

The shell is of ovo-cylindical to spindle-like shape with a short spire or with convolute coiling. The last whorl is large and smooth and the aperture is narrow and only slightly widened abapically. The outer lip is simple, the columella bears one to three plicae. The protoconch is heterostrophic with sinistral coiling that grades into the dextral coiling in the shell of the metamorphosing animal.

The shell shape is like that of some Ellobiidae, but there is no internal resorbtion of shell walls. The shells are usually larger and thicker than those of most Cephalaspidea but similar to them in general shape.

Genus *Acteonella* D'ORBIGNY, 1843

Type species: *Acteonella laevis* D'ORBIGNY, 1843 from the Turonian, Uchaux basin, France.

Description: The shells are spindle shaped, have a narrow aperture and usually three columellar folds.

Remarks: *Acteonella* lived in shallow water or full marine lagoons and is commonly associated with corals and rudists (KOLLMANN 1965, KOWALKE & BANDEL 1996). An infaunal mode of living has been suggested by SOHL & KOLLMANN (1985).

Acteonella agricolai VIDAL, 1921

Plate 34, Figures 10-11

1921 *Acteonella agricolai* VIDAL: 103, pl. 7, figs. 14-16.
1949 *Acteonella agricolai* VIDAL - BATALLER: 131.

Material: Ten specimens from the Campanian of Torallola, Spain.

Description: The round protoconch is about 0.15 mm in diameter and appears to consist of one whorl with its axis perpendicular to the axis of coiling of the teleoconch. The first two teleoconch whorls are smooth and high-conical. In the third whorl the increase in whorl height is dramatic, so that the posterior margin reaches the spire and covers the spire. The typical convolute, spindle-like shape is thus reached within a little less than one volution. With the fifth whorl, the shape of the adult shell is acquired which is slender, smooth and convolute. Its apical end is pointed and the columella bears three ridges. The largest diameter of the shell lies in its middle. The aperture is slit like and as high as the whole shell, is apically pointed and ends anteriorly in a narrow notch. The largest specimen is 26 mm high and 10 mm wide.

Remarks: SOHL & KOLLMANN (1985) pointed out that in case of *Acteonella laevis* the diameter does not exceed 30% of its height. This relation is about 2.5:1 in *Acteonella agricolai*. Also *Acteonella caucasia* ZEKELI as figured by KOLLMANN (1968: pl. 2, fig. 13) is more elongate than *A. agricolai*. Here the columellar ridges have the same distance to each other, whereas the first ridge of *Acteonella marchmontenses* SOHL & KOLLMANN, 1985 is a bit set apart.

Genus *Trochactaeon* MEEK, 1863

Type species: *Acteonella renauxiana* D'ORBIGNY, 1842 from the Uchaux basin, Turonian, France.

Description: The elongate ovate to subcylindrical, moderately thick walled shells have an almost flat to high conical spire. The elongate aperture is broadening anteriorly and has a callused inner lip that normally bears three prominent folds.

Trochactaeon gigantea SOWERBY, 1832

Plate 34, Figures 12-13

Material: About 60 species from the Campanian of Torallola, Spain.
Description: The spire is flat or of moderate height. Young specimens usually have a subcylindrical body whorl with smooth, convex sides that taper more or less towards the columellar folds. Larger shells show a broader variability in the shape of the body whorl from conical to rounded cylindrical. There are always three columellar folds of which the uppermost is stronger than the anterior two. The largest specimen is 122 mm high and 75 mm wide.
Remarks: The specimens of *Trochactaeon* found in Torallola are mostly corroded and exhibit a broad variability from conical or cylindrical to well rounded, barrel-shaped shells with spires ranging from flat to broadly conical and moderately high. In contrast, they all show three oblique columellar plates of which the posterior one is a little stronger than the anterior two. Since all specimens found in Torallola show transitions into each other, they are all assigned to the same species.

Family Acteonidae D'ORBIGNY, 1842

This family holds elongate to egg-shaped shells with a sinistrally coiled protoconch and often a sculpture of incised spirals. The columella may bear one or more plications and the outer lip is not extended.

Genus *Actaeon* MONTFORT, 1810

Type species: *Voluta tornatilis* GMELIN, 1788, Recent, Mediterranean.
Description: Same as the family.
Remarks: Generic separation within the Actaeonidae is carried out mainly according to the number of columellar and parietal folds. The relative height of the spire is also considered but remains a minor character (WENZ & ZILCH 1959-60, SOHL 1964).

Actaeon cicatricosus SOHL, 1964

Plate 37, Figures 1-2

1964 *Acteon cicatricosus* SOHL: 288, pl. 47, figs. 17-18, 22.

Material: Six specimens from the Maastrichtian of Temalac, Mexico.
Description: The protoconch measures 0.3 to 0.4 mm in diameter, forms an angle of about 45° with the teleoconch and the last protoconch whorl is thicker than the first teleoconch whorl. The egg-shaped teleoconch consists of five moderately to well rounded volutions and is sculptured with fine spiral grooves with fine axial costae inside. The sutures are deep and the whorl shoulder bears a spiral groove. The columellar lip is reflected, the aperture is elongate, narrow and rounded on both ends. The largest specimen is 7 mm high and 3.5 mm wide
Remarks: The specimen from the Ripley Formation of Mississippi is only about half as high as the Mexican ones.

Actaeon sp.

Plate 37, Figures 5-6

Material: One specimen from the Maastrichtian of Temalac, Mexico.
Description: The large, smooth protoconch measures 0.45 mm across, is deeply imbedded in the teleoconch and has an inclined axis. The one teleoconch whorl shows numerous nodular spiral cords connected vertically by fine axial lamellae.
Remarks: Only half a teleoconch whorl is preserved, its ornament resembles that of *Actaeon cicatricosus* but the protoconch has a different mode of coiling, is larger and more deeply imbedded in the teleoconch. A very similar ornament is known from the mid-Jurassic *Actaeon* cf. *ooliticus* HUDLESTON (SCHRÖDER 1995: pl. 11, figs. 7-10).

Genus *Tornatellaea* CONRAD, 1860

Type species: *Tornatellaea belle* CONRAD, 1860.
Description: This genus comprises subovate shells with the spire making less than half of the total shell height. Sculpture consists of fine, punctate furrows that are narrower than their interspaces. The aperture is posteriorly narrowed and shows two columellar plates.
Remarks: *Tornatellaea* is distinct from *Actaeon* MONTFORT, 1810 by the presence of two columellar plates while there is only one in *Actaeon*. *Eoactaeon* STEPHENSON, 1955 differs according to SOHL (1964) by a higher spire, by the presence of only one columellar plate which is not visible in the aperture and its larger size. Although STEPHENSON (1955) mentioned a weak, second columellar plate, SOHL (1964) was unable to verify this diagnosis.

Tornatellaea sp. 1

Plate 34, Figures 14-15

Material: Four specimens from the Campanian of Torallola, Spain.
Description: The egg-shaped shell consists of three volutions and has an apical angle of about 65°. Its columella possesses two folds, the base of the body whorl shows incised spiral cords. The shell is 9 mm high and 5 mm wide.
Remarks: *Tornatellaea* sp. 1 and *Tornatellaea* sp. 2 are distinct only by the presence of a parietal fold in *Tornatella* sp. 2. Too few specimens are available to decide whether this justifies separation on the species-level. Similar species from the Ripley formation include *Tornatellaea cretacea* WADE, 1926 and *Tornatellaea globulosa* WADE, 1926 but they appear generally higher spired. From the Aachen greensands, HOLZAPFEL (1888) described *Actaeon mülleri* BOSQUET, 1861 also with a higher spire.

Tornatellaea sp. 2

Plate 34, Figures 16-17

Material: One specimen from the Campanian of Torallola, Spain.
Description: The spire of this small shell makes less than one third of the total shell height The whorls are subsuturally grooved and sculptured with fine incised spiral lines. The aperture is rather narrow, its outer side is denticulate and the columella bears two plates, there is one weak parietal plate. The protoconch is only little elevated from the spire. The shell is 9 mm high and 5 mm wide.

Family Ringiculidae FISCHER 1883

The ringiculid shell is globular to elongated egg-shaped and sculptured with pitted spirals or zigzagged grooves. The columella bears several plications, the outer lip is thickened and extends onto the spire and may have denticles on its inner side.

Genus *Ringicula* DESHAYES, 1838

Type species: *Auricula ringens* LAMARCK, 1804.
Description: Same as the family.

Ringicula abundanta n. sp.

Plate 35, Figures 1-2

Holotype: GPI 3990, figured at pl. 35, figs. 1-2.
Material: About 100 specimens from the Campanian of Torallola, Spain.
Derivation of name: This is the most abundant ringiculid in the Campanian fauna of Torallola.
Diagnosis: A *Ringicula* with a small spire, weakly developed spiral grooves, the inner lip has three ridges and the outer lip has five small denticles at its base.
Description: The protoconch is coaxial and embedded in the teleoconch. Adult shells are small, made of six straight sided volutions and the body whorl makes about two thirds of the total shell height. Sculpture consists of fine spiral grooves, the outer lip is reinforced with a thick callus that extends onto the spire. This callus shows axial growthlines on its dorsal side, the ventral side is smooth, with a large groove on the posterior end and a ridge with five denticles near the base. The inner lip is heavy callused, shows two sinuses and a keeled ridge between them. The shell is 9 mm high and 6 mm wide.
Remarks: A similar apertural dentition show *R. pulchella* SHUMARD, 1861 and *R. yochelsoni* SOHL, 1964 from the Maastrichtian of the Ripley Formation, but both differ with their zigzagged sculpture.

Ringicula larteti CHAVAN, 1947

Plate 35, Figures 5-7

1959 *Ringicula* (*Ringiculopsis*) *larteti* CHAVAN – WENZ & ZILCH: 20, fig. 53.

Material: Nine specimens from the Campanian of Torallola, Spain.
Description: This small shell is made of seven volutions, has a large body whorl which is about two to and a half times as high as spire. Sculpture consists of fine spiral grooves, the outer lip is reinforced with a thick callus that has a carinate ornament of strong axial and spiral lines on the dorsal side. These spiral lines become the dominant ornament on the ventral side. Its inner lip is also thickened with a band of callus that is keeled at the aperture. The columella bears four ridges, the first is the weakest, the third the strongest. The base of inner lip shows a similar ornament as the dorsal outer lip. The shell is 8.5 mm high and 6 mm wide.
Remarks: *Ringicula larteti* was used as type species of the subgenus *Ringicula* (*Ringiculopsis*) CHAVAN, 1947. WENZ & ZILCH (1959-60) described this subgenus as ”a precursor of *Ringicula* which unites characters of *Ringiculina* and other genera”. Due to the broad variability within *Ringicula* this subgenus is not used here. A species with similarly sculptured outer lip and also two columellar folds was described by KOLLMANN (1976) from the Albian/Cenomanian of Austria. However, that species lacks the callused inner lip of *Ringicula larteti.*

Ringicula multidenta n. sp.

Plate 35, Figures 3-4

Holotype: GPI 3992, figured at pl. 35, figs. 3-4.
Material: Ten specimens from the Campanian of Torallola, Spain.
Derivation of name: Named for the numerous denticles on the outer lip.
Diagnosis: This *Ringicula* has three columellar folds and a ridge on the inside of the outer lip which has one strong denticle at its base, three small ones in the middle and three further ones on its apical side.
Description: This species is small and relatively high spired for the genus. It shows no ornament and a columella with three ridges. The inner side of the outer lip shows two denticles, followed by a denticulate ridge and another strong denticle near the base. The outer lip is reinforced with a thick band of callus that bears one strong basal denticle, three small median denticles and three more at the upper end. The shell is 5 mm high and 3 mm wide.
Remarks: The anterior spout of the aperture is bordered by a strong denticle on the outer side in this species, neither *Ringicula exceptionalia* nor *Ringicula abundanta* show such a denticle.

Ringicula corona n. sp.

Plate 37, Figure 3

2000 *Ringicula (Ringiculina*) cf. *clarki* GARDNER – PERRILLIAT, VEGA & CORONA: 19, fig. 7.10.
Holotype: The specimen illustrated in pl. 37, fig. 3.
Material: About 20 specimens from the Maastrichtian of Temalac, Mexico.
Derivation of name: In honour of R. CORONA, Mexico City, who worked on the mollusca of the Temalac fauna.
Diagnosis: A *Ringicula* with smooth and slender early whorls, two oblique plaits on the columella and the outer lip is dented within.
Description: The protoconch forms an angle of 180° with the teleoconch and has a diameter of about 0.15 mm. The teleoconch is egg-shaped with six volutions, the first two are smooth and straight sided, but later whorls are convex and sculptured with fine spiral grooves. These grooves are only weak on the central body whorl and interspaces are much closer next to the upper suture than elsewhere. The outer lip is thickened with callus and reaches up to the two preceding volutions. Its outer side shows axial grooves, the inner side is dented. The parietal lip is thickened with callus and the columellar lip is reflected and bears two oblique plates. The aperture is convex and narrow. The holotype is 8 mm high and 5 mm wide.
Remarks: *Ringicula clarki* GARDNER, 1916 shows no denticles on the outer lip and the outer lip does not reach as high on the spire as *Ringicula corona* n. sp. *Ringicula pulchella* SHUMARD, 1861 and *Ringicula yochelsoni* SOHL, 1964 have a denticle on the parietal lip and a zigzagged ornament.

Genus *Avellana* D'ORBIGNY, 1843

Type species: *Avellana avellana* (BROGNIART) from the Cenomanian of France.
Description: *Avellana* is characterized by rounded shell shape, a low dome shaped spire and a thickened inner lip callus. There is one strong plication on the columellar lip and the inner side of the outer lip is denticulated within or smooth. Additional denticles and plicae may be present on the inner and outer lip. The outer lip forms a thickened varix and there is a shallow canal on the posterior side of the aperture and a rounded notch at the anterior side of the aperture. The ornament

consists of a pattern of spiral grooves that are crossed by collabral bridges to form a row of pits.

Remarks: KOLLMANN (1976) discussed the *Avellana-Oligoptychia*-group and, based on a species which he found to intermediate, proposed to synonymize the two genera. KASE (1984) stated that discrimination between *Eriptychia* and *Avellana* is difficult. A character distinguishing *Avellana* and *Eriptychia* might be the double-toothed, basal columellar fold of the latter. Due to these uncertainties and the lack of better evidence, *Eriptychia* is treated as a subgenus of *Avellana*.

Subgenus *Avellana* (*Eriptychia*) MEEK, 1876

Type species: *Eriptychia decurata* SOWERBY, 1835 from the Turonian.

Avellana (*Eriptychia*) *decurata* (SOWERBY, 1835)

Plate 35, Figures 8-9

1959 *Eriptychia decurata* (SOWERBY) – WENZ & ZILCH: 22, fig. 64.

Material: One specimen (figured: GPI 3993).

Description: The low spired, egg-shaped shell is made of about three volution. Sculpture consists of numerous strong incised spirals with fine axial ribbletts. The outer lip is reinforced, reaches the penultimate whorl and is dented within. The aperture is long and narrow, its inner lip bears one strong, bilobed columellar fold and two strong parietal denticles. The shell is 6.5 mm high and 5 mm wide.

Informal group Bullomorpha

Due to the strong convergence among the shells of Recent bullomorph gastropods, the species desribed here are placed either in exclusively fossil genera or tentatively in Recent genera of similar shell-shape. However, they are not assigned to a certain bullomorph family because this would pretend a more precise classification than it is possible using shell-characters alone.

Genus *Goniocylichna* WADE, 1926

Type species: *Gonicylichna bisculpturata* WADE, 1926 from the Coon Creek Maastrichtian in Tennessee, USA.

Description: The small, subcylindrical shell has a low to flat spire. Sculpture is axial on the adapertural margin of the whorl and spiral on the basal portion of the whorl. The aperture is narrow and the columella is smooth.

Remarks: Members of *Cylindrotruncatum* SOHL, 1963 with the type species *C. demersum* SOHL, 1963 from the Maastrichtian Ripley Formation have similar shell shapes with slender, adapically truncate, cylindical shells, but the whorls terminate adapically in a sharply carinate edge that borders the apical depression.

Goniocylichna laeviata n. sp.

Plate 35, Figures 12-13

Holotype: GPI 3994, figured at pl. 35, figs. 12-13.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: This species of *Goniocylichna* lacks any sculpture.

Diagnosis: This flat-topped *Goniocylichna* is smooth and slightly constricted below the top.

Description: The cylindrical shell is smooth and constricted near the top, its aperture is long and narrow and widens anteriorly. Aperture is anteriorly expanded and rounded, posteriorly with shallow notch and the columella has a distinct fold that begins just behind the aperture. The columellar lip thus appears reflected. The top is flat to a little concave and sculptured with spiral lines, the protoconch can still be seen in the middle probably uncovered by erosion. The shell is little higher than 3 mm.

Remarks: WADE (1926: 106) considered the ”abruptly truncate posterior extremity and its dual type of sculpture” as characteristic for *Goniocylichna*. The smooth species from Torallola is tentatively placed here due to its truncated spire, although it lacks any sculpture.

Genus *Cylindrotruncatum* SOHL, 1963

Type species: *Cylindrotruncatum demersum* SOHL, 1964 from the Maastrichtian Ripley Formation.

Description: The cylindrical shell is small and apically truncated with the spire visible in the concave apical depression. The whorls terminate above in a sharply carinate edge that borders the apical depression. Ornament consists of faint spiral grooves that are pitted and fine collabral transverse elements restricted to the posterior part of the whorl. The aperture is narrow and expands anteriorly. The columella is basally truncate (SOHL 1964, pl. 49, figs. 8-12).

Remarks: The unusual depressed open spire and carinate upper whorl edge separated *Cylindrotruncatum* from *Cylichna* and other similar genera.

Cylindrotruncatum caldera n. sp.

Plate 35, Figures 10-11

Holotype: GPI 3995, figured at pl. 35, figs. 10-11.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: For the caldera-shaped apical side.

Diagnosis: As for the genus.

Description: The cylindrical shell has volutions which are little convex and smooth except for faint growthlines. On the apical side, the whorls are in one plane and form a sharp crest. The aperture is straight and narrow and it widens at the base. There are some faint spirals on the base. The shell is 6 mm high and 2.7 mm wide.

Cylichna-like shells

Description: *Cylichna* is based on the Recent *Cylichna cylindracea* (PENNANT, 1777), shells are convolute, cylindrical with more or less rounded sides, the columella is smooth and the shell might be sculptured with incised spirals.

”Cylichna” recta GABB, 1860

Plate 37, Figure 4

1860 *Cylichna recta* GABB: 302, pl. 48, fig. 16.
1916 *Cylichna recta* GABB - GARDNER: 411, pl. 18, figs. 10-11.
2000 *Cylichna secalina* SHUMARD – PERRILLIAT, VEGA & CORONA: 19, fig. 7.9.

Material: 14 specimens from the Maastrichtian of Temalac, Mexico.

Description: A cylindrical, convolute shell with an apical umbilicus that measures about one third of the whorls diameter. The top is flattened and the margin marked by a weak ridge. The aperture is long and narrow, ends anteriorly in a sinus, posteriorly it widening as the whorl is constricted near the base and the outer lip is only very little convex. The columella is a little reflected and has a rounded base. The sculpture of weak spiral grooves is best developed in the lower half of the whorl. The largest shell is about 1.8 mm high.
Remarks: *Cylichna secalina* SHUMARD, 1861 and *Cylichna recta* are most probably synonymous as the only difference reported and visible is the distribution of the fine spiral grooves. The weaker development of this ornament on the Mexican species than on those figured by GARDNER (1916) probably is a matter of corrosion rather than a distinctive character.
Cylichna diversilirata SOHL, 1964 is distinct by having a strongly reinforced columellar lip (SOHL 1964, pl. 49, figs. 34-36). *Cylichna incisa* can be distinguished by its punctate ornament, and it has a narrower apical depression than the other species of the region. *Cylichna intermissia intermissia* SOHL, 1964 is distinguished by lack of a pronounced columellar fold, the presence of an umbilical slit, and the absence of sculpture upon the medial parts of the body (SOHL 1964, pl. 49, figs. 22-23). *Cylichna pessumata* SOHL, 1964 has a similar ornament as *C. intermissia* but possesses an apical plug.

”Cylichna” actaeonelliformis n. sp.

Plate 35, Figure 14

Holotype: GPI 3996, figured at pl. 35, fig. 14.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: This species is spindle-shaped like *Acteonella*.
Diagnosis: This spindle-shaped shell is made of smooth and convolute whorls. Its aperture is long, narrow and posteriorly elevated, anteriorly there is a canal.
Remarks: A related species could be *Cylichna incisa* STEPHENSON, 1941 which is also spindle-shaped but differs in having numerous incised spiral cords.

”Cylichna” sp. 1

Plate 35, Figure 15

Material: One specimen from the Campanian of Torallola, Spain
Description: The *Cylichna*-like shell has a smooth exterior except for some fine axial ribs on the adapical side of the shell. The aperture is long and narrow and the columella is smooth. The shell is 7 mm high and 2.5 mm wide.

Discussion: Although the fossil record is of limited value in retracing opisthobranch evolution in many cases, it tells us the major steps of their history. BANDEL (1994b) commented on the Carboniferous *Girtyspira* KNIGHT, 1936 and considered these shells to represent Caenogastropods due to their dextrally coiled protoconchs. Typical opisthobranchiate shells are clearly recognizable since the Triassic with *Zardinella* BANDEL, 1994 and *Cylindrobullina* AMMON, 1878 (not to be confused with the Recent *Cylindrobulla*) (BANDEL 1994b). Of these, *Zardinella* has a teleoconch similar to that of *Actaeon*, but its protoconch shows strong radial ribbing on its base (BANDEL 1994b: pl. 3, figs. 11-14). This feature is unknown from any post-Triassic opisthobranch.
Apparently, shell-morphologies like those of Recent *Actaeon*, *Ringicula* and *Cylichna* appear more or less simultaneously in the Jurassic (GRÜNDEL 1997c).

During the Early Cretaceous, the Actaeonellidae with *Acteonella* and *Trochactaeon* occurred and dominated the Tethyan carbonate and lagoonal facies until the end of the Mesozoic.

A placement of *Actaeon* closer to the allogastopod *Gegania* than to the Opisthobranchia as supposed by MIKKELSEN (1996) does not coincide with the fossil record.

SOHL & KOLLMANN (1985) described the ontogenetic changes in *Acteonella cubensis* SOHL & KOLLMANN, 1985. They found the protoconch to be 0.24 mm in diameter and thus quite a bit larger than that of *Acteonella agricolai*. The change from conical to convolute coiling was found to start after the third whorl and to take more than one volution. In *Acteonella agricolai* this process takes only a little more than half of a volution and starts within the fourth whorl. This indicates some variation in protoconch size and the timing of the change of coiling behaviour with the species of the genus *Acteonella*.

Order Pulmonata CUVIER, 1817

Suborder Archaeopulmonata MORTON, 1955

Family Ellobiidae ADAMS & ADAMS in PFEIFFER, 1854

Ellobiids have a high-spired, dextral and comparatively thick-walled shell. Most species have well-developed palatal, parietal and/or columellar teeth. The family is further characterised by the gradual resorbtion of internal shell-structure during growth (BEESLEY et al. 1998: 1077-78).

Genus *Laemodonta* PHILIPPI, 1846

Type species: *Laemodonta striata* PHILIPPI, 1846 from the Island of Hawaii (WENZ & ZILCH 1959-60).

Description: The small, egg-shaped shell has whorls that are little convex and show spiral sculpture. The aperture is narrow and shows two folds on the inner lip, and some denticles on the inner side of the outer lip.

Laemodonta cretacea n. sp.

Plate 35, Figure 16

Holotype: GPI 3998, figured at pl. 35, fig. 16.

Material: One specimen from the Campanian of Torallola, Spain.

Derivation of name: This is the first Cretaceous species of *Laemodonta* known to me.

Diagnosis: This *Laemodonta* has a reticulate ornament made of equally strong axial and spiral elements. There are three plates on the inner lip, numerous fine denticles on the base of the aperture and a strong pallatal plate.

Description: Spire and last whorl are of about equal height in this ellobiid shell. Sculpture consists of fine axial and spiral cords which form small tubercles at their intersections. The inner lip possesses three plates, the outer lip shows fine denticles at the base, and a strong denticle opposite the central one of the inner lip. The shell is 13 mm high and about 6.5 mm wide.

Remarks: The similarly sculptured Recent species *Laemodonta exarata* H. & A. ADAMS, 1854 was reported by MARTINS & TRISTÃO DA CUNHA (1992) from a salt water meadow in the Sai Kong Peninsula, Hong Kong, China.

Family Siphonariidae GRAY, 1840

The limpet-like shell is circular to elliptical in outline with a central or subcentral apex. The protoconch is sinistrally coiled. Sculpture on the adult shell consists of radial ribs and concentric growthlines. A siphonal groove is located internally on the right side of the shell and may be seen as a ridge externally.

Genus *Siphonaria* SOWERBY, 1823

Type species: *Patella laciniosa* LINNÉ, 1758 living around the Salomon Islands.
Remarks: Since DOCKERY (1993: pl. 17, figs. 8-10) was able to demonstrate a sinistrally coiled protoconch for *Anisomyon* MEEK & HAYDEN, 1860, that genus can quite safely be placed within the Siphonariidae. SOHL (1964: 232) pointed out that the siphonal groove is on the left side of the shell in *Anisomyon*, while it is on the right in *Siphonaria*. Additionally, *Anisomyon* is smooth or shows concentric growthlines but no radial sculpture in contrast to *Siphonaria*, it also appears higher conical than the rather flat-shelled limpets of *Siphonaria*.

Siphonaria revillaria n. sp.

Plate 35, Figures 17-18

Holotype: GPI 3999, figured at pl. 35, fig. 18.
Paratype: GPI 4000, figured at pl. 35, fig. 17.
Material: Two specimens from the Campanian of Torallola, Spain.
Derivation of name: Named in honour of JOSÉ DE LA REVILLA who described several gastropods from the Campanian of Torallola.
Diagnosis: A *Siphonaria* with equally strong radial and concentric sculpture.
Description: The protoconch is sinistrally coiled and measures about 0.6 mm in diameter, the transition to the teleoconch is indistinct. The limpet-like adult-shell has a carinate pattern of fine radial and concentric striae. The concentric lines are initially closely spaced and their interspaces gradually become wider. About half way between apex and margin, they are again very closely spaced and widening of the interspaces begins again. Just at the basal margin, as far as it is preserved, they become closely spaced again. The shell is 8 mm in diameter.
Remarks: *Siphonaria wieseri* (WADE, 1926) appears to have radial sculpture only.

