

## About *Heterostropha* (Gastropoda) of the Campanian of Torallola, Spain



### *Heterostropha* (Gastropoda) kampanského stáří z Toralloly, Španělsko

(3 plates)

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27 species of the *Heterostropha* (Gastropoda) are reported from the Campanian of Torallola in north-eastern Spain, including 17 new species and two new genera. They belong to a broad variety of families, including the Mathildidae, Amphitomariidae, Ebalidae, Pyramidellidae, Misurinellidae, Acteonellidae, Actaeonidae, Ringiculidae, Ellobiidae, Siphonariidae, and the bullomorph group of the Opisthobranchia. The new genera are *Haszprunariella* with sinistrally and dextrally coiled members within each species, and *Ponsia* for a small, trochispiral mathildid sculptured with two strong, nodular spirals and a weak one in between. The new species are: *Mathilda campania*, *Gymnothilda torallolensis*, *Tirolthilda hispanica*, *Ponsia catalania*, *Lemniscolittorina elongata*, *Ebala gruendeli*, *Amphitomaria dockeryana*, *Neamphitomaria torallolia*, *Haszprunariella laevis*, *Haszprunariella spiralis*, *Ringicula abundanta*, *Ringicula multidentata*, *Cylindrotruncatum caldera*, *Gonicyclichna laeviata*, “*Ctychna*” *acteonelliformis*, *Laemodonta cretacea* and *Siphonaria revillaria*.

**Key words:** Cretaceous, Gastropoda, *Heterostropha*, taxonomy, new species

### Introduction

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 used the term Heterobranchia. Within them, he recognized 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 *Cyllichna* Lovén, 1846, *Retusa* Brown, 1827, *Acteocina* Gray, 1847 and *Scaphander* Montfort, 1810 etc. on the other.

### Material

The gastropods described in this study are from the grey marls exposed on the slopes of the Barranc de Sensui valley between Torallola, Toralla and Sensui in the Tresp basin of the Spanish Pyrenees. The material was collected by us and colleagues from Hamburg University during the last ten years. Fossils from this locality were previously described by Vidal (1921), Bataller (1949), Quintero – Revilla (1966) and Baron-Szabo (1998). According to Rosell et al. (1972) the big slump mass which holds the fossils was deposited in a submarine depression during the Campanian. All specimens are deposited in the collection of the Geologisch-Paläontologisches Institut und Museum, Hamburg University.

### Systematic paleontology

Class Gastropoda Cuvier, 1798  
Subclass *Heterostropha* Fischer, 1885  
Order Allogastropoda Haszprunar, 1985  
Family Mathildidae Dall, 1889

**Description:** 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.

**Remarks:** The Mathildidae are an often described but little known group of marine gastropods. Wenz (1938–1944) listed no less than 15 genera and subgenera. Gründel (1976, 1997a) 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. In all more than 20 species described by him the number of spiral ribs inserting with begin of the first whorl of the teleoconch amounts to 4 to 6. Usually four of them remain visible on the spire; one of them develops into the peripheral keel within the course of the first teleoconch whorl. Of the mathildids from Torallola two fit in this scheme of *Mathilda* while one fragmental one has less ornament and can not be placed here.

### Genus *Mathilda* Semper, 1865

**Type species:** *Turbo quadricarinata* Brocchi, 1814 lives in the sublittoral rubble down to 30 m depth in the Mediterranean Sea of southern Italy (Sabelli – Spada 1978).

**Description:** The description of the family applies to the genus. Among the modern species of the genus Bieler (1995) noted that in the elongated shell the sculptural pattern succeeding the smooth protoconch abruptly consists of 4–6 strong spiral costae crossed by fine to coarse collabral radial ribs, forming a reticulated pattern. The whorl side is featured by one or two keels and the first teleoconch whorl on its exposed side carries 3–4 spiral ribs, often with interspaced additional ones. Only the anterior 1 or 2 of these are more prominent than the others and form the whorl angulation. The aperture is roundish, and the margin of the apertural lip is not continuous at the inner lip, which represents only a glazed cover surface on the prior whorl. There is usually an indistinct anterior apertural notch.

The protoconch is sinistral, forms a low helical coil, and is immersed in the apex of the teleoconch at 90° or less. The embryonic shell may lie free at the apex or may be partly covered by the first whorl of the teleoconch.

#### *Mathilda campania* sp. nov.

Pl. I, Fig. 1

**Holotype:** GPI 3969, figured at Pl. I, Fig. 1.

**Material:** One specimen.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla – Sensui in the Tresp basin in northern Spain.

