

Trochidae (Archaeogastropoda) from the Campanian of Torallola in northern Spain

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ABSTRACT:

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30 species of the archaeogastropod family Trochidae are described from the Campanian of the southern Pyrenees, 15 of them are new. The new genus *Amphigibbula* is introduced and the genus *Chilodontoidea* is renamed as *Hudledonta*. Apparently several trochid lineages with living species can be traced back into the Late Cretaceous. This regards the Eucyclinae, Margaritinae, and Solariellinae, and the Tegulinae with some reservations. Among the groups examined here, only the members of the Trochinae appear to be of rather different character than their modern representatives. The fossil record of the Umboniinae can go far beyond that of the Late Cretaceous and connect even to Palaeozoic genera. The 15 new species are: *Eucyclomphalus reminiscens*, *Calliotropis torallolensis*, *Calliotropis seguris*, *Ilerdus pyrenaeus*, *Eucycloscala cretacea*, *Hudledonta nicolae*, *Danilia kosslerae*, *Margarites kasei*, *Margarites nielsenii*, *Margarites kowalkei*, *Tectus quinteroi*, *Thoristella marshalli*, *Suavotrochus ponsi*, *Ethalia vinxae*, and *Protorotella herberti*.

Kew words: Cretaceous, Campanian, Trochidae, Northern Spain.

INTRODUCTION

The Late Cretaceous was a time when numerous modern gastropod groups made their first appearance and subsequently radiated (SOHL 1987). In contrast, archaeogastropods of this period are rarely described and reports on them are scattered throughout the literature. This scarcity may not reflect their actual abundance but may rather be an artefact resulting from their habitat-preferences of rocky shores. This opinion is based on the antiquity of archaeogastropods which have their base in the Ordovician and have radiated since. But rocky shores, where they have been and still are most commonly living, are usually areas of erosion rather than sedimentation, so the potential of fossilisation of their inhabitants is poor. When such shores are preserved in the fossil record, as it

is not infrequently the case in the carbonate environment, rock diagenesis usually has resulted in a hard limestone, from which fossils are difficult to extract.

The sediments of the Puimanyons Olisthostrom near Torallola in northern Spain are the result of a series of events when entire shorelines became unstable, broke off, and were slumped down into the basin (ROSELL & al. 1972). During these events everything composing the beach including the organisms living there became buried surrounded by sediments of the slope. The occurrence of rudists as well as numerous species of corals (BARON-SZABO 1998) indicates that the paleoenvironment was located within the tropical Tethys Realm.

The occurrence of Cretaceous gastropods near Sensui and Torallola (Text-fig. 1) has been known for 80

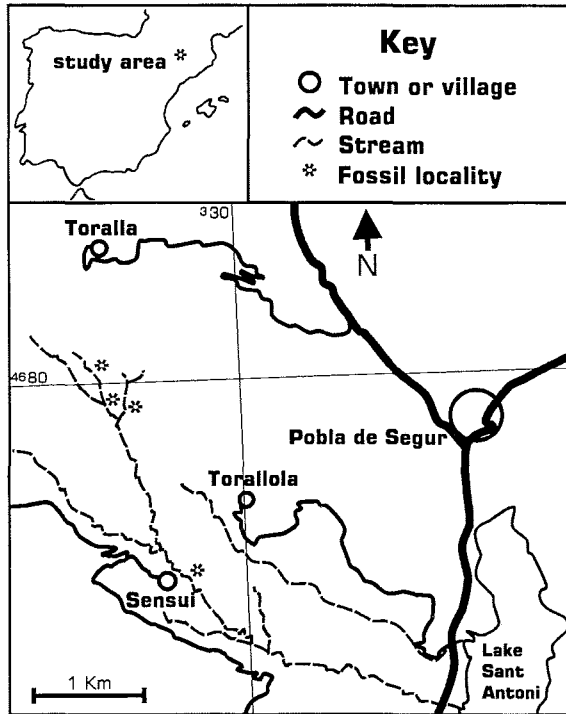


Fig. 1. The fossil localities around Torallola in the Tremp Basin of the Spanish Pyrenees

years when VIDAL (1921) first reported fossils from this locality. It has since been revisited by several workers and many new species have been described (BATALLER 1949, CALZADA 1989, QUINTERO & REVILLA 1966). Later, its stratigraphical age was determined by ROSELL & *al.* (1972) as Campanian. We have been collecting at this locality on several field trips since 1989. Sediment samples were also taken to obtain the small, early ontogenetic shells that have been proven an important character to classify fossil and recent gastropods (BANDEL 1982).

A study on shell structure of some species has been carried out by HÄNSEL (1992) in an unpublished master thesis at the University of Hamburg. She used peels of polished and etched shells to determine the shell structure. Thin sections through shells were coloured with solutions of Alizarin S- and Potassium Hexacyanoferrat III to distinguish Aragonite, Calcite and Fe-Calcite. The archaeogastropod shells examined usually consisted of three layers: An inner layer with no or lamellar structure of recrystallised Fe-Calcite which is usually thick in the early whorls and becomes thinner or absent on the last. It is followed by a nacreous layer still in the original aragonitic state (some exceptions occurred), this layer becomes gradually thicker from early to later whorls. The third is a thin, homogenous outer layer of recrystallised Fe-Calcite. Where the shell structure is known it is noted in the description of each species.

Among the Gastropoda of Torallola, more than 50 species of Archaeogastropoda have been discovered so far, providing us with the opportunity to study their diversity at a time that has been proven to be crucial for gastropod evolution. This report deals with members of the family Trochidae RAFINESQUE, 1815, comprising 30 species.

