Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus*, based on morphology of the early shell

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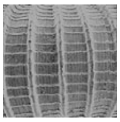

The aim of this study is to document the relationship that may exist between Triassic species of *Eucycloscala*, *Ampezzotrochus*, *Sabrinella*, *Microcheilus, Eunemopsis* and *Pseudoclanculus* and living species of genera such as *Pagodatrochus*, *Turcica, Calliotropis, Danilia,* and *Euchelus*. Their shell has a nacreous inner layer and ornament of axial ribs on the early teleoconch. This ornament distinguishes from living and fossil Vetigastropoda with *Trochus*, and *Turbo*-like shells. Eucycloscalidae, containing the Triassic genera *Eucycloscala* and *Ampezzotrochus,* can be distinguished from *Eunemopsis* and *Pseudoclanculus* and the Eunemopsidae fam. nov. by folds on the inner lip and Sabrinellidae fam. nov. with *Sabrinella* and *Microcheilus* by the varix of the aperture of the last whorl. *Lanascala* with Lanascalidae belongs here. *Neoeunema* gen. nov. represents a Triassic member of Eucyclidae, which contains numerous Jurassic genera and species. Pseudoturcicidae fam. nov. differs by the ornament of the early teleoconch. The Chilodontidae form a characteristic Cretaceous group with teeth on the inner side of their outer lip. Three families of modern genera can be distinguished by the arrangement of teeth in the radula: four pairs in Pagodatrochidae fam. nov. and Turcicidae fam. nov., and three pairs in Calliotropidae, documented with *Euchelus*. The Seguenzioidea represents a related group having a distinctive radula with two lateral pairs of teeth and a variety of shell shapes and ornament. The early teleoconch of Seguenziidae (with slit in the aperture) and Ancistrobasidae fam. nov. (without such a slit) resembles that of the Eucycloscalidae, but has a strong spiral rib in addition to the axial ribs. The new species *Microcheilus maxwelli* sp. nov., *Eucycloidea madagascariensis* sp. nov., new genera *Pseudoturcica* and *Heterodiscohelix,* and new families Sabrinellidae fam. nov., Euemopsidae fam. nov., Pseudoturcidae fam. nov., Pagodatrochidae fam. nov. Turcicidae fam. nov., and Ancistrobasidae fam. nov. are introduced. The fossil record confirms existence of two independent branches of Vetigastropoda since more than 220 Ma, and within one of these branches parallel to the Eucycloidea the Seguenzioidea since Mesozoic times. • Key words: Vetigastropoda, phylogeny, shell morphology.

BANDEL, K. 2010. Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus,* based on morphology of the early shell. *Bulletin of Geosciences 85(3)*, 435–486 (16 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received March 7, 2010; accepted in revised form August 23, 2010; published online September 20, 2010; issued September 30, 2010.

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Based on the results of molecular analysis it has quite recently become evident that the Vetigastropoda (formerly Archaeogastropoda, in part) have evolved into quite different groups. One of them that have been in existence for a long time is seen in the Seguenzioidea, into which also the *Calliotropis* and *Turcica* relation had been included (Kano 2008, Kano *et al*. 2009). Previously both genera had been interpreted to belong to the Trochoidea by Hickman & McLean (1990) including almost all Vetigastropoda without a slit-bearing shell, and families and groups within them had been distinguished by anatomical characters, predominantly the morphology and arrangement of the teeth of their radula. When it comes to the interpretation of fossil species neither molecular data nor the morphology of the teeth of the radula can be applied. Hickman & McLean (1990) included in their interpretation earlier suggestions based on general shell shape, summarized by Knight *et al*. (1960) and this is also the basis on which, for example, Kano *et al*. (2009) elaborate on the fossil species. Knight *et al*. (1960) collected existing earlier data especially from the compilation of Wenz (1938) based on the studies of former authors who compared shell shape of fossils with Recent species. They noted that species of Triassic *Eucycloscala*, *Eunemopsis* and *Pseudoclanculus* have a shell morphology that allows their relatives to be traced through succeeding times, even though species with similar shells have often been regarded as belonging in different genera. Some of the Mesozoic species connect in shell shape with living species belonging to Eucyclidae Koken, 1897, Calliotropidae Hickman & McLean, 1990 and Pagodatrochidae fam. nov., established below. Besides species with thin shells belonging to such genera as *Calliotropis, Bathybembix, Lischkeia*, and those mostly with thicker shells belonging to genera such as *Euchelus*, *Danilia, Turcica, Mirachelus,* some Cretaceous genera such as *Agnathodonta, Ilerdus* and *Hudledonta* with relatively thick shell also belong here. In particular, Kaim (2004) interpreted some of the Jurassic and Early Cretaceous species studied by him from Poland as representing genera with modern type species, such as *Calliotropis*, *Turcica* and *Adeuomphalus*. Other genera based on living species such as *Pagodatrochus* and *Perrinia* also have characters of the general morphological relationship of Calliotropidae.

Kano *et al*. (2009) summarized that Vetigastropoda are an archaic and diverse group of Gastropoda, comprising several thousand living species. Their systematic interpretation has changed former classification schemes and reconstruction of phylogeny considerably due to the molecular analysis and by including data presented by Warén *et al*. (2003), Geiger & Thacker (2005), Williams & Ozawa (2006), Kano (2008) and Williams *et al*. (2008, 2010).

Hickman & McLean (1990) placing their main emphasis on the characters of living species suggested that the Eucyclinae represent a subfamily of the Trochidae, in turn a family of the Trochoidea. Szabo (1995) grouped Mesozoic (especially Jurassic) species differently, noting that the Eucycloidea have their shell in shape and ornament differing from that of the Trochoidea. An even more uniting factor is the change from embryonic shell of the protoconch to the early ontogenetic shell. Here the embryonic shell is characteristically succeeded by juvenile teleoconch with ornament of axial ribs.

All species belonging to the Eucycloidea have a nacreous inner shell layer, as is also found in the Trochoidea. They differ from the later by ornament of the early teleoconch, which has distinctly axial ornament rather than spiral ribs. Moreover, the radula of living species of this group is quite distinct from that of other groups that have been included in the Trochidae (Trochoidea) by Hickman & McLean (1990). Apparently Trochoidea and Eucycloidea have lived side-by-side since at least the Triassic that is since about 220 Ma. A similar derivation in time was also speculated by Kano *et al*. (2009) based on molecular studies of living species considered to belong to the Seguenzioidea.

Among the Eucyloidea, two families are recognized from the Triassic. The Eucycloscalidae can be traced to the end of the Cretaceous and may be interpreted as connecting with the living species of the genus *Pagodatrochus*. The Eunemopsidae consist of two genera with species only in the Triassic. *Neoeunema* gen. nov. connects with the predominantly Jurassic Eucyclidae and, among the modern taxa, with Calliotropidae and Pagodatrochidae, which are distinguished from each other predominantly by the number of teeth in the central zone of their radulae.

Molecular analysis by Warén *et al*. (2003) suggest to Bouchet *et al.* (2005) the presence of a superfamily Seguenzioidea Verrill, 1884 within the Vetigastropoda, including the families Seguenziidae and Chilodontidae with living species, and Eucyclidae and Laubellidae with fossil species. Their classification scheme in not totally compatible to the paleontological record and the data presented below suggests a new interpretation of their taxonomic relationships. Laubellidae have recently been reinterpreted by Bandel (2009) including a revaluation of the phylogeny of slit bearing Vetigastropoda with nacreous shell living since the Triassic.

Note. – Studied specimens are housed in the collection of the Geologisch-Paläontologisches Institut der Universität Hamburg, SGPHM No. 4664–4698, Germany. Other material cited is to be found in the Naturhistorisches Museum in Vienna, Austria (NHM Wien) and the collection of the Senckenberg Museum, Frankfurt a. M., Germany (SMF).

Systematic paleontology

Phylum Mollusca Linné, 1758
Class Gastropoda Cuvier, 1797
Subclass Vetigastropoda Salvini-Plawen, 1980

Superfamily Eucycloidea Koken, 1897

Diagnosis. – Nacreous shell has protoconch succeeded by rounded first whorls of teleoconch with ornament of axial ribs. Characters of the aperture differ among families included here. Within superfamily, family Eucycloscalidae has a slender shell with keel on sides of whorls and simple inner lip, whereas family Eunemopsidae has a ridge on inner lip. Family Sabrinellidae has a small shell with strongly expressed adult aperture. All three are based on Triassic species. Eucyclidae is based on a Jurassic type with conical and often shorter shell, some taxa of which are very similar in shape with some Triassic genera, others to modern genera. Lanascalidae, with Triassic representatives, has rounded whorls and a simple aperture.