**Etymology:** Named after its Campanian age.

**Diagnosis:** The smooth, sinistral protoconch is of lowly helicoidal shape, consists of 2.25 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 2.25 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 holotype is 2.0 mm high.

**Comparison:** 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?* sp. 1

Pl. I, Fig. 2

**Material:** Two specimens (figured: GPI 3970).

**Description:** The turriform shell bears a protoconch of about 0.4 mm width at an angle of about 45° to the teleoconch. The adult shell consists of six angular whorls sculptured with fine axials and spirals. The shell is about 10 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.

**Comparison:** The shell is very similar to that of *Mathilda*, *Tirolthilda*, *Promathildia*, *Teretrina*, or *Tricari-ida*, but differs by having very little or no axial ribbing.

#### *Gymnothilda torallolensis* sp. nov.

Pl. I, Fig. 3

**Holotype:** GPI 3971, figured at Pl. I, Fig. 3.

**Material:** One specimen.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla – Sensui in the Tresp basin in northern Spain.

**Etymology:** Named for its occurrence in the vicinity of Torallola.

**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 sub-suturally 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 *Tirolthilda* Bandel, 1995

Type species: *Tirolthilda seelandica* Bandel, 1995 from the Upper Triassic St. Cassian Formation.

**Description:** The high-spired, slender, turritiform 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* sp. nov.

Pl. I, Fig. 4

Holotype: GPI 3972, figured at Pl. I, Fig. 4.

Material: One specimen.

Type strata: The Campanian Puimanyons Olisthostrom.

Type locality: The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

Etymology: 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.

**Comparison:** 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.

### Genus *Ponsia* gen. nov.

Type species: *Ponsia catalanica* sp. nov.

Etymology: Named for our colleague Jose Maria Pons of the Universidad Autonoma in Barcelona, Spain.

**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 twists from sinistral to dextral coiling in its transition to the teleoconch.

**Comparison:** *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 *Pon-*

*sia*. 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, Kiel et al. 2000).

#### *Ponsia catalanica* sp. nov.

Pl. I, Figs 5–6

Holotype: GPI 3973, figured at Pl. I, Figs 5–6.

Material: One specimen.

Type strata: The Campanian Puimanyons Olisthostrom.

Type locality: The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

Etymology: Named for the Spanish province of Catalonia.

**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.

**Comparison:** *Ponsia catalanica* sp. nov. 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 one 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.

**Description:** The *Littorina*-like shell has rounded whorls and nodular spiral ornament. The protoconch is smooth and sinistrally coiled, while the teleoconch is dextral.

*Amphitomaria elongata* sp. nov.

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GPI 3974, figured at Pl. I, Figs 7–8.

Material: Two specimens.

Type strata: The Campanian Puimanyons Olisthostrom.

Type locality: The valley system between Torallola, Toralla and the Tremp basin in northern Spain.

Etymology: For its elongate shape.

**Diagnosis:** This elongate *Lemniscolittorina* has four bed spiral cords and no umbilicus.

**Description:** The relatively high spired shell has at least five volutions and is sculptured with four axially spiral cords. Its base is rounded, sculptured with spiral cords and has no umbilicus. The roundish aperture shows a smooth columella. The holotype is 12 mm high and 12 mm wide.

**Comparison:** *Lemniscolittorina elongata* is larger and more elongate than *L. berryi* from the Ripley Formation, USA. It differs from *L. yonkersi* Dockery, 1993 in 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. Bandel (2000) described from Santonian/Campanian Trichinopoly Formation of Indiana *Lemniscolittorina kuthurensis* which differs by having 6–7 broad spiral ribbons on the whorl of the spire and 16–18 on the last whorl.

Family Amphitomariidae Bandel, 1996

**Description:** 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.

**Comparison:** 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 sinistraly coiled with the larval shell grading into planispiral coiling before the onset of the teleoconch.

***Amphitomaria dockeryana* sp. nov.**

Pl. I, Figs 9–12

Holotype: GPI 3983, figured at Pl. I, Figs 9–12.

Material: One specimen.

Type strata: The Campanian Puimanyons Olisthostrom.

Type locality: The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

Etymology: The species is named for David Dockery (Jackson, Mississippi) who described a very similar species from the Campanian of the Coffee Sand, Mississippi.

**Diagnosis:** This *Amphitomaria* has a protoconch made of 1.5 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 sinistraly 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.