The comprehensive recent evaluation of the taxonomy of trochoidean gastropods provided by HICKMAN & MCLEAN (1990) was based mainly on anatomical characters. Consequently, their attempts to trace certain lineages into the fossil record were not complete, sometimes not very trustworthy, and they did not go very far back in time. Still their account on the classification of the trochoidean gastropods living now is so valuable that we tried to use it for the classification of the Late Cretaceous species from Torallola as far as possible. HICKMAN & MCLEAN (1990) came to the conclusion that Trochoidea can only be traced to the Triassic even though they may have an older origin, similar as was assumed by WENZ (1938) and KNIGHT & *al.* (1960). It has been difficult to characterize the shell of a gastropod in such a way, that it can securely be placed with the Archaeogastropoda. This has been improved as it was shown that archaeogastropods produce their early ontogenetic shell in such a way that they can be distinguished from all other gastropod subclasses (BANDEL 1982). In addition, there seem to have been no gastropods outside of the Archaeogastropoda that constructed their shell with nacreous layers (BANDEL 1979, 1990). BANDEL (1993a) suggested relations between several Palaeo-Meso- and Cenozoic taxa based on the well preserved Triassic gastropod fauna of St. Cassian in the Italian Alps. But he also pointed out that connecting recent species with fossils beyond the Tertiary is difficult due to the scarcity of the fossil record.

All specimens are deposited in the type collection of the Geologisch-Paläontologisches Institut und Museum, University of Hamburg, labelled GPI 3908-3946.

SYSTEMATIC PART

Class Gastropoda CUVIER, 1797
 Subclass Archaeogastropoda THIELE, 1925
 Superfamily Trochoidea RAFINESQUE, 1815

REMARKS: The Trochoidea have been evaluated extensively by HICKMAN & MCLEAN (1990) and according to their diagnosis they can be characterized as having a shell without slit or foramen. The shape of the shell is conspiral 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 characterizing 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 recognized 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 Trochidae RAFINESQUE, 1815

Subfamily Tegulinae KURODA, HABE & OYAMA, 1971

REMARKS: Tegulinae represent one of the 12 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)* OLSSON & 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 pellisserperts* (WOOD, 1828) living in the shallow sea of the Central American Pacific.

DESCRIPTION: The turbinat 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)

(Pl. 1, Fig. 1)

1966. *Trochus simplex* sp. n.; I. QUINTERO & J. REVILLA, p. 49, Pl. 8, Fig. 3.

1989. *Clanculus simplex* (QUINTERO & REVILLA); S. CALZADA, p. 31, Pl. 2, Figs 1a, b.

MATERIAL: Seven specimens (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 (1939, 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 viridunensis* BUVIGNIER (in: LORIOU & PELLAT 1874) from the Upper Jurassic of Northern France, but that species seems to lack a columellar denticle.

Subfamily Eucyclinae KOKEN, 1897

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

REMARKS: 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 (see BANDEL 1993a, p. 61). On the other hand, the Calliotropini are defined as thin shelled, whereas the included *Cidarina* DALL, 1909 and *Calliophthalus* 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 we only recognize the Eucyclini and Chilodontini with *Calliotropis* and *Cidarina* included in the latter tribe.

Tribe Eucyclini KOKEN, 1897

REMARKS: Recent Eucyclini occur world wide mainly in depths 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, fig. 369).

REMARKS: The genus *Eucyclomphalus* was treated by WENZ (1938) as a member of the Cirridae 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 reminiscencius sp. n. (Pl. 1, Fig. 3)

1992. *Trochus carinatus*? QUINTERO & REVILLA; HÄNSEL, p. 74, Pl. 4, Fig. 17.

HOLOTYPE: The specimen illustrated in Pl. 1, Fig. 3 (GPI 3946).

MATERIAL: Two specimens.

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 8 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 specimens (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 otto* (PHILIPPI, 1844) living on the shelf of the eastern Atlantic Ocean near New England.

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 sp. n. (Pl. 1, Fig. 7)

HOLOTYPE: The specimen illustrated in Pl. 1, Fig. 7 (GPI 3909).

MATERIAL: 14 specimens.

DIAGNOSIS: The higher than wide *Calliotropis* has three, in the last whorl four rows of pointed, delicate tubercles. 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 (1848) from the Vaals Greensands is very similar in shape but has stronger tubercles.

Calliotropis securis sp. n.
(Pl. 1, Figs 4, 5)

HOLOTYPE: The specimen illustrated in Pl. 1, Figs 4, 5 (GPI 3911).

DERIVATION OF NAME: Named after the town of Pobra de Segur near the locality of Torallola.

MATERIAL: One specimen.

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. The margin of umbilicus is denticulate. The shell is 10 mm high, 9 mm wide and has an apical angle of about 70°.

REMARKS: *Calliotropis torallolensis* has small spines, which are unknown from *Calliotropis securis*.

Calliotropis sp.
(Pl. 1, Fig. 2)

MATERIAL: Three specimens (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 tubercles. The basal margin is rounded, the base flat and umbilicate and sculptured with three weak tuberculate spiral cords. The shell is 8 mm high, 8 mm wide and has an apical angle of about 60°.

REMARKS: The three equally sized cords distinguish this species from *Calliotropis securis* sp. n. 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)
(Pl. 1, Figs 6, 10, 13)

1949. *Trochus Melgari* sp. n.; J.R. BATALLER, p. 20.

1989. *Ilerdus melgari* (BATALLER); S. CALZADA, p. 27, Pl. 2, Figs 7a, b.

1992. *Trochus maestrichtiensis* VIDAL; K.N. HÄNSEL, p. 61, Pl. 2, Fig. 9.

MATERIAL: About 90 specimens and fragments (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 nodose 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 8 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 proto-

conch of this species to consist of two smooth whorls. This is superficially the case on worn adult shells. However, as shown in Pl. 1, 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 number of spirals increases on latter whorls up to number eight.

Ilerdus pyrenaeus sp. n.
(Pl. 1, Figs 8, 9, 11, 12)

HOLOTYPE: The specimen illustrated in Pl. 1, Figs 8, 9 (GPI 3914).

PARATYPE: The specimen illustrated in Pl. 1, Figs 11, 12 (GPI 3915).

MATERIAL: Nine specimens.

DIAGNOSIS: The high spired *Ilerdus* is sculptured with beaded spiral cords which increase in number during growth from 3 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 trochi-form 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-pearl-like cords. Their number increases from 3 to 8 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 specimens 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 sp.n.
(Pl. 1, Figs 14, 15)

HOLOTYPE: The specimen illustrated in Pl. 1, Figs 14, 15 (GPI 3916).