Discussion: The Archaeopulmonata are represented with two species in the fauna of Torallola, *Laemodonta cretacea* n. sp. and *Siphonaria revillaria* n. sp. While a Cretaceous origin of the Siphonariidae has long been supposed (WENZ & ZILCH 1959-60, SOHL 1964), the ellobiid *Laemodonta* was previously only reported from the Neogene (WENZ & ZILCH 1959-60). Shells which resemble modern Ellobiidae were found in Jurassic-Early Cretaceous intertidal and brackish-water sediments (BANDEL 1991d).

Suborder Stylommatophora SCHMITT, 1855

Six species of terrestrial gastropods are present in the material from Torallola. Two of them, one sinistrally and one dextrally coiled species probably belong to a new genus of the Clausiliidae GRAY, 1855 (NORDSIECK, 2000). These species are characterised by few (8-9) whorls and a strongly descending aperture, which may be apostrophic (e.g. it is detached from the spire and sits at the end of a short tube).

The most conspicuous species belongs to *Lychnus* MATHERON, 1832. This genus first builds a trochispiral shell and then wraps the bodywhorl around the spire, giving the shell a rounded triangular shape. The specimen available is fairly large (43 mm in diameter) and shows very fine spirals on the upper side of the last whorl. It probably represents a new species, since it does not match any of the descriptions and figures of the seven species of *Lychnus* provided by BATALLER (1949). *Lychnus* is only known from the Late Cretaceous of northern Spain and southern France (WENZ & ZILCH 1959-60).

The last three species may be classified as *Palaeostoa* ANDREAE, 1884. Whether this genus represents a natural group or just a waste-basket for fossil, elongate-pupiform and axially ribbed terrestrial gastropods remains doubtful. OPPENHEIM (1895) described several species of *Palaeostoa* from the Spanish Late Cretaceous, but my material from Spain is too poorly preserved to assign them to any of these species.

BIOGEOGRAPHY

In current reconstructions of Late Cretaceous gastropod biogeography, much emphasis is laid on a clear distinction between a tropical Tethys-belt and temperate or cool-temperate provinces north and south of this belt (SOHL 1971, 1987, ZINSMEISTER 1979, 1982). Strong similarities between the northern and the southern temperate faunas have been discerned with astonishment, because respective relatives were unknown from the Tethys (SOHL 1964). No satisfying explanation has been offered for this phenomenon.

The classification of fossil gastropods has strongly improved in recent years, especially since protoconch morphology has been recognised as a powerful tool in gastropod taxonomy (see BANDEL 1997 for a review). Based on a better classification, numerous fossil gastropods can now be assigned to a certain paleo-environment, which is of great value in paleobiogeographic reconstructions.

Distribution-patterns in the Campanian-Maastrichtian

The gastropods of the rudist facies

Four groups of gastropods are considered typical representatives for the circum-equatorial rudist facies: the Nerineoidea, *Pileolus*, *Discotectus*, and the Acteonellidae. In previous reconstructions of Late Cretaceous gastropod biogeography, these gastropods of the rudist facies have been treated synonymously with "tropical" gastropods. This must be reconsidered.

The northern and southern boundaries of the tropical faunas today are marked by the latitudes 30-35°S in the Indian Ocean and 35-40°N and 30-35°S in the western and central Pacific (EKMAN 1935). In contrast, the Late Cretaceous northern boundary of the rudist facies in the Mediterranean apparently stayed quite constantly at about 30°N (VOIGT et al. 1999). The present-day tropical fauna in the western Atlantic extends to about 35°N and 24°S (EKMAN 1935), the Caribbean Late Cretaceous rudists ranged up to 35°N (JOHNSON et al. 1996). Thus, the Late Cretaceous rudist facies and its gastropods apparently had an equal or even narrower latitudinal distribution than the Recent tropical fauna. This is quite surprising considering the warm, equable Cretaceous climate. Therefore, temperature alone is obviously insufficient to explain the boundaries of the rudist facies and its gastropods. HALLAM (1969) has already noticed this phenomenon for the Jurassic.

A change in the climate regime from arid to humid at 30°N was offered as an explanation for the northern boundary of Mediterranean rudist build-ups at this latitude by VOIGT et al. (1999). Accordingly, rudist build-ups (and carbonate platforms in general) could only grow in environments with a negative freshwater balance which resulted in basins of slightly hypersaline, nutrient-depleted waters. Also KAUFFMAN & JOHNSON (1988) suggested that rudists favoured warm, hypersaline waters. Nerineans, *Pileolus*, and *Discotectus* arose in carbonate platform environments during the Jurassic (WENZ, 1938-44) and only rarely left this habitat during their almost 100 ma of evolutionary history. This may have led to such close ties with this environment - for example regarding water chemistry - that temperature played only a secondary role in controlling their distribution. Their contemporaneous extinction with the rudists at the end of the Cretaceous may further support this suggestion. However, palecologic reconstructions concerning nerineans, *Discotectus* and *Pileolus* are more speculative than those of other groups because no close living relatives exist.

The habitats of the Acteonellidae, on the other hand, are not restricted to the rudist facies; they have been reported from California (ANDERSON 1958), central Europe

(HOLZAPFEL 1888), and South Africa (WOODS 1906, RENNIE 1930). Furthermore, some are known to tolerate brackish water.

The tropical Atlanto-Indian Province

The existence of typical ”temperate” gastropods within the Tethys belt (this work, see also LEES 1928, RIEDEL 1932, DARTEVELLE & BREBION 1956, MUNIZ 1993) indicates that the classical distinction of Tethys and temperate faunas needs to be reconsidered.

As shown in the previous chapter, the term "tropical" cannot be applied to the gastropods of the rudist facies alone. Most gastropods today are not as sensitive to the substrate and the nutrient-content of the water as corals are (BANDEL & WEDLER 1987). This was most likely the case with Cretaceous gastropods, too, perhaps with the exception of the Nerineidae, *Discotectus* and *Pileolus*. Considering the latitudinal range of Recent tropical gastropods and taking the warmer and more equable Cretaceous climate into account, the latitudinal distribution of Late Cretaceous tropical gastropods should range far beyond the average recent 35°N and S. The almost equal latitudinal ranges of coral reefs and tropical gastropods today may be coincidental because the 20°C isotherm and the change from a negative to a positive freshwater balance lies at almost the same latitude. However, the water-chemistry controlled range of the rudist facies could well be decoupled from the temperature controlled range of the tropical gastropods in the warm, equable Cretaceous climate.

The most stable features of the modern ocean are the stratified tropical-subtropical gyres with warm saline surface waters. These lie in each hemisphere between ~15° and ~45° latitude. The same conditions are assumed for the Late Cretaceous oceans (HAY 1995). While today the 20°C isotherm lies within this zone, climate models for the Campanian-Maastrichtian predict its position at around 45°N and S, and thus on the poleward margins of the tropical-subtropical gyres (HAY & DECONTO 1999). In plate-tectonic reconstructions of the Late Cretaceous, the northern shores of the Atlantic lie at about 40°N in the Campanian, and there were no deep-water connections with the Arctic Ocean (SCOTESE et al. 1988, HAY et al. 1999). Therefore, the entire gastropod fauna of the Late Cretaceous North Atlantic, including the rich and diverse faunas of the American Gulf coast plains and the European Atlantic coast may well be regarded as tropical. Probably no temperate gastropod fauna existed in the North Atlantic during the Late Cretaceous, analogously to the situation in the present-day northern Indian Ocean. Changes in the gastropod assemblages northward through the Western Interior Seaway as noted by SOHL (1971) may be interpreted as a change to a temperate fauna. The data on Cretaceous gastropod assemblages of the Arctic Ocean are yet too sparse to allow a postulation of a ”Boreal” Province (SOHL 1971). Assuming a similar latitudinal range of tropical gastropods to the south, the faunas of India and perhaps even South Africa can be included in the tropical realm as well.

The postulation of a broad tropical Atlanto-Indian faunal province explains the diversity of Gulf coast plain and European faunas as well as the obviously close relationships between faunas of the northern and southern hemisphere previously considered "temperate". A tropical character of these faunas is also indicated for example by the presence of *Xenophora* in the Aachen greensands of Germany, the Ripley and Coffee Sand formations and the Navarro group of the Gulf coast plains, or by the strombid *Hippocrenes* in Maastricht. Both *Xenophora* and strombids today are confined to the tropical realm. The current evaluation of the faunas of Torallola and Temalac has shown that numerous gastropods previously considered as typical inhabitants of "temperate" waters also lived on clastic substrate within the range of the rudist facies.

Comparison to other organisms provides further evidence. Based on fish otolithes, NOLF & DOCKERY (1990) considered the climatic conditions of the Coffee Sand as tropical/subtropical. The delineated province falls within the range of the "megathermal" flora of WOLFE & UPCHURCH (1987), or the "tropical-paratropical" flora of SAWARD (1992).

The more equable climate of the Late Cretaceous may also have resulted in broader transitional zones between faunal realms, as for example documented by SOHL (1971) from the Western Interior Seaway. Here, the more tropical *Anomalofusus* and *Liopeplum* interfinger with the more northern *Serrifusus* and *Vanikoropsis* on a width of more than 1000 km. On the southern margin of the tropical Atlanto-Indian Province, the fauna of the Umzamba formation in South Africa shows numerous tropical elements. But its aporrhaids show also affinities to the Antarctic Weddellian Province (KIEL & BANDEL, in review). From the floristic point of view, the area lies in a transitional zone (WOLFE & UPCHURCH 1987, SAWARD 1992), and the Foraminifera show a transitional character from Tethyan to polar forms as well (HUBER 1992).

Although a distinct North Atlantic temperate gastropod fauna is doubted here, gastropods which preferred the cooler margins of the tropics could well have existed. An example may be *Sargana* which occurs on the Gulf coast plains (SOHL 1964) as well as in South Africa (RENNIE 1930), but has never been reported from Tethyan waters. Whether this represents true bipolarity or a case of tropical submergence is not yet clear. The latter hypothesis is supported by the habitat of their present day relatives, the Trichotropidae, which occur in depth from 10 to 5000 m (RIEDEL 2000). Accordingly, *Sargana* could have crossed the equator in cooler central-waters. Unfortunately, supporting data are difficult to obtain because sediments from deeper waters are unlikely to be exposed along central and southern Atlantic coasts; both are passive continental margins and therefore no tectonic processes exist which could uplift deeper water sediments.

The proposed tropical Atlanto-Indian Province includes the entire North Atlantic from the American Gulf coastal plains in the west, to the European Atlantic coast and interior basins, it ranges eastwards through the central Tethys to the Oman and India, and to the south through the South Atlantic to the southwestern Indian Ocean. Eastward from the Indian Ocean, however, the vast Pacific Ocean might have prevented exchange between the tropical faunas on its eastern and western shores, as it does today. This suggestion is in contrast to the proposed trans-Pacific spread of tropical shallow marine benthos (SKELTON & WRIGHT 1987) in the Campanian/Maastrichtian.

Common and widespread genera include *Campanile*, the stromboideans *Graciliala*, *Pterocerella*, *Hippocrenes*, *Pugnellus* and *Bizarrus*, the neo- and neomesogastropods *Sargana*, *Liopeplum*, *Bellifusus*, *Drilluta*, *Mitridomus*, *Mesorhytis*, and *Koenenia*; and *Lemniscolittorina* of the Mathildidae.

The northern and eastern Pacific

The Late Cretaceous Pacific differed markedly from the Atlantic. The ocean basins reached considerably further north and south, to about 70° latitude in both hemispheres (see BARRERA & SAVIN 1999: fig. 1). This allowed the development of temperate gastropod faunas, perhaps with broad transitional zones analogously to that of the Western Interior Seaway. Distinction between tropical and temperate gastropods along the American westcoasts is not yet well understood. Non-framework building rudists are known from northwestern Mexico and even from central California (SOHL 1987, WHITE 1885). In the same region other typical inhabitants of tropical waters like *Xenophora*, the neritoids *Otostoma* and *Neritoplica*, and the *Anchura*-clade of the Aporrhaidae occurred (WEBSTER 1983, CUSHING WOODS & SAUL 1986, SAUL & SQUIRES 1997, SAUL 1998, own data). The climatic affinities of other groups, such as *Biplica*, the Perissityidae (*sensu* POPENOE & SAUL 1987), and the Pugnellidae, which are all extinct, are more difficult to evaluate.

The best known gastropod faunas of the South American Pacific coast are those of the Amotape and Paita-region in northern Peru (OLSSON 1934, 1944) and of Quiriquina in central Chile (PHILIPPI 1887, WILKENS 1904, BANDEL & STINNESBECK 2000) and they are usually considered highly endemic. ZINSMEISTER (1982) emphasised relationships of the Quiriquina fauna to those of the Weddellian Province (see following chapter). However, Paita and Quiriquina show faunal relationships with each other as well as to the northern Pacific faunas (POPENOE 1957, own data). Compared to the distribution of Maastrichtian Foraminifera, Quiriquina is located within the transitional zone from Tethyan to polar forms (HUBER 1992).

The Miocene gastropod fauna of the Ranquil/Navidad formation which overlies the Quiriquina formation, contains numerous tropical elements such as *Nerita*, *Sinum*, *Semicassis*, *Ficus*, *Distorsio* and *Terebra* (PHILIPPI 1887, NIELSEN pers. comm.). This was due to the absence of a cold current such as the Humboldt current today. The Humboldt current, which branches off the circum-Antarctic current, is responsible for the extremely northern position of the southern boundary of the Recent tropical fauna at 4°S according to EKMAN (1935). There were no circum-Antarctic deep-water connections in the Late Cretaceous so that a "paleo-Humboldt current" presumably did not exists at that time either. In conclusion, some tropical affinities of the Quiriquina gastropods can be expected.

Bipolar distribution and tropical submergence today occurs most commonly along the westcoast of the Americas due to cool currents and upwelling of cooler central waters (EKMAN 1935). Such cooler central water which underlayed the surface water must also have existed during the Campanian/Maastrichtian albeit with a smaller difference in temperature than today. Thus, upwelling would have been easier (HAY 1995). Additionally, sediments of deeper waters are more likely to be uplifted on this active continental margin. These factors must also be considered in interpretations of American westcoast faunas and may account for the wide latitudinal distribution of certain taxa.

Characteristic gastropods for this province are the Perissityidae, which are known from Japan to California and as far south as central Chile. The ringiculid *Biplica* seems to have had a similar distribution. There is a distinct Californian lineage within *Pyktes*. *Pseudoperissitys* and *Taniella* seem endemic to Japan. *Lysis* occurred in California and Japan, but has also been reported from South Africa (STEWARD 1927, RENNIE 1930, POPENOE 1957, 1983, HAYAMI & KASE 1977, POPENOE & SAUL 1987, KASE 1990, KIEL & BANDEL 1999).

The Weddellian Province

A cool-temperate fauna apparently existed in the southern Pacific (ZINSMEISTER 1979, 1982, STILWELL 1997). It ranged from New Zealand and the Chatham Islands along the Antarctic Pacific coast to the Pacific and Atlantic coasts of southern South America, and was named Weddellian Province by ZINSMEISTER (1979). According to this author, the gastropods of this province have been isolated from Early Cretaceous through Eocene and consequently evolved quite independently from those of the outside world.

However, there is some doubt on this hypothesis. BANDEL & STINNESBECK (2000) showed that *Austrosphaera* which has been considered a typical representative of the Weddellian Province in the Paleocene (OLEINIK & ZINSMEISTER 1996), was already abundant in the Quiriquina Maastrichtian; the same genus also occurred in the Paita Maastrichtian (own data). Two aporrhaids characteristic for the Weddellian Province have been found in the Umzamba formation in South Africa (KIEL & BANDEL, in review). RICCARDI (1991) noted a ”Santonian-Campanian increase in ammonoid similarity between southern South America and southeast Africa”. Finally, relationships to South America and to South Africa are also demonstrated for the echinoids of Seymour Island in the Weddellian Province (NÉRAUDEAU et al. 2000).

In conclusion, a transitional zone of considerable width between the Weddellian and the tropical eastern Pacific faunas appears more likely than an highly isolated Weddellian Province. Faunal exchange might even have existed with South Africa.

Local and Evolutionary aspects

The taxonomic level

The genus is usually considered the most reliable taxonomic unit in paleobiogeographic reconstructions (KAUFFMAN 1973). The following example shows that the comparison of genus- and species-level relationships can become crucial in the interpretation of ancient distribution patterns.

Recent *species* of Caribbean crabs show closer relationships to those of the Westafrican coast than to those of the Indo-Pacific. Concerning the *genera*, the opposite is the case. The relationships on genus-level have *historical* reason; faunal exchange with the Indo-Pacific was possible until only about 3.1 ma ago, when the Isthmus of Panama closed. Relationships on the species level, on the other hand, are the result of *present* migration-routes, which are open towards Westafrica but closed towards the Indo-Pacific (EKMAN 1935).

The Caribbean – seaway or landbridge?

In current reconstructions of the Caribbean, the distance between the American continents reached its maximum during the Campanian/Maastrichtian (PINDELL & BARRETT 1990, MESCHEDE & FRISCH 1998, HAY et al. 1999). Surprisingly, exchange of marine gastropods between Atlantic and Pacific appears quite limited at this time. A similar observation was made by RICCARDI (1991), who considered the affinities of Campanian-Maastrichtian ammonoids of the central South Atlantic clearly Tethyan but noted low similarities to those of northwestern South America. Exchange of terrestrial vertebrates between North and South America took place in the Campanian (BENTON 2000). This led to the postulation of some kind of landbridge between the two continents at this time.

Comparing only gastropod-*genera* between the present-day Pacific and Atlantic coasts of Central America, a landbridge would seem highly unlikely. However, an examination on species-level reveals obvious differences between the east- and the westcoast (EKMAN 1935).

A preliminary survey of Campanian/Maastrichtian gastropods in the eastern Pacific and western Atlantic displays a noticeable pattern of relationships. For example, affinities can be observed between mangrove-snails from Paita and those from Pernambuco in eastern Brazil (WHITE 1887, OLSSON 1944), and the pugnellids of Paita show relations to those of the European Tethys (KIEL & BANDEL 1999). Interestingly, these similarities exist only on genus-level but not on species-level. Additionally, none of the typical post-Turonian East Pacific gastropods are known from the Atlantic. Thus, the distribution of gastropod species and genera supports the hypothesis of a temporary landbridge, and it suggests that it may even have been continuous rather than a chain of islands.

The Sierra Madre Occidental and the evolution of the north Pacific fauna

Several gastropod genera regarded here as typical for the Campanian-Maastrichtian Atlanto-Indian Province (*Sargana, Liopeplum,* and *Gymnarus* the *Drilluta-Paleopsephaea-Remera*-group) also occur in the Turonian of California, but seem to have disappeared afterwards. Almost simultaneously, the development of the typical Pacific fauna began (POPOENOE 1983, POPENOE & SAUL 1987). SAUL (1986) considered the post-Turonian cooling responsible for this development. Another event which might have intensified the effect of this cooling could be the contemporaneous rise of the Sierra Madre Occidental in western Mexico. The closure of shallow marine connections across central Mexico was documented by IMLAY (1944: figs. 2-6) and ALENCÁSTER (1984: figs. 4-7), and belts of plutonic rock in southeastern Mexico are dated as Late Cretaceous by SCHAAF et al. (1995). Together with the possible central American landbridge, this mountain chain could have effectively prevented faunal exchange between the western Atlantic and the eastern Pacific, and thereby made the development of distinct faunal realms possible.

The early history of the Neogastropoda

The Neogastropoda are considered one of the rare examples of a large and successful group of animals which did not originate in the tropics but in cooler regions (TAYLOR et al. 1980, SOHL 1987). It was suggested that they originated in the temperate European seas and had their maximum diversity and centres of evolution in the Late Cretaceous temperate realms north and south of the Tethys. After the K/T-boundary they switched to their present-day distribution with a maximum of diversity in the tropics.

This implies that a large number of gastropods confined to temperate waters repeatedly travelled across the tropical realm - e.g. from northern Europe through the tropical Caribbean into the eastern Pacific, in the opposite direction into the western Pacific, and perhaps three times across the equator to the southern Pacific, Indic and Atlantic - without becoming adopted to this environment.

The hypothesis of a temperate origin needs to be reassessed in the light of the new biogeographic interpretation outlined here. The earliest abundant occurrences of Neomeso- and Neogastropoda are known from the later Albian of central western Europe (MARLIÈRE 1939, KOLLMANN 1976, TAYLOR et al. 1983). The paleoposition of this part of the world was situated at around 35-40°N latitude (SCOTESE et al. 1988, HAY et al. 1999) and a warm, equable climate is assumed for the later Albian (see FASSELL & BRALOWER 1999 for discussion). Consequently, a tropical habitat is a more likely model for evolutionary breeding grounds of the earliest Neomeso- and Neogastropoda.

Temperature and its role in faunal distributions

Today, temperature is the most important factor controlling faunal distribution (EKMAN 1935). However, the temperature-control hypothesis fails to explain several biogeographic patterns of past periods with warm, equable climate. HALLAM (1969) discussed several objections on the temperature-control hypothesis concerning Jurassic faunal realms, and considered facies to be more important. VOIGT et al. (1999) proposed that the northern boundary of rudist-buildups in the Mediterranean was controlled by the change from a negative to a positive freshwater balance in the basins north of 30° latitude. As discussed herein, distribution of Late Cretaceous tropical gastropods was mostly controlled by the 20°C isotherm. Only in those few cases where gastropods were apparently tied to the rudist facies, other factors became more important.

During times of warmer, more equable climates, the significance of temperature in faunal distribution apparently decreases. The extent to which the importance of other factors like salinity, turbidity, nutrients, substrate, length of the day, and wave-energy increases, depends mostly on the ecological needs of the individual taxon. It can thus be expected that the distribution patterns of different groups of organisms show a considerably higher variability in times of warm, equable climate than today.

This trend might be enhanced by another factor. EKMAN (1935) showed that in areas with very gradual transitions between climate zones, such as the modern-day eastern North Atlantic, the faunal realms have their broadest transitional zones, too. During times of more equable climates, transitional zones between faunal realms consequently were much broader. This could account for the extremely wide transitional zone reported by SOHL (1971) from the Western Interior Seaway, and for the apparent difficulties to distinguish tropical from temperate faunas along the Pacific coasts of the Americas during the Late Cretaceous.

CONCLUSIONS

Members of all four gastropod subclasses – Archaeogastropoda, Neritimorpha, Caenogastropoda, and Heterostropha – were present in the outcrops of Torallola and Temalac. The 186 described species belong to 53 families and subfamilies, and 120 genera and subgenera.

Among the Archaeogastropoda, 56 species of 31 genera of 15 families and subfamilies are described (see fig. 3). Most of these families have a long history, ranging from the Triassic or even the Paleozoic until today. Most species reported here fit well into these lineages and do not differ much from living species. However, there are exceptions. Those of the Trochinae have a unique character and differ from their Recent as well as from their earlier Mesozoic relatives. Some Eucyclinae, like *Eucyclomphalus* and *Hudledonta* have Mesozoic affinities, while *Danilia kossleri* n. sp. represents the oldest species of this modern genus.

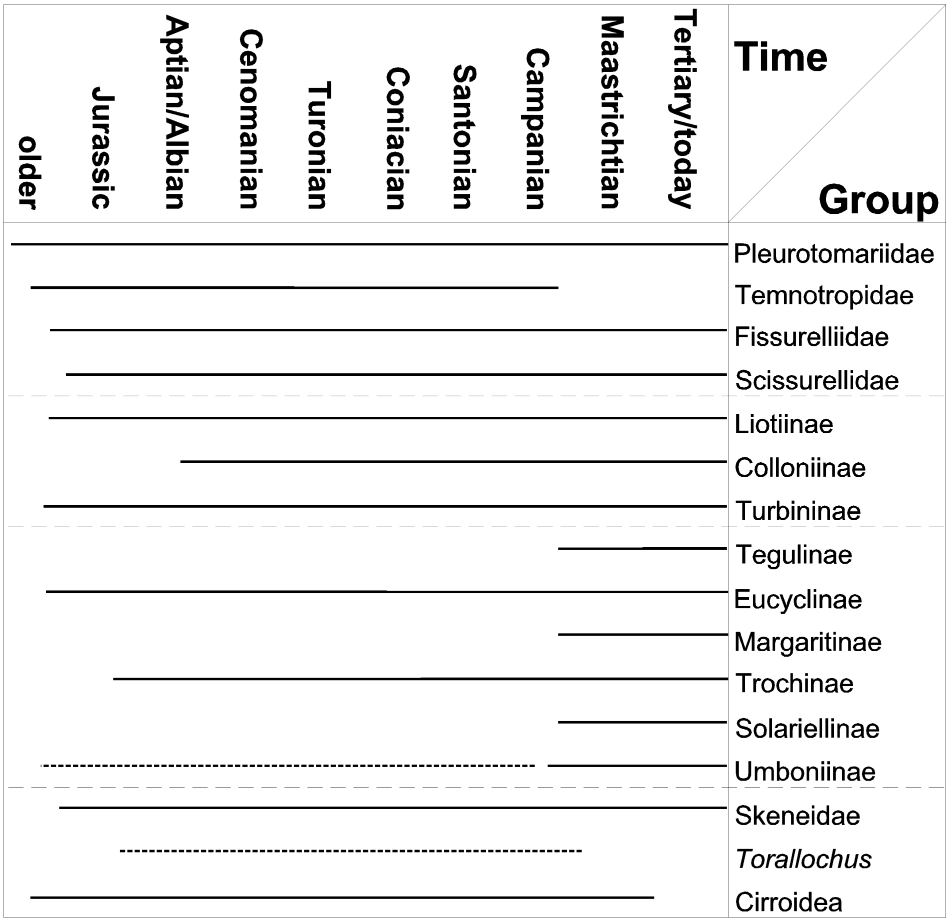


Figure 3. Geologic ranges of the concerned Archaeogastropoda.

Of three subfamilies, the Tegulinae, Margaritinae and Solariellinae, some of the oldest known representatives are described. Whether these families actually originated during the Late Cretaceous or older members just had different shell-morphologies remains unknown. In three cases, the Temnotropidae, Cirroidea and

Torallochus, the species described represent the last of their group. The Cirroidea and *Torallochus* became extinct at the end of the Cretaceous, the Temnotropidae apparently gave rise to the modern Haliotidae.