Remarks. – Among the modern groups the Pagodatrochidae fam. nov. consists of few small species living in the tropical Pacific and resembling some Mesozoic genera. The radula connects with the Calliotropidae, which has many modern species with simple aperture, and many deep water taxa with thin shell. Mesozoic Chilodontidae, with a thick shell and the aperture bearing teeth, is based on Jurassic species and includes several Cretaceous genera. The shell of some species of the modern Turcicidae fam. nov. have only one or two teeth on the inner lip. Several genera are rather similar in shell shape to Mesozoic representatives of the Eucycloidea.

The superfamily has been suggested by Conti & Monari (2001) following advice of Szabo (1995). They discussed the history of the taxonomy of *Eucyclus* and those genera they suggested to be related to *Eucyclus*.

Family Eucycloscalidae Gründel, 2007

Type genus. – *Eucycloscala* Cossmann, 1895.

Diagnosis. – Conical shell is higher than wide, with ornament of axial and spiral ribs, a simple circular aperture, nacre forming inner part of its walls. First whorl of teleoconch surrounds protoconch, forming a flat or wide conical apex, and only in the second whorl of teleoconch the more slender trochispiral shape is introduced, which in further growth forms an elongate conical shell. On first whorls of the teleoconch predominant ornament consists of axial ribs. Later two or three spiral ribs are added. One or both of these spiral ribs form keels or angulations on the teleoconch whorls. Base is convex with spiral ornament and aperture of last whorl is circular and has a continuous margin. The family is based on *Eucycloscala* Cossmann, 1895 with the type species *Trochus binodosus* Münster, 1844 from the Late Triassic St. Cassian Formation (Knight *et al.* 1960, fig. 171, 10).

Remarks. – Cossmann (1918, pl. 11, figs 6–8) interpreted *Eucycloscala* as a member of the Liotidae and connected the Triassic type with the Cretaceous *Eucycloscala cretacea* (Boury). Gründel (2004; 2007a) considered *Eucycloscala* as representative of the Eucyclidae. Gründel (2007b) based on that genus the Eucycloscalinae Gründel, 2007. This latter approach is accepted here and the subfamily is raised to family status. Eucycloscalidae can be traced from the Triassic to the Late Cretaceous and even Paleocene, and the relationship possibly continued as *Pagodatrochus,* which has rather similar shell. The Eucycloscalidae thus may have lasted for more than 220 Ma. Gründel (2007c) noted as characteristic feature of the Eucycloscalinae the appearance of three spiral ribs on the early teleoconch whorls, while Gründel (2004) suggested that 2–3 spiral ribs were also present in the members of the genus *Eucycloscala*. Within the genus *Eucycloscala* of the Triassic St. Cassian Formation, there are species with two and others with three spiral ribs on the early teleoconch whorls. While the type species to the genus *Eucycloscala binodosa* (Münster, 1841), has two spiral ribs (the third spiral ribbon at the base is covered by the succeeding whorl), *Eucycloscala baltzeri* (Klipstein, 1889) has three of them on the visible part of the second or third teleoconch whorl (Figs 1, 2A–C).

Gründel (2007c) suggested that besides *Eucycloscala,* the Jurassic genera *Gerasimovcyclus* Gründel, 2003, which is very similar to *Riselloidea* Cossmann, 1909, and *Trypanotrochus* Cossmann, 1918 among others, should be included in the Eucycloscalinae. These genera all have a more triangular shell and I prefer to regard them as members of the Eucyclidae (discussed in detail below).

Genus *Eucycloscala* Cossmann, 1895

Type species. – *Trochus binodosus* Münster, 1841, Late Triassic, St. Cassian Formation, Southern European Alps (Zardini 1978, pl. 16, figs 1–3; 1980, pl. 3, fig. 9).

Diagnosis. – Slender conical shell (apical angle 40° or less) has an aragonitic nacreous inner shell layer. Axis of coiling of the planispiral protoconch, with rounded whorls, may deviate from axis of coiling of teleoconch. First teleoconch whorl is ornamented by simple axial costae, to which more or less distinct spiral lines are added on later whorls. Later teleoconch whorls are ornamented with strong axial ribs, which are crossed by two or three spiral ribs forming short, sharp spines with each other. Ornament of base is spiral and some taxa have an umbilicus. Aperture is circular and simple and the peristome is continuous in the fully grown shell. The genus has been recognized from Late Triassic to the Late Cretaceous (Bandel 1993, Kiel & Bandel 2001), and also the Paleocene (Ravn 1933, Anderson 1975) (Figs 2H, I, 3A).

Remarks. – *Eucycloscala binodosa* has a shell that is more than 8 mm high and 6 mm wide (Fig. 1A–C). It is about half as wide when it has about 8 whorls. The protoconch is 0.22 mm wide with wrinkle pattern and three fine spiral ribs, which reflect the deformation. The first teleoconch whorl is coiled in a plane and bears axial ribs that are weak at first, strengthening around the whorl. With second whorl spiral coiling begins to form a cone with an apical angle of about 40°. Ornament consists of up to 10 straight, broadly rounded axial ribs. From beginning of the fourth teleoconch whorl the axial ribs are transected by two spiral keels, forming spines where they cross each other. The weakly rounded base has three spiral ribs. The umbilicus is narrow at the first five whorls and later wider and deeper, with a nodular spiral around it. The last whorl has a circular aperture that is thickened and almost vertical in orientation (Fig. 1A–C). The inner layer of the shell is nacre (Zardini 1978, pl. 16, figs 1–3; Bandel 1993, pl. 10, figs 2, 3, 1994, pl. 2, fig. 4).

The shape of the first teleoconch whorls differs among the 5 species of *Eucycloscala* that have been recognized from St. Cassian. The embryonic shell lies in the plane formed by the first teleoconch whorl, which contrasts to *Eucycloscala baltzeri* (Klipstein, 1843) (Fig. 1E, F) and *Eucycloscala supranodosa* (Klipstein, 1843) (Fig. 1G–I), in which the first whorls are conical and helically coiled (Bandel 1993, pl. 11, figs 1, 2, 4, 5). The embryonic whorl of *Eucycloscala spinosa* (Klipstein, 1843) (Fig. 2A–C) and *Eucycloscala elegans* (Münster, 1841) is surrounded by a planispiral first teleoconch whorl. This early shell has its axis of coiling inclined to that of the succeeding shell (Bandel 1993, pl. 11, figs 6, 7) (Fig. 2D–G).

Eucycloscala baltzeri (Fig. 1E, F) has three spiral ribs on teleoconch whorls (Zardini 1978, pl. 16, figs 9–11; Bandel 1993, pl. 10, figs 4–6; pl. 11, fig. 1) and is a little smaller than *E. binodosa*. *E. spinosa* (Fig. 2A–C) is more slender than *E. binodosa* (7 mm high and 3 mm wide, with 7 whorls) and has the inclined axial ribs aligned in succeeding whorls (Zardini 1978, pl. 16, fig. 12; Bandel 1993, pl. 9, fig. 8). *E. elegans* (Fig. 2D–G) has a similar shell shape to *E. binodosa* but has more rounded early teleoconch whorls and has later whorls more angular with more numerous axial ribs on each whorl (Bandel 1993, pl. 10, fig. 7, pl. 11, fig. 6). The first whorls of some specimens of *E. elegans* and *E. spinosa* appear detached and inclined to the later whorls, and their axis coils at an angle to that of the later teleoconch (Fig. 2B–G). All five species from St. Cassian have slender conical shells.