DERIVATION OF NAME: This is a Cretaceous representative of its genus.

MATERIAL: Two specimens.

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 2.5 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.

Tribe Chilodontini WENZ, 1938

REMARKS: This group is characterised by some kind of apertural thickening or apertural denticles and the shells mostly possess a carinate ornament. Recent Chilodontini live on hard substrate in shallow tropical seas.

Genus *Hudledonta* nom. n.

TYPE SPECIES: *Chilodontoidea oolitica* HUDLESTON, 1896 from the Bajocian of Dorsetshire, UK (WENZ 1938, Fig. 649).

DESCRIPTION: The small pupoid shell has a high spire and well developed sutures. Ornament consists of spiral and axial ribs forming a reticulated 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 we introduce here the new name *Hudledonta*, honouring W.H. HUDLESTON who introduced the genus *Chilodontoidea* HUDLESTON, 1896.

According to statements of WENZ (1938) 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 sp. n.
(Pl. 2, Figs 1, 2)

HOLOTYPE: The specimen illustrated in Pl. 2, Figs 1, 2 (GPI 3917).

DERIVATION OF NAME: Named for KATHARINA NICOLA HÄNSEL who worked on the shell structure of the gastropods of Torallola.

MATERIAL: Four specimens.

DIAGNOSIS: This *Hudledonta* has concave whorlsides 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 decreases 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 relictus* White, 1887 from north-eastern Brazil.

Genus *Chilodonta* ÉTALLON, 1859

TYPE SPECIES: *Chilodonta clathrata* ÉTALLON, 1859 from the Late Jurassic of France (WENZ 1938: fig. 651).

DESCRIPTION: The rounded conical shell is higher than wide with narrow whorls separated by deep sutures and a large body whorl occupying 60% of the 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)
(Pl. 2, Figs 5-8)

1921. *Clanculus ilerdensis* sp. n.; L.M. VIDAL, p. 101, Pl. 5, Figs 5-7.

1949. *Clanculus ilerdensis* VIDAL; J.R. BATALLER, p. 26.

1966. *Trochus pseudoclanculosus* sp. n.; I. QUINTERO & J. REVILLA, p. 50, Pl. 8, Fig. 4.

1989. *Chilodonta ilerdensis* (VIDAL); S. CALZADA, p. 25, Pl. 2, Figs 4-5.

1992. *Clanculus ilerdensis* VIDAL; K.N. HÄNSEL, p. 43, Pl. 1, Fig. 1.

MATERIAL: 19 specimens (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 is small, 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 (DESHAYES 1866) 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
(Pl. 2, Figs 3, 4)

1959. *Chilodonta crespelli* sp. n.; J.R. BATALLER, p. 59.

1989. *Chilodonta crespelli* BATALLER; S. CALZADA, p. 26, Pl. 2, Figs 2a, b.

MATERIAL: Six specimens (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, which differs by the presence of wrinkles and tubercles on the callus of the inner lip, that of *Chilodonta crespelli* is smooth. *Chilodonta jamaicensis* 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 gestini* (D'ARCHIAC), as figured by WEINZETTL (1910, Pl. 2, Figs 16-19) from the Late Cretaceous of the Czech Republic is a very similar species but possesses more spiral cords. Much larger and ornamented with numerous nodose 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).

DIAGNOSIS: 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 sp. n.
(Pl. 2, Figs 9-11)

HOLOTYPE: The specimen illustrated in Pl. 2, Figs 9, 10 (GPI 3932).

DERIVATION OF NAME: Named after our colleague ANNETTE KOSSLER, Hamburg.

MATERIAL: Three specimens (figured: GPI 3921, 3932).

DIAGNOSIS: This high-conical *Danilia* has a large last whorl and is sculptured with rows of gutter-like spines. The columella bear 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 species of 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.

Subfamily Margaritinae STOLICZKA, 1868

REMARKS: 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.

Tribe Margaritini STOLICZKA, 1868

Genus *Margarites* GRAY, 1847

TYPE SPECIES: *Margarites margarita* (MONTAGU, 1815) living off the shore of England in the eastern Atlantic Ocean (WENZ 1938, 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 sp.n.
(Pl. 2, Figs 16, 17)

HOLOTYPE: The specimen illustrated in Pl. 2, Figs 16, 17 (GPI 3922).

DERIVATION OF NAME: In honour of TOMOKI KASE, Tokyo, who is and has been working on Cretaceous gastropods.

MATERIAL: Four specimens.

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 11mm high, 10 mm wide and has an apical angle of about 80°.

REMARKS: *Margarites kowalkei* sp. n. and *Margarites nielseni* sp. n. have a lower spire as is present in *Margarites kasei*. With this feature it is also distinguished from the type species.

Margarites nielseni sp. n.
(Pl. 2, Figs 12, 13)

HOLOTYPE: The specimen illustrated in Pl. 2, Figs 12, 13 (GPI 3923).

DERIVATION OF NAME: For our colleague SVEN NIELSEN who helped to collect this material.

MATERIAL: One specimen.

DIAGNOSIS: This *Margarites* is wider than high and sculptured with 5-6 weak spiral cords posteriorly and 3 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* sp. n. by the broad spiral cords of its ornament.

Margarites kowalkei sp.n.
(Pl. 2, Figs 14, 15)

HOLOTYPE: The specimen illustrated in Pl. 2, Figs 14, 15 (GPI 3924).

DERIVATION OF NAME: In honour of THORSTEN KOWALKE who works in our group and helped collecting in Torallola.

MATERIAL: One specimen.

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* sp. n. 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.

Subfamily Trochinae RAFINESQUE, 1815
Tribe Trochini RAFINESQUE, 1815

REMARKS: 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 mauritanus* (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)
(Pl. 3, Figs 1, 4)

1966. *Trochus carinatus* sp. n.; I. QUINTERO & J. REVILLA, p. 49, Pl. 8, Fig. 2.

1989. *Tectus carinatus* (QUINTERO & REVILLA); S. CALZADA, p. 31, Pl. 1, Fig. 5.

1992. *Trochus sensuyi* VIDAL; K.N. HANSEL, p. 53, Pl. 1, Fig. 5.