Neritimorpha are few, the eleven species belong to six genera of three families (see fig. 4). The Neritopsidae have a long history and the species described here does not differ much from its few living relatives. Among the Neritidae, *Otostoma* is an exclusively Cretaceous genus, while *Dontostoma* is herein reported from the Cretaceous for the first time. *Neritoplica* probably gave rise to the modern brackish- to freshwater inhabiting Neritininae, and *Neritoptyx* combines characters of *Nerita* and *Neritoplica*. The two species of *Pileolus* are among the last of the Pileolidae, a family which arose during the Jurassic and became extinct at the end of the Cretaceous.

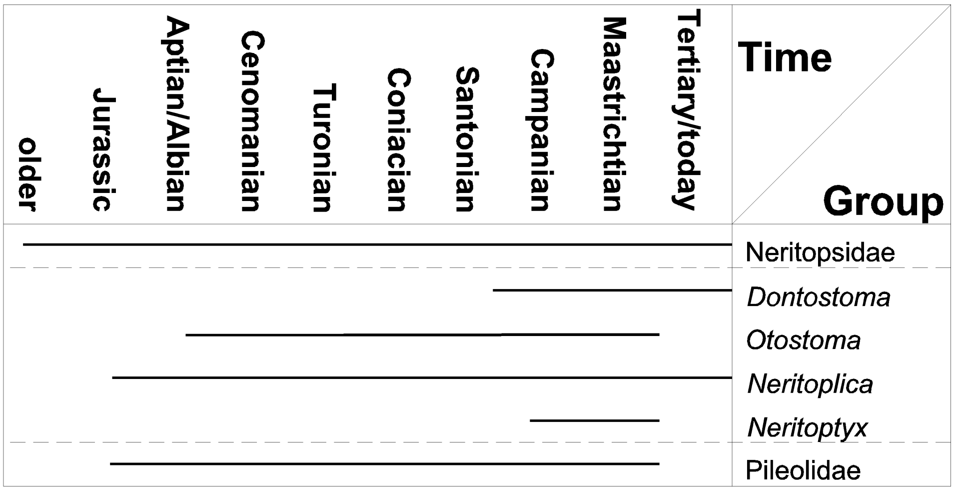
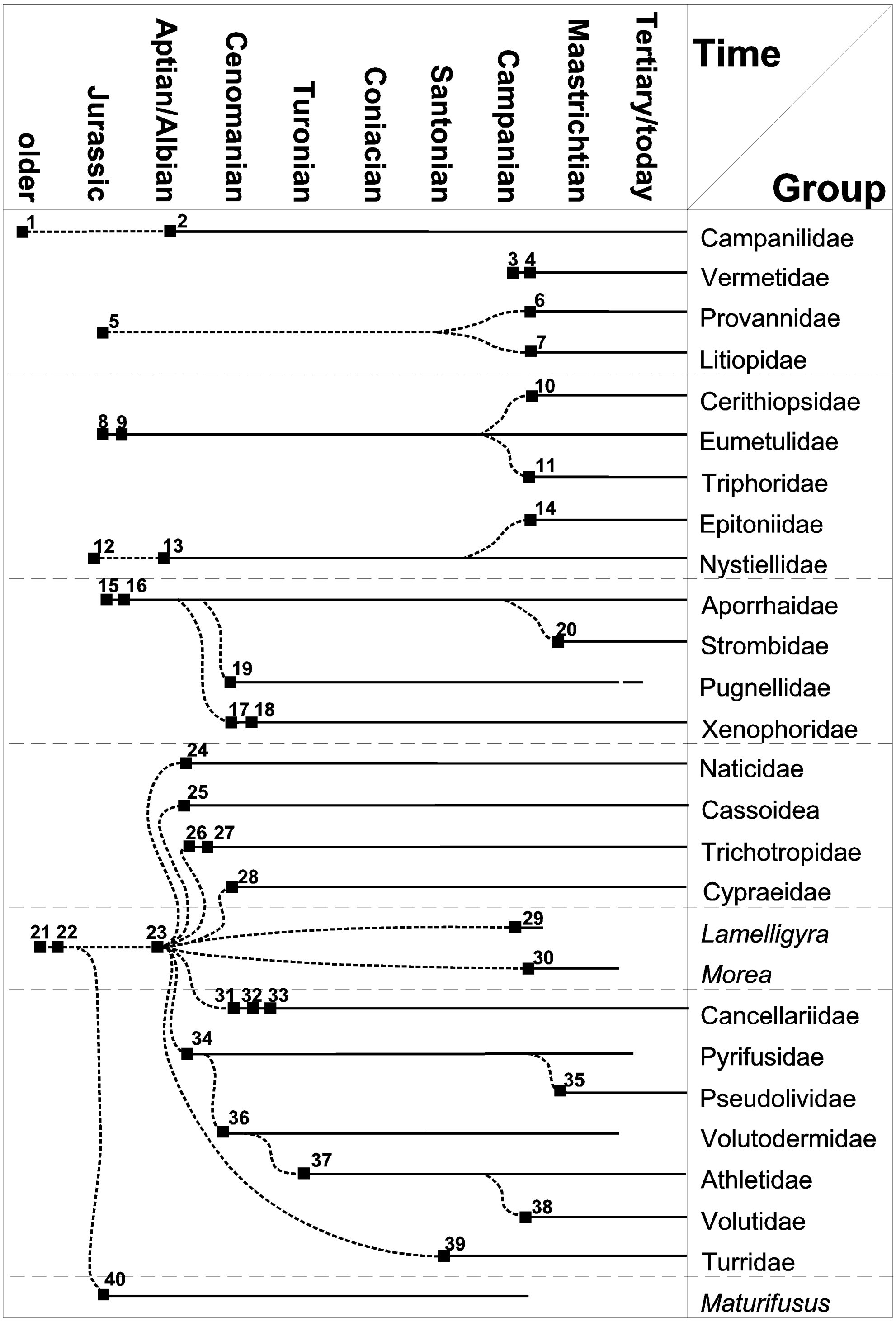


Figure 4. Geologic ranges of the concerned Neritimorpha.

Figure 5 (opposite page). Geologic ranges and suggested relationships of the concerned Caenogastropoda. **1**: larval shell small, smooth, globular, strong terminal varix; **2**: teleoconch high spired, with dominant spiral sculpture; **3**: protoconch conical with rounded whorls and sculptured with small tubercles; **4**: teleoconch openly coiled or uncoiled; **5**: larval shell turriform, with collabral ribs; **6**: adaptation to life at hydrothermal vents?; **7**: adaptation to the sea-grass environment?; **8**: reticulate teleoconch sculpture; **9**: turriform protoconch with collabral ribs; **10**: protoconch smooth; **11**: sinistral coiling, larval shell bicarinate; **12**: turriform protoconch with collabral ribs; **13**: *Epitonium*-like shell; **14**: protoconch smooth; **15**: protoconch large, convex-conical, smooth; **16**: extended outer lip; **17**: trochiform shell, agglutination of particles; **18**: low-spired protoconch; **19**: low-spired teleoconch, blunt projections, extended callus-cover; **20**: posterior canal extends from the aperture to the spire and bents down near the apex; **21**: large, multiwhorled protoconch?; **22**: siphonate teleoconch; **23**: embryonic shell larger than 0.15 mm; **24**: predation by drilling; **25**: protoconch larger than 1 mm diameter, with carinate sculpture; **26**: teleoconch with dominant spiral sculpture; **27**: protoconch initially flatly coiled (planorbid); **28**: typical cowrie shell; **29**: teleoconch with strong spiral ridges, axial lamellae, columellar plates, and varices; **30**: teleoconch with umbilical slit and one columellar plate; **31**: protoconch initially flatly coiled or truncate; **32**: cancellate teleoconch, columellar plates; **33**: sucking mode of feeding?; (continued on opposite page)



(continued) **34**: smooth, conical protoconch of 0.6-1 mm diameter; **35**: basal groove; **36**: straight basal slope, growthlines strongly opisthocline; **37**: strombiform shell, callus-glaze; **38**: large protoconchs reflecting lecithotrophic ontogeny; **39**: anal sinus; **40**: bicarinate larval shell.

With 23 families, 54 genera and 83 species, the Caenogastopoda are the most diverse gastropod subclass in the present study (see fig. 5). For the first time, a *Campanile* with preserved larval shell is documented. This opens the possibility to identify fossil members of this group by its protoconch morphology, and to trace the history of this group back in time, perhaps even to the Carboniferous, when gastropods with a similar larval shell lived.

Members of the Vermetidae, Provannidae and Litiopidae with a protoconch similar to those of their living relatives existed already in the Campanian. The latter two familes show similar protoconch morphologies and might be related.

Among the Ptenoglossa, the oldest known species of the Cerithiopsidae and Triphoridae occurred in Torallola. Thus, all modern ptenogloss families except the Janthinidae and Triforidae existed in the Late Cretaceous.

The modern stromboideans Strombidae and Xenophoridae first occurred in the Late Cretaceous. The strombid *Rimella* is documented for the first time from the Maastrichtian. The Aporrhaidae had their origin in the Jurassic and the species described here resemble those of other Late Cretaceous faunas but not the modern ones.

The largest caenogastropod group are the Neomeso- and Neogastropoda, which arose during the Aptian/Albian and subsequently underwent a rapid diversification. Many Late Cretaceous species resemble each other more closely than they resemble their modern relatives. Thus, they can only be assigned to stem- or sister groups of the living families. Others, however, show distinct characters of certain modern families and are assigned to those (see fig. 5). *Maturifusus*, previously only known from the Jurassic and Lower Cretaceous, is documented for the first time from the Late Cretaceous. It may represent an early offshoot of the neomeso- and neogastropod stem-group.

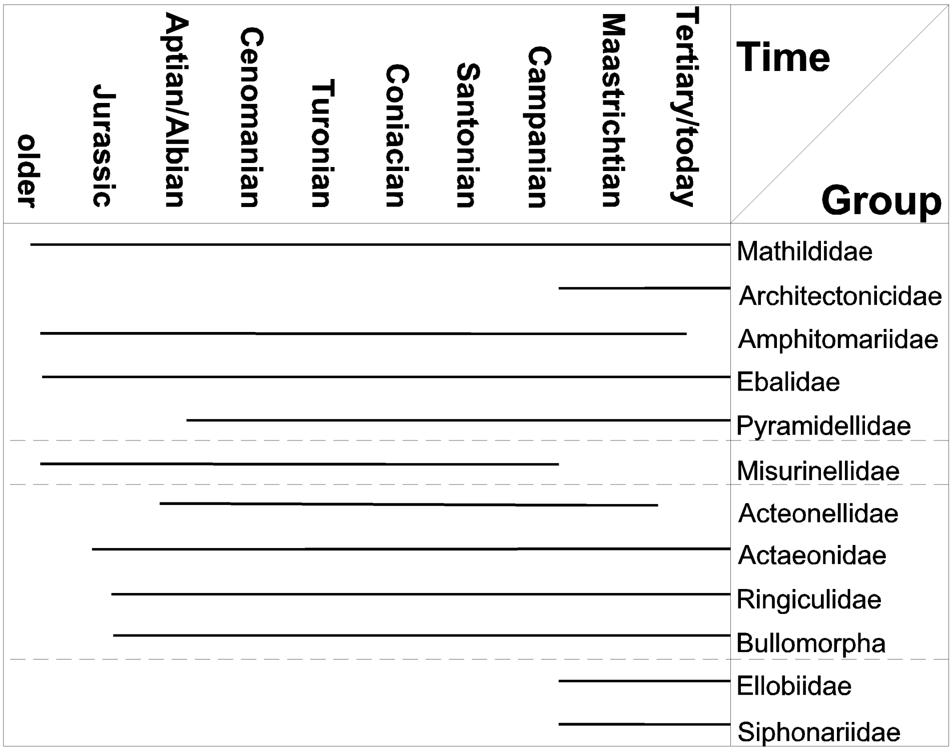


Figure 6. Geologic ranges of the concerned Heterostropha.

Most Heterostropha reported here belong to groups which have a Jurassic or even earlier origin (see fig. 6). Among them, only the Misurellidae apparently are restricted to the Mesozoic. Two families appeared as late as Aptian/Albian, of which the Pyramidellidae are a diverse and successful group today. The Acteonellidae, on the other hand, dominated Late Cretaceous tropical lagoons but became extinct at the K/T boundary. Two families of the Pulmonata appeared in the Late Cretaceous, and among the Ellobiidae, the oldest known *Laemodonta* is presented.

In conclusion, the documented gastropods belong to groups that behaved in ways which can be expected in a transitional time: some old groups became extinct at the end of the Mesozoic, some long-ranging ones survived through all environmental changes until today, some lived exclusively in the Late Cretaceous, and some are among the oldest stem-group representatives of successful modern groups.
Gastropods have been called an extinction resistant clade, a statement which seems supportable. Of the 53 familes and subfamilies concerned in this study, only seven – about $^{1}/_{8}$ - apparently became extinct at or before the K/T boundary. Regarding genera, 30 out of 120 - which equals one quarter - presumably did not survive the end of the Cretaceous.

The gastropod biogeography of the Campanian/Maastrichtian was characterised by a broad tropical belt with two more or less distinct faunal provinces: the Atlanto-Indian Province and the East Pacific Province. Between the Americas, they have probably been separated by a landbridge. How far the Atlanto-Indian Province extended into the western Pacific is still unclear due to insufficient data. Within the tropical belt, zones of slightly hypersaline, nutrient depleted water facilitated the development of the rudist facies and their typical gastropods. Temperate gastropod provinces apparently existed in the northern Pacific, and in the south the

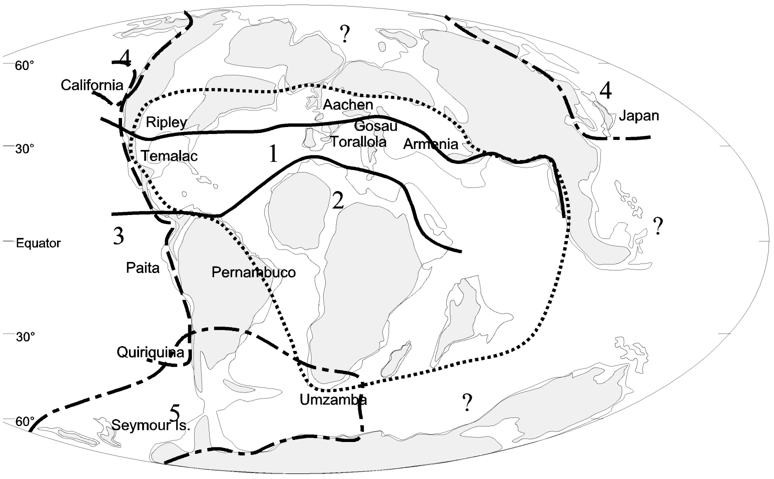


Figure 7. Paleogeographic reconstruction for the Campanian (modified from HAY et al., 1999) with the outlined gastropod provinces. 1 (solid line): Gastropods of the rudist facies, 2 (dotted line): tropical Atlanto-Indian Province, 3 (broken line): tropical East Pacific Province, 4 (dotted and dashed line): temperate North Pacific Province, 5 (dotted and dashed line): cool-temperate Weddellian Province. The gastropods of the northern Polar Ocean, the western Pacific and the southern Indian Ocean are not yet well known.

Weddellian Province included the southern Pacific and perhaps parts of the South Atlantic (see fig. 7). Where known, the transitional zones between tropical and temperate faunas are broad, as documented for the Western Interior Seaway and along the South American westcoast. Others, such as those along the South American eastcoast or from Southeast Asia to Japan are yet poorly documented. Whether the biogeographical features outlined here for gastropods also apply to other marine groups remains to be tested.

In future biogeographic reconstructions of gastropod provinces in geologic history, it should be considered that the distribution of reefs does not necessarily coincide with ”tropical realm”. Tropical gastropods (and perhaps other marine groups, too) could well have had a much broader latitudinal distribution. During most of the Phanerozoic the poles were free of permanent ice and the climate was warmer and more equable than today. The present day similarity between reef and tropical gastropod distribution might be coincidental and rather exceptional in earth history.

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PLATES

1-37

PLATE 1

Slit bearing Archaeogastopoda from Torallola

Figs. 1-2. *Perotrochus* cf. *distincta* (Goldfuss, 1841); **1** – adult shell; GPI 3960; greatest width 43 mm; **2** – juvenile shell showing the protoconch and the smooth initial whorls; GPI 3961; width 2.5 mm.

Figs. 3-4. *Stuorella cretacea* n. sp.; GPI 3962; front and back view; height 7 mm.

Figs. 5-7. *Temnotropis frýdai* n. sp.; **5** – paratype showing the transition from the smooth early shell to the sculptured adult shell; GPI 3963; greatest width 3.1 mm; **6** – umbilical view on the holotype; GPI 3964; greatest width 3.3 mm; **7** – detail of the holotype showing the slit; width 0.9 mm.

Figs. 8-9. *Scissurella hispanica* n. sp.; apical and frontal view on the holotype; GPI 3965; width 1.0 mm.

Figs. 10-11. *Scissurella lleidania* n. sp.; **10** – frontal view on the holotype; GPI 3966; height 1.0 mm; **11** – apical view on the paratype; GPI 3967; width 1.5 mm.

Figs. 12-14. *Emarginula radiocostata* n. sp.; three views on the holotype; GPI 3968; greatest width 7.0 mm, height 5.0 mm.


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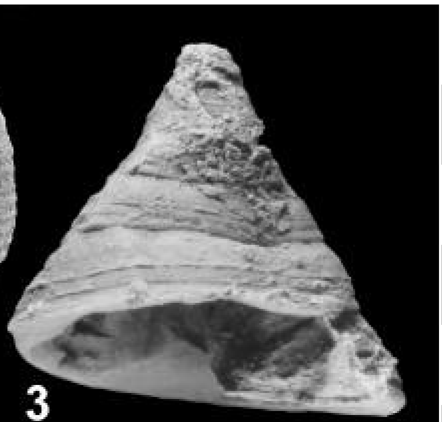
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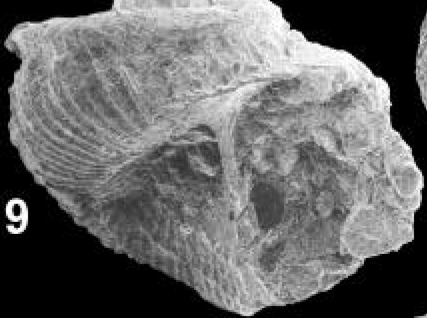
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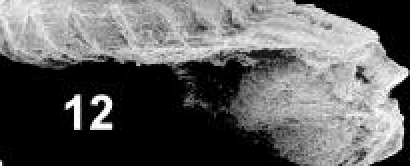
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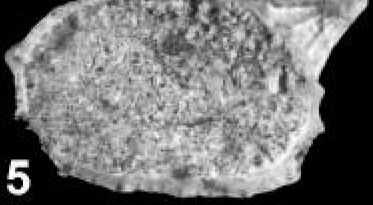
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PLATE 2

Turbinidae from Torallola

Figs. 1-2. *Pseudoliotina sensuyi* (VIDAL, 1921); diameter 11 mm.

Figs. 3-5. *Pseudoliotina stinnesbecki* n. sp.; holotype; diameter 18 mm.

Figs. 6-7. *Arene mcleani* n. sp.; holotype; height 2.6 mm.

Fig. 8. *Homalopoma schroederi* n. sp.; holotype; height 5 mm.

Figs. 9-10. *Barbotella maestrichtiensis* (QUINTERO & REVILLA, 1966); **9** – adult specimen; height 44 mm; **10** – juvenile specimen; height 12 mm.

Fig. 11. *Homalopoma minimum* QUINTERO & REVILLA, 1966; height 4 mm.

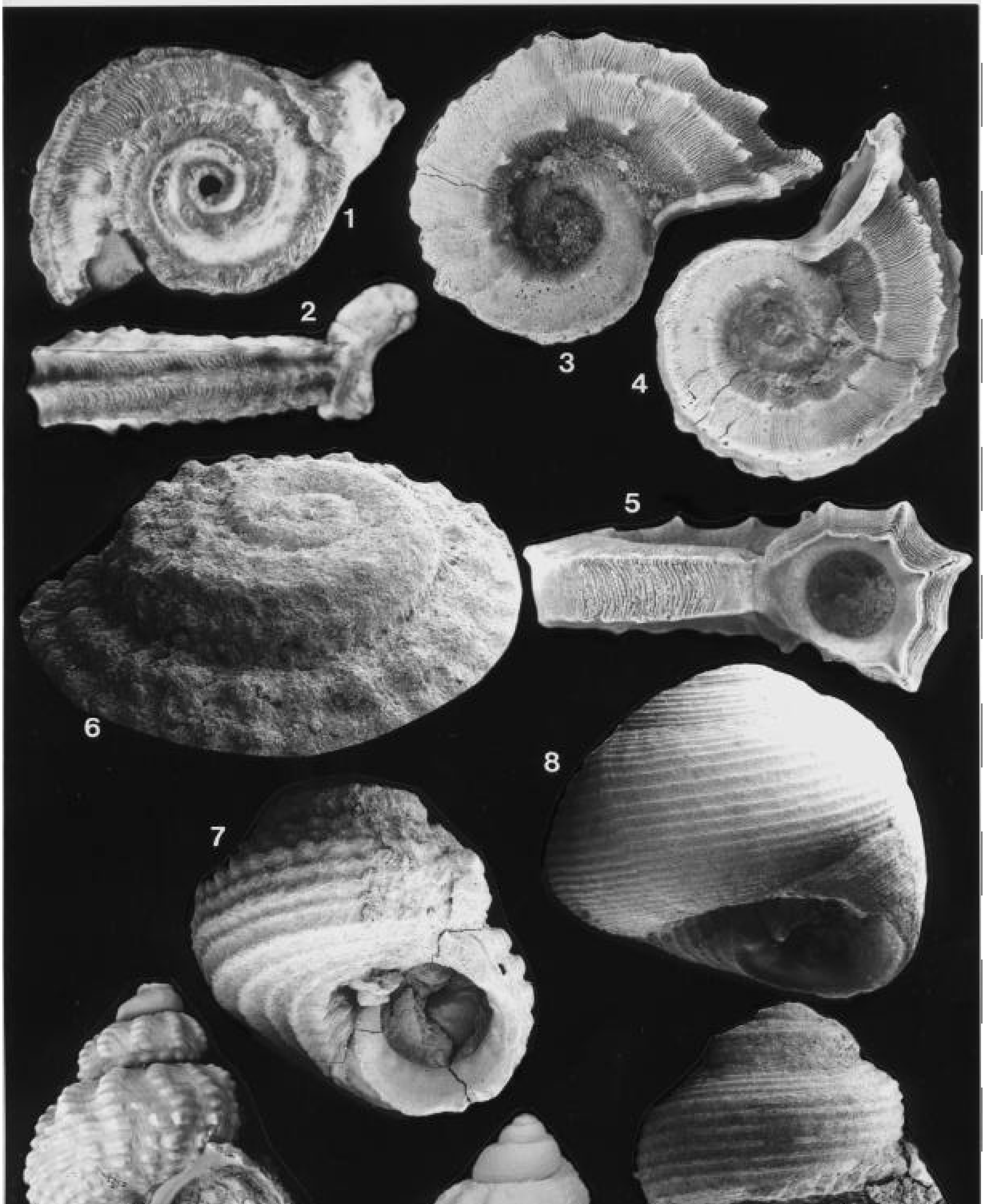
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PLATE 3

Turbinidae from Torallola

Figs. 1-3. *Marmorostoma sensuyi* (VIDAL, 1924); **1-2** – adult specimen; diameter 18 mm, height 15 mm; **3** – juvenile specimen showing the protoconch; diameter 11 mm.

Figs. 4-6. *Astraea batalleria* n. sp.; holotype, diameter 25 mm.

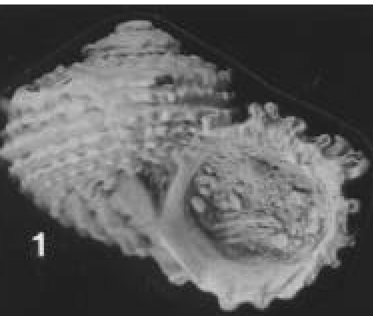
Figs. 7-9. *Callopoma iredalei* n. sp.; holotype; diameter 17 mm.

Figs. 10-11. *Astraea hickmanae* sp.; holotype; diameter 15 mm.

Figs. 12-14. *Astraea* sp.; diameter 17 mm.

Fig. 15. *Skenea wareni* n. sp.; holotype; height 1.7 mm.

Fig. 16. *Skenea sutura* n. sp.; holotype; height 2.2 mm.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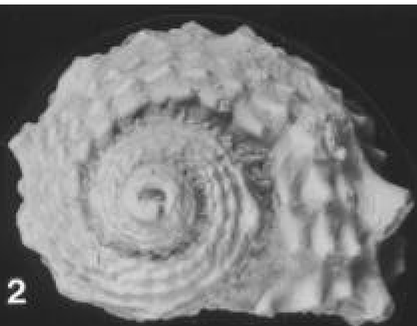
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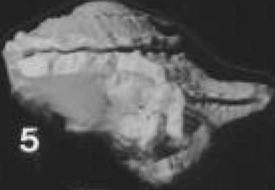
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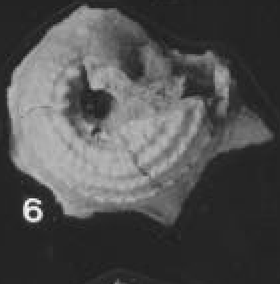
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PLATE 4

Tegulinae and Eucyclinae from Torallola

Fig. 1. *Tegula*? *simplex* (QUINTERO & REVILLA, 1966); x 3.

Fig. 2. *Calliotropis* sp.; x 3.

Fig. 3. *Eucyclomphalus reminescencius* n. sp.; holotype; x 2.3.

Figs. 4-5. *Calliotropis seguris* n. sp.; two views on the holotype; x 4.

Figs. 6, 10, 13. *Ilerdus melgari* (BATALLER, 1949); **6, 10** – two views on a juvenile shell; x 25; **13** – Adult shell; x 3.

Fig. 7. *Calliotropis torallolensis* n. sp.; holotype; x 3.3.

Figs. 8-9, 11-12. *Ilerdus pyrenaeus* n. sp.; **8-9** – two views on the holotype; x 3; **11** – paratype represented by an early shell; x 20; **12** – apical view on the same specimen as Fig. 11; x 120.

Figs. 14-15. *Eucycloscala cretacea* n. sp.; holotype; **14** – side view; x 50; **15** – apical view; x 100.