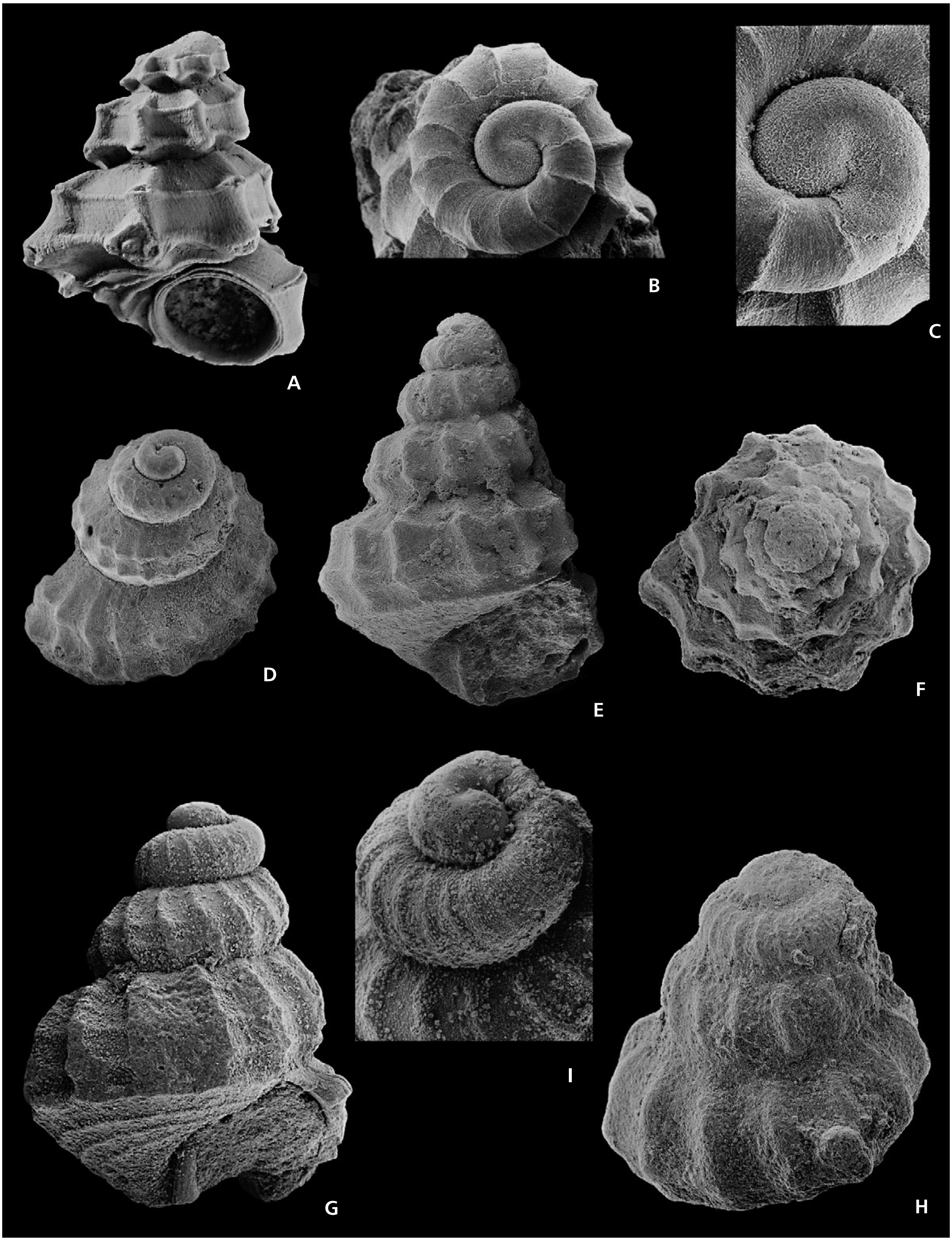
Gründel (2007a, pl. 2, figs 10–13) determined a species from Pliensbachian sediments of Reinberg in northeastern Germany as *Eucycloscala elegans* (Münster, 1844) that has a protoconch about 0.3 mm wide. This would extend the record of this species from the St. Cassian living on a tropical reef of the Tethys, to a species of a soft bottom environment on the northern European shelf, and also indicate duration of this species lasted for at least 15 Ma.

The Jurassic *Eucycloscala dunkeri* (Goldfuss, 1844) has a protoconch of 0.27 mm in width that is succeeded by rounded trochispiral whorls of the early teleoconch, ornamented by axial ribs and a fine honey-comb pattern. Two spiral ribs appear with beginning of the second teleoconch whorl. The later whorls are angular and more spiral ribs appear (Gründel 2007a, pl. 3, figs 4–7). Contrasting with some species of *Eucycloscala* from the Triassic, the apical angle of the Jurassic fossils placed in this genus by Gründel is larger than 40°, ranging from 60° upwards. *E. dunkeri* is placed below with *Pseudoturcica* gen. nov.

Eucycloscala torulosa Bandel, Gründel & Maxwell, 2000 from the Mid Jurassic of New Zealand has its protoconch 0.2 mm wide that is raised from the teleoconch. Two convex, rounded teleoconch whorls with axial ribs follow. Later whorls have ornament of one tubercular spiral rib crossed by axial ribs. The base carries spiral ribs. A shell with six whorls is about 3.4 mm high (Bandel *et al.* 2000, pl. 2, figs 11–13). *E. tortulosa* resembles *Eucycloscala supranodosa* from St. Cassian Formation regarding the early teleoconch. A quite similar shaped early ontogenetic shell is also found in the Jurassic species *Eucycloscala praetor* (Goldfuss, 1844), *Eucycloscala orbignyana* (Hudleston, 1893) and the very similar *Eucycloidea bianor* (Orbigny, 1853) from southern Germany (Gründel 2003c). In shell shape as well as ornament *E. tortulosa* closely resembles *Perrinia stellata* A. Adams, 1854 living in the tropical Pacific (Fig. 15D–F) and is also similar to modern *Turcica maculata* Brazier, 1877 that lives off the Philippines, and *Perrinia elisa* (Gould, 1849) from the Australian Barrier Reef (Fig. 15A–C). Among the species from the Mid Jurassic of southern Germany with very similar shell shape, a species with somewhat weaker ornament is identified as *Eucyloidea bianor* (Orbigny, 1853). Species from the Early and Middle Jurassic have changed their determination back and forth among the genera *Eucycloscala*, *Eucyloidea* and *Eucyclus* (see, for example, the lists of synonyms in Gründel 2003c).

Eucycloscala cretacea Kiel & Bandel, 2001 from the Campanian of Spain has a shell similar in shape to that of *E. binodosa*. It has a flat first teleoconch whorl surrounding the protoconch. This species lived near or on the shore of the tropical Tethys (Kiel & Bandel 2001, pl. 1, figs 14, 15). *E. cretacea* has the shell with nacreous internal wall. The protoconch is 0.2 mm in diameter and deviates only slightly from the axis of coiling of the teleoconch. The early whorls are convex with axial ribs, and later on the third teleoconch whorl they are angulated by two spiral keels. The later shell succeeding the juvenile with 3.5 whorls remains unknown.

Figure 1. *Eucycloscala* and *Eunemopsis* from St. Cassian Formation at Cortina d'Ampezzo. • A–C – *Eucycloscala binodosa* (Münster, 1841). A – fully grown shell; loc. Alpe di Specie (height about 8 mm) (SGPHM, No. 4664). B – first teleoconch whorl (diameter about 0.5 mm). C – detail of Fig. 1B (embryonic whorl 0.22 mm wide). • D – *Eunemopsis obliquecostata* Zardini, 1978, juvenile shell of from St. Cassian (about 1.5 mm high) (SGPHM, No. 4665). • E, F – *Eucycloscala baltzeri* (Klipstein, 1843) from loc. Campo (SGPHM, No. 4666). E – with axial ribs on the first two teleoconch whorls and later three ribs (shell about 1.3 mm high). F – apical view of the juvenile shell of *E. baltzeri* with helicospiral first whorls and appearance of the first spiral ornament only in the third teleoconch whorl (shell about 1 mm wide). • G–I – *Eucycloscala supranodosa* (Klipstein, 1843) from loc. Campo SGPHM, No. 4667). G – apical view with flattened base ornamented by spiral ribs (1.5 mm high). Spiral ornament begins in the second teleoconch whorl. H – first whorls rounded with conical shape, and more axial ribs on the first teleoconch whorl than later (1.6 mm high). I – initial whorls of as in Fig. 1G with smooth rounded protoconch (0.2 mm wide), ornament of simple axial ribs on first teleoconch whorl with background of growth lines with tubercles.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Eucycloscala ultima Ravn, 1933 from the Early Paleocene (Danian) of Denmark has a flat protoconch and three teleoconch whorls with apical angle of 65°. While the protoconch is smooth, the teleoconch is ornamented with about 15 lamellar axial ribs per whorl (Ravn 1933, pl. 2, fig. 2). Accordingly the shell consists of about five whorls and is 2.3 mm high and 2 mm wide. The rounded base has the umbilicus surrounded by a spiral row of tubercles and the aperture is circular. Actually, the first whorl has only about 12 ribs and 15–16 ribs ornament the second and third whorl (Fig. 2H). The protoconch is almost 0.4 mm across, and ends at the first axial rib. Its aperture is round, the whorls are rounded, and the umbilicus is open. Fine spiral ornament lies between small indentations in the lamellar axial ribs of the first teleoconch whorl, with coarser spiral ribs developing with begin of the second teleoconch whorl (Fig. 2I). The edge of the base is rounded and here the ornament of spiral ribs is more obvious. The umbilicus becomes relatively narrower with the increasing number of teleoconch whorls (Figs 2H, I, 3A). A similar species with spirals on the base was reported by Anderson (1975) as *Eucycloscala basistriata* from the Paleocene of western Germany. The relatively large protoconch is evidence for a lecithotrophic development with young emerging from their spawn as crawling individuals and not as swimming veliger. It also resembles that of modern species of the superfamily which live in colder and deeper water, such as the species of *Calliotropis* from deep water reefs on the edge of the slope (Fig. 16D, E).