MATERIAL: Eleven specimens (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 specimens when they are prepared by peel technique but the shell material is recrystallized into Fe-Calcite (HANSEL 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 and figured by WEINZETTL (1910, Pl. 2, Fig. 3) from the Czech Cenomanian appears to be closely related as well.

Tectus convallii (VIDAL, 1874)
(Pl. 3, Fig. 14)

1874. *Trochus convallii* sp. n.; L.M. VIDAL, p. 31, Pl. 5, Figs 28, 28a.

1949. *Trochus convallii* VIDAL; J.R. BATALLER, p. 18.

MATERIAL: Two specimens (figured: GPI 3926).

DESCRIPTION: The small trochiform shell has whorls that are ornamented with four nodose 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)
(Pl. 3, Figs 2, 5)

1921. *Trochus sensuyi* sp. n.; L.M. VIDAL, p. 100, Pl. 6, Figs 19-20.

1949. *Trochus sensuyi* VIDAL; J.R. BATALLER, p. 24.

1989. *Tectus sensuyi* (VIDAL); S. CALZADA, p. 32, Pl. 1, Fig. 3.

MATERIAL: Five specimens (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 *Tectus novoatus* (DESHAYES, 1866, Pl. 59, Figs 5-6) from the Paris Basin, but this species has fewer ribs per whorl.

Tectus revillai (BATALLER, 1959)
(Pl. 3, Figs 3, 6)

1959. *Trochus revillai* sp. n.; J.R. BATALLER, p. 57.

1989. *Tectus revillai* (BATALLER); S. CALZADA, p. 32, Pl. 1, Fig. 5.

1992. *Trochus revillai* BATALLER; K.N. HANSEL, p. 51, Pl. 1, Fig. 4.

MATERIAL: 19 specimens (figured: GPI 3928).

DESCRIPTION: This moderate to large trochiform shell consists of at least eight volutions, is sculptured with three nodose 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)
(Pl. 3, Figs 7, 10)

1959. *Trochus almelai* sp. n.; J.R. BATALLER, p. 58.

1989. *Sensuitrochus almelai* (BATALLER); S.CALZADA, p. 30, Pl. 1, Fig. 6.

1992. sp.indet. HÄNSEL, p. 55, Pl. 1, Fig. 6.

MATERIAL: Nine specimens (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 nodose 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 specimens (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) we consider *Sensuitrochus* synonymous with *Hamusina* GEMMELLARO, 1878 (unpubl., see also BANDEL 1993b).

Tectus quinteroi sp. n.
(Pl. 3, Figs 8, 11)

HOLOTYPE: The specimen illustrated in Pl. 3, Figs 8, 11 (GPI 3930).

DERIVATION OF NAME: In honour of INDALECIO QUINTERO who described several molluscs from Torallola in 1966.

MATERIAL: Four specimens.

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 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, 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) and HICKMAN & MCLEAN (1990). The latter authors characterized the genus as „an abundant element in some Mesozoic Tethyan carbonate-platform fauna“ (HICKMAN & MCLEAN (1990: 95).

Discotectus pallarsensis (QUINTERO & REVILLA, 1966)
(Pl. 3, Fig. 13)

1966. *Trochus pallarsensis* sp. n.; I. QUINTERO & J. REVILLA, p. 49, Pl. 7, Fig 10.

1989. *Discotectus pallarsensis* (QUINTERO & REVILLA); S. CALZADA, p. 24, Pl. 2, Figs 8a, b.

1992. *Trochus pallarsensis* QUINTERO & REVILLA; K.N. HÄNSEL, p. 66, Pl. 2, Fig. 12.

MATERIAL: 22 specimens (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 specimens 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 1 mm 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 nodose 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: LORIOU 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)
(Pl. 3, Figs 9, 12, 15)

1949. *Trochus gavalai* sp. n.; J.R. BATALLER, p. 20.

1992. *Trochus gavalai* BATALLER; K.N. HÄNSEL, p. 57, Pl. 2, Fig. 7.

MATERIAL: About 100 specimens and fragments (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 nodose 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-pattern 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 Campanian/Maastrichtian of Puerto Rico shows a very similar ornamentation but has a higher spire, and the basal keel is 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, a little convex, and sculptured with fine spirals.

REMARKS: *Thoristella* is distinct from *Trochus* by larger cephalic tentacles and the lack of umbilical spiral cords (MARSHALL 1998). This author also indicated the earliest fossil record of this genus as Miocene.

Thoristella marshalli sp. n.
(Pl. 4, Figs 1-3)

HOLOTYPE: The specimen illustrated in Pl. 4, Figs 1-3 (GPI 3937).

DERIVATION OF NAME: Named in honour of BRUCE MARSHALL, who contributed to our knowledge of Recent gastropods from Australia and New Zealand.

MATERIAL: Two specimens.

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.

Tribe Gibbulini STOLICZKA, 1868
Genus *Amphigibbula* gen. n.

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

DERIVATION OF NAME: A combination of *Amphitrochus* and *Gibbula*, two similar genera.

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

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) tentatively placed *Semisolarium* in the Omalaxidae within the Cerithioidea FÉRUSAC, 1819. However, its protoconch type places the species concerned here within the Archaeogastropoda. Its early shell resembles that of *Amphitrochus*, a genus which was assigned to the Angariinae THIELE, 1921 by KNIGHT & 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)
(Pl. 4, Figs 4-7)

1915. *Semisolarium vidali* sp. n.; COSSMANN, 157, Pl. 6, Figs 26-27.
1921. *Semisolarium vidali* COSSMANN; VIDAL, 102, Pl. 1, Figs 12-16.
1949. *Semisolarium vidali* COSSMANN; BATALLER, p. 35.
1992. *Semisolarium vidali* COSSMANN; HÄNSEL, 83-86, Fig. 24.

MATERIAL: 80 specimens and some fragments (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 revolution. The adult shell is conical; the first four and half whorls are straight-sided with a nodose 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 growth-lines 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

REMARKS: 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. 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).