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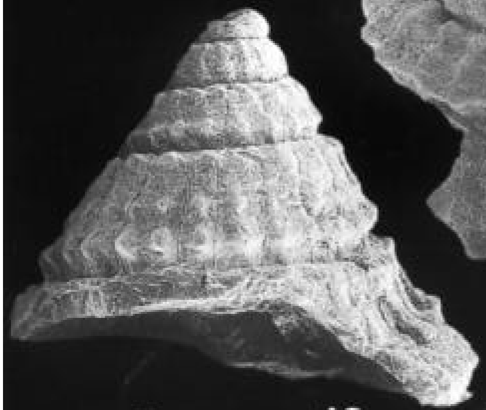
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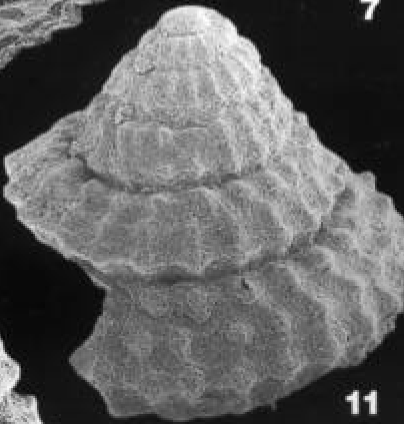
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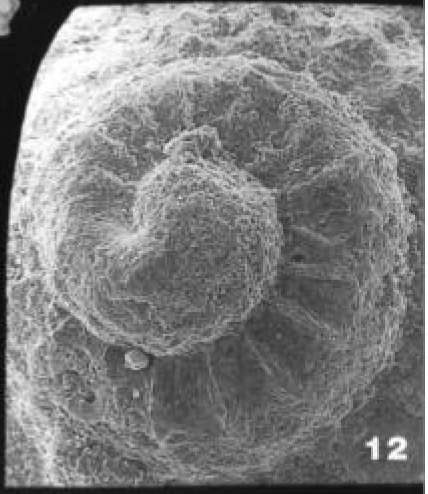
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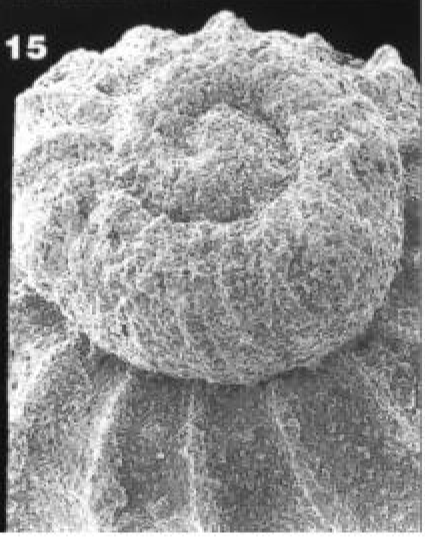
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PLATE 5

Eucyclinae and Margaritinae from Torallola

Figs. 1-2. *Hudledonta nicolae* n. sp.; holotype; **1** – apertural view; x 3; **2** – aperture in detail; x 6.

Figs. 3-4. *Chilodonta crespelli* BATALLER, 1959; **3** – side view; x 6; **4** – aperture in detail; x 8.

Figs. 5-8. *Chilodonta ilerdensis* (VIDAL, 1921); **5** – apical view; x 30; **6-7** – two views on an adult specimen; x 4; **8** – aperture of the same specimen as Fig. 6, 7; x 5.

Figs. 9-11. *Danilia kosslerae* n. sp.; **9-10** – two views on the holotype; x 4.5; **11** – apical view on a juvenile specimen; x 40.

Figs. 12-13. *Margarites nielseni* n. sp.; holotype; x 2.5.

Figs. 14-15. *Margarites kowalkei* n. sp.; holotype; x 5.

Figs. 16-17. *Margarites kasei* n. sp.; holotype; x 3.5.


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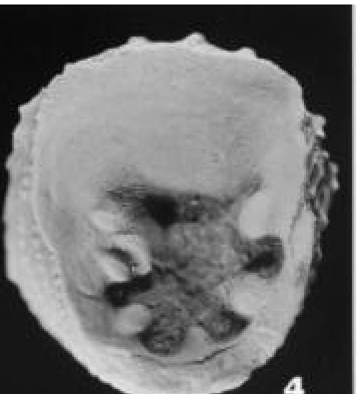
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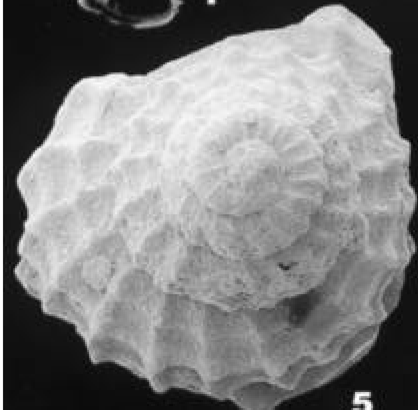
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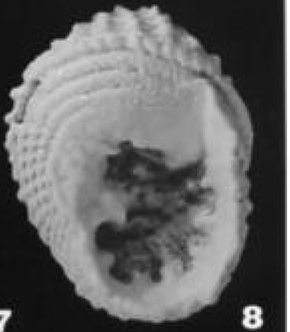
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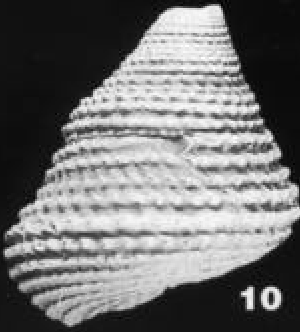
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PLATE 6

Trochinae from Torallola

Figs. 1, 4. *Tectus carinatus* (QUINTERO & REVILLA, 1966); two views; x 2.5.

Figs. 2, 5. *Tectus sensuyi* (VIDAL, 1921); two views; x 3.

Figs. 3, 6. *Tectus revillai* (BATALLER, 1949); two views; x 1.3.

Figs. 7, 10. *Tectus almelai* (BATALLER, 1959); **7** – apertural view; x 1.6; **10** – basal view; x 1.3.

Figs. 8, 11. *Tectus quinteroi* n. sp.; holotype; **8** – apertural view; x 2.5; **11** – basal view; x 2.7.

Figs. 9, 12, 15. *Discotectus gavalai* (BATALLER, 1949); **9** – apertural view; x 3.3; **12** – basal view; x 2.8; **15** – specimen showing colour pattern; x 3.

Fig. 13. *Discotectus pallarsensis* QUINTERO & REVILLA, 1966; x 8.

Fig. 14. *Tectus convallii* (VIDAL, 1874); x 7.


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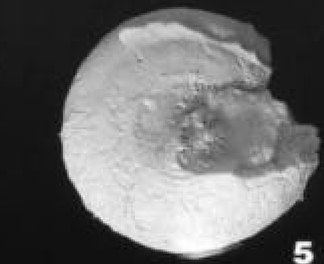
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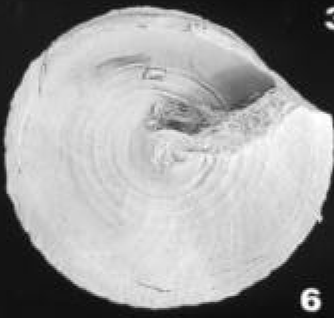
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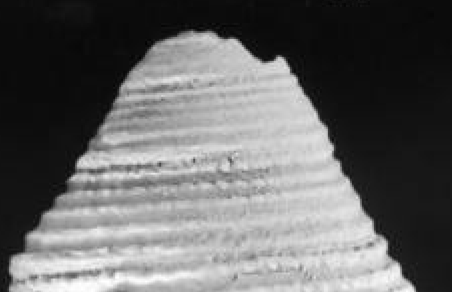
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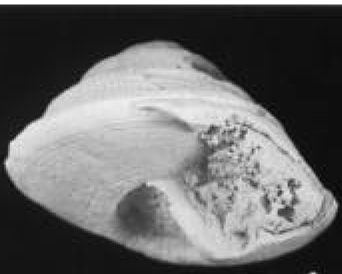
PLATE 7

Trochinae and Solariellinae from Torallola

Figs. 1-3. *Thoristella marshalli* n. sp.; three views on the holotype; x 5.

Figs. 4-7. *Amphigibbula vidali* (COSSMANN, 1915); **4, 7** – adult specimens; x 2.7; **5** – juvenile specimen; x 15; **6** – apical view on the same specimen as Fig. 5; x 115.

Figs. 8-10. *Solariella montsecana* (VIDAL, 1921); **8** – adult shell; x 5; **9-10** – juvenile shell showing the protoconch and the transition from spiral to axial sculpture; x 38.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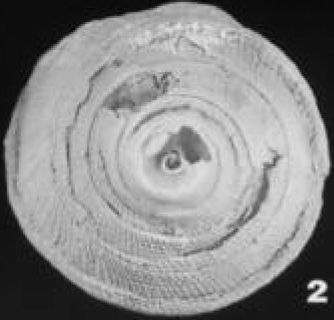
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PLATE 8

Solariellinae and Umboniinae from Torallola

Fig. 1. *Solariella cossmanni* VIDAL, 1921; x 5.

Figs. 2-3. *Suavotrochus ponsi* n. sp.; **2** – juvenile specimen; x 15; **3** – holotype; x 6.5.

Figs. 4, 6, 8. *Ethalia vinxae* n. sp.; three views on the holotype; x 3.8.

Figs. 5, 7, 9. *Protorotella herberti* n. sp.; three views on the holotype; x 2.2.


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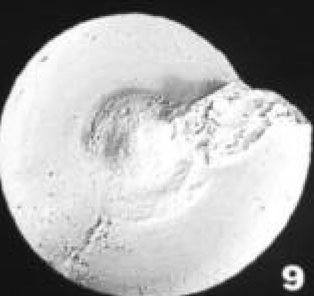
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PLATE 9

Skeneidae, Cirridae and *Torallochus* from Torallola

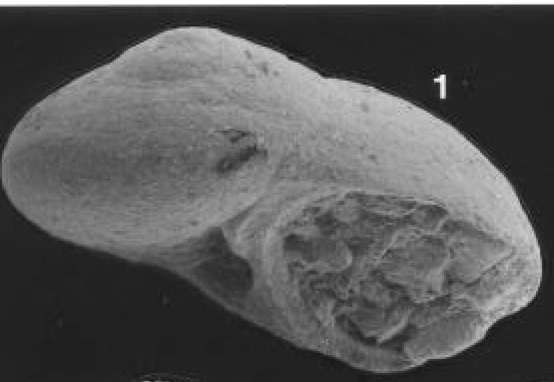
Fig. 1. *Skenea torallolensis* n. sp.; holotype; width 2.1 mm.

Figs. 2-3, 11. *Torallochus discus* n. sp.; holotype; diameter 2.4 mm; **2-3** – apical and ventral view; **11** – view on the protoconch.

Figs. 4-6. *Torallochus torallochus* n. sp.; holotype; height 5 mm; **4-5** – two view on the holotype; **6** – view on the protoconch.

Figs. 7-8. *Torallochus pupiformis* n. sp.; holotype; height 1.7 mm.

Figs. 9-10. *Hamusina ferreri* (QUINTERO & REVILLA, 1966); height 16 mm.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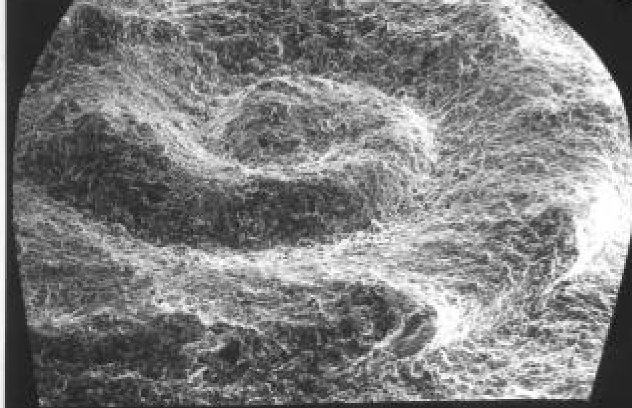
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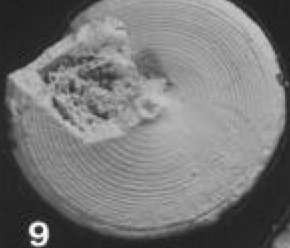
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PLATE 10

Archaeogastropoda and Neritimorpha from Temalac

Figs. 1-2. *Homalopoma chica* n. sp.; holotype; height 1.8 mm.

Figs. 3-4. *Solariella mexcalensis* (PERRILLIAT, VEGA & CORONA, 2000); **3** – adult shell; height 6 mm; **4** – view on the protoconch.

Fig. 5. *Skenea buitronae* n sp.; holotype; height 2.5 mm.

Figs. 6-7. *Dontostoma*? sp.; width 5 mm.

Figs. 8-10. *Otostoma* sp.; width 4 mm.

Figs. 11-13. *Pileolus cozatli* n. sp.; **11, 13** – apical views on the paratype; length 7.5 mm; **12** – holotype; diameter 2.1 mm.

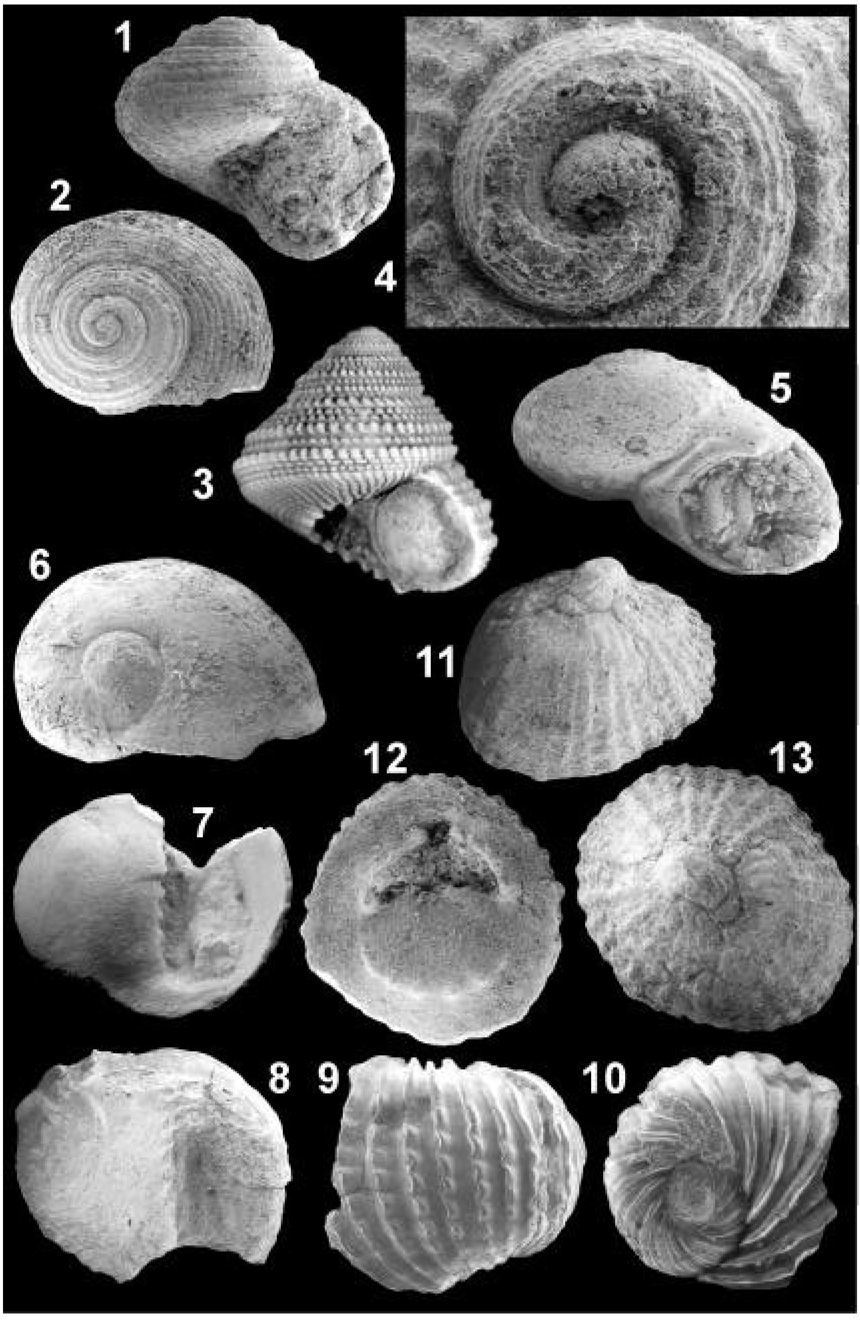
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PLATE 11

Neritimorpha (*Neritopsis, Dontostoma* and *Otostoma*)

Figs. 1-3. *Neritopsis ilerdensis* VIDAL, 1921 from Torallola; height 14 mm.

Figs. 4-6. *Dontostoma bergadana* (VIDAL, 1921) from Torallola; width 13 mm.

Figs. 7-9. *Otostoma vidali* n. sp. from Torallola; holotype; width 20 mm.

Figs. 10-12. *Otostoma trempense* n. sp. from Torallola; holotype; width 20 mm.

Figs. 13-15. *Otostoma* sp. from Temalac; width 4 mm.


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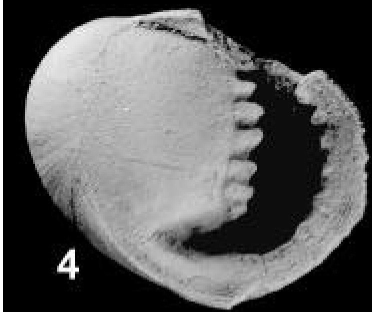
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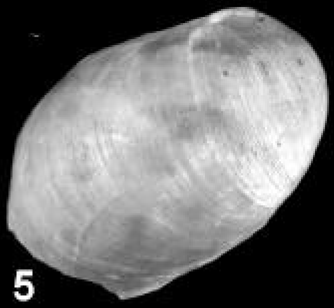
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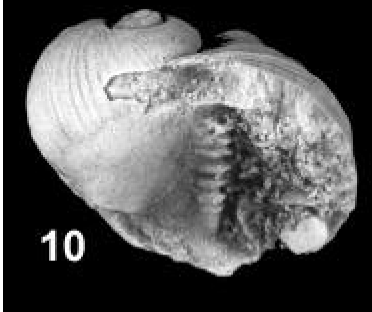
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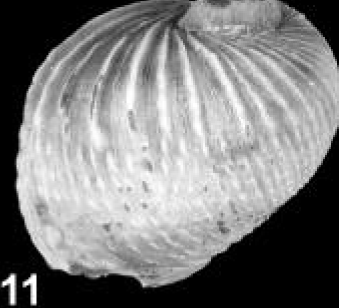
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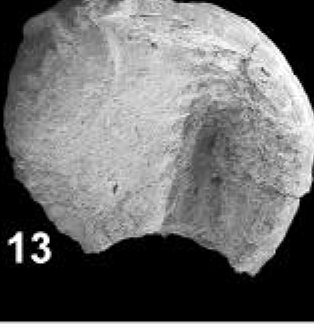
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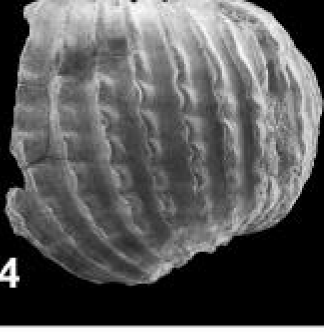
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PLATE 12

Neritimorpha (*Neritoplica, Neritoptyx* and *Pileolus*)

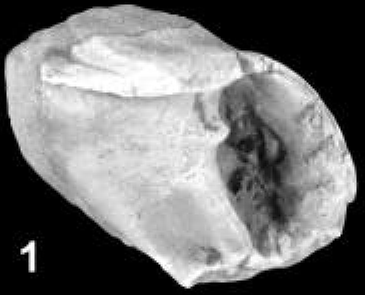
Figs. 1-3. *Neritoplica torallolensis* n. sp. from Torallola; holotype; width 15 mm.

Fig. 4. *Neritoplica trochispira* n. sp. from Torallola; holotype; height 7 mm.

Figs. 5-6. *Neritoptyx reticulirata* (DOCKERY, 1993) from the Coffee Sand Formation of the USA; **5** – specimen showing the denticle on the inner lip; height 2.1 mm; **6** – specimen showing sculpture; height 2.1 mm.

Figs. 7-9. *Pileolus ponsi* n. sp. from Torallola; holotype; diameter 6 mm.

Figs. 10-11. *Pileolus cozatli* n. sp. from Temalac; **10** – apertural view on the holotype; **11** – paratype; length 7.5 mm.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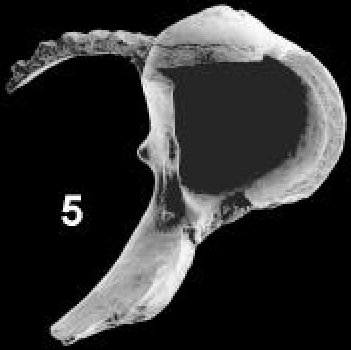
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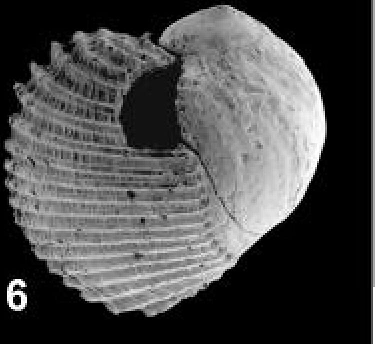
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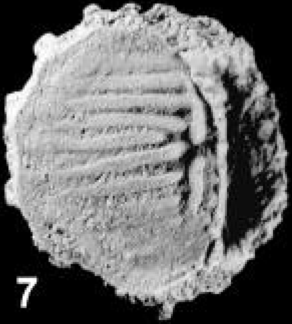
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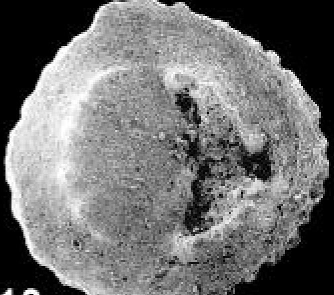
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PLATE 13

Campaniloidea (*Campanile*)

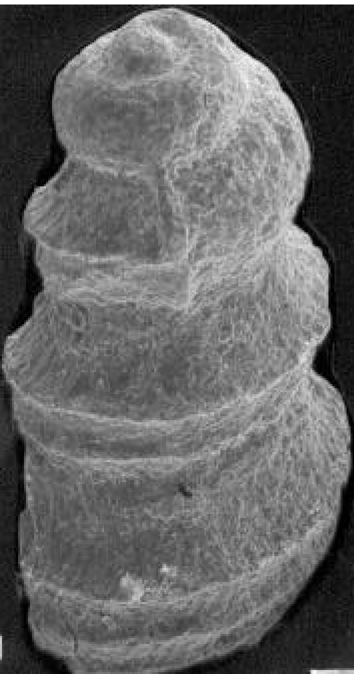
Figs. 1-5. *Campanile houbricki* n. sp. from Temalac; **1** – early ontogenetic shell with protoconch and two teleoconch whorls, IGM 7810, x 100; **2** – juvenile shell showing ontogenetic changes in sculpture, IGM 7809, x 75; **3** – small specimen showing the transition to the adult sculpture, IGM 7807, x 5; **4** – holotype, IGM 7806, x 3; **5** – cross-section showing the smooth interior, IGM 7808.

Fig. 6. *Campanile*? *regens* PETHÖ, 1906 from Čerević stream, cross-section showing the internal plates, GPI 3950, x 0.9.

Fig. 7. *Campanile inauguratum* (Stoliczka, 1868) from Čerević stream, GPI 3949, x 0.9.

Figs. 8-9. *Campanile*? *carezi* VIDAL, 1917 from Torallola, GPI 3951; **8** – frontal view of the corroded shell, x 0.7; **9** – basal view showing the parietal folds and their disappearance near the aperture, x 0.9.

Figs. 10-11. *Campanile cossmanni* VIDAL, 1917 Torallola, two views, GPI 3948, x 1.8.



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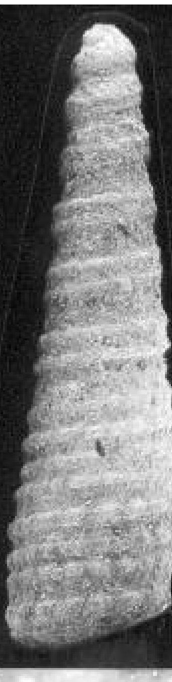

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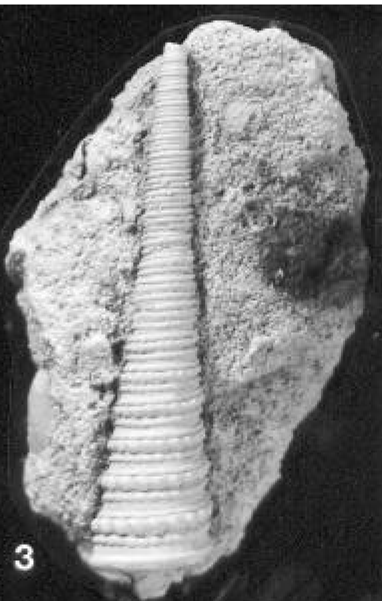

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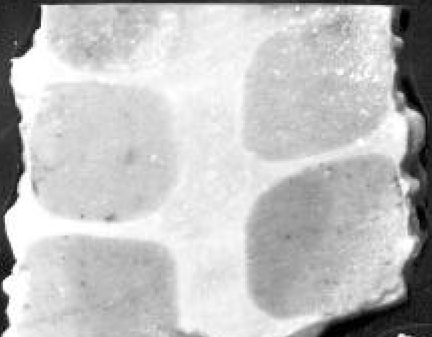

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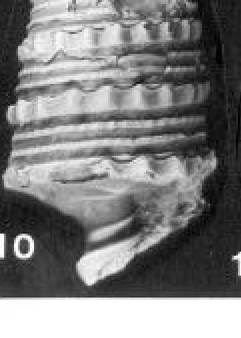

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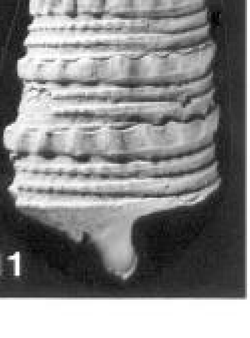

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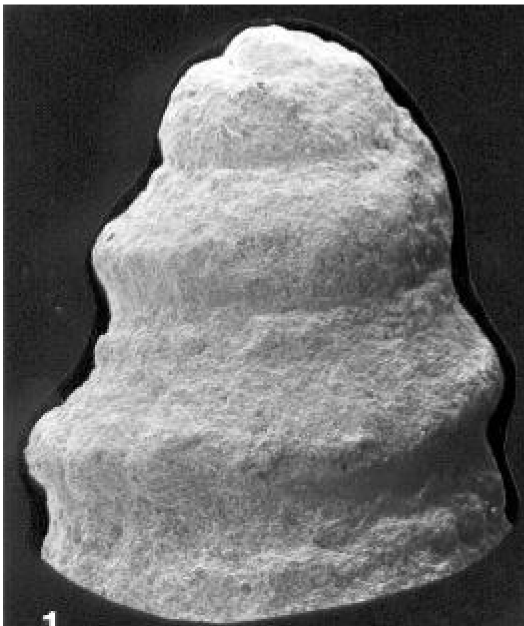
PLATE 14

Campaniloidea (*Metacerithium* and *Plesiotrochus*)

Figs. 1-4. *Metacerithium ponsi* n. sp. from Torallola; **1** – protoconch of the holotype, GPI 3953, x 144; **2** – protoconch of another specimen, showing the characteristic varix, GPI 3954, x 125; **3** – holotype, GPI 3953, x 20 ; **4** – paratype, GPI 3952, x 7.