The shape of the early ontogenetic shell could be regarded as more distinctive than that of the later teleoconch. It is flat in case of the type species of the Eucyloscalidae as well as in the Pagodatrochidae fam. nov., here based on living *Pagodatrochus* (Fig. 10A–C) (see below). In Calliotropidae and Turcicidae and their fossil counterparts, the Chilodontidae, the ornament of the early teleoconch is similar but its shape is trochispiral from the beginning of the first whorl.

Genus *Ampezzotrochus* Bandel, 1993

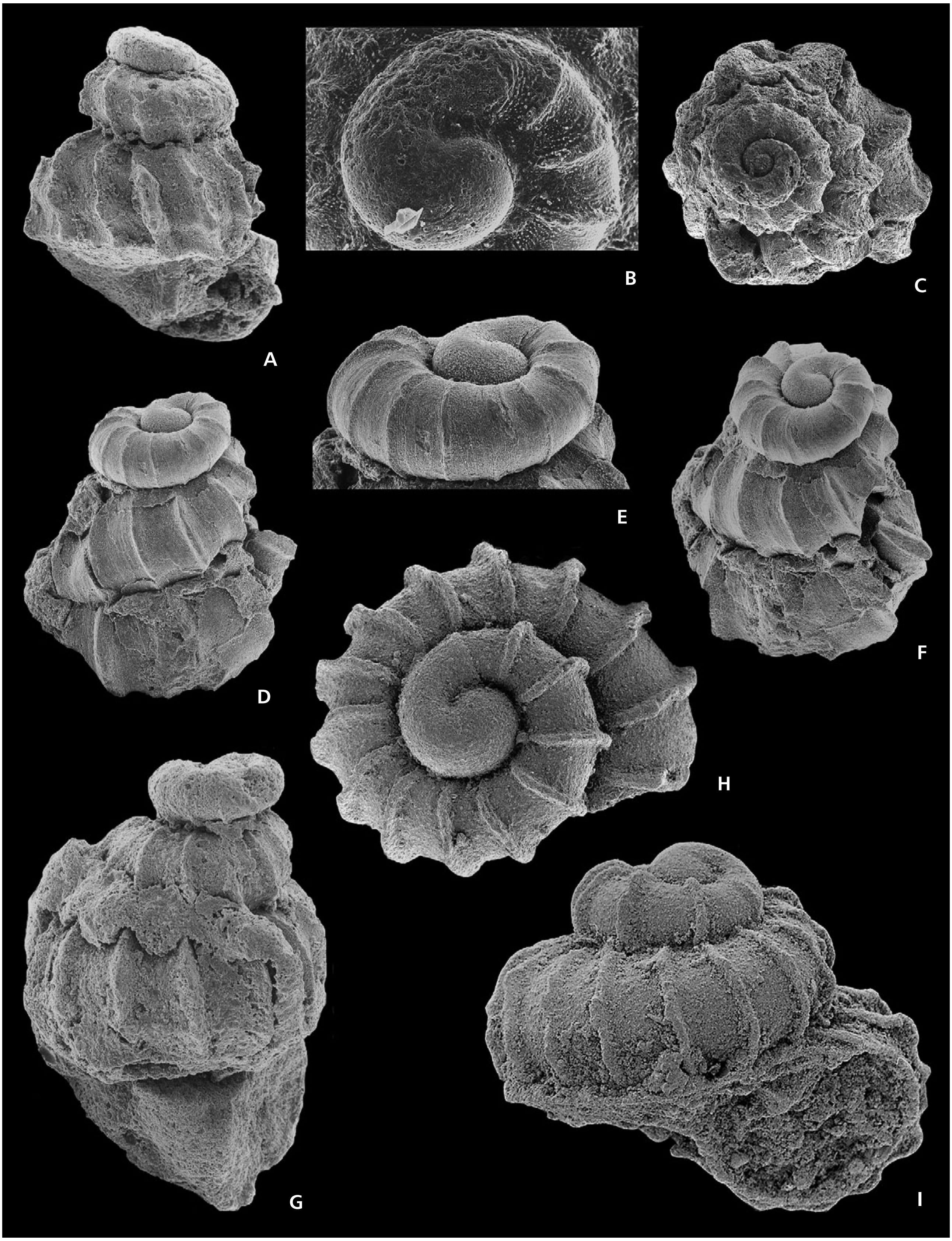
Type species. – *Ampezzotrochus rinaldus* Bandel, 1993 from St. Cassian Formation (Bandel 1993, pl. 9, figs 4–7).

Diagnosis. – Small *Rissoa*-like shell has a rounded base and consists of up to seven whorls. Shell wall is predominantly composed of nacre (Fig. 3H). Smooth protoconch is about 0.2 mm wide and has an aperture with wide, rounded rim and lobed outer lip. Its axis of coiling forms an angle with that of the teleoconch. Following trochispiral rounded whorls of the teleoconch have ornament of prominent axial ribs for three whorls. On the fourth whorl the ribs are weaker and more numerous and the last three whorls are smooth, including the large last whorl. Base has a few spiral ribs and a narrow umbilicus. Aperture is circular and simple with the inner lip slightly detached in the fully grown shell. Its shell is up to about 3.5 mm high and 1.5 mm wide when fully grown. Protoconch is succeeded by three teleoconch whorls with straight axial ribs. On the last two teleoconch whorls the ornament disappears on the sides while the base has spiral ribs around the narrow umbilicus (Figs 3B–I, 4A–E).

Remarks. – *Ampezzotrochus rinaldus* was common in the shallow reef flats of St. Cassian. It was formerly identified as *Natica argus* (Zardini 1978, pl. 20, figs 15, 16; 1980, pl. 3, figs 15, 16). *Ampezzotrochus* has a smooth, rounded body whorl, which differs from that of *Eucycloscala* and resembles that of species of the Carboniferous *Microdoma* Meek & Worthen, 1867 (Microdomatidae Wenz, 1938) which differs regarding the ornament of the juvenile teleoconch. *Eucochlis* Knight, 1933 with *Eucochlis perminuta* Knight, 1933 (Carboniferous) as type species (Knight 1933, fig. 2), is presented by a species in the Jurassic of New Zealand. Here the shell is small, conical and ovate with rounded whorls, and consists of 4.5 whorls, 2.2 mm in height and 1.6 mm in width. The apical whorls are smooth, including the first part of the teleoconch, and axial ornament appears later. The Jurassic species, *Eucochlis costata* Bandel, Gründel & Maxwell, 2000, resembles the Carboniferous type species of the genus, differing in details of basal ornament.

Two species from the St. Cassian Formation have been referred to *Tylotrochus* Koken, 1886, which is based on incompletely preserved species *Trochus konincki* Hörnes, 1856 from the Carnian of the northern Alps (Koken 1897). *T. semipunctatus* (Münster, 1841) has almost smooth slender shell with fine spiral ornament in the early teleoconch,

Figure 2. *Eucycloscala* from St. Cassian Formation near Cortina d'Ampezzo, H, I – juvenile shell of *Eucycloscala ultima* Ravn, 1933 from the Paleocene of Faxe (SGPHM, No. 4670). • A–C – *Eucycloscala spinosa* (Klipstein, 1843) from loc. Specie. A – juvenile shell of with plane and slightly inclined first teleoconch whorl (about 1.1 mm high) (SGPHM, No. 4668). B – protoconch (about 0.2 mm wide) succeeded by teleoconch with axial ribs. C – early teleoconch is almost plane and with axial ribs (shell about 1 mm wide). • D–G – *Eucycloscala elegans* (Münster, 1841) from loc. Specie (SGPHM, No. 4669). D – protoconch surrounded by a plane first teleoconch whorl and inclined axis of coiling inclined (1.2 mm high shell). E – detail to Fig. 2D (0.5 mm wide shell), first teleoconch whorl with few axial ribs and background of fine growth lines and tubercles. F – shape of shell more rounded than *E. binodosa* (shell 1.2 mm high, same in Fig. 2G). G – early teleoconch slightly detached (shell about 1.2 mm high). • H, I – *Eucycloscala ultima* (0.4 mm wide protoconch). H – rounded teleoconch whorls with 12 lamellar axial ribs (shell 0.8 mm wide). I – with as fine spiral ornament imprinted on the lamellar axial ribs, begin of several spiral keels on the second teleoconch whorl (shell 0.8 mm high).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whereas *T. elongatus* Bandel, 1993 has an early teleoconch with spiral ribs at first, later also developing weak axial elements, and later still with only smooth whorls (Bandel 1993, pl. 7, figs 2, 4 and figs 3, 5). *T. elongatus* has the conical shell with the early teleoconch whorls rounded and ornamented with axial ribs, later also developing spiral ribs. Later teleoconch whorls are flat and smooth with inclined growth lines, reflecting the oblique orientation of the aperture. The juvenile shell of *Tylotrochus semipunctatus* is documented here (Fig. 4F–H). The embryonic whorl of the protoconch is smooth, about 0.23 mm wide, and has a sinuous outer lip margin. The succeeding teleoconch whorls are rounded up until the third whorl, becoming flattened later on. Ornament consists of narrow spiral ribs and fine granular surface. The number of ribs increases in succeeding whorls and ribs are indistinct in the more fully grown shell. *T. semipunctatus* and *Tylotrochus keuppi* Bandel, Gründel & Maxwell, 2000 from the Jurassic of New Zealand have the early ontogenetic part of the teleoconch preserved well, documenting that *Tylotrochus* does not belong in the relationship of *Eucycloscala*. The first ornament on the teleoconch consists of spiral ribs, and axial ribs or traces of such elements only appear later (Bandel *et al.* 2000, pl. 4, figs 4, 6–9) (Fig. 4F).