Genus *Solariella* WOOD, 1842

TYPE SPECIES: *Solariella maculata* WOOD, 1842 from the Pliocene of Suffolk, England (WENZ 1938, 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)
(Pl. 4, Figs 8-10)

1921. *Margarita montsecana* sp. n.; L.M. VIDAL, p. 100, Pl. 6, Figs 12-14.

1925. *Margarita montsecana* VIDAL; M. COSSMANN, p. 289

1949. *Margarita montsecana* VIDAL; J.R. BATALLER, p. 26.

1992. *Margarita montsecana* VIDAL; K.N. HÄNSEL, p. 59, Pl. 2, Fig. 8.

MATERIAL: 80 specimens and some fragments (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, turbiform and consists of eight convex volutions separated by deep sutures. The spiral cords become more nodose 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 specimens (HÄNSEL 1992).

REMARKS: Very similar 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, *Turbo zekeli* BINKHORST, and *Turbo rimosus* BINKHORST (see HOLZAPFEL 1888 and KAUNHOWEN 1897). Their early ornament is unknown but they may belong to *Calliomphalus*.

Solariella cossmanni VIDAL, 1921
(Pl. 5, Fig. 1)

1921. *Solariella cossmanni* sp. n.; L.M. VIDAL, p. 100, Pl. 6, Figs 17-18.

1949. *Solariella cossmanni* VIDAL; J.R. BATALLER, p. 27.

MATERIAL: Four specimens (figured: GPI 3940).

DESCRIPTION: The small turbiform 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 inclined with 45°. 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.

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, p. 111). These authors also recognized 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, p. 41) in the Gulf of Mexico.

Suavotrochus ponsi sp. n.
(Pl. 5, Figs 2, 3)

HOLOTYPE: The specimen illustrated in Pl. 5, Fig. 3 (GPI 3942).

PARATYPE: The specimen illustrated in Pl. 5, Fig. 2 (GPI 3943).

DERIVATION OF NAME: In honour of JOSE MARIA PONS, University of Barcelona who introduced us to the geology of the Tremp Basin and the locality of Torallola.

MATERIAL: Ten specimens.

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 nodose 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), which in *Suavotrochus ponsi* is only present on the last whorl.

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 sp. n.

(Pl. 5, Figs 4, 6, 8)

HOLOTYPE: The specimen illustrated in Pl. 5, Figs 4, 6, 8 (GPI 3944).

DERIVATION OF NAME: For EVA VINX who helped to photograph some of the species described here in a very good way.

MATERIAL: Four specimens.

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, 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, own observations).

Genus *Protorotella* MAKIYAMA, 1925

TYPE SPECIES: *Protorotella yuantaniensis* MAKIYAMA, 1925 from the Miocene of the Yuyanotani Province, Yamashiro/Japan (WENZ 1938, 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 covered with callus.

Protorotella herberti sp. n.

(Pl. 5, Figs 5, 7, 9)

1992. sp.indet.; HÄNSEL, 47, Pl. 1, Fig. 3.

HOLOTYPE: The specimen illustrated in Pl. 5, Figs 5, 7, 9 (GPI 3945).

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.

MATERIAL: Five specimens.

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 specimens (HÄNSEL 1992).

DISCUSSION

The abundance and the state of preservation of the Campanian gastropods from *Torallola* allows us to trace quite a few trochid lineages back across the K/T-boundary and connect them with more ancient species from Jurassic and Triassic times.

According to WENZ (1939) 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. From the discovery of *Tegula? simplex* presented here, a Cretaceous origin for *Tegula* is suggested with some reservations. BANDEL (1993a) indicated possible relations even to Jurassic genera such as *Tylotrochus* KOKEN, 1896.

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 our data (see systematic part). Therefore, we do not recognize the Calliotropini, but include them in the Eucyclini. We propose 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) *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.

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 the Trochinae, as also indicated by the constricted aperture.

The Chilodontini have been treated as an exclusively Mesozoic family by WENZ (1938), but MCLEAN (1984) 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.

The Late 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 margaritidins (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) also indicated a Late Cretaceous origin of this group with *Atira* STEWARD, 1927.

The Trochinae are abundant in the fauna of *Torallola* with eight species assigned to *Tectus*, two to *Discotectus*, and one to *Thoristella*. 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, p. 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. The Trochinae represent the only trochid subfamily to which a new genus, *Amphigibbula* had to be introduced, due to the lack of a sufficiently similar Recent genus.

Periaulax and *Solariella* are considered to represent Late Cretaceous members of the Solariellinae (HICKMAN & MCLEAN 1990), we also report a species of *Suavotrochus*. 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. Our 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).

Of the Umboniinae, two species belonging to *Ethalia* and *Protorotella* are described here. 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* sp. n. which is formed by an umbilical denticle. Although HICKMAN & MCLEAN (1990) mentioned a Late Cretaceous *Umbonium* from Oman, they only recognized 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, p. 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.

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PLATES 1 – 5

PLATE 1

- 1 – *Tegula? simplex* (QUINTERO & REVILLA, 1966); × 3
2 – *Calliotropis* sp.; × 3
3 – *Eucyclomphalus reminiscencius* sp. n.; holotype; × 2.3
4-5 – *Calliotropis securis* sp. n.; two views on the holotype; × 4
6, 10, 13 – *Ilerdus melgari* (BATALLER, 1949); 6, 10 – two views on a juvenile shell; × 25; 13 – Adult shell; × 3
7 – *Calliotropis torallolensis* sp. n.; holotype; × 3.3
8, 9, 11, 12 – *Ilerdus pyrenaicus* sp. n.; 8, 9 – two views on the holotype; × 3;
11 – paratype represented by an early shell; × 20; 12 – apical view on the same specimen as fig. 11; × 120
14, 15 – *Eucycloscala cretacea* sp. n.; holotype; 14 – side view; × 50;
15 – apical view; × 100