**Comparison:** *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.

**Description:** The teleoconch is like that of *Amphitomaria* but the protoconch consists only of a large, globular embryonic shell and lacks a sinistraly coiled larval shell (Bandel 1988).

***Neamphitomaria torallolina* sp. nov.**

Pl. I, Figs 13–14

Holotype: GPI 3984, figured at Pl. I, Figs 13–14.

Material: One specimen.

Type strata: The Campanian Puimanyons Olisthostrom.

Type locality: The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

Etymology: Named for the village of Torallola, near to the crop where it was found.

**Diagnosis:** The small discoid shell with angular whorls consists of 2.5 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 diameter and 0.2 mm high.

**Comparison:** *Neamphitomaria stantoni* (Sohl, 1960) and *N. planospira* Dockery, 1993 both differ in having smaller but sculptured protoconchs. *N. stantoni* additionally has a keel on the upper side of the whorls.

#### Family Ebalidae Warén, 1994

**Description:** 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* sp. nov.

Pl. I, Fig. 15–17

**Holotype:** GPI 3982, figured at Pl. I, Figs 15–17.

**Material:** Two specimens.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** Named for our colleague 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 1.5 lowly and sinistrally coiled whorls. The teleoconch consists of 3.5 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.

**Comparison:** *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.

#### Family Pyramidellidae Gray, 1840

**Description:** In a recent examination of living species, Wise (1996) showed that pyramidellids 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 1938–1944).

**Description:** The small, turritiform 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 (1938–1944) 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)

Pl. II, Figs 1–2

1888 *Odostomia cretacea* Holzapfel: 134, Pl. 14, Fig. 16; Pl. 21, Fig. 14.

**Material:** Four specimens (figured: GPI 3975 and 3976).

**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 figured specimens are 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.**

Pl. II, Fig. 3

Material: One specimen (figured: GPI 3977).

**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.

Order uncertain

Family Misurinellidae Bandel, 1994

**Description:** Bandel (1994) 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* gen. nov. with dextral and sinistral coiling within the same species, we extend the original family diagnosis to include also the dextrally coiled counterparts of sinistrally coiled species. **Comparison:** 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* gen. nov.**

**Type species:** *Haszprunariella laevis* sp. nov. 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.

**Etymology:** Named for Gerhard Haszprunar (München) who recognized the independence of the Allogastropoda among the Heterostropha.

**Comparison:** 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.

**Remarks:** 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 1.25 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.

However, 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 snails are found alongside in these sediments. Therefore, it is impossible to determine the habitat in which these unusual gastropods have lived in the Campanian.

***Haszprunariella laevis* sp. nov.**

Pl. II, Figs 4–6

**Holotype:** The sinistrally coiled specimen GPI 3979, figured at Pl. II, Figs 4, 6.

**Paratype:** The dextrally coiled specimen GPI 3978, figured at Pl. II, Fig. 5.

**Material:** About 10 specimens.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** 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* sp. nov.**

Pl. II, Figs 7–9

**Holotype:** The sinistrally coiled specimen GPI 3980, figured at Pl. II, Fig. 7.

**Paratype:** The dextrally coiled specimen GPI 3981, figured at Pl. II, Figs 8, 9.

**Material:** About 10 specimens.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** 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 ter-

minates in a strong varix. The teleoconch consists of up to five straight and keeled volutions. On the first 1–3 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.

**Comparison:** This species is distinct from *Haszprunariella laevis* sp. nov. by its keeled whorls.

Order Opisthobranchia Milne-Edwards, 1848  
Family Acteonellidae Zilch, 1959

**Description:** The shell is of ovo-cylindrical to spindle-like shape with a short spire or with involute 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.

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

**Remark:** The spelling of *Actaeon* and derived names is quite misleading. Among generic names subsequently derived from *Actaeon*, Adams, Aldrich, Cossmann, Dall, Gabb, Meek, Thiele, and Wenz used "ae", while d'Orbigny, Gray, Stephenson, and Vokes used "e". Wenz – Zilch (1959–1960) considered *Actaeon* Adams, 1854 as a synonym of *Acteon* Montfort, 1810. The original work of Montfort was not available to the authors, however, according to Schröder (1995) the name was written with the French "æ". The same author pointed out that this name is derived from the latinised Greek name of the grandchild of Kadmos, "Actaeon" and this being the correct spelling. Thus, *Actaeon* and Actaeonidae are used here. In d'Orbigny's (1843) original description of *Acteonella*, it is spelled with "e" only, thus, *Acteonella* and Acteonellidae are used here.