Figs. 5-6. *Plesiotrochus* spp. from Lizard Island, Australia, GPI 3955; **5** – apertural view on the adult shell, x 34; **6** – protoconch of the same specimen, x 185.



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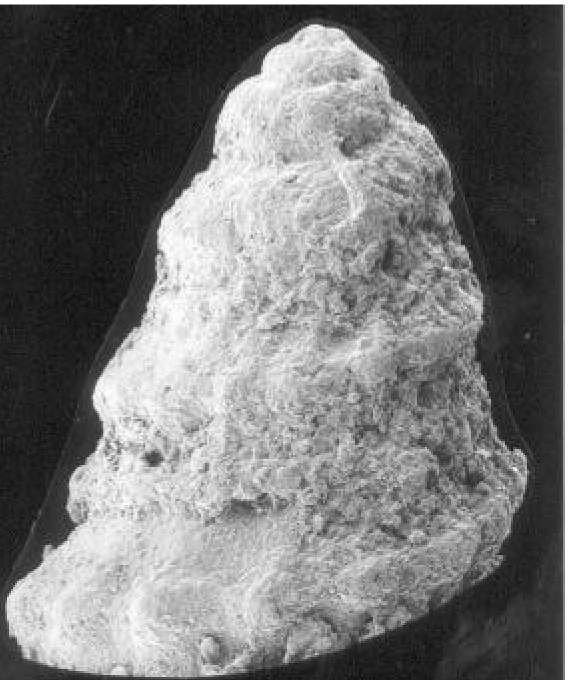

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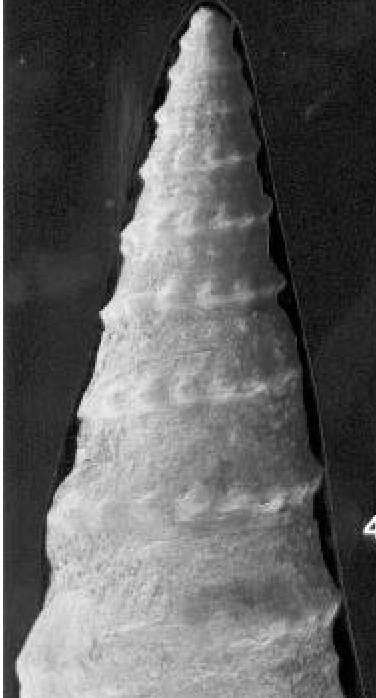

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PLATE 15

Vermetidae, Provannidae and Litiopidae from Torallola

Figs. 1-3. *Vermetus nielseni* n. sp.; **1** – view on the holotype; x 50: **2** – view on the protoconch of the holotype; x 70; **3** – paratype; x 50.

Figs. 4-5. *Desbruyeresia antigua* n. sp.; holotype; **4** – apertural view; x 32; **5** – protoconch; x 100.

Figs. 6-7. *Litiopella schoeningi* n. gen. n. sp.; holotype; **6** – apertural view; x 15; **7** – protoconch; x 62.

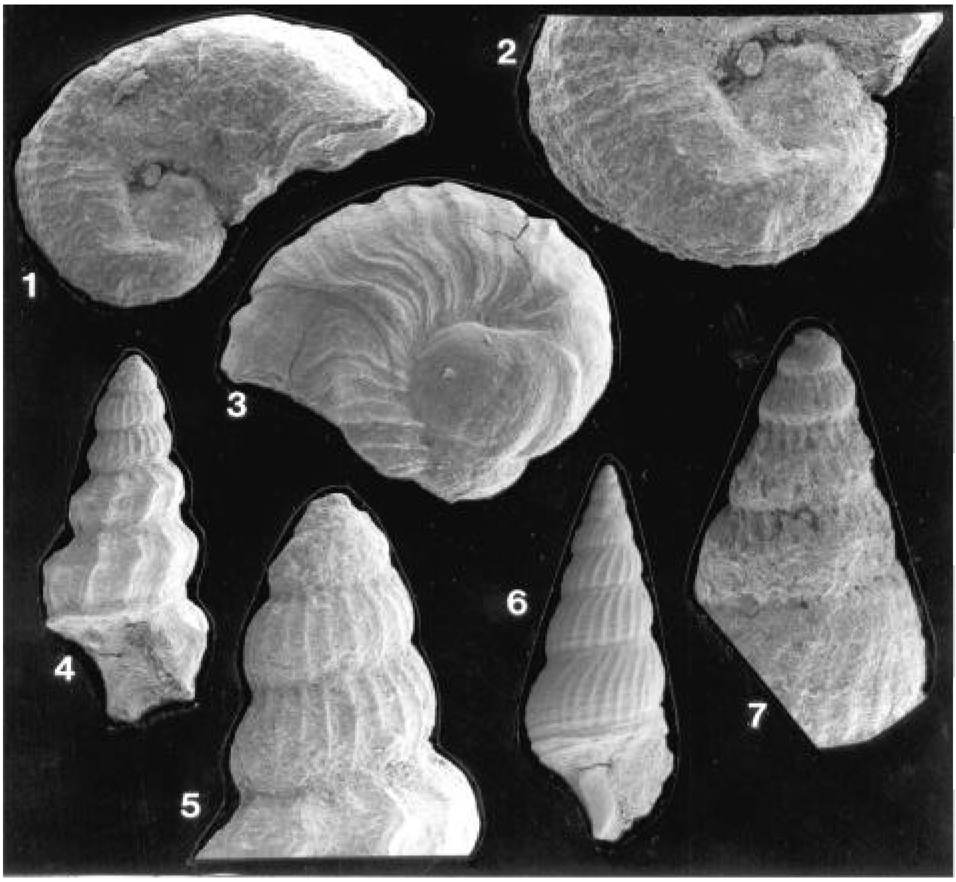
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PLATE 16

Cerithiopsidae and Eumetulidae

Fig. 1. *Cerithiopsis seguris* n. sp. from Torallola; holotype, height 1.0 mm.

Fig. 2. *Vatopsis nodoliratum* (WADE, 1926) from Temalac; height 1.7 mm.

Fig. 3. *Variseila catalania* n. sp. from Torallola; height 1.0 mm.

Fig. 4. *Ataxocerithium heliclina* (DOCKERY, 1993) from Temalac; height 2.2 mm.

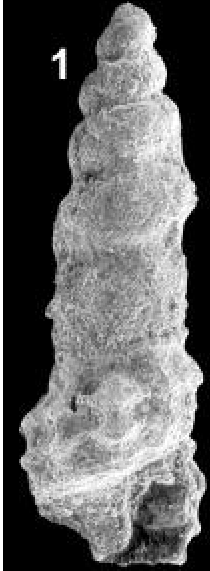
Figs. 5-6. *Eumetula monospiralia* n. sp. from Torallola; holotype; height 0.62 mm; **5** – apertural view; **6** – view on the transition from proto- to teleoconch.

Figs. 7-8. *Eumetula risbeci* n. sp. from Torallola; holotype; height 1 mm.

Fig. 9. *Eumetula marshalli* n. sp. from Torallola; holotype; height 1.8 mm.

Fig. 10. *Marshallaskeya nuetzela* n. sp. from Torallola; holotype; height 4 mm.

Figs. 11-12. *Eumetula* (*Cerithina*) *vaalsensis* HOLZAPFEL, 1888 from Torallola; **11** – juvenile specimen with preserved protoconch; **12** – adult shell; height 12 mm.



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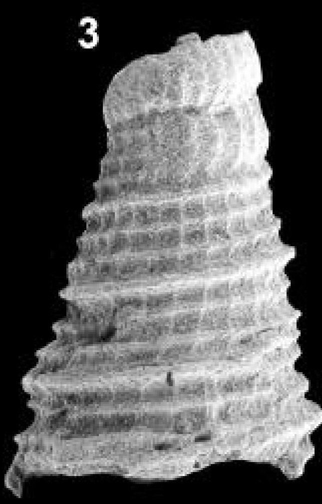

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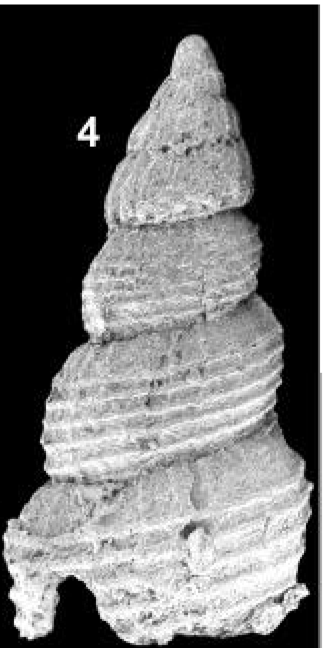

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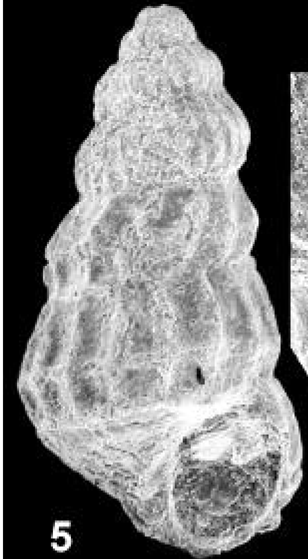

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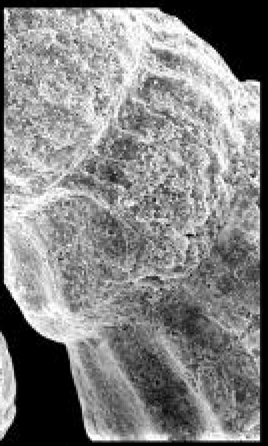

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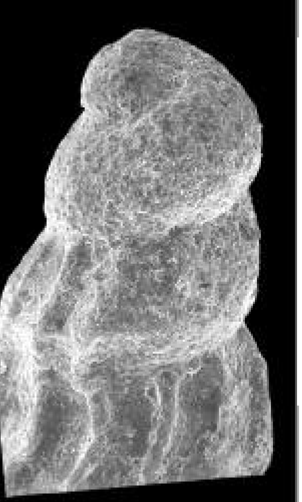

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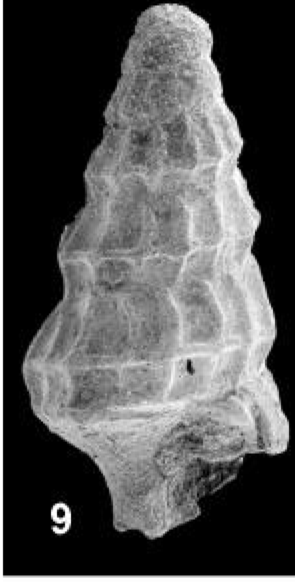

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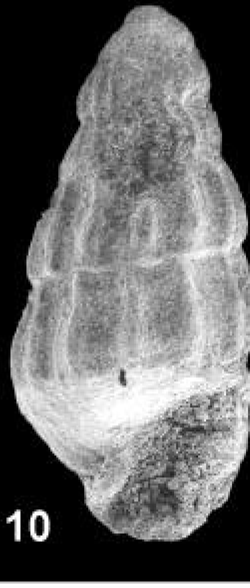

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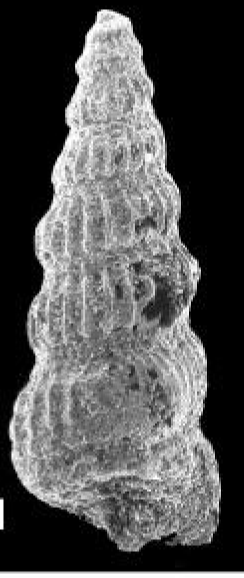

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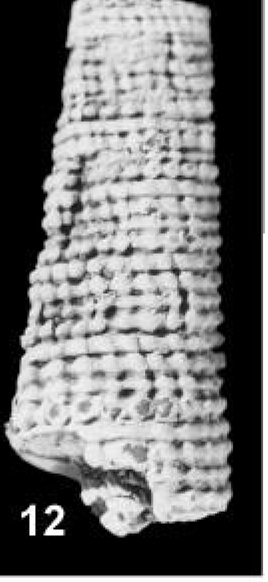

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PLATE 17

Cerithiopsidae, Triphoridae Epitoniidae and Nystiellidae

Fig. 1. *Eumetula (Cerithina) dockerya* n. sp. from Temalac; holotype; height 1.6 mm.

Figs. 2-3. *Trempinella sensuyi* (VIDAL 1921) from Torallola; **2** – adult shell; height 9 mm; **3** – larval shell; height 0.66 mm.

Fig. 4. Triphorid larval shell from Temalac; height 0.58 mm.

Fig. 5. *Cylindriscala mexcalia* n. sp. from Temalac; holotype; height 3.2 mm.

Fig. 6. *Opaliopsis punctata* n. sp. from Torallola; holotype; height 1 mm.

Fig. 7. *Opaliopsis temalacia* n. sp. from Temalac; holotype; height 1.2 mm.

Figs. 8-9. *Proscala campaniana* n. sp. from Torallola; **8** – adult shell, height 15 mm high; **9** – holotype with preserved protoconch; height 3 mm.

Fig. 10. *Atorcula americana* n. sp.; holotype; height 1.4 mm.

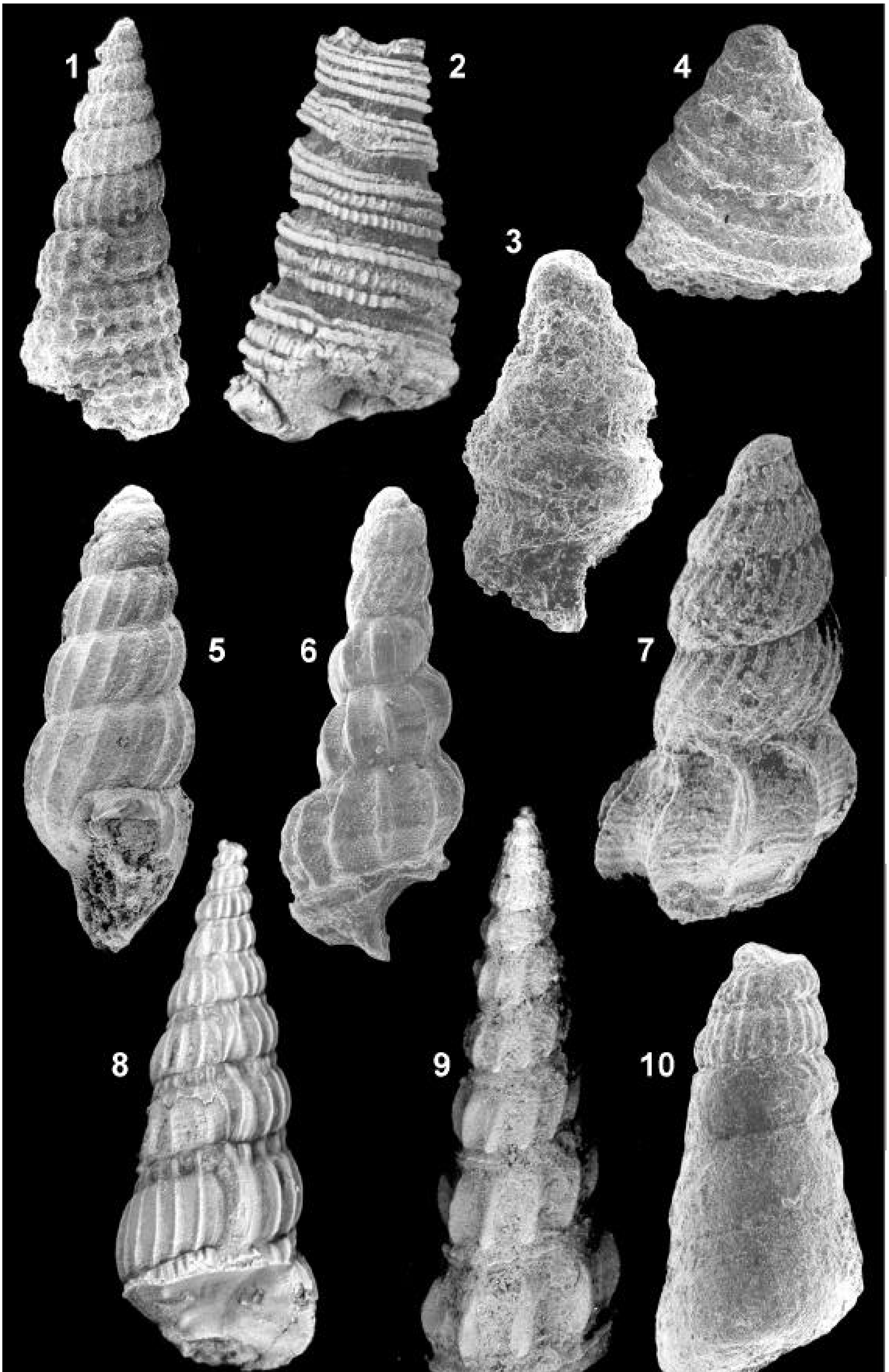
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PLATE 18

Strombidae from Temalac

Figs. 1-3. *Rimella mexcala* n. sp.; **1, 3** – paratype; height 21 mm; IGM 7783; **2** – holotype; height 17 mm; IGM 7782.

Figs. 4-5. *Calyptraphorus binodiferus* PERRILLIAT & VEGA, 1997, specimen with well developed canal; height 21 mm; IGM 7784.

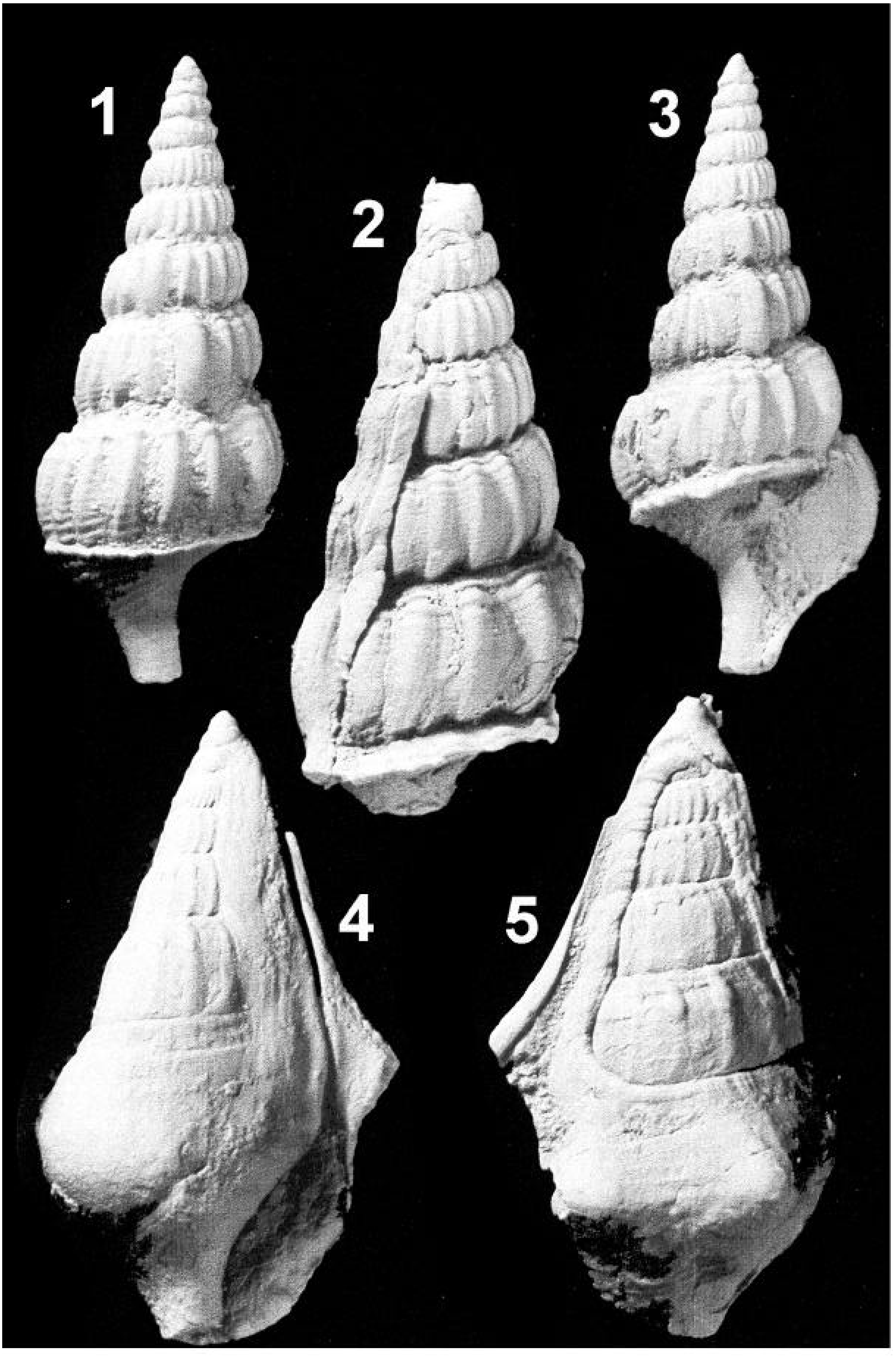
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PLATE 19

Strombidae and Aporrhaidae from Temalac

Figs. 1-3. *Calyptraphorus binodiferus* PERRILLIAT & VEGA, 1997; **1-2** – fully grown specimen with large callus deposit; height 29 mm; IGM 7785; **3** – protoconch; height 1.5 mm.; IGM 7786.

Figs. 4-5. *Anchura denticulata* n. sp.; holotype; height 15 mm; IGM 7787.

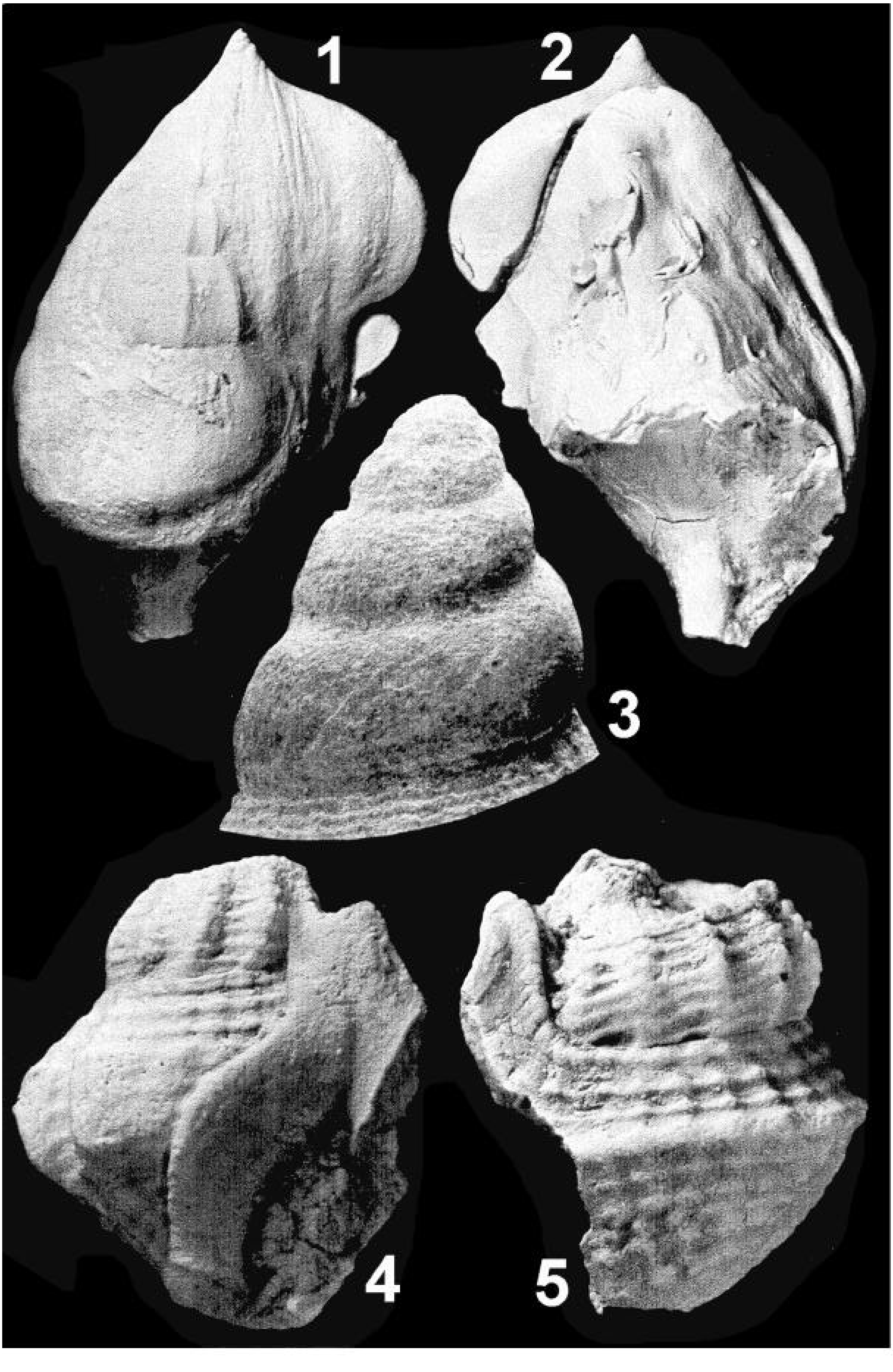
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PLATE 20

Aporrhaidae from Temalac

Fig. 1. *Anchura denticulata* n. sp.; protoconch; height 1.4 mm; IGM 7788.