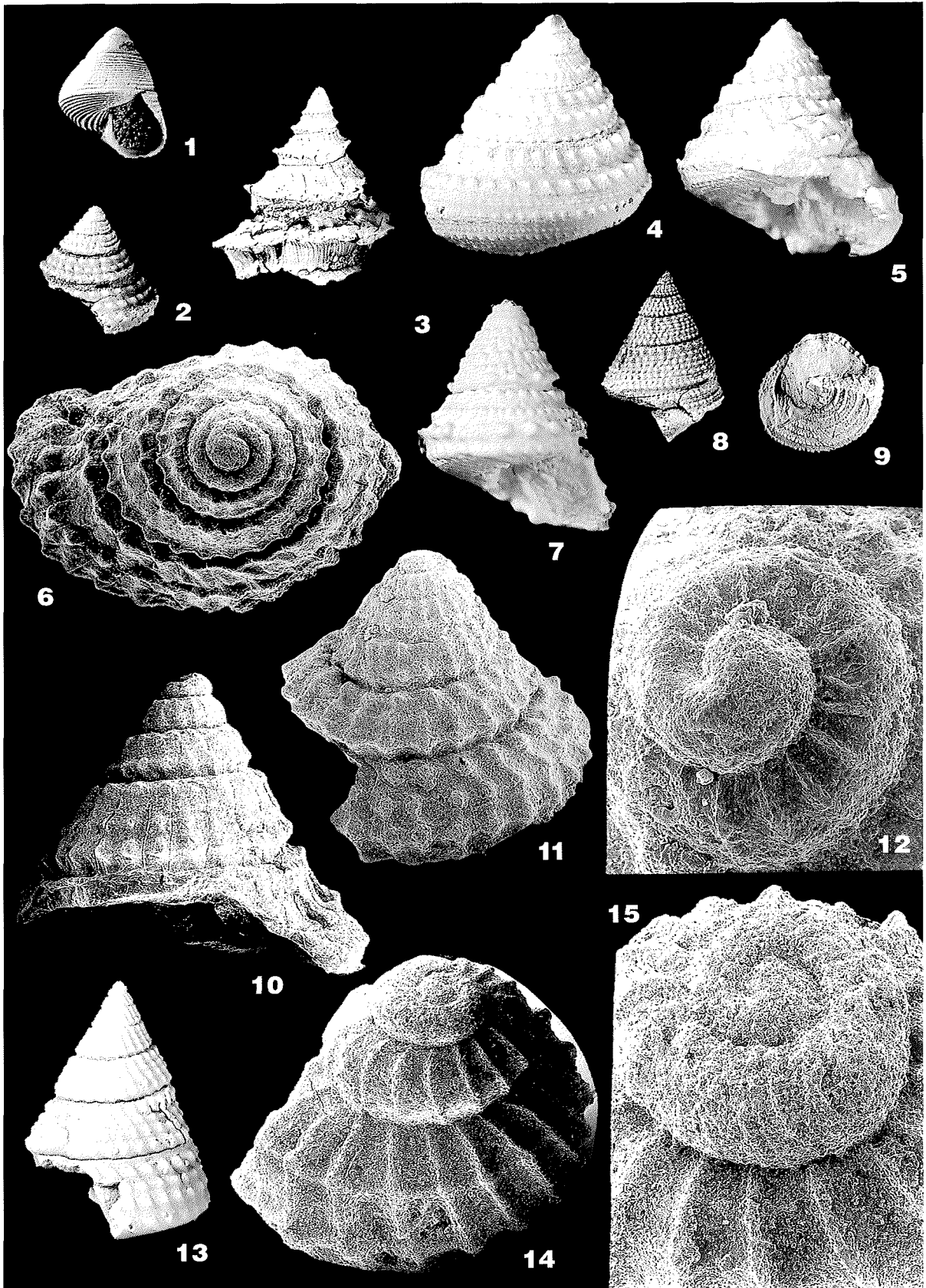


PLATE 2

- 1, 2 – *Hudledonta nicolae* sp. n.; holotype; 1 – apertural view; $\times 3$; 2 – aperture in detail; $\times 6$
- 3, 4 – *Chilodonta crespelli* BATALLER, 1959; 3 – side view; $\times 6$; 4 – aperture in detail; $\times 8$
- 5-8 – *Chilodonta ilerdensis* (VIDAL, 1921); 5 – apical view; $\times 30$; 6, 7 – two views on an adult specimen; $\times 4$; 8 – aperture of the same specimen as fig. 6, 7; $\times 5$
- 9-11 – *Danilia kosslerae* sp. n.; 9, 10 – two views on the holotype; $\times 4.5$; 11 – apical view on a juvenile specimen; $\times 40$
- 12, 13 – *Margarites nielseni* sp. n.; holotype; $\times 2.5$
- 14, 15 – *Margarites kowalkei* sp. n.; holotype; $\times 5$
- 16, 17 – *Margarites kasei* sp. n.; holotype; $\times 3.5$