### 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

Pl. II, Figs 10–11

1921 *Acteonella agricolai* Vidal: 103, Pl. 7, Figs 14–16.  
1949 *Acteonella agricolai* Vidal – Bataller: 131.

**Material:** Ten specimens (figured: GPI 3985).

**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 involute, 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 involute. 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 percent of its height. This relation is about 2.5 : 1 in *Acteonella agricolai*. Also *Acteonella caucasica* Zekeli, 1852 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, 1843 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)

Pl. II, Figs 12–13

**Material:** About 60 species (figured: GPI 3986 and 3987).

**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 our specimens show transitions into each other, they are all assigned to the same species.

Family *Actaeonidae* d'Orbigny, 1843

**Description:** 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 *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.

**Comparison:** *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

Pl. II, Figs 14–15

**Material:** Four specimens (figured: GPI 3988).

**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.

**Comparison:** *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

Pl. II, Figs 16–17

**Material:** One specimen (figured: GPI 3989).

**Description:** The spire of this small shell makes less than 1/3 of the total shell height. The whorls are sub-structurally 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

**Description:** 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:** As for the family, with elongate shells.

*Ringicula abundanta* sp. nov.

Pl. III, Figs 1–2

**Holotype:** GPI 3990, figured at Pl. III, Figs 1–2.

**Material:** About 100 specimens.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** 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 2/3 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.

**Comparison:** 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 multidenta* sp. nov.

Pl. III, Figs 3–4

**Holotype:** GPI 3992, figured at Pl. III, Figs 3–4.

**Material:** Two specimens.

**Type strata:** The Campanian Puimanyons Olisthostrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** 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.

**Comparison:** The anterior spout of the aperture is bordered by a strong denticle on the outer side in this species, neither *Ringicula larteti* Chavan, 1947 nor *Ringicula abundanta* show such a denticle.

#### ***Ringicula larteti* Chavan, 1947**

Pl. III, Figs 5–7

1959 *Ringicula (Ringiculopsis) larteti* Chavan – Wenz – Zilch: 20, Fig. 53.

**Material:** Nine specimens (figured: GPI 3991).

**Description:** This small shell is made of seven volutions, has a large body whorl which is about 2–2.5 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.

**Comparison:** *Ringicula larteti* was used as type species of the subgenus *Ringicula (Ringiculopsis)* Chavan, 1947. Wenz – Zilch (1959–1960) described this subgenus as “a precursor of *Ringicula* which unites characters of *Ringiculina* and other genera”. Due to the broad variability within *Ringicula* we doubt the validity of this subgenus. 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*.

#### **Genus *Avellana* Orbigny, 1843**

**Type species:** *Cassis avellana* Brogniart, 1810 from the Cenomanian of France.

**Description:** As for the family, with globular shells. **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, we treat *Eriptychia* as a subgenus of *Avellana*.

#### **Subgenus *Avellana (Eriptychia)* Meek, 1876**

**Type species:** *Auricula decurata* Sowerby, 1835 from the Turonian.

#### ***Eriptychia decurata* (Sowerby, 1835)**

Pl. III, Figs 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 volutions. Sculpture consists of numerous strong incised spirals with fine axial ribblets. 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***

**Remarks:** Due to the strong convergence among Recent bullomorph gastropods, we place our species 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 is possible using shell-characters alone.

#### **Genus *Cylindrotruncatum* Sohl, 1963**

**Type species:** *Cylindrotruncatum demersum* Sohl, 1963 from the Maastrichtian Ripley Formation.

**Description:** The cylindrical shell is small and apically truncated with all spires 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).

**Comparison:** The sharply carinate upper whorl edge separates *Cylindrotruncatum* from *Cylichna* Lorén, 1846 and other similar genera.

#### ***Cylindrotruncatum caldera* sp. nov.**

Pl. III, Figs 10–11

**Holotype:** GPI 3995, figured at Pl. III, Figs 10–11.

**Material:** One specimen.

Type strata: The Campanian Puimanyons Olisthostrom.  
 Type locality: The valley system between Torallola, Toralla and Sensui in the Tresp basin in northern Spain.  
 Etymology: For the caldera-shaped apical side.

Diagnosis: 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, it widens at the base and the apical margin appears to be open. There are some faint spirals on the base. The shell is 6 mm high and 2.7 mm wide.

### Genus *Goniocylichna* Wade, 1926

Type species: *Goniocylichna 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.

Comparison: Members of *Cylindrotruncatum* Sohl, 1963 have similar shell shapes with slender, adapically truncate, cylindrical shells, but the whorls terminate adapically in a sharply carinate edge that borders the apical depression.