Fig. 2. *Anchura* sp.; width 19 mm; IGM 7789.

Figs. 3-5. *Lispodesthes lilipus* n. sp.; **3** – juvenile specimen; height 15 mm; IGM 7790; **4-5** – holotype; height 21 mm; IGM 7791.

Fig. 6. *Pterocerella* sp.; height 26 mm; IGM 7792.

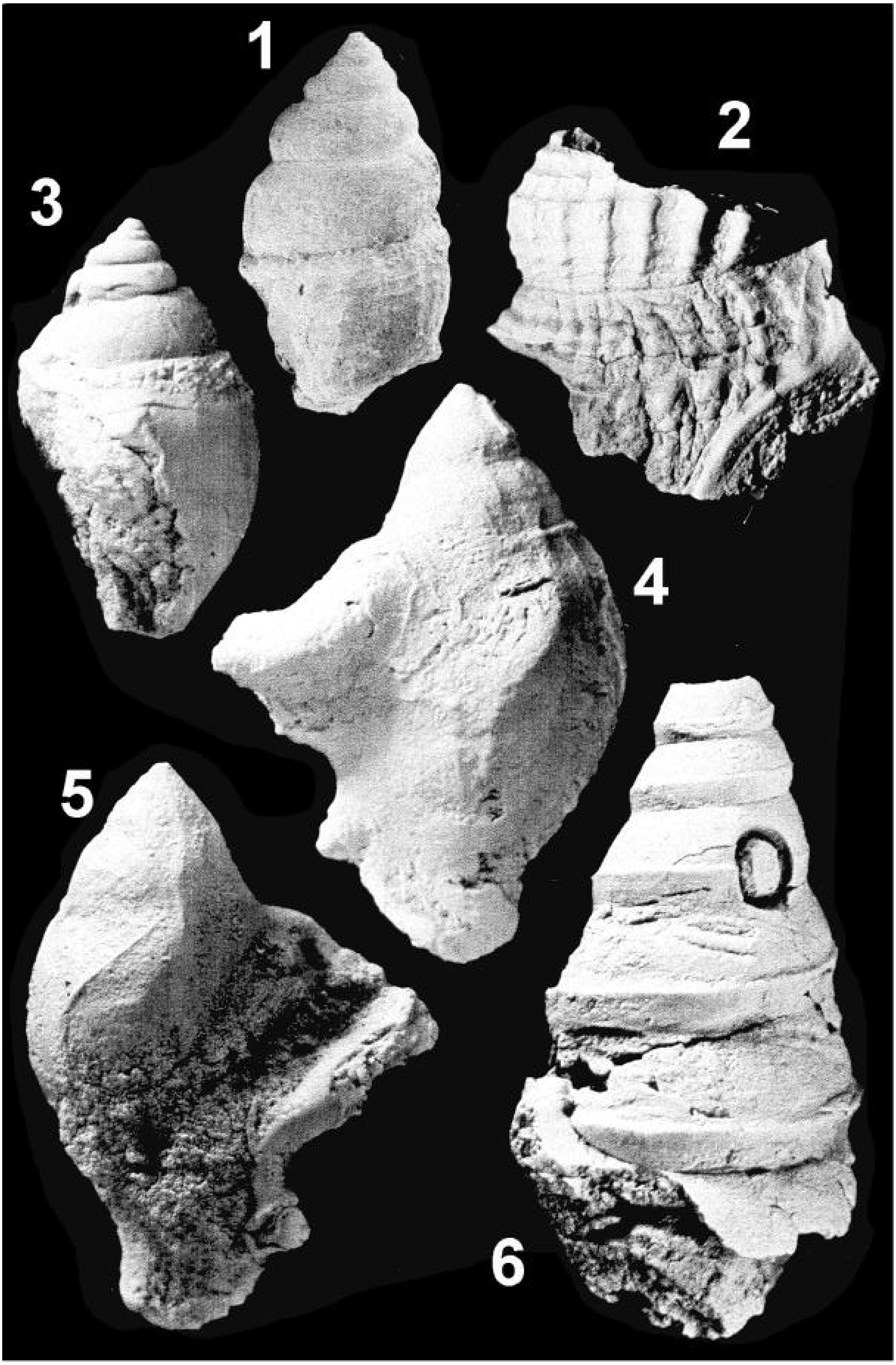
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PLATE 21

Aporrhaidae from Temalac

Figs. 1-3. *Mexopus mexicanus* n. gen. n. sp.; **1-2** – holotype; height 20 mm; IGM 7793; **3** – juvenile shell with preserved protoconch; height 8 mm; IGM 7794.

Figs. 4-5. *Mexopus robustus* n. gen. n. sp.; holotype; height 30 mm; IGM 7795.

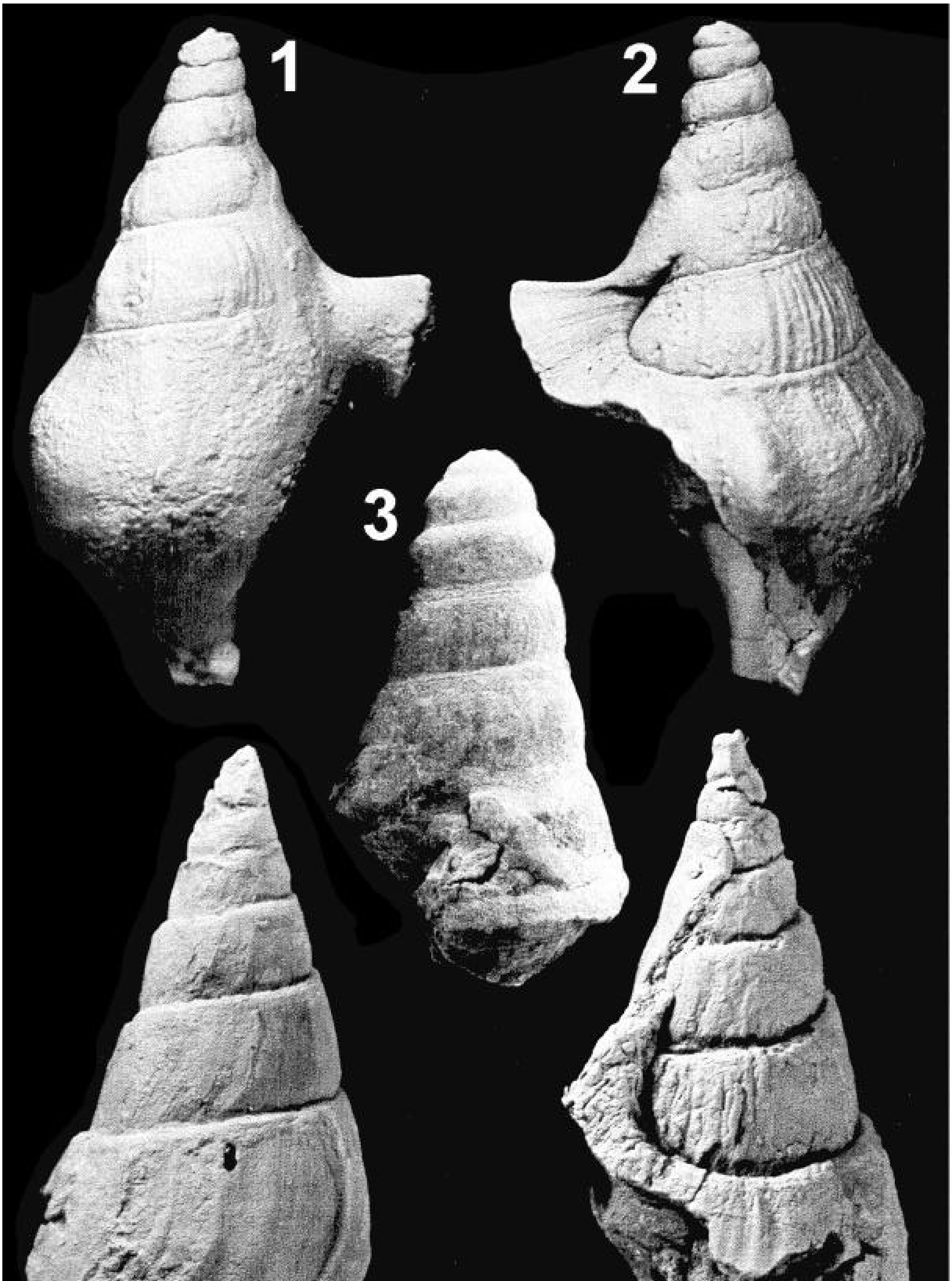
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PLATE 22

Pugnellidae and Xenophoridae from Temalac

Figs. 1-2. *Torgnellus* sp.; height 24 mm; IGM 7796.

Figs. 3-5. *Acanthoxenophora sinuosa* PERRILLIAT & VEGA, 2000; **3** – specimen with remains of an attached *Turritella*; height 4 mm; IGM 7797; **4** – adult shell; height 14 mm; IGM 7798; **5** – specimen with preserved protoconch; width 2.1 mm; IGM 7799.

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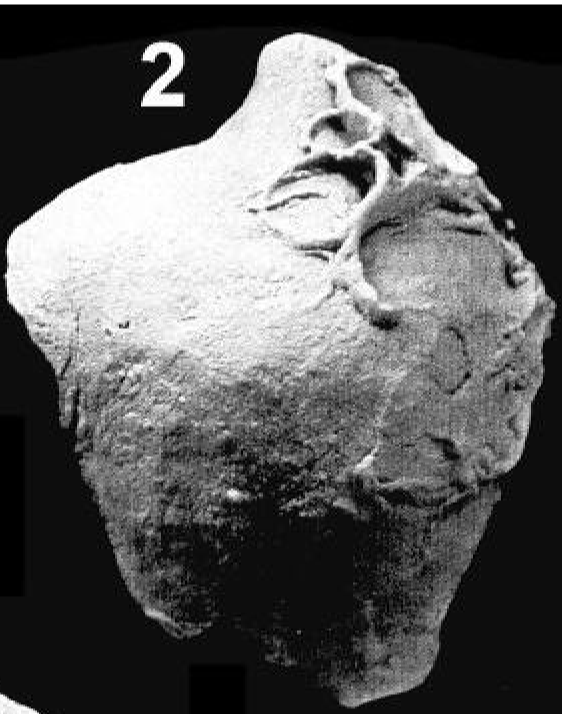

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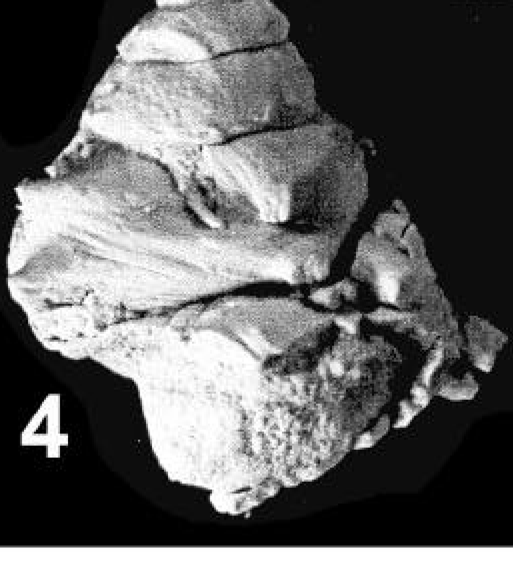

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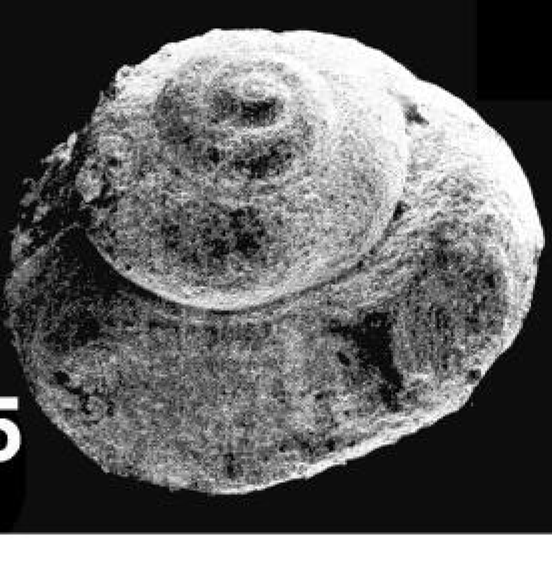


PLATE 23

Neomesogastropoda from Temalac

Figs. 1-2. *Gyrodes supraplicatus* (CONRAD, 1858); height 9 mm.

Figs. 3-4. *Gyrodes* (*Dockeryella*) cf. *major* (WADE, 1926); height 10 mm.

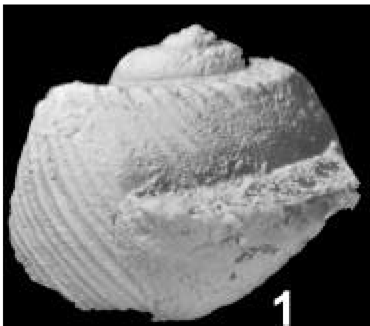
Figs. 5-6. *Natica* cf. *perspecta* WHITFIELD, 1865; height 11 mm.

Figs. 7-9. *Anomalofusus alani* n. sp.; **7** – specimen with preserved columella; height 14 mm; **8** – holotype; height 13 mm; **9** – juvenile specimen with preserved protoconch; diameter of the smooth protoconch 1.3 mm.

Fig. 10. C*antharulus* sp.; height 19 mm.

Figs. 11. Neomesogastropod larval shell type 1; width 0.8 mm.

Figs. 12-14. Neomesogastropod larval shell type 2; three views; height 0.6 mm, width 0.8 mm.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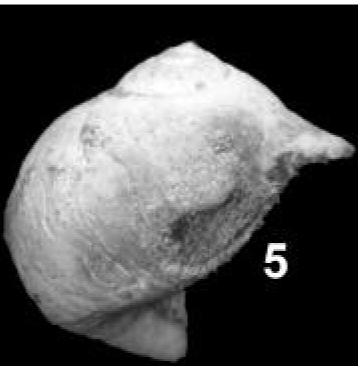
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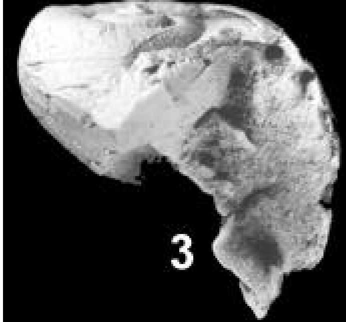
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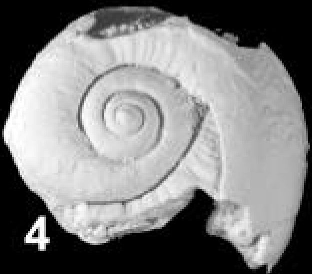
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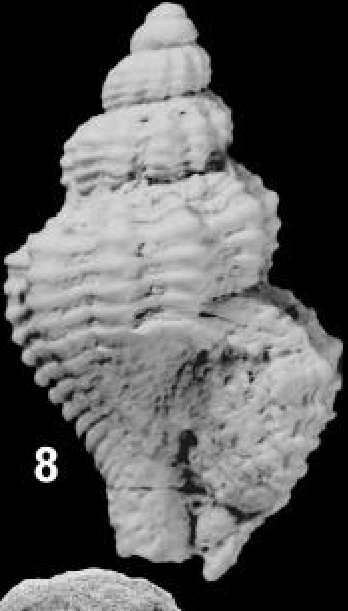
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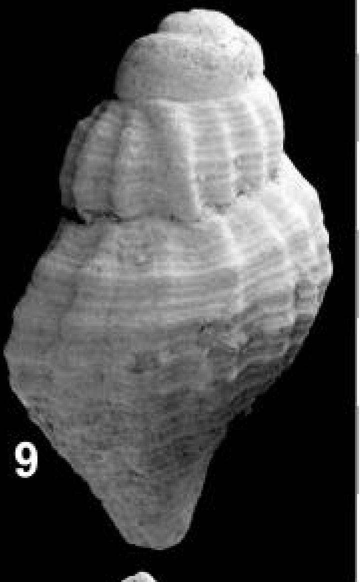
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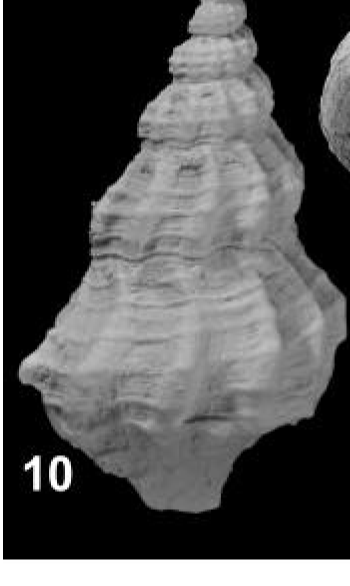
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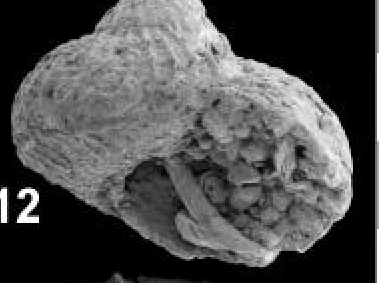
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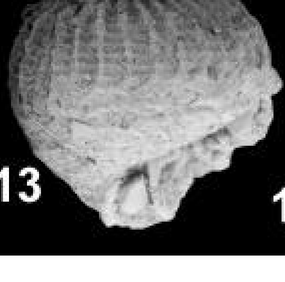
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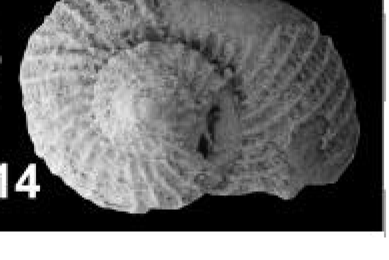
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PLATE 24

Neomesogastropoda from Torallola

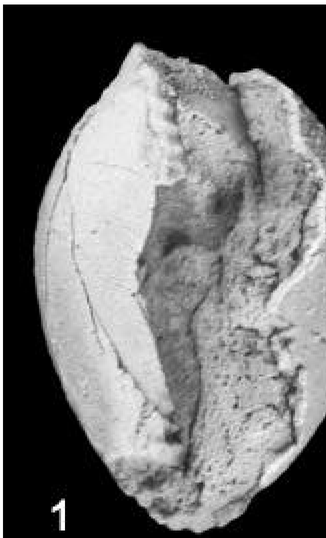
Figs. 1-2. *Cypraea* sp.; height 10 mm.

Fig. 3. *Gyrineum gwinae* DOCKERY, 1993; height 28 mm.

Figs. 4-6. *Sassia praegranosum* (COTTREAU, 1922); **4** – adult specimen showing the distorted whorls; height 21 mm; **5** – specimen with preserved protoconch which shows a cancellate pattern; height 3.5 mm; **6** – isolated larval shell; diameter 1.2 mm.

Fig. 7. *Trichotropis konincki* (MÜLLER, 1851); height 2.5 mm.

Figs. 8-9. *Lamelligyra lamellaris* n. gen. n. sp.; holotype; height 23 mm.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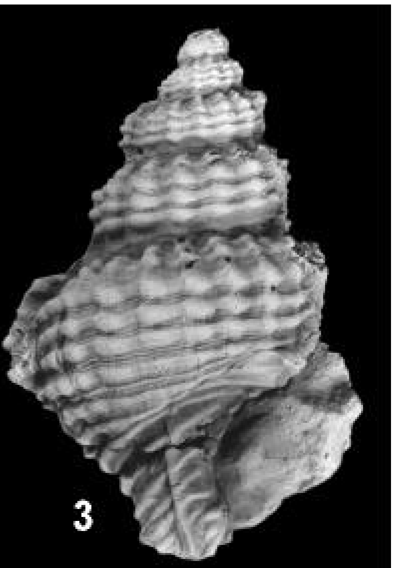
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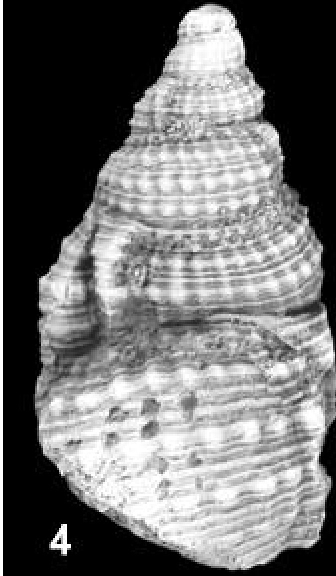
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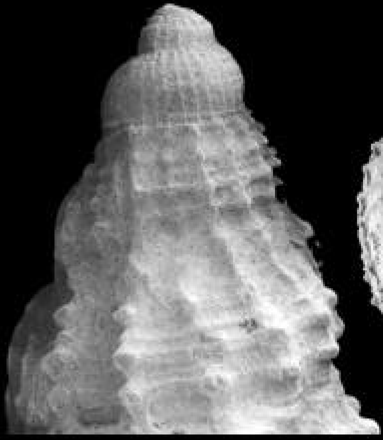
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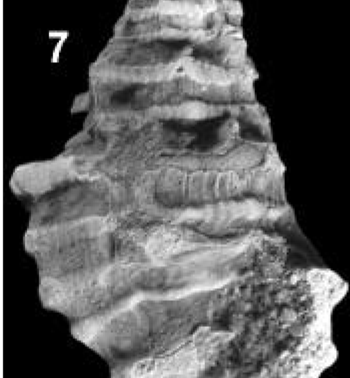

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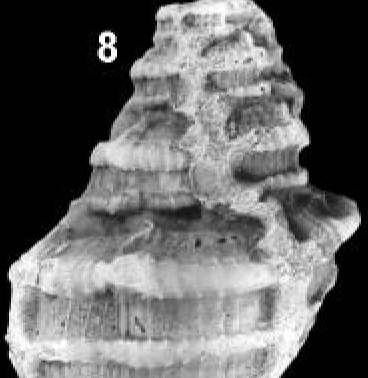

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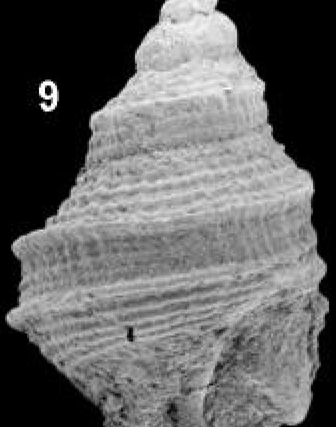

PLATE 25

Maturifusus, Cancellariidae and Turridae from Torallola

Fig. 1. *Maturifusus* sp.; height 2.2 mm.

Figs. 2-3. *Cancellaria puimanyonsia* n. sp.; holotype; height 6.5 mm; two views on proto- and teleoconch.

Fig. 4. *Koenenia* sp. 1; height 38 mm.

Figs. 5-6. *Koenenia* cf. *octocostata* n. sp.; height 15 mm.

Fig. 7. *Koenenia* sp. 2; height 42 mm.

Figs. 8-9. *Eupleurotoma formosa* (BINKHORST, 1861); height 20 mm.


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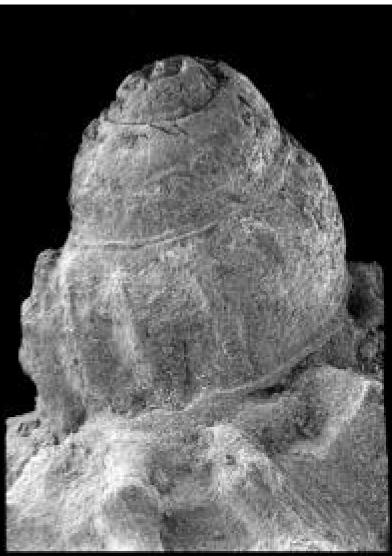
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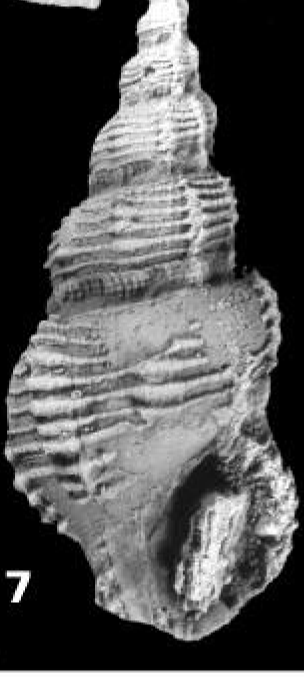
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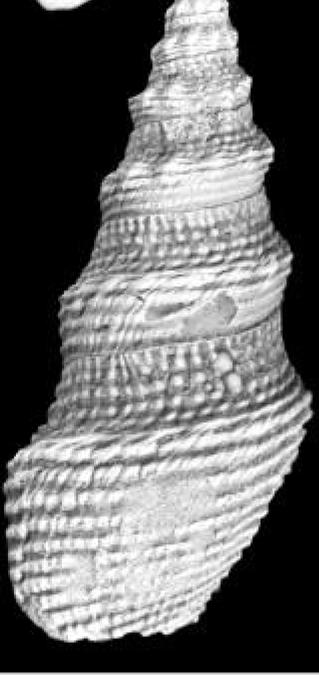
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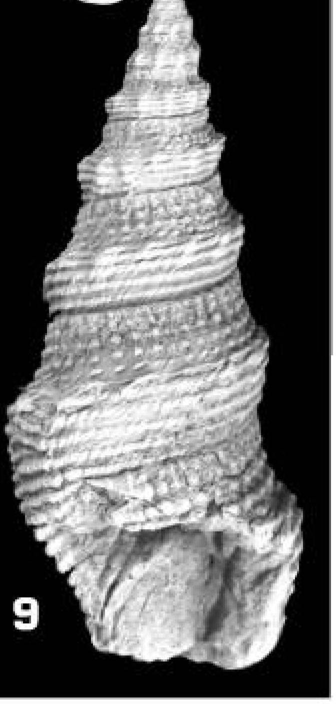
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PLATE 26

Turridae, Athletidae, Volutodermidae and Volutidae from Torallola

Figs. 1-2. *Eupleurotoma formosa* (BINKHORST, 1861); juvenile specimen with preserved protoconch which is 0.9 mm high.