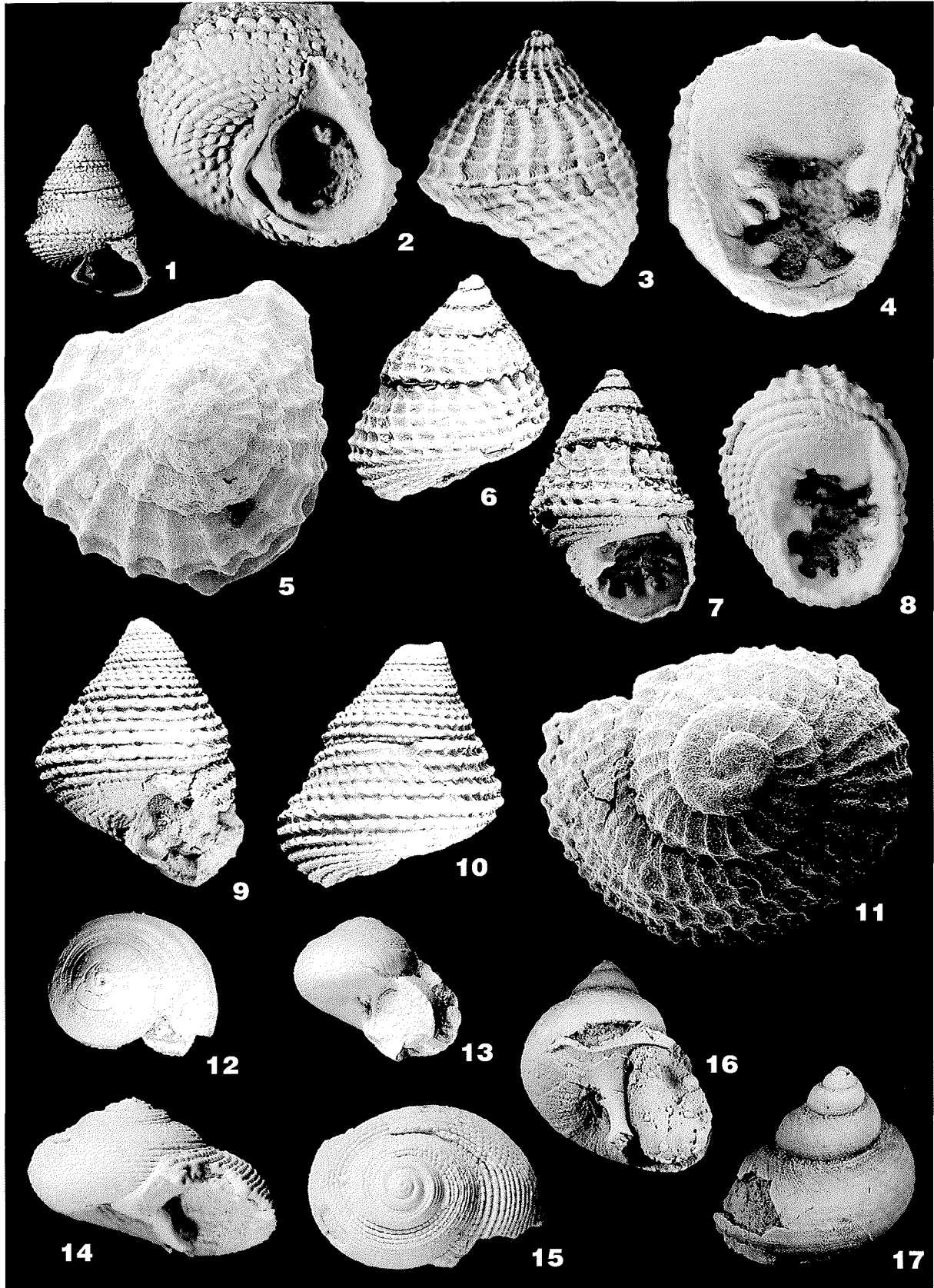


PLATE 3

- 1, 4 – *Tectus carinatus* (QUINTERO & REVILLA, 1966); two views; \times 2.5
2, 5 – *Tectus sensuyi* (VIDAL, 1921); two views; \times 3
3, 6 – *Tectus revillai* (BATALLER, 1949); two views; \times 1.3
7, 10 – *Tectus abmelai* (BATALLER, 1959); 7 – apertural view; \times 1.6;
10 – basal view; \times 1.3
8, 11 – *Tectus quinteroi* sp. n.; holotype; 8 – apertural view; \times 2.5;
11 – basal view; \times 2.7
9, 12, 15 – *Discotectus gavalai* (BATALLER, 1949); 9 – apertural view; \times 3.3;
12 – basal view; \times 2.8; 15 – specimen showing colour pattern; \times 3
13 – *Discotectus pallarsensis* QUINTERO & REVILLA, 1966; \times 8
14 – *Tectus convallii* (VIDAL, 1874); \times 7