### *Goniocylichna laeviata* sp. nov.

Pl. III, Figs 12–13

Holotype: GPI 3994, figured at Pl. III, Figs 12–13.  
 Material: One specimen.  
 Type strata: The Campanian Puimanyons Olisthostrom.  
 Type locality: The valley system between Torallola, Toralla and Sensui in the Tresp basin in northern Spain.  
 Etymology: 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.  
 Comparison: Wade (1926: 106) considered the “abruptly truncate posterior extremity and its dual type of sculpture” as characteristic for *Goniocylichna*. Our smooth species is tentatively placed here due to its truncated spire, although it lacks any sculpture.

### *Cylichna*-like shells

#### “*Cylichna*” *acteonelliformis* sp. nov.

Pl. III, Fig. 14

Holotype: GPI 3996, figured at Pl. III, Fig. 14.  
 Material: Two specimens.  
 Type strata: The Campanian Puimanyons Olisthostrom.  
 Type locality: The valley system between Torallola, Toralla and Sensui in the Tresp basin in northern Spain.  
 Etymology: This species is spindle-shaped like *Acteonella*.

Diagnosis: This spindle-shaped shell is made of smooth and involute whorls. Its aperture is long, narrow and posteriorly elevated, anteriorly there is a canal. The shell is 3.3 mm high.

Comparison: A related species could be *Cylichna incisa* Stephenson, 1941 which is also spindle-shaped but differs in having numerous incised spiral cords.

#### “*Cylichna*” sp.

Pl. III, Fig. 15

Material: One specimen (figured: GPI 3997).

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.

Order Pulmonata Cuvier, 1817

Suborder Archaeopulmonata Morton, 1955

Family Ellobiidae H. and A. Adams in Pfeiffer, 1854

Description: 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 resorption of internal shell-structure during growth (Beesley et al. 1998: 1077–1078).

### Genus *Laemodonta* Philippi, 1846

Type species: *Laemodonta striata* Philippi, 1846 from the Island of Hawaii (Wenz – Zilch 1959–1960).

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* sp. nov.

Pl. III, Fig. 16

Holotype: GPI 3998, figured at Pl. III, Fig. 16.  
 Material: One specimen.  
 Type strata: The Campanian Puimanyons Olisthostrom.  
 Type locality: The valley system between Torallola, Toralla and Sensui in the Tresp basin in northern Spain.

Etymology: This is the first Cretaceous species of *Laemodonta* known to us.

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.

**Comparison:** The similarly sculptured Recent species *Laemodonta exarata* H. and A. Adams, 1854 was reported by Martins – Tristão da Cunha (1992) from a salt water meadow in the Sai Kong Peninsula, Hong Kong.

#### Family Siphonariidae Gray, 1840

**Description:** 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. According to Hubendick (1945) the shell is more or less bilaterally symmetrical and limpet shaped, with smooth surface or radial ribs. The apex lies posteriorly, far back or near the centre. Often the siphonal side of the shell is extended.

#### Genus *Siphonaria* Sowerby, 1823

**Type species:** *Patella laciniosa* Linné, 1758 living around the Solomon Islands.

**Description:** As for the family.

#### *Siphonaria revillaria* sp. nov.

Pl. III, Figs 17–18

**Holotype:** GPI 3999, figured at Pl. III, Fig. 18.

**Paratype:** GPI 4000, figured at Pl. III, Fig. 17.

**Material:** Two specimens.

**Type strata:** The Campanian Puimanyons Olisthstrom.

**Type locality:** The valley system between Torallola, Toralla and Sensui in the Tremp basin in northern Spain.

**Etymology:** 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.

**Comparison:** *Siphonaria wieseri* (Wade, 1926) appears to have radial sculpture only.

#### Discussion

Among the Allogastropoda, typical members of the Mathildidae can be recognized since Triassic time (Bandel 1995) and were abundant also in the Jurassic (Gründel 1997a). The mathildids described herein can well be connected to early Cretaceous and Jurassic forms, in the case of *Tirothilda* 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.

Our 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.

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 (1994, 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*, the latter of which closely resembles *Donaldina*, both share a similar “jaw-apparatus” (Warén 1994), but appear to have different mantle cavities (Bandel, pers. obs.). However, the ebalid described here is similar to its Triassic, Cretaceous as well as living relatives, identifying *Ebala* as a fairly conservative lineage.