Figs. 3-4. *Liopeplum pyrenaeum* n. sp.; holotype; height 36 mm.

Figs. 5-6. *Volutomoderma* cf. *zitteliana* HOLZAPFEL, 1888; height 17 mm.

Figs. 7-10. *Volutifusus olssoni* n. sp.; **7** – holotype with preserved protoconch; height 16 mm; **8** – adult shell; height 25 mm, **9-10** – paratype; height 25 mm.

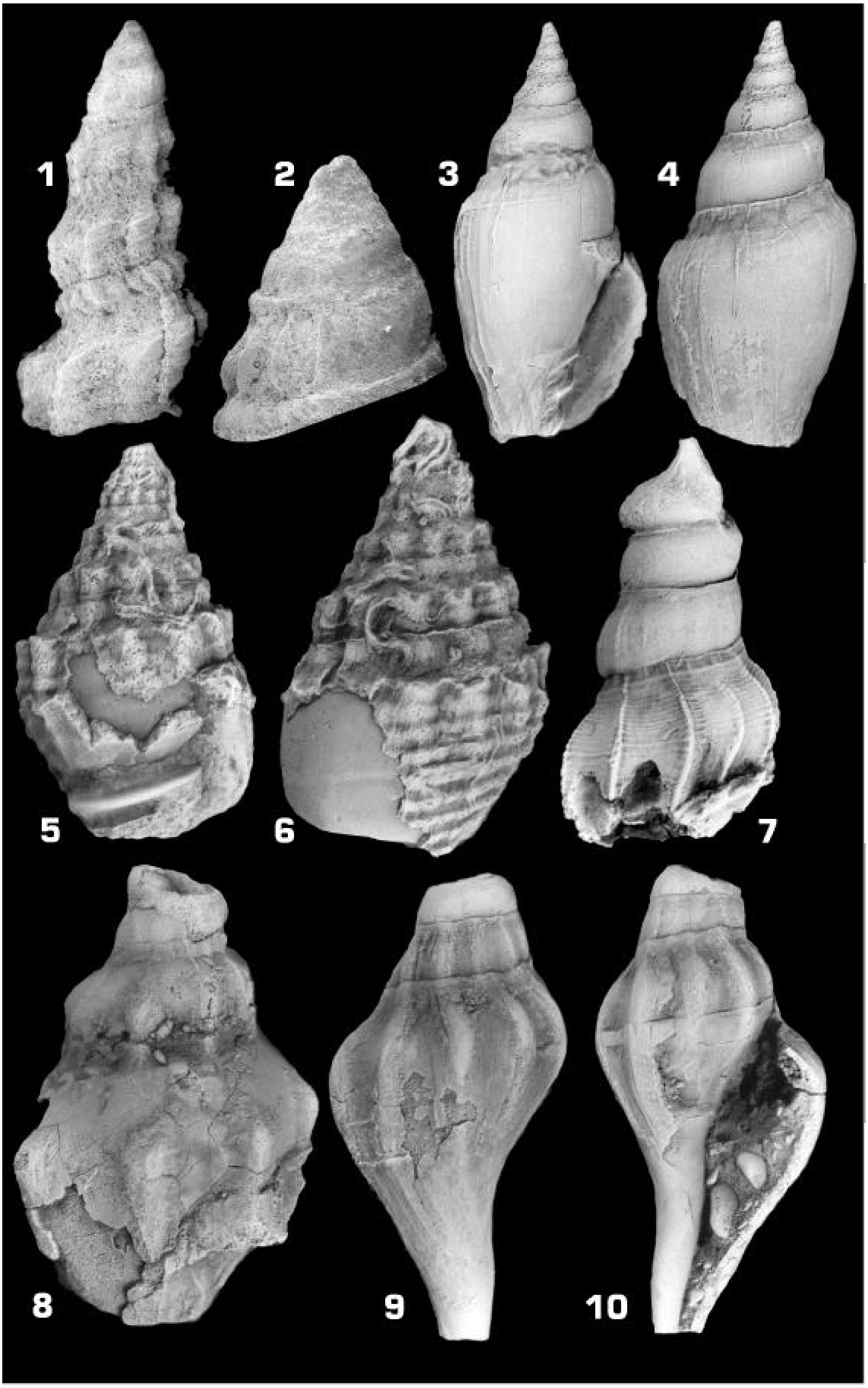
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PLATE 27

Pyrifusidae from Torallola

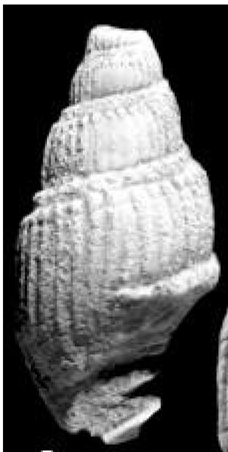
Fig. 1. *Drilluta* sp.; height 10 mm.

Figs. 2-5. *Graphidula maestrichtiensis* (KAUNHOWEN, 1897); **2-3** – specimen without columellar folds; height 25 mm; **4** – cross-section of a specimen with one columellar fold; **5** – cross-section of a specimen with two columellar folds.

Figs. 6-7. *Paleopsephaea octacostata* n. sp.; holotype; height 31 mm.

Figs. 8-9. *Paleoplephaea stephensoni* n. sp.; holotype; height 21 mm.

Figs. 10-11. *Paleopsephaea wadei* n. sp.; holotype; height 17 mm.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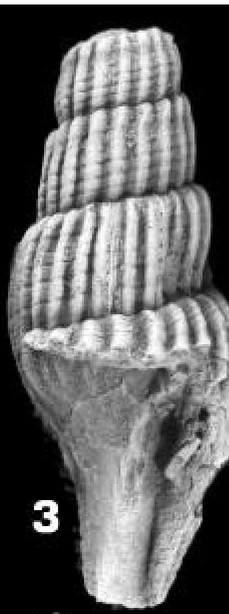
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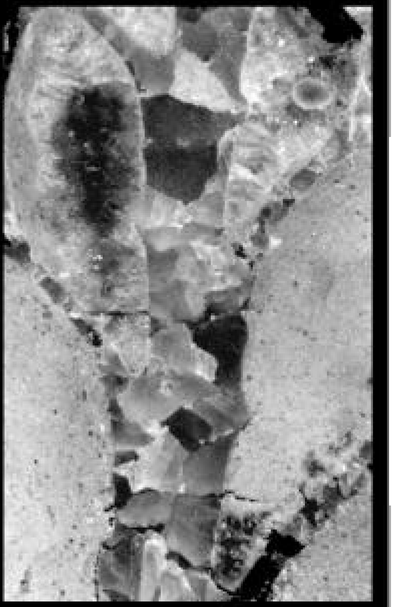
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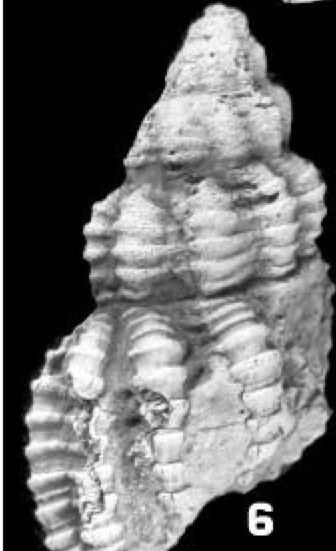
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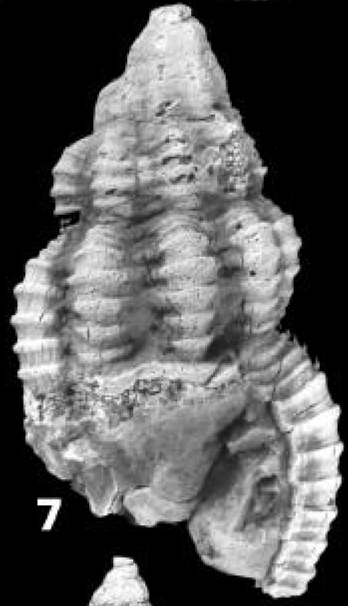
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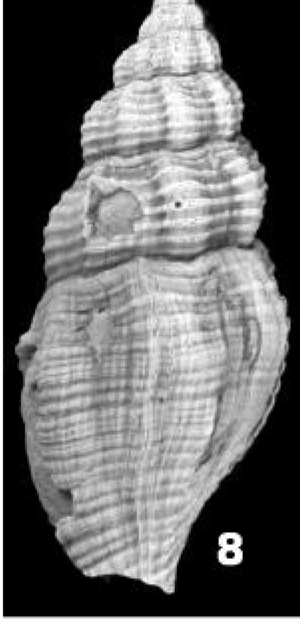
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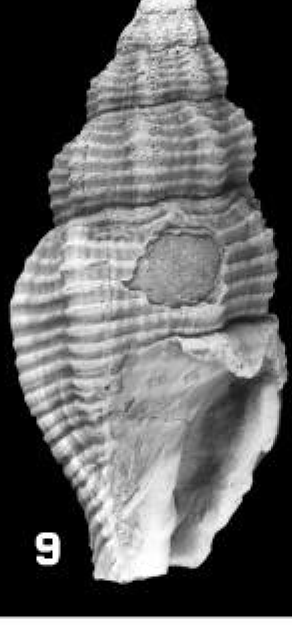
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PLATE 28

Pyrifusidae from Torallola

Figs. 1-2. *Bellifusus* sp.; height 25 mm.

Figs. 3-4. *Mitridomus pseudocostellarius* n. sp.; holotype; height 40 mm.

Figs. 5-7. *Mitridomus conomitriformis* n. sp.; **5-6** – holotype; height 25 mm; 7 – specimen with preserved protoconch.

Figs. 8-9. *Mitridomus varicicousus* n. sp.; holotype; height 17 mm.

Figs. 10-11. *Mesorhytis* sp.; height 17 mm.

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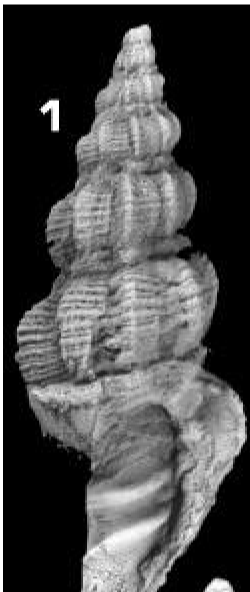

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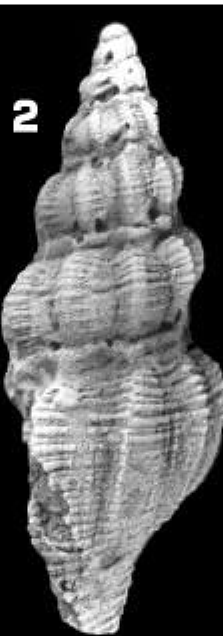

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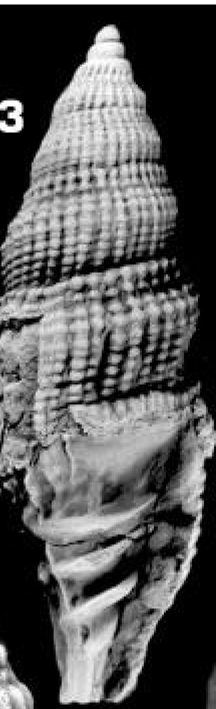

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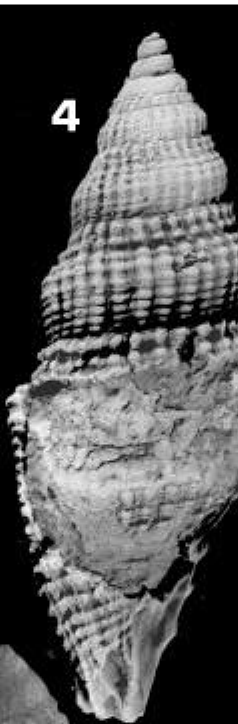

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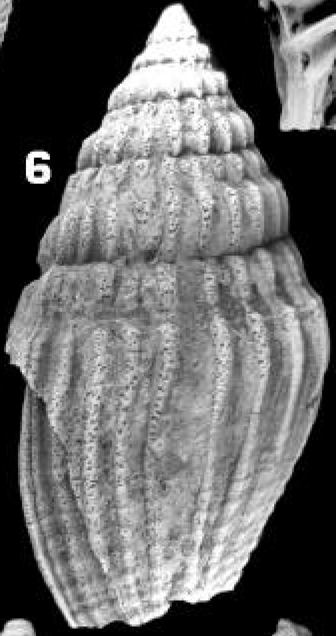

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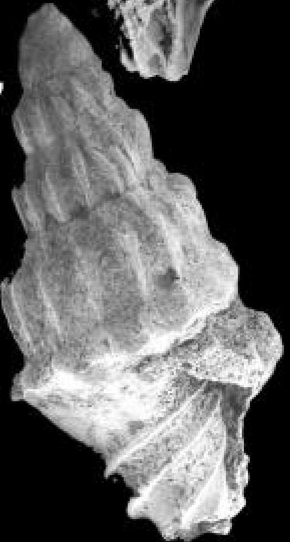

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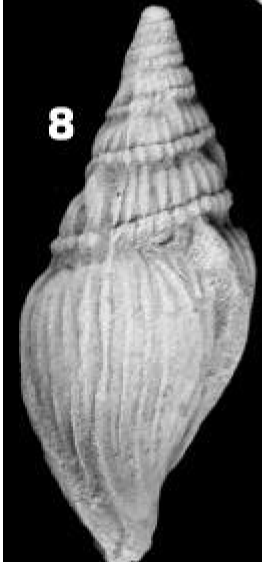

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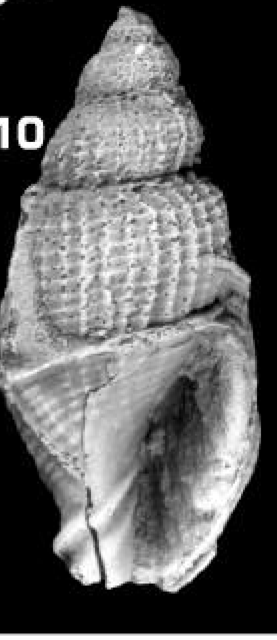

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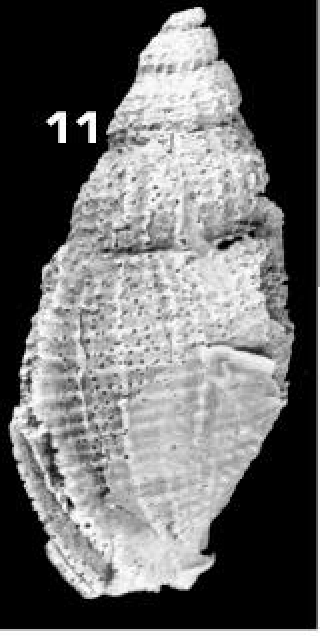

PLATE 29

Buccinopsis, Pyrifusus **and** ***Morea*** **from Torallola**

Figs. 1-2. *Buccinopsis crassiaxialis* n. sp.; holotype; height 13 mm.

Fig. 3. *Pyrifusus* sp.; height 10 mm.

Figs. 4-5. *Morea* sp.: height 11 mm.

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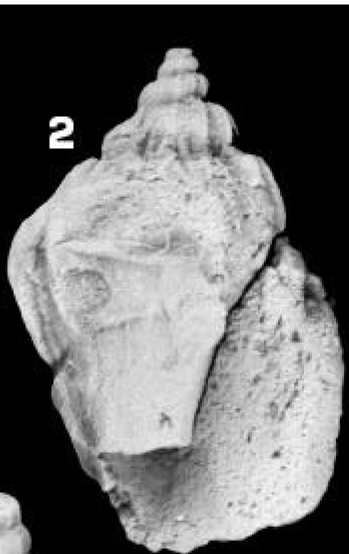

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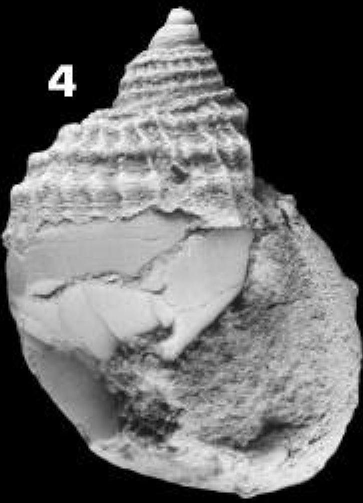

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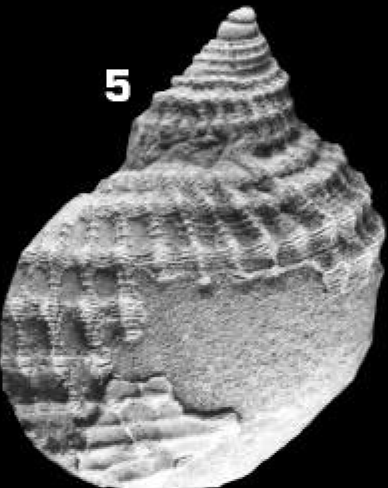

PLATE 30

Cancellariidae, Turridae and Pseudolividae from Temalac

Figs. 1-4. *Cancellaria nissenae* n. sp.; **1, 4** – juvenile specimen with protoconch and a drill-hole near the aperture, probably caused by a naticid; height 4.6 mm; **2** – adult showing the aperture; height 11 mm; **3** – holotype; height 10 mm.

Figs. 5-6. *Koenenia kilburni* n. sp.; holotype; height 33 mm.

Fig. 7. *Koenenia octacostata* n. sp.; holotype; height 23 mm.

Fig. 8. *Beretra ornatula* STEPHENSON, 1941; height 17 mm.

Figs. 9-10. *Koenenia kirsteni* n. sp.; holotype; height 16 mm.

Figs. 11-12. *Koenenia multispirata* n. sp.; **11** – holotype; height 14 mm; **12 –** specimen with preserved columella.

Figs. 13-14. *Koenenillia typica* n. sp.; **13** – juvenile specimen with preserved protoconch; height 4.2 mm; **14** – holotype; height 14 mm.

Figs. 15-17. Pseudolivide? **15** – specimen showing the columellar fold; height 3.6 mm; **16** – specimen with the smooth protoconch, which is 0.6 mm wide; **17** – back-view on an adult specimen, height 4.5 mm.

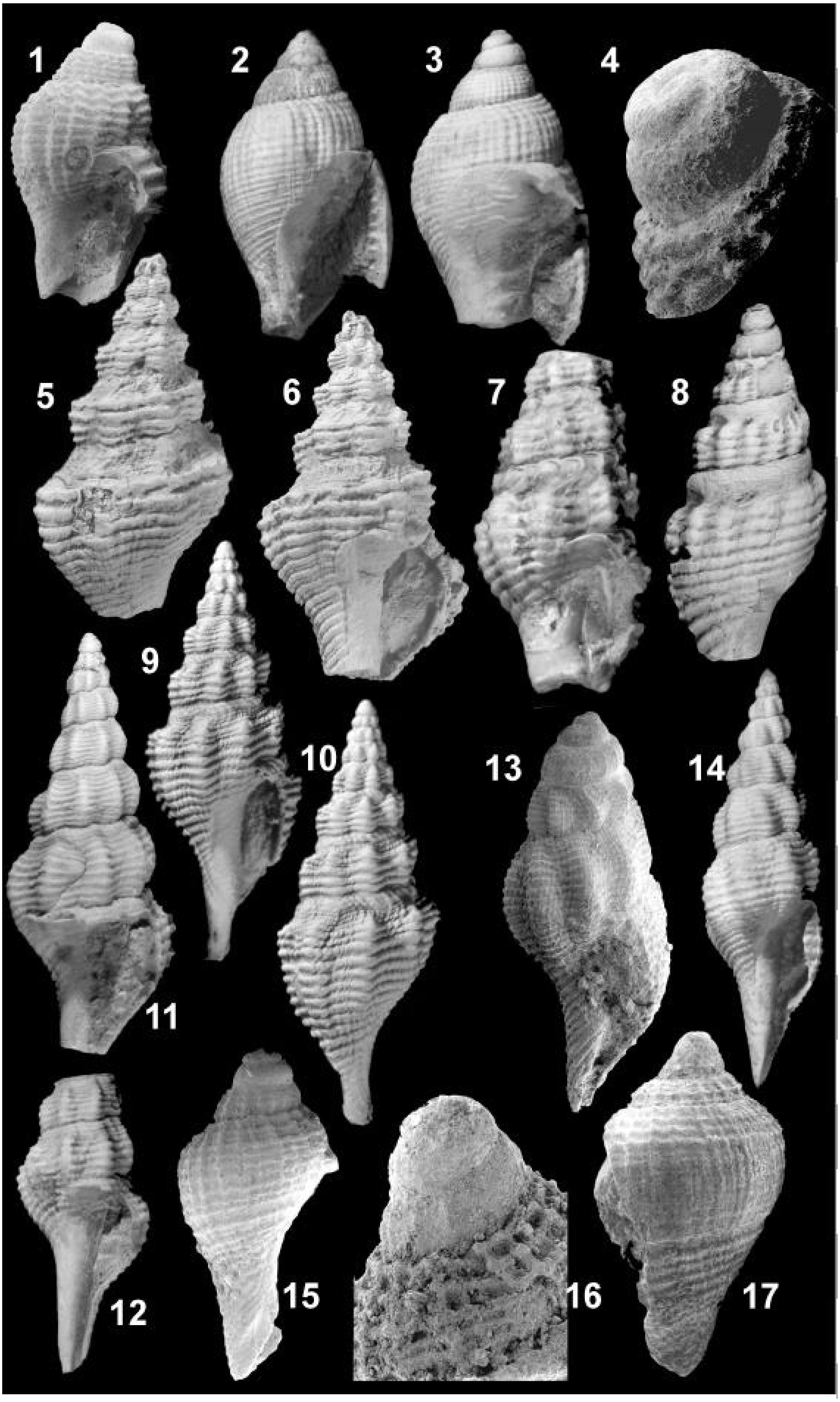
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PLATE 31

Athlitidae, Volutidae, Volutodermidae and Pyrifusidae from Temalac

Figs. 1-2. *Liopeplum cretaceum* (CONRAD, 1858); height 27 mm.

Figs. 3-6. *Liopeplum costatum* n. sp.; **3-4** – holotype; height 46 mm; **5-6 –** juvenile shell showing the spiral sculpture on the early whorls.

Figs. 7-9. *Lyria*? sp.; **7-8** – adult shell; height 15 mm; **9** – specimen with preserved columella; height 7 mm.

Figs. 10-12. *Volutoderma*? sp.; **10-11** – adult shell; height 34 mm; **12** – juvenile shell with parts of the smooth protoconch preserved.

Fig. 13. *Drilluta* cf. *communis* WADE, 1916; height 16 mm.

Figs. 14-15. *Paleopsephaea* cf. *tenulirata* SOHL, 1964; height 30 mm.

Figs. 16-17. *Bellifusus curvicostatus* (WADE, 1926); height 19.5 mm.

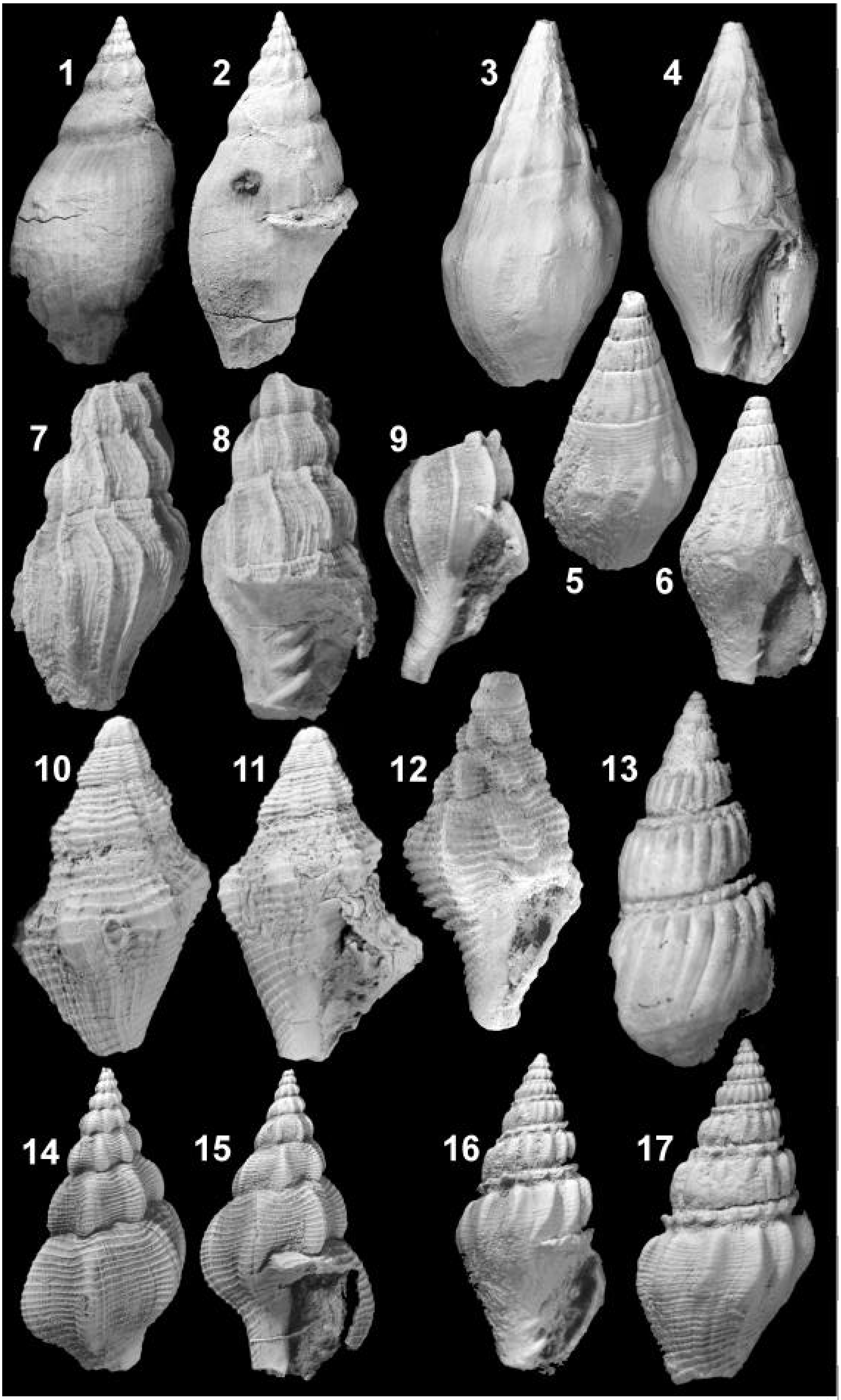
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PLATE 32

Pyrifusidae from Temalac

Figs. 1-4. *Drilluta gloriae* PERRILLIAT, VEGA and CORONA, 2000; **1-2** – two views on a well-preserved specimen with three columellar folds; height 16 mm; **3** – cross-section of a specimen showing the development of a fourth posterior fold within half a volution (compare left and right side of the columella); **4** – large specimen with four columellar folds; height 22 mm.