Family Sabrinellidae fam. nov.

Type genus. – *Sabrinella* Bandel, 1993.

Diagnosis. – Small conical shell with the final margin of the aperture thickened, expanded and inclined backwards. Shell has internal nacreous layer. Ornament consists of regular, inclined, axial ribs crossed by fine spiral lines. Protoconch succeeded by rounded teleoconch whorls with axial ribs. Outer lip of the last whorl is thickened by concentric addition of shell added to and the aperture is circular (Fig. 5A–D).

Remarks. – The thickened aperture and small size distinguish *Sabrinella* Bandel, 1993 from the Eucycloscalidae and perhaps from the whole relationship assumed here for that group. A species of *Munditia* Finlay, 1927 occurring in the Gulf of Aqaba has axial ribs on the early teleoconch, but these are more lamellar in their arrangement and this member of the Liotiinae H. Adams & A. Adams, 1854 is not related to the fossil Sabrinellidae. *Sabrinella* is also not related to the living genus *Pagodatrochus*. The shell of *Microliotia* Boettger, 1901 resembles that of *Sabrinella* and *Microcheilus* when fully grown, but represents a member of the caenogastropod family Pickworthiidae Iredale, 1917 with very different early ontogenetic shell (Le Renard & Bouchet 2003, Bandel 2006). This similarity in size ornament and shape of the adult shell with *Sabrinella* documents good evidence of the dangers of convergence when fossils species are compared with each other and especially with such taxa living much later.

Genus *Sabrinella* Bandel, 1993

Type species. – *Delphinula doris* Laube, 1869 from St. Cassian Formation (Fig. 5A–D).

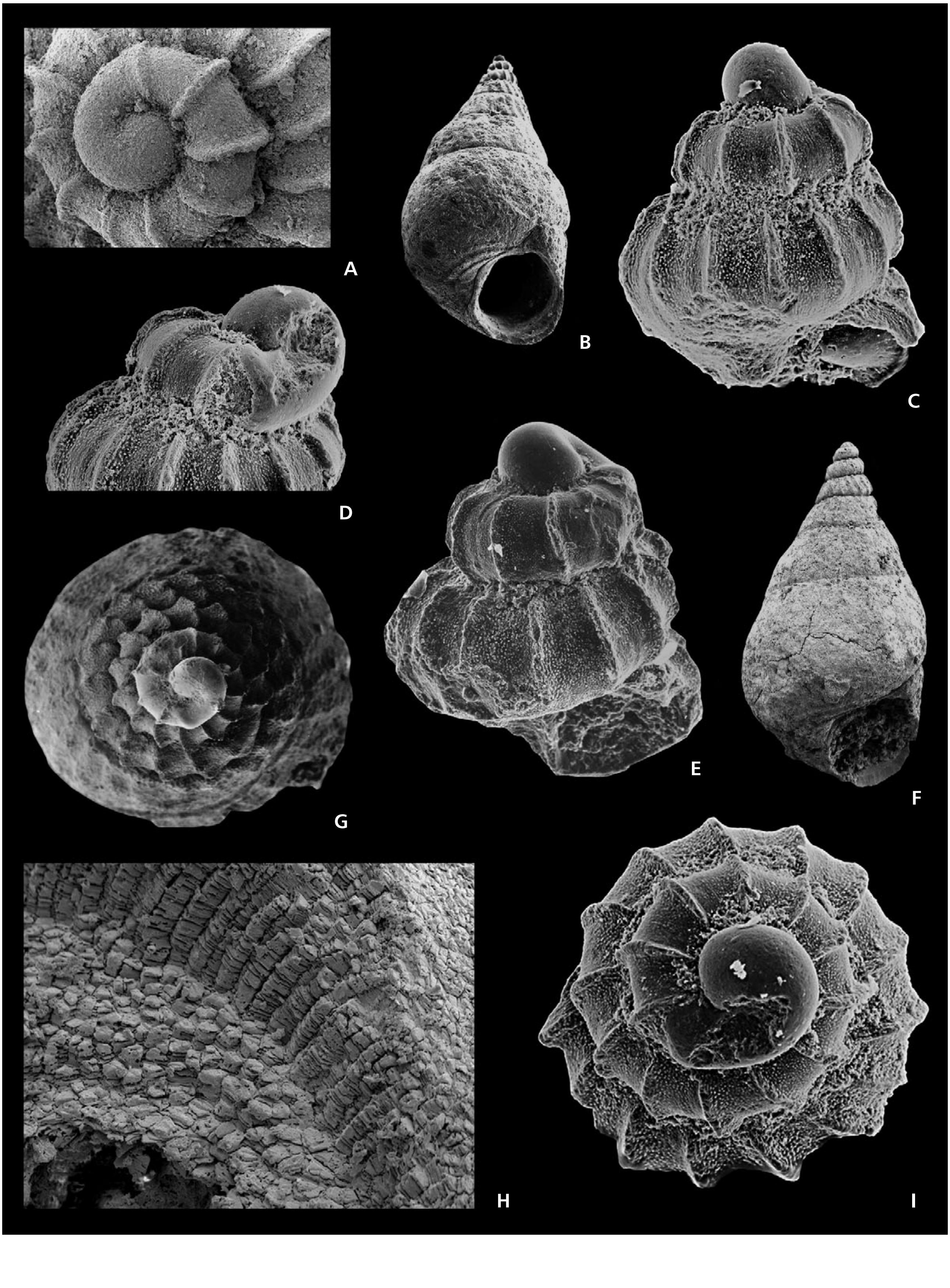
Diagnosis. – Small conical shell when fully grown has a wide and thickened rim around circular aperture. Ornament consists of collabral axial ribs and a few spiral ribs. Protoconch lies inclined in apex and first teleoconch whorl is evenly rounded, whereas later whorls are flattened and well separated by the suture. Thickened rim around the aperture is characteristic to *Sabrinella doris,* type species of the genus.

Remarks. – *Sabrinella doris* with a teleoconch of 5.5 whorls is about 2 mm high and fully grown. The protoconch is about 0.2 mm wide and is surrounded by the first teleoconch whorl, which has widely spaced axial ribs. Teleoconch whorls have about ten collabral ribs on the first whorl, later they increase to twenty, to decrease again to 14 on the last whorl. Spiral lines ornament the base. The aperture is inclined with about 45° (Bandel 1993, pl. 11, figs 8–10; 1994, pl. 1, fig. 10). Its periphery is widened and a rim with concentric construction is added to, decreasing width of the final aperture and making it perfectly circular. The shell shape is taller but the aperture resembles that found among modern species of the Liotiidae.

Genus *Microcheilus* Kittl, 1894

Type species. – *Microcheilus brauni* (Klippstein, 1845) (as *Cochlearia brauni*) from St. Cassian Formation.

Figure 3. A – *Eucycloscala ultima* (detail to Fig. 2H) from Paleocene of Faxe has a 0.4 mm wide protoconch with rounded whorls and the first teleoconch ornamented by strong axial ribs. • B–I –*Ampezzotrochus rinaldus* Bandel, 1993 from St. Cassian Formation, Cortina d'Ampezzo. B – fully grown shell is about 2.5 mm high (coll. NHM Wien 1992/116). C – juvenile shell with regular ornament of axial ribs (shell about 0.5 mm high) (SGPHM, No. 4671). D – protoconch with thickened margin (0.2 mm wide). E – protoconch lies inclined in the top of the teleoconch (shell about 0.45 mm high) (SGPHM, No. 4672). F – fully grown shell (3 mm high), loc. Specie (SGPHM, No. 4673). G – apex with teleoconch ornament of axial ribs changing into smooth shell in the fourth whorl (shell about 1 mm wide). H – fractured shell with stacks of nacre tablets composing the bulk of the shell wall. I – apex with early teleoconch with regular axal ornament (shell about 0.5 mm wide).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Remarks. – The small turriculate shell has spiral keels around the whorls. The last whorl has a circular aperture with a wide, thickened margin (Kittl 1894). Knight *et al.* (1960, fig. 171, 1a) noted the similarity with *Eucycloscala*. The genus was renamed *Pseudocochlearia* Cossmann, 1895 since *Microchilus* was preoccupied. However, as noted by Knight *et al*. (1960), the name was originally spelled *Microcheilus* and not *Microchilus*, and therefore is valid. The thick margin of the circular aperture is characteristic to the genus.