In the fossil record, members of the Pyramidellidae are difficult to distinguish from those of the 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.

Of uncertain taxonomic position are the two species of the new misurinellid genus *Haszprunariella*. Today, sinistrally coiled adult shells with dextrally coiled protoconch are only known from the archaeopulmonate *Blauneria*. Consequently, Bandel (1994) discussed relationships of the Misurinellidae with the Pulmonata. On the other hand, the adult shells of *Haszprunariella* resemble those of living *Bacteridium* and *Eulimella*, which are undoubtedly pyramidellid Allogastropoda.

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 (1994) 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, 1994). Of these, *Zardinella* has a teleoconch similar to that of *Actaeon*, but its protoconch shows strong radial ribbing on its base (Bandel 1994,

Pl. 3, Figs 11–14). This feature is unknown from post-Triassic opisthobranchs.

Apparently, shell-morphologies like those of Recent *Actaeon*, *Ringicula* and *Cyliclha* appear more or less simultaneously in the Jurassic (Gründel 1997b). During the Early Cretaceous, the Acteonellidae with *Acteonella* and *Trochactaeon* occurred and dominated tropical carbonate platforms and lagoons until the end of the Mesozoic.

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*.

Diversity of shell-shapes among the bullomorpha increased during the Late Cretaceous (see Sohl 1964). *Goniocyliclha* with its apically flattened, and in the case of *Goniocyliclha laeviata* sp. nov. constricted whorls, resembles shells of the modern Diaphanidae.

The Archaeopulmonata are represented with two species in the fauna of Torallola, *Laemodonta cretacea* sp. nov. and *Siphonaria revillaria* sp. nov. While a Cretaceous origin of the Siphonariidae has long been supposed (Wenz – Zilch 1959–1960, Sohl 1964), the ellobiid *Laemodonta* was previously only reported from the Neogene (Wenz – Zilch 1959–1960). On the other hand, gastropods which might belong to the Ellobiidae are known since the Jurassic (Bandel 1991).

**Acknowledgements.** We would like to thank Jose Maria Pons, Barcelona, for his introduction to the locality of Torallola; Sven Nielsen and Silke Nissen, Hamburg, who helped to improve the quality of this manuscript; and Jiří Fryda, Prague, for the Czech translations.

Submitted November 15, 2000

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### Explanation of plates

#### Plate I

- 1 – *Mathilda campania* sp. nov.; holotype; height 2.0 mm
- 2 – *Mathilda* sp.; height 10 mm
- 3 – *Gymnothilda toralloensis* sp. nov.; holotype; height 1.2 mm
- 4 – *Tirolthilda hispanica* sp. nov.; holotype; height 1.2 mm
- 5–6 – *Ponsia catalania* gen. et sp. nov.; holotype: 5 – apertural view; 6 – view on the protoconch
- 7–8 – *Lemnicolittorina elongata* sp. nov.; holotype; height 22 mm
- 9–12 – *Amphitomaria dockeryana* sp. nov.; 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
- 13–14 – *Neamphitomaria torallolia* sp. nov.; holotype; diameter 1.2 mm: 13 – view on the bulbous embryonic shell which measures about 0.2 mm across; 14 – frontal view
- 15–17 – *Ebala gruendeli* sp. nov.; holotype; height about 1 mm: 15 – close-up on the protoconch; 16, 17 – two views on the entire shell.

#### Plate II

- 1–2 – *Syrnola? cretacea* (Holzapfel, 1888): 1 – slightly deformed specimen; height 1.8 mm; 2 – smooth specimen; height 1.7 mm
- 3 – *Herewardia?* sp.; height 0.5 mm
- 4–6 – *Haszprunariella laevis* gen. et sp. nov.: 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
- 7–9 – *Haszprunariella spiralis* gen. et sp. nov.: 7 – the sinistrally coiled holotype; height 1.1 mm; 8 – the dextrally coiled paratype; height 0.9 mm; 9 – apical view on the paratype

- 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
- 12–13 – *Trochactaeon gigantea* (Sowerby, 1832): 12 – specimen with a low spire; height 28 mm; 13 – specimen with a high spire; height 23 mm
- 14–15 *Tornatellaea* sp. 1; height 9 mm
- 16–17 *Tornatellaea* sp. 2; height 9 mm