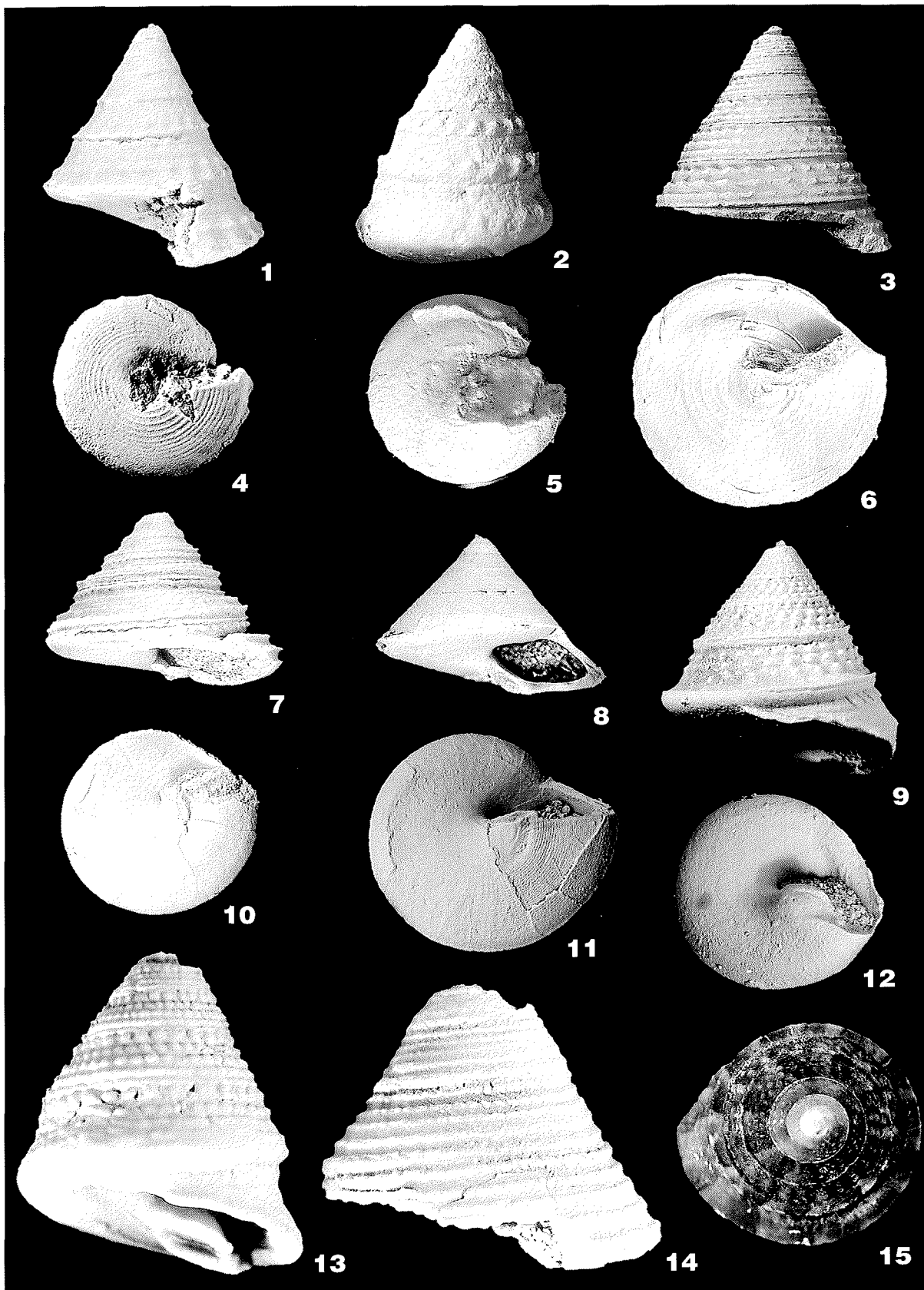


PLATE 4

- 1-3 – *Thoristella marshalli* n.sp; three views on the holotype; $\times 5$
4-7 – *Amphigibbula vidali* (COSSMANN, 1915); 4, 7 – adult specimens; $\times 2.7$; 5 – juvenile specimen; $\times 15$; 6 – apical view on the same specimen as fig. 5; $\times 115$
8-10 – *Solariella montsecana* (VIDAL, 1921); 8 – adult shell; $\times 5$; 9, 10 – juvenile shell showing the protoconch and the transition from spiral to axial sculpture; $\times 38$

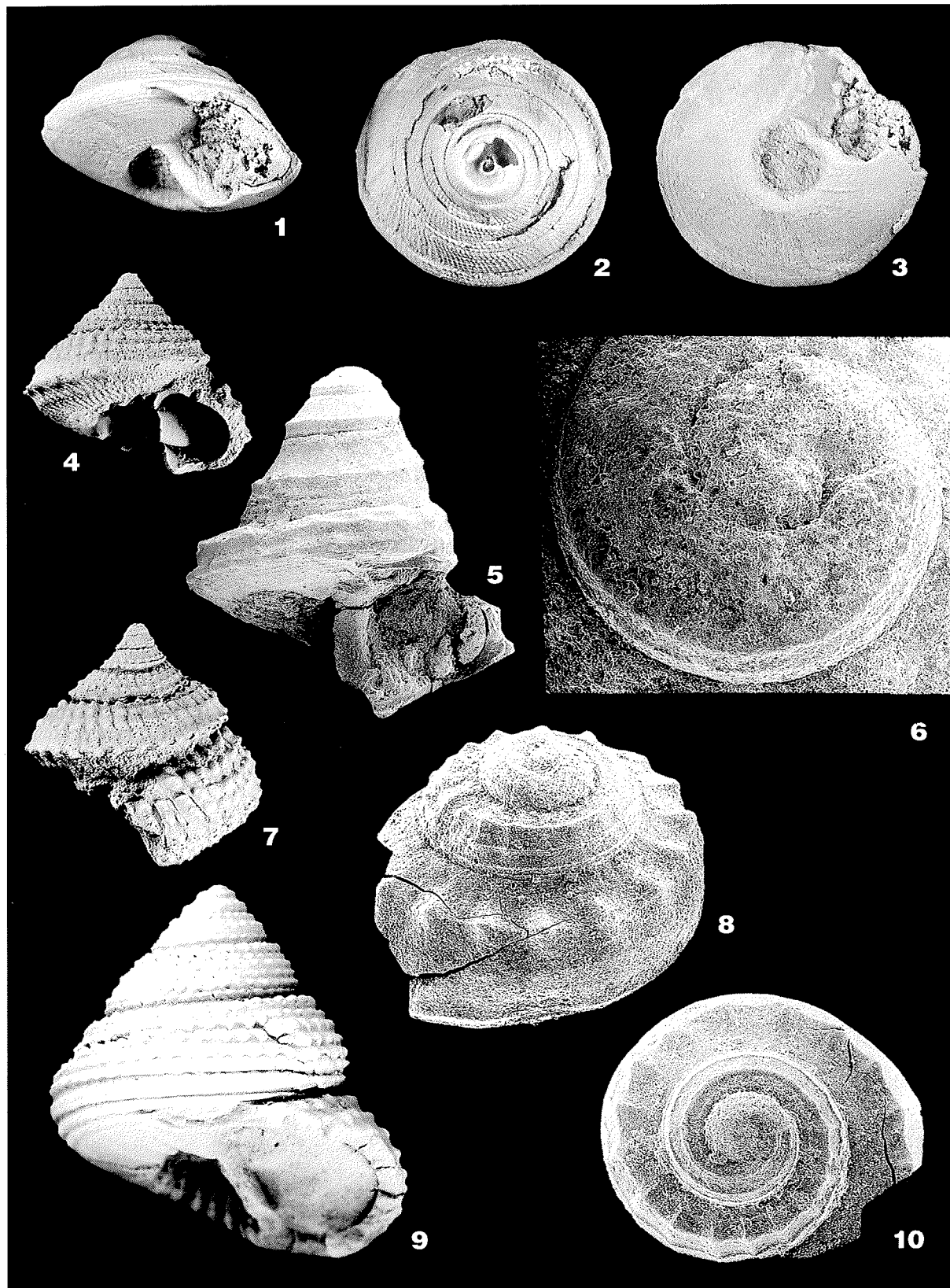


PLATE 5

- 1 – *Solariella cossmanni* VIDAL, 1921; × 5
2, 3 – *Suavotrochus ponsi* sp. n.; 2 – juvenile specimen; × 15; 3 – holotype; × 6.5
4, 6, 8 – *Ethalia vinxae* sp. n.; three views on the holotype; × 3.8
5, 7, 9 – *Protorotella herberti* sp. n.; three views on the holotype; × 2.2