Figs. 5-6. *Mesorhytis eleganza*n. sp.; **5** – juvenile specimen showing the protoconch which measures 0.6 mm in diameter; **6** – holotype; height 18 mm.

Fig. 7. *Ripleyella truncata* n. sp.; holotype; height 27 mm.

Figs. 8-9. *Ripleyella elevata* (WADE 1916); height 14 mm.

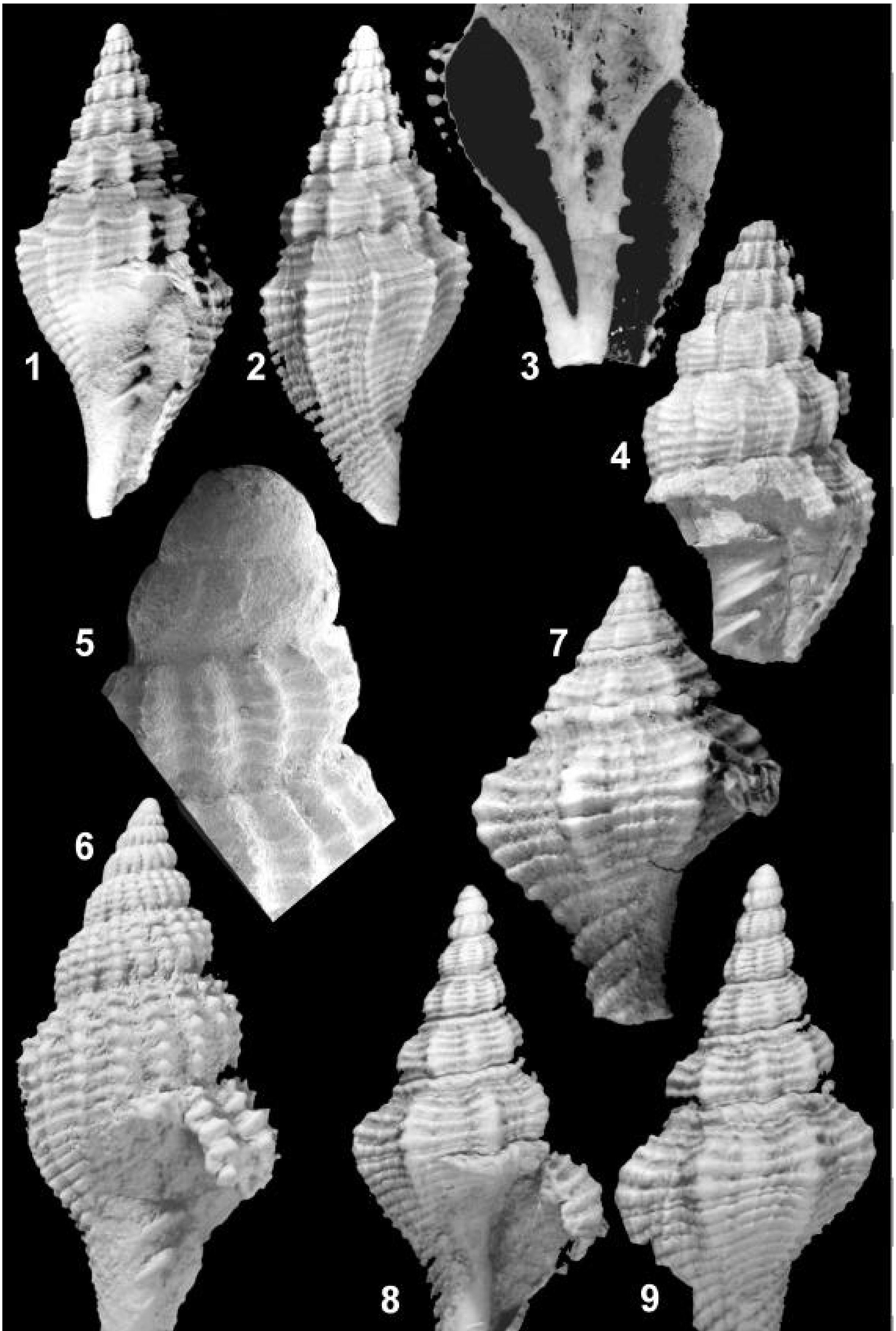
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PLATE 33

Mathildidae, Amphitomariidae and Ebalidae from Torallola

Fig. 1. *Mathilda campania* n. sp.; holotype; height 2.0 mm.

Fig. 2. *Mathilda* sp.; height 10 mm.

Fig. 3. *Gymnothilda torallolensis* n. sp.; holotype; height 1.2 mm.

Fig. 4. *Tirolthilda hispanica* n. sp.; holotype; height 1.2 mm.

Figs. 5-6. *Ponsia catalanica* n. gen. n. sp.; holotype; **5** – apertural view; **6** – view on the protoconch.

Figs. 7-8. *Lemniscolittorina elongata* n. sp.; holotype; height 22 mm.

Figs. 9-12. *Amphitomaria dockeryana* n. sp.; holotype; diameter 6 mm. **9** – apertural view; **10** – apical side; **11** – view on the imbedded, sinistrally coiled larval shell which has a diameter of about 0.36 mm; **12** – umbilical side.

Figs. 13-14. *Neamphitomaria torallolina* n. sp.; holotype; diameter 1.2 mm; **13** – view on the bulbous embryonic shell which measures about 0.2 mm across; **14** – frontal view.

Figs. 15-17. *Ebala gruendeli* n. sp.; holotype; height about 1 mm; **15** – close-up on the protoconch; **16-17** – two views on the entire shell.

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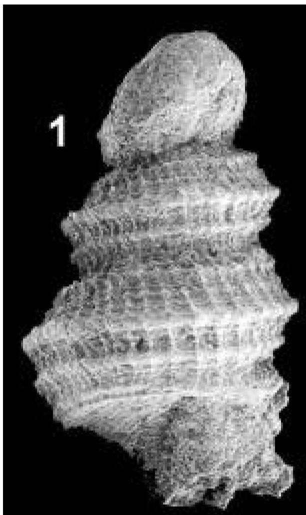

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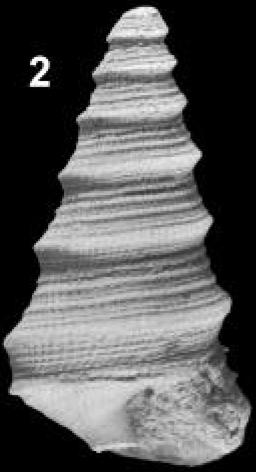

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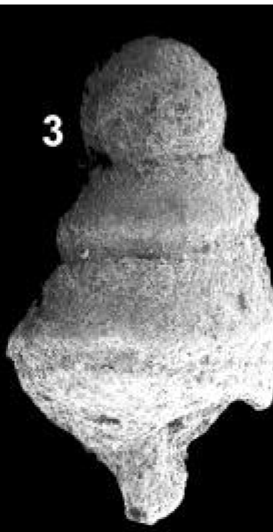

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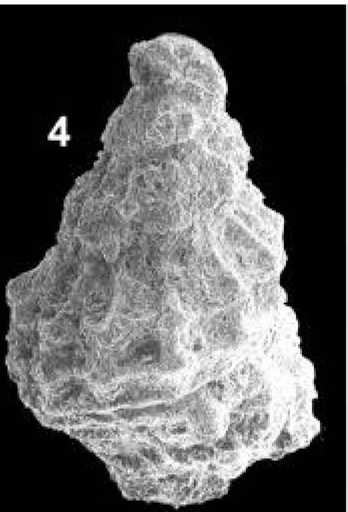

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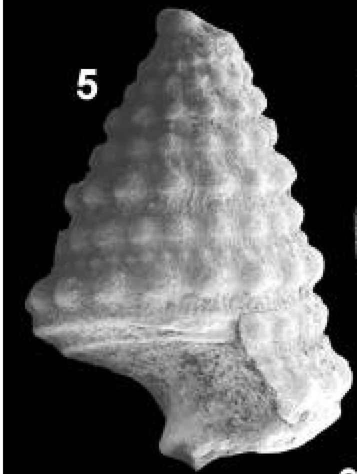

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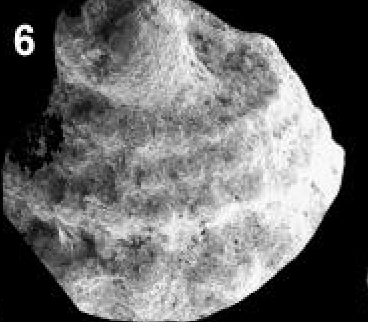

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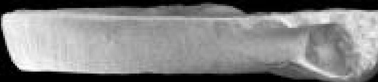

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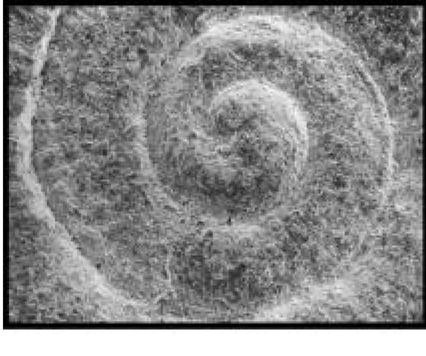

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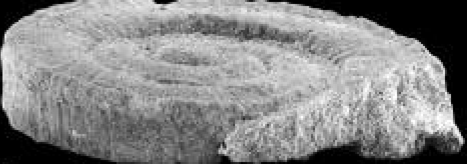

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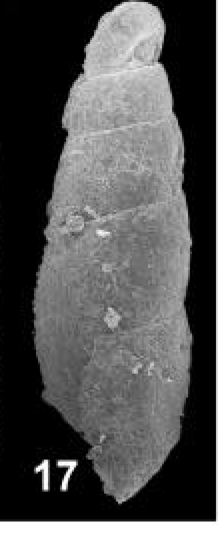


PLATE 34

Pyramidellidae, *Haszprunariella* Acteonellidae and Actaeonidae from Torallola

Figs. 1-2. *Syrnola*? *cretacea* (Holzapfel, 1888); **1** – slightly deformed specimen; height 1.8 mm; **2** – smooth specimen; height 1.7 mm.

Fig. 3. *Herewardia*? sp.; height 0.5 mm.

Figs. 4-6. *Haszprunariella laevis* n. gen. n. sp.; **4** – the sinistrally coiled holotype; height 1.9 mm; **5** – the dextrally coiled paratype; height 0.5 mm; **6** – the dextrally coiled protoconch of the holotype.

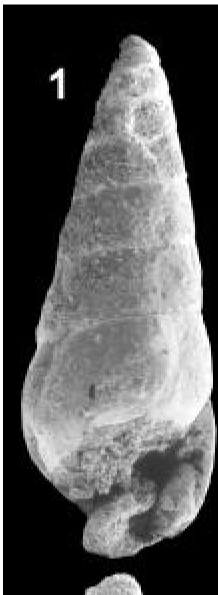
Figs. 7-9. *Haszprunariella spiralis* n. gen. n. sp.; **7** – the sinistrally coiled holotype; height 1.1 mm; **8** – the dextrally coiled paratype; height 0.9 mm; **9** – apical view on the paratype.

Figs. 10-11. *Acteonella agricolai* VIDAL, 1921; **10** – view on the spire showing the change from trochispiral to convolute coiling; height of the visible aperture 0.7 mm; **11** – apertural view on the entire specimen; height 2.4 mm.

Figs. 12-13. *Trochactaeon gigantea* (SOWERBY, 1832); **12** – specimen with a low spire; height 28 mm; **13** – specimen with a high spire; height 23 mm.

Figs. 14-15. *Tornatellaea* sp. 1; height 9 mm.

Figs. 15-16. *Tornatellaea* sp. 2; height 9 mm.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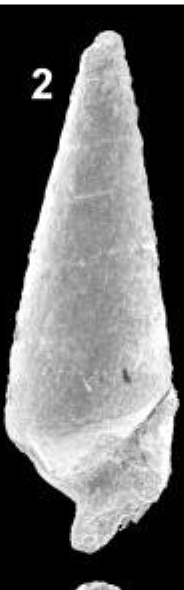
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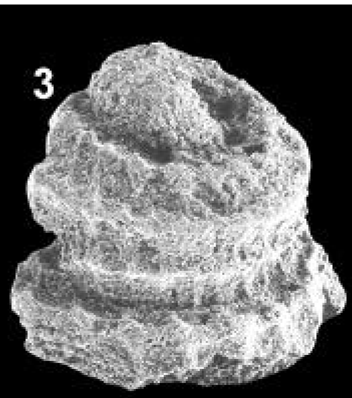
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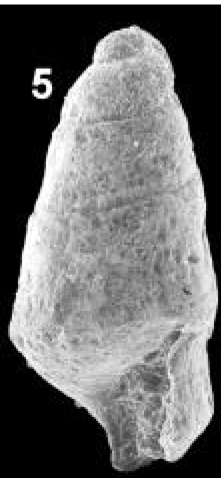
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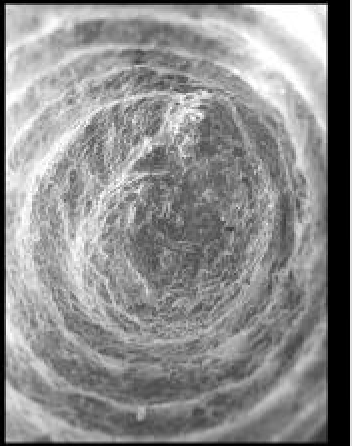
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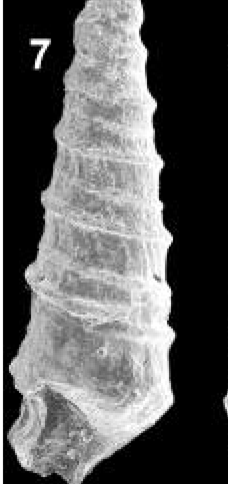
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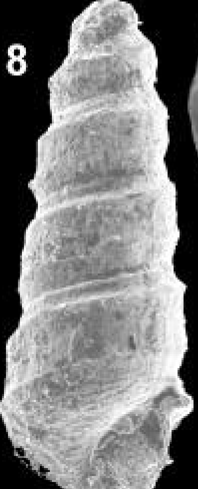
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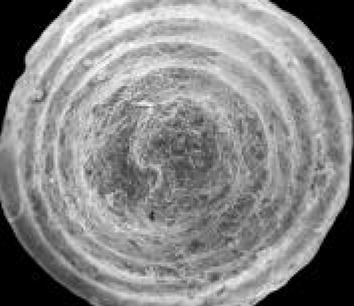
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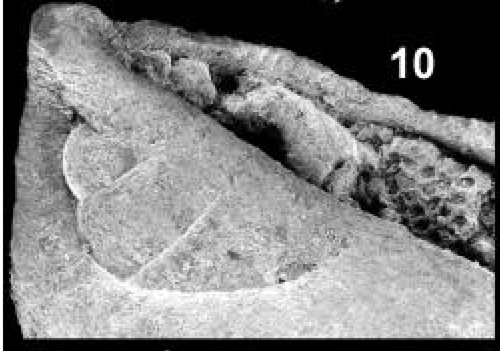
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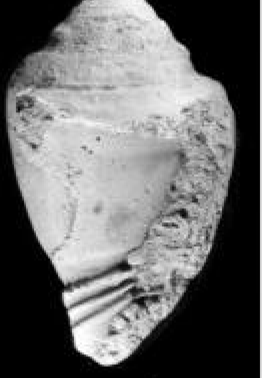
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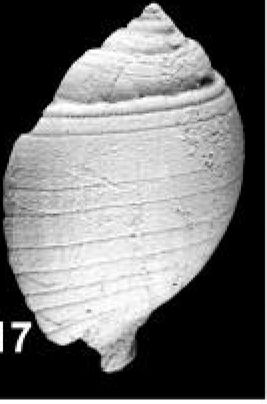
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PLATE 35

Ringiculidae, Bullomorpha, Ellobiidae and Sophonariidae from Torallola

Figs. 1-2. *Ringicula abundanta* n. sp.; holotype; **1 -** apertural view; height 2.5 mm; **2** – protoconch; width of the detail 0.27 mm.

Figs. 3-4. *Ringicula multidentata* n. sp.; holotype; **3** – apertural view; height 5 mm; **4 –** protoconch; width of the detail 0.4 mm.

Figs. 5-7. *Ringicula* cf. *larteti* (CHAVAN, 1947); height 8.5 mm.

Figs. 8-9. *Avellana* (*Eriptychia*) *decurata* (SOWERBY, 1832); height 6.5 mm.

Figs. 10-11. *Cylindrotruncatum caldera* n. sp.; holotype; height 6 mm, width 2.5 mm; **10** – apertural view; **11** – view on the apical side.

Figs. 12-13. *Goniocylichna laeviata* n. sp.; holotype; height 3 mm, width 1.4 mm; **12** – apertural view; **13** – view on the apical side.

Fig. 14. "*Cylichna*" *acteonelliformis* n. sp.; holotype; height 3.3 mm.

Fig. 15. "*Cylichna*" sp.; height 7 mm.

Fig. 16. *Laemodonta cretacea* n. sp.; holotype; height 13 mm.

Figs. 17-18. *Siphonaria revillaria* n. sp.; **17** – paratype showing the protoconch; width 5 mm; **18** – holotype with the two strong radial ribs on the right side indicating the postion of the lung; width 8 mm.

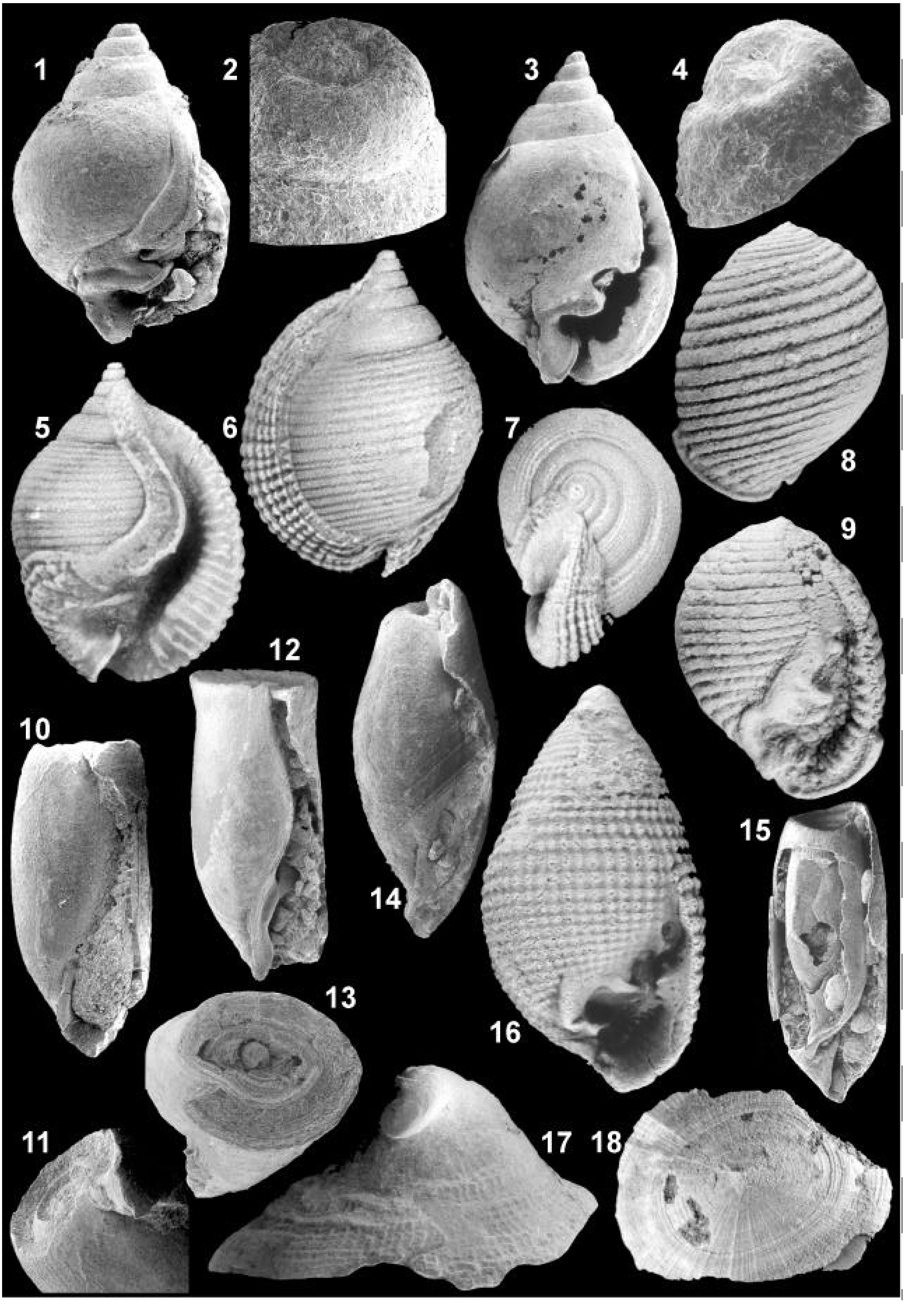
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PLATE 36

Mathildidae and Architectonicidae from Temalac

Figs. 1-2. *Mathilda mexicana* n. sp.; **1** – holotype with preserved protoconch; height 0.8; **2** – paratype; height 8 mm.

Fig. 3. *Mathilda gardnerae* n. sp.; holotype; height 9.5 mm.

Fig. 4. *Carinathilda diminuta* (PERRILLIAT, VEGA & CORONA, 2000); height 8 mm.

Figs. 5-6. *Heliacus alencasterae* n. sp.; holotype; height 3 mm.

Fig. 7. *Granosolarium* sp.; diameter 3 mm.

Figs. 8-9. *Pseudomalaxis pateriformis* STEPHENSON, 1955; diameter 1.5 mm.

Figs. 10-11. *Herewardia*? sp.; height 0.45 mm.

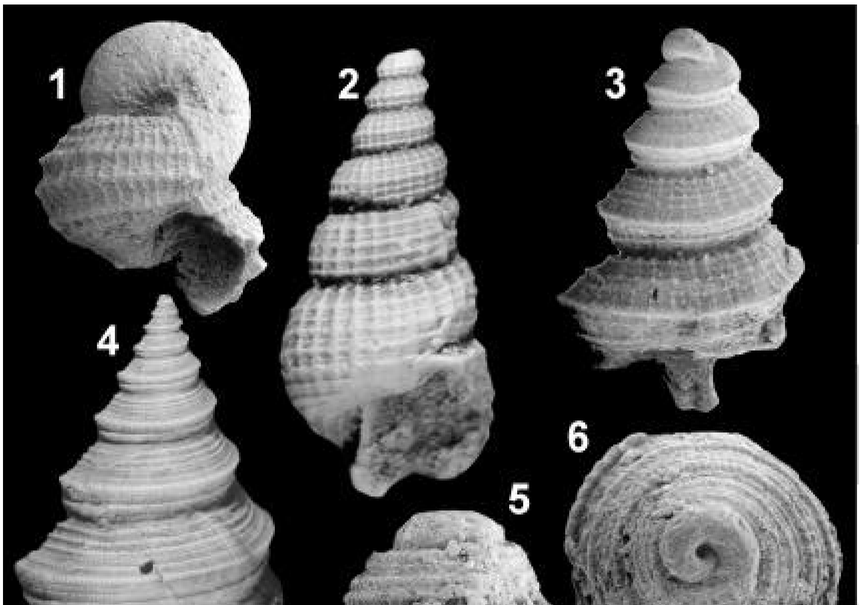
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PLATE 37

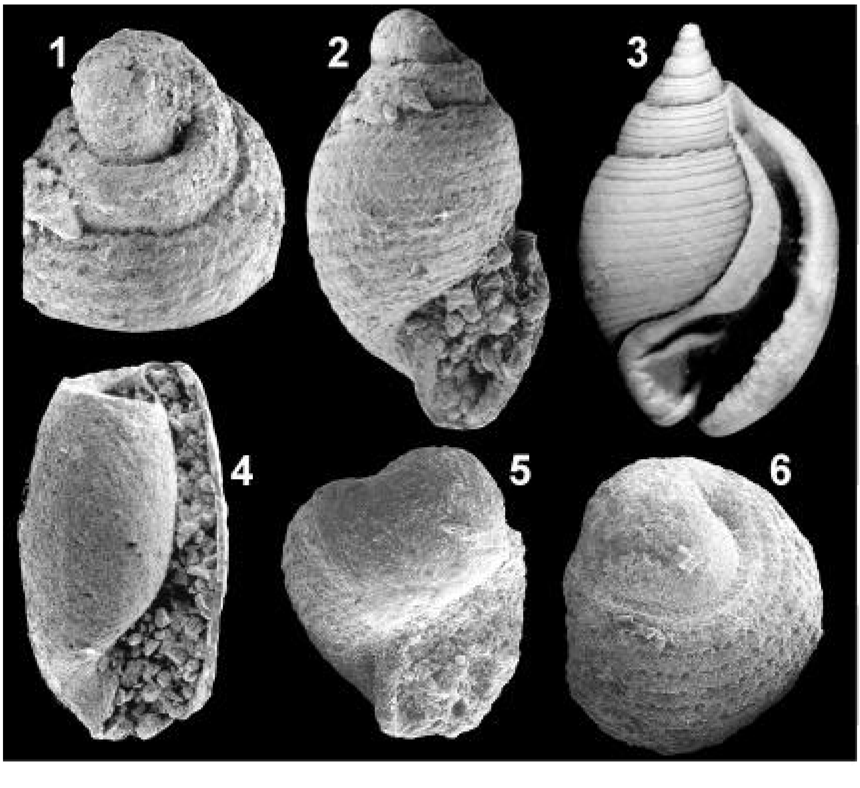
Actaeonidae, Ringiculidae and Bullomorpha from Temalac

Figs. 1-2. *Actaeon cicatricosus* SOHL, 1964; height 7 mm.

Fig. 3. *Ringicula corona* n. sp.; holotype; height 8 mm.

Fig. 4. *Cylichna recta* GABB, 1860; height 1.8 mm

Figs. 5-6. *Actaeon* sp.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