#### Plate III

- 1–2 – *Ringicula abundanta* sp. nov.; holotype: 1 – apertural view; height 2.5 mm; 2 – protoconch; width of the detail 0.27 mm
- 3–4 – *Ringicula multidentata* sp. nov.; holotype: 3 – apertural view; height 5 mm; 4 – protoconch; width of the detail 0.4 mm
- 5–7 – *Ringicula* cf. *larteti* (Chavan, 1947); height 8.5 mm
- 8–9 – *Avellana (Eriptychia) decurata* (Sowerby, 1832); height 6.5 mm
- 10–11 – *Cylindrotruncatum caldera* sp. nov.; holotype; height 6 mm, width 2.5 mm: 10 – apertural view; 11 – view on the apical side
- 12–13 – *Goniocylicchna laeviata* sp. nov.; holotype; height 3 mm, width 1.4 mm: 12 – apertural view; 13 – view on the apical side
- 14 – “*Cylicchna*“ *acteonelliformis* sp. nov.; holotype; height 3.3 mm
- 15 – “*Cylicchna*“ sp.; height 7 mm
- 16 – *Laemodonta cretacea* sp. nov.; holotype; height 13 mm;
- 17–18 – *Siphonaria revillaria* sp. nov.: 17 – paratype showing the protoconch; width 5 mm; 18 – holotype with the two strong radial ribs on the right side indicating the position of the lung; width 8 mm