Microcheilus maxwelli **sp. nov.**
Figure 5E–I

Diagnosis. – Shell has the protoconch surrounded by an almost plane whorl with axial ribs. This first whorl of the teleoconch lies inclined on the apex of the following whorls, which form a pupa-like shell shape. Its last whorl has a downward twist in its final part and the circular aperture is oblique. It lies in a widened final portion of the shell (varix) and is surrounded by an angular rim. Ornament of the last teleoconch whorls includes axial ribs and three spiral ribs that angulate the outline.

Etymology. – The name of this tiny, unusual species of *Microcheilus* from St. Cassian is in honor of Phillip A. Maxwell.

Description. – The small species has a juvenile teleoconch with characteristics of *Eucycloscala* and the final whorl with expanded and thickened aperture as in *Sabrinella* (Fig. 5E–I). The shell is less than 2 mm high and the teleoconch consists of five whorls. The protoconch is surrounded by a plane first whorl sculptured with about 8 sharp, straight axial ribs. The coiling axis of the protoconch deviates a little from that of the later shell. On the second and third teleoconch whorls about 15 keel-like axial ribs are developed, whereas the last whorl has about 10, of which the last one forms the final varix of the aperture. Two spiral ribs appear on the second teleoconch whorl and on the last whorl they form two angles. A third spiral rib is present on the convex base. The margin of the aperture is angular and surrounds the circular opening of the aperture. Near the inner side, growth increments surround the aperture. The holotype (Fig. 5E–I) is 1.8 mm high and 1.5 mm in wide.

Type material. – The shell documented in Fig. 5E–I is the holotype deposited in the collection of the Geologisch-Paläontologisches Institut of the University of Hamburg with registration number SGPHM No. 4675.

Remarks. – *Microcheilus brauni* (Klipstein, 1868) differs from *M. maxwelli* sp. nov. by having more numerous whorls and a different ornament (Fig. 5J). The name *Cochlearia brauni* Klipstein, 1845, used by Laube (1869, pl. 23, fig. 4), was changed to *Microcheilus brauni* by Kittl (1894). The shell consists of 8 whorls with the last one deviating towards the base. Ornament at first consists of one row of nodules, later there are two rows. The aperture is circular with wide margin and is twisted towards the side. Shell size is about 1.5 mm high and 1.2 mm wide.

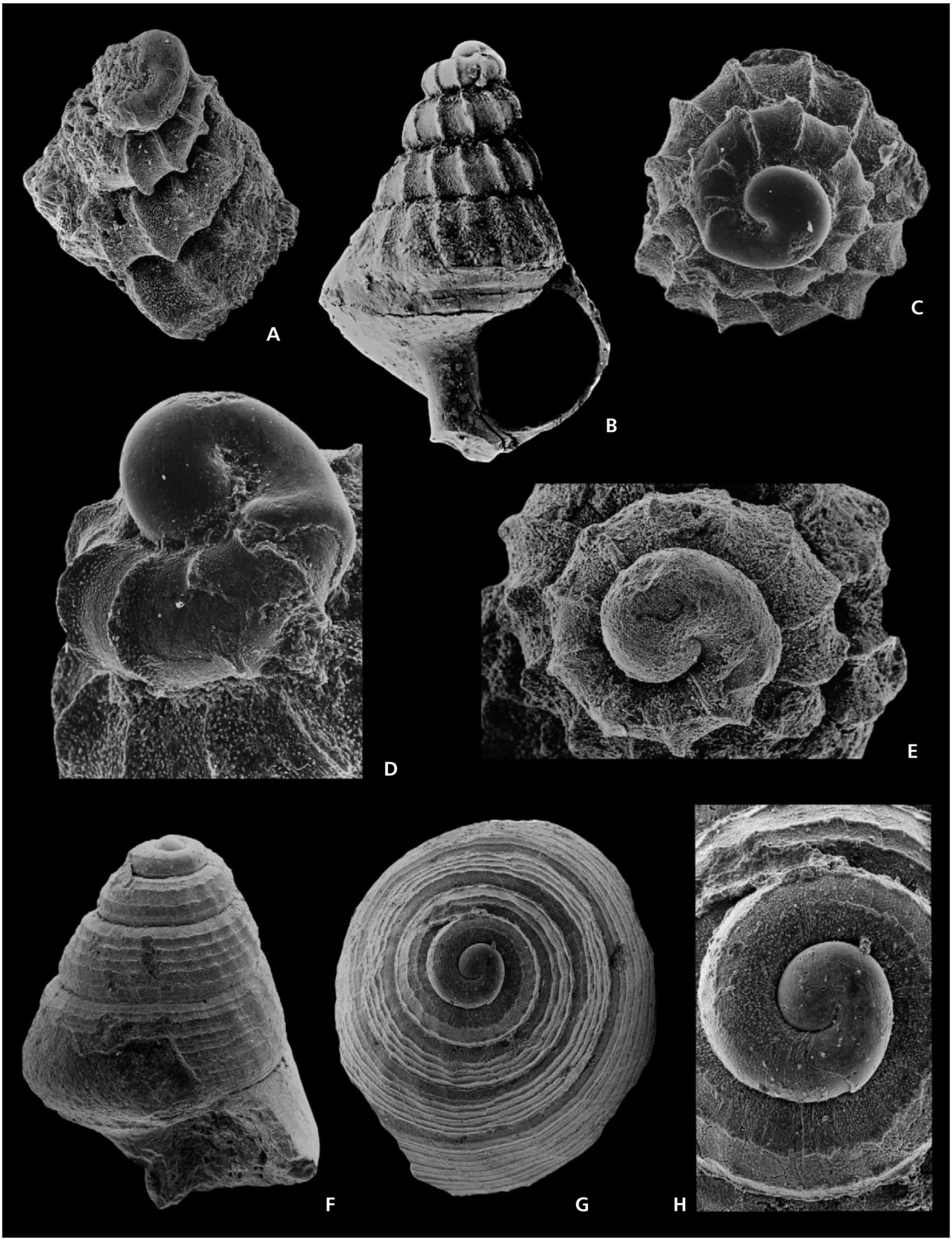
Among living species a similar aperture is found among the Halistylinae Keen, 1958, which is based on *Halistylus* Dall, 1890, with a pupa-like shell and rounded whorls, *Botelloides* Strand, 1928 with a similar shape but flattened sides and indistinct sutures, and *Charisma* Hedley, 1915 with short rounded shell. All have thick walls, small size, and a downward twist of the final aperture with margin thickened and a circular outline. The ornament of the early teleoconch consists of spiral lines and the radula resembles that in the Umboniidae (Hickman & McLean 1990, figs 76, 78). The ornament of the early teleoconch clearly distinguishes from that of the Sabrinellidae with its axial ornament. A widened aperture with thickened margin is also found among the Liotiidae, which have a small shell with flat spire, but have ornament of lamellar collabral ribs.

Family Eunemopsideae fam. nov.

Type genus. – *Eunemopsis* Kittl, 1991.

Diagnosis. – Conical shell has a prominent ridge on its inner lip that continues into the shell interior. Wall of shell consists predominantly of nacre. Early teleoconch whorls have inclined axial ribs, and later ones also have also 2–3 spiral ribs, the lowermost on the edge to rounded base. Family is based on *Eunemopsis* Kittl, 1891 from St. Cassian Formation (Fig. 6) and includes also *Pseudoclanculus* Cossmann, 1918 (Fig. 7A–C) from the Triassic.