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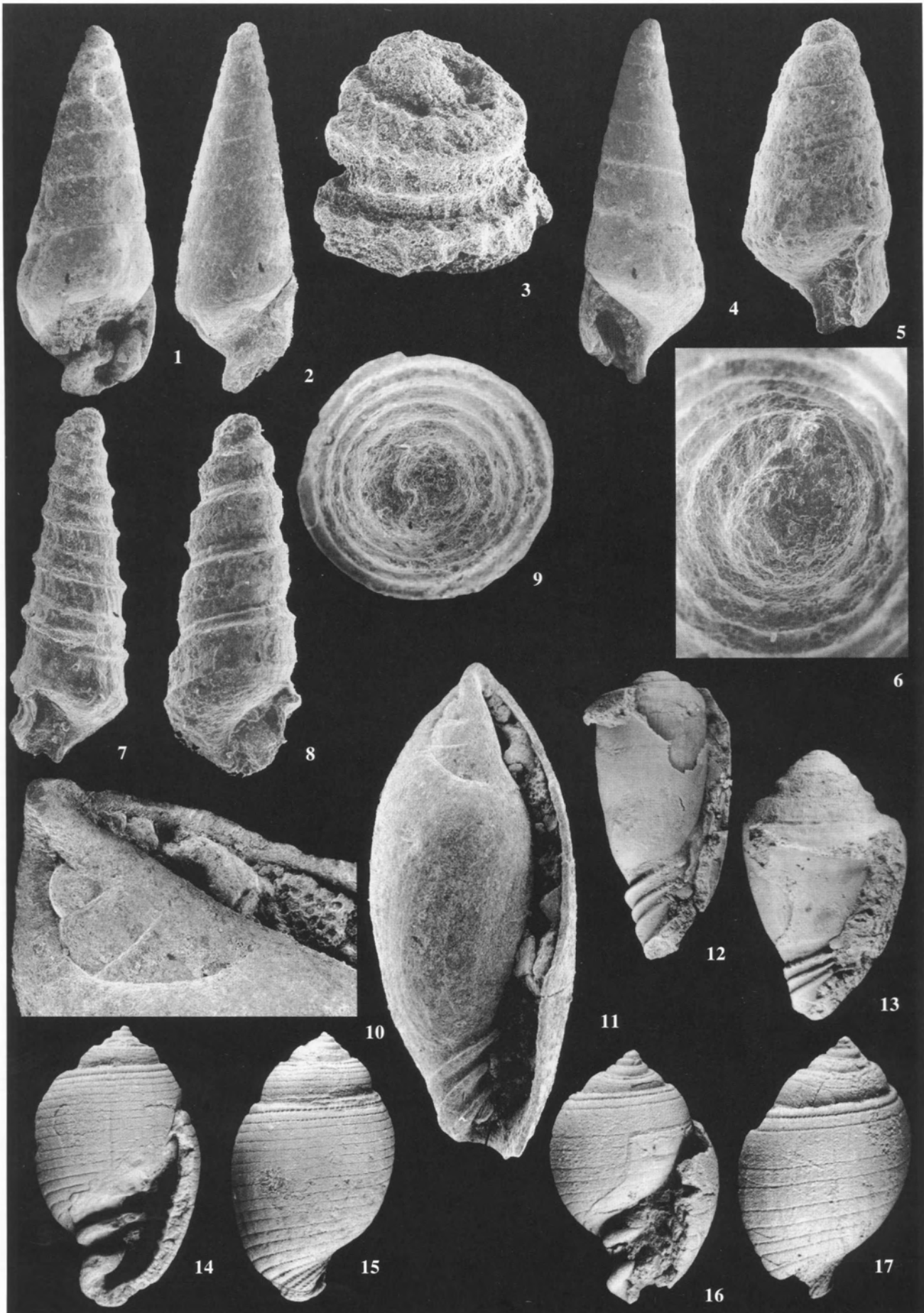
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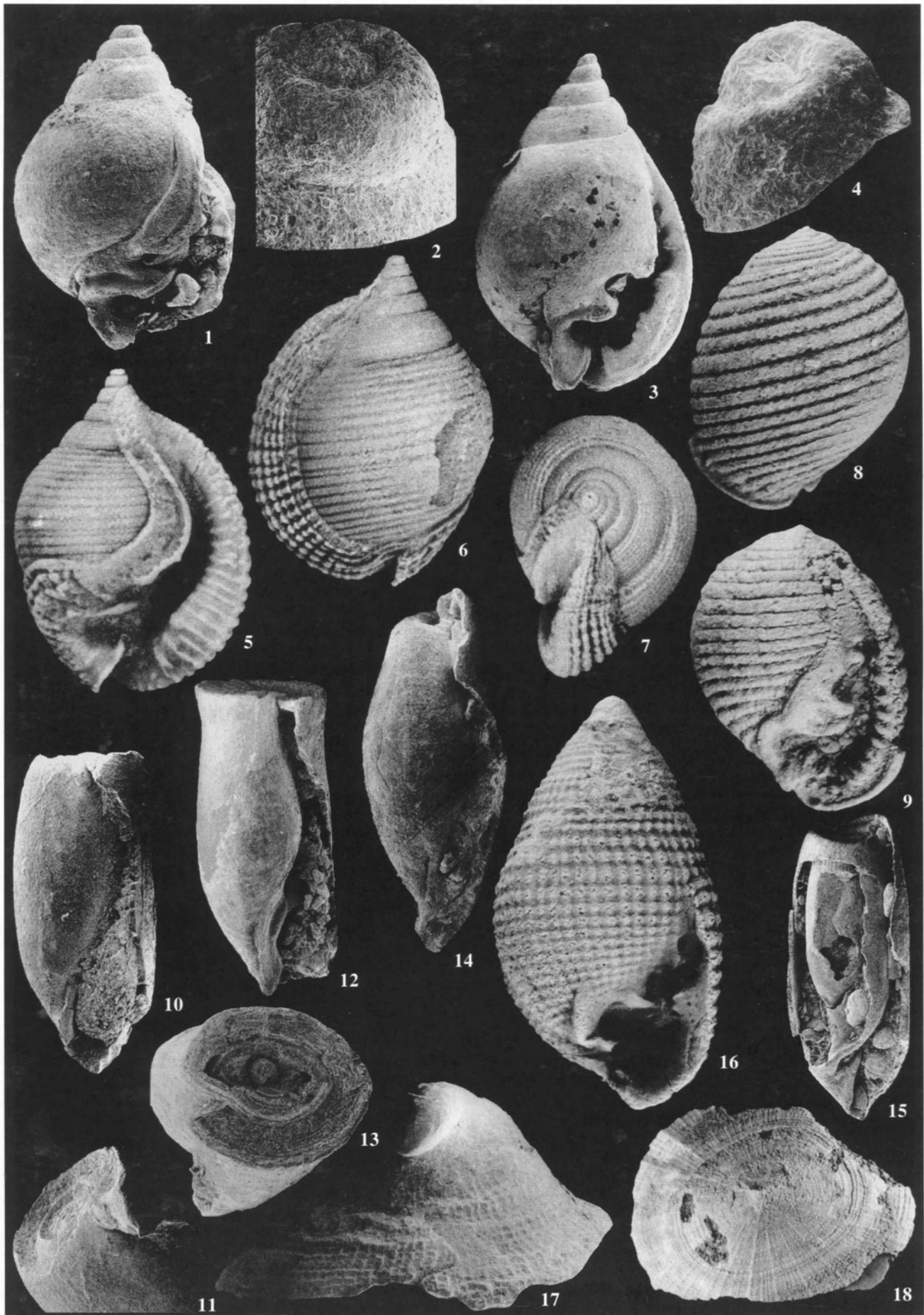
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For explanation see p. 331