Figure 4. All are from St. Cassian Formation at Cortina d'Ampezzo. • A–E – *Ampezzotrochus rinaldus* Bandel, 1993. A – juvenile shell (0.8 mm high). B – juvenile shell with ornamented whorls, ribs weaker in last whorls and base as in *Eunemopsis* (Fig. 6B) (shell about 1 mm high) (SGPHM, No. 4674). C – apex of *A. rinaldus* with regular axial ornament of juvenile teleoconch and smooth protoconch (shell 0.35 mm wide). D – wide margin of the protoconch (0.2 mm wide) lies inclined on the teleoconch. E – rim on the aperture and angular lateral fold of protoconch (about 0.2 mm wide). • F–H – *Tylotrochus semipunctatus* (Münster, 1841). F – lateral view of juvenile shell with teleoconch whorls initially rounded, later flattened and ornament of narrow spiral ribs on fine granular surface (shell about 2 mm high). G – apical shell with spiral ornament of the early teleoconch, later also axial folds (shell about 1.7 mm wide). H – protoconch smooth with sinuous margin (about 0.23 mm wide).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Remarks. – Kittl (1891) suggested a phylogenetic relationship with some living species, such as *Clanculus,* and noted that previously, *Eunemopsis* had usually been thought to be related to *Trochus* and *Turbo* (Münster 1841, Laube 1869, Zittel 1895) and also to *Eunema* and *Amberleya*. The later connection to *Eunema* and *Amberleya* (*Eucyclus*) is here supported by the morphology of the early teleoconch. No ridge on the inner lip is present in *Neoeunema,* which connects the Triassic Eunemopsidae with the Jurassic genera such as *Eucyclus* and *Riselloidea*.

Cossmann (1918) suggested a transfer from *Clanculus* and from the Trochinae to his new family Polydontinae Cossmann, 1918. Polydontinae is an invalid taxon (Bouchet *et al.* 2005) and was changed to Chilodontinae Wenz, 1938, which is based on *Chilodonta* Etallon, 1859, with Late Jurassic type species (Wenz 1938, fig. 651). This suggestion agrees to the morphology of the early teleoconch, but characters of the inner lip differ between *Chilodonta* and *Pseudoclanculus*. In case of *Eunemopsis* and *Pseudoclanculus,* species have not been recognized from Jurassic strata, but genera with similar shell shape are known from Pagodatrochidae, Turcicidae and Calliotropidae which have living species. The relationship of *Pseudoclanculus* to *Clanculus*, suggested by Kittl (1891), is not confirmed by the characters of the early teleoconch, which were not considered when Cossmann (1918) suggested the taxonomic change from *Clanculus* to *Pseudoclanculus.*

Genus *Eunemopsis* Kittl, 1891

Type species. – *Eunemopsis epaphus* (Laube, 1869) from the St. Cassian Formation. It resembles in shape and ornament the specimen illustrated in Fig. 6A.

Diagnosis. – Conical shell has somewhat flattened whorls with angular sutures and consists of 7–8 whorls. Early teleoconch whorls have inclined axial ribs; later ones have also 2–3 spiral ribs, the lowermost on the edge to the rounded base. The base has spiral lines and a narrow umbilicus surrounded by a keel with tubercles. Aperture is rectangular with rounded angles, a concave inner lip with callus cover, and with a fold. Inner shell layer consists of nacre (Kittl 1891, Bandel 1993) (Fig. 6H, I).

Remarks. – *Eunemopsis epaphus* has a shell of 9 whorls. It is slender, conical, 6 mm high and 2.7 mm wide, with apical angle about 50°. The embryonic shell is 0.2 mm wide and is smooth. Spiral and axial ribs form nodules where they cross. Those in the more apical row are strongest. The base has 7 spiral ribs and one bearing nodes around the narrow umbilicus. The tooth on the inner lip lies on its upper edge (Zardini 1978, pl. 14, fig. 5; Bandel 1993, pl. 13, fig. 4; 1994, pl. 2, fig. 3).

Eunemopsis dolomitica Kittl, 1891 has a conical shell with apical angle about 60°, flattened whorls with a double keel, and basal spiral ribs around the umbilicus (Fig. 6B, E–I). The apical angle of *Eunemopsis campense* Zardini, 1978 is smaller, about 48°, and whorls are more rounded (Fig. 6C) and the base has no umbilicus. An apical angle of 50° distinguishes *Eunemopsis obliquecostata* Zardini, 1978 (Figs 1D, 6D) from *Eunemopsis campense.* Its shell is more slender and smaller than that of *E. dolomitica* (Zardini 1978, pl. 14, figs 7, 8; Bandel 1993, pl. 13, figs 7, 8, pl. 14, fig. 1). *Eunemopsis seelandica* has a more nodular ornament than in *Eunemopsis obliquecostata* (Zardini 1978, pl. 14, figs 9–12; Bandel 1993, pl. 14, fig. 2).

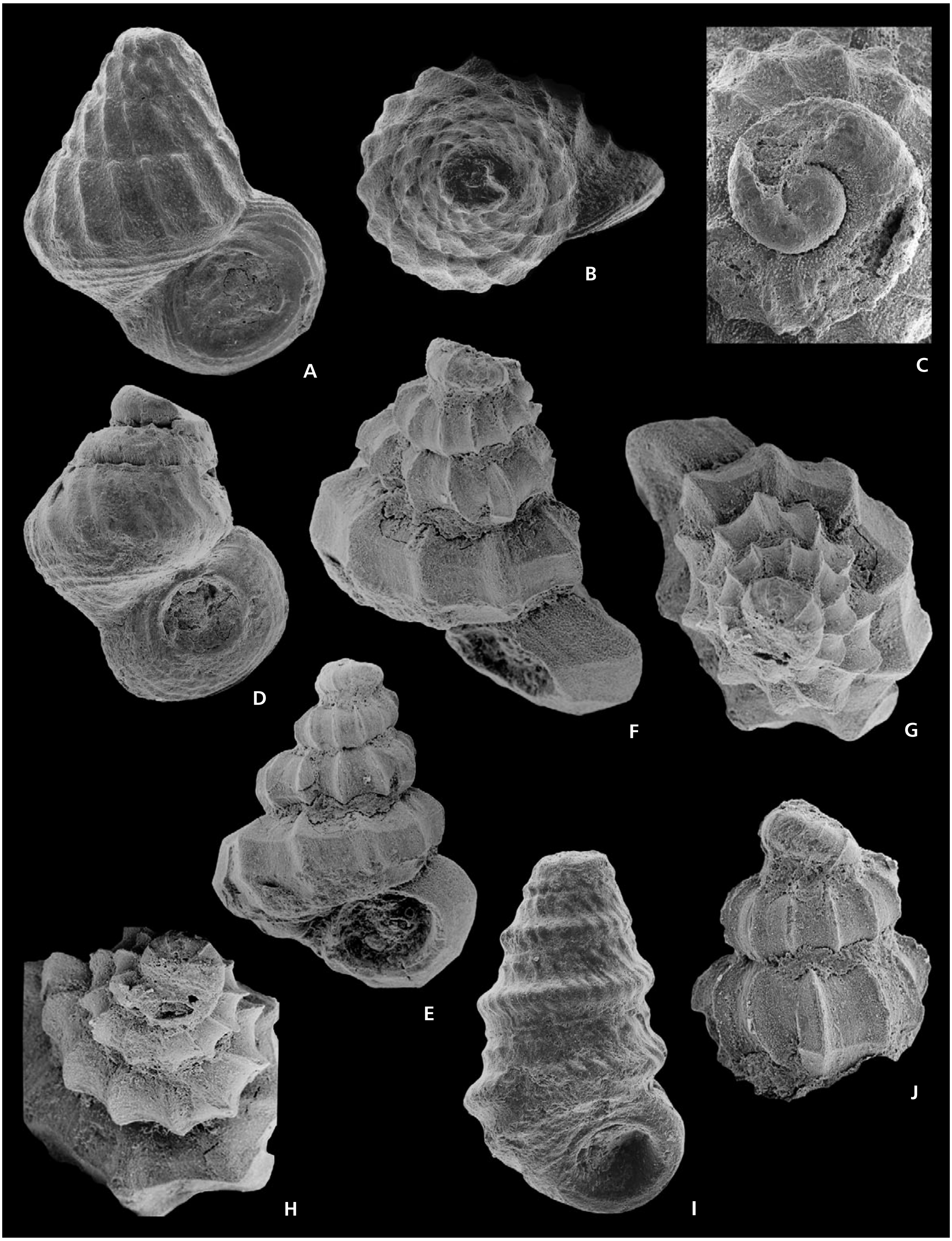
Genus *Pseudoclanculus* Cossmann, 1918

Type species. – *Pseudoclanculus cassianus* (Wissmann, 1841) (*Monodonta*) from St. Cassian Formation (Fig. 7C).

Diagnosis. – Small shell is low-conical in shape and ornamented by axial ribs having tubercles and spiral ribs crossing them. Whorls are flattened on their sides and also the base is flattened with only spiral ribs, and a callus from the inner lip closes the umbilicus. Oval aperture is thickened and inclined and there is a strong tooth on the inner lip that continues into a fold on the inner lip. Protoconch is surrounded by two teleoconch whorls with axial ribs. Shell consists of an outer layer and an inner nacreous layer.

The fully grown shell of *Pseudoclanculus cassianus* is 7 mm wide and 6 mm high, consisting of seven whorls. The embryonic shell is more than 0.25 mm wide and larger than that of *Pseudoclanculus nodosus* (Kittl, 1891). The first whorl of the teleoconch is ornamented by about 16 axial ribs (Fig. 7C). The shell is relatively higher in its early

Figure 5. All from St. Cassian Formation at Cortina d'Ampezzo. • A–D – *Sabrinella doris* Bandel, 1993. A – fully grown shell (about 2 mm high) with aperture thickened and inclined with about 45°, loc. Specie (SGPHM, No. 4674). B – apical view with aperture widened and inclined. C – protoconch (0.2 mm in diameter) and first teleoconch whorl with axial ribs. D – shell (about 2 mm high) with round aperture with thickened margin (coll. NHM Wien 1992/125). • E–I – *Microcheilus maxwelli* sp. nov. E – with final whorl expanded and with thickened aperture (shell 1.8 mm high) (holotype). F – with thickened aperture that has obique orientation. G – seen from apex, the final whorl has expanded and thickened aperture (1.5 mm wide shell) loc. Misurina (SGPHM, No. 4675). H – juvenile whorls of *Microcheilus maxwelli* sp. nov. resemble *Eucycloscala* and change from rounded to angular whorls of the teleoconch (SGPHM, No. 4677). I – juvenile teleoconch detached from the later teleoconch and surrounding the protoconch in a plane whorl as in Fig. 5F. • J – *Microcheilus brauni* (Laube, 1868) with the last whorl deviating towards the base and apertural margin thickened. Ornament first of one row of short rounded ribs and later a second rib is added below the suture (shell 1.6 mm high).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whorls, with the last whorls relatively broader. Spiral ribs form the dominant ornament, dissolved into rows of nodes. The base is covered by about 11 spiral ribs. The first three whorls resemble those of *Pseudoclanculus nodosus* but spiral elements dominate later (Fig. 7A, B). The callus of the inner lip is smaller than in *Pseudoclanculus nodosus*. The tooth on the inner lip is thickened and split into two, partly narrowing the umbilical slit (Zardini 1978, pl. 13, fig. 8; Bandel 1993, pl. 12, figs 4, 6–8).

Remarks. – *Rumerloella* Bandel, 1993 has a conical shell with the first three whorls rounded (Fig. 7D–H). Later whorls develop a flat flank with peripheral edge just above the suture, and the base is flattened. The first teleoconch whorl has initially two, later three spiral rows of nodules on the side connected to narrow axial ribs near the suture. The third whorl is ornament with spiral rows of nodules. The type species is *Trochus reflexus* Münster, 1841 from St. Cassian Formation. The shell resembles that of modern species of *Collonia* Gray, 1850 in shape but differs in ornament. Kittl (1891, pl. 7, figs 22–26) determined the species as *Collonia reflexa*. *Rumerloella reflexa* (Münster, 1841) is about 6 mm high with 4.5 whorls. The base is rounded and has a narrow umbilicus (Bandel 1993, pl. 6, fig. 10, pl. 7, fig. 1). Specimens known from St. Cassian may not be fully grown, even though individual shown in Fig. 7F, G are 6 mm high. *Rumerloella* differs from the Eucycloscalidae, Eunemopsidae, and Lanascalidae by the initially spiral ornament of the early teleoconch that is connected to interrupted axial elements. The position of *Rumerloella* in the system still needs to be determined. A similar early teleoconch ornament is found in some Seguenziidae and Ancistrobasidae (see below).

A family Lanascalidae Bandel, 1992 based on *Lanascala* Bandel, 1992 with type species *L. cassiana* Bandel, 1992 (Fig. 11A–C) from St. Cassian Formation was introduced as group of small Caenogastropoda. *Lanascala* was found distinct from the similar *Ampezzoscala ornata* (Münster, 1841) by a relatively smaller and shorter shell and the more rounded protoconch, from *Eucycloscala* by the short shell and helicoidal early shell. *Lanascala* has the conical shell 3 mm high and 2 mm wide with about five whorls. The protoconch remained incompletely known, and in the third teleoconch whorl spiral ornament is added forming a regular net with wide rectangular mesh. The convex base of the fully grown shell has a narrow umbilicus surrounded by spiral ribs (Bandel 1992, pl. 4, figs 6, 7, pl. 5, figs 1, 2). The aperture is oriented parallel to the shell axis, with a straight inner and rounded outer lip. It was suggested that Lanascalidae are related to Ladinulidae Bandel, 1992 of the Cerithioidea Fleming, 1822 (Bandel 1992, 2006). Conti & Monari (2001), in contrast, suggested that *Lanascala* resembles *Riselloidea*. The early teleoconch whorls of new individuals studied since indicate that the protoconch of the archaeogastropod type with spiral ornament is surrounded by a first teleoconch whorl with regular axial ribs (Fig. 11A–C). *Lanascala,* thus, belongs to the Vetigastropoda and may be included with the Eucycloidea in case its shell is constructed of nacre, and not of crossed lamellae, as was stated by Bandel (1992).

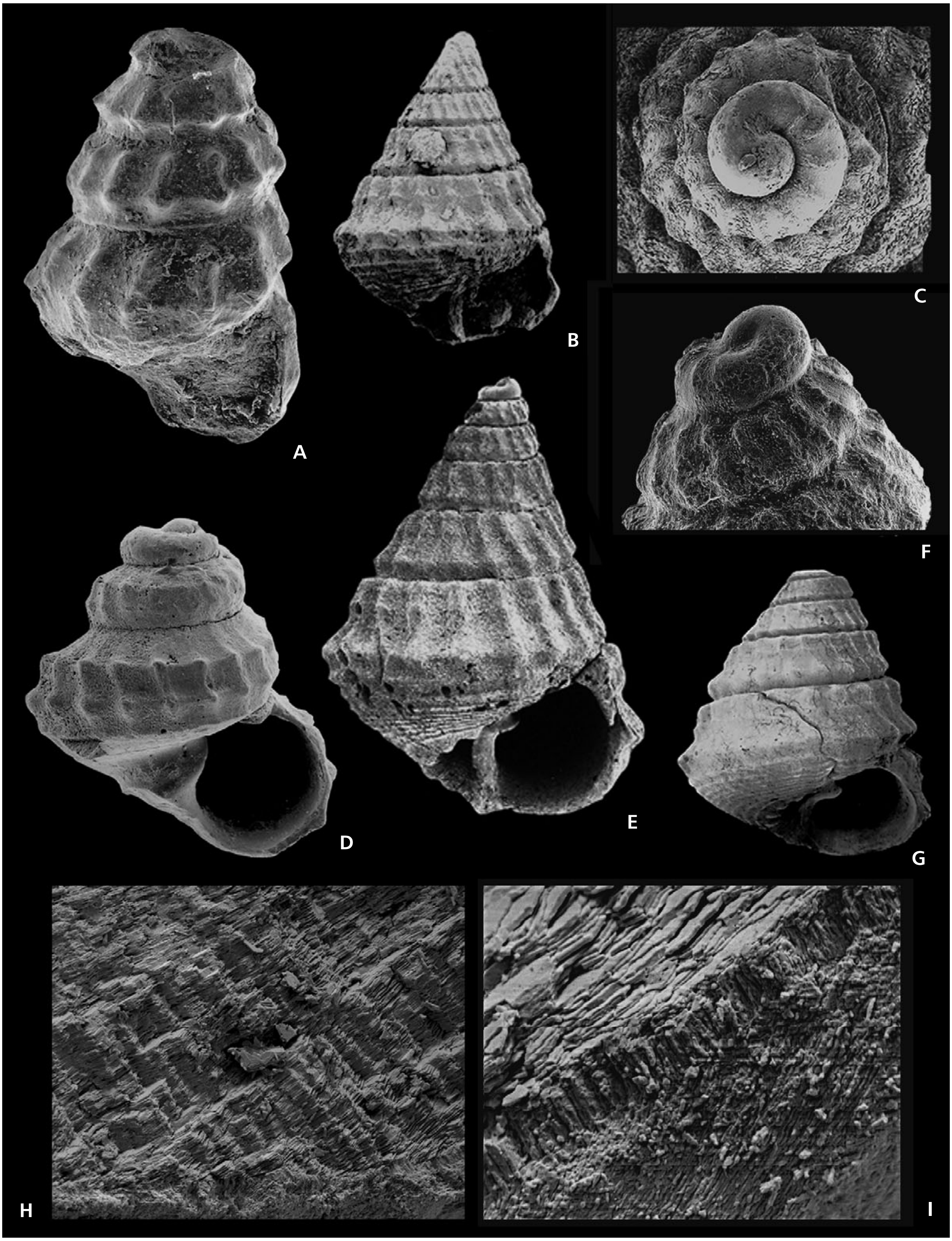
Family Eucyclidae Koken, 1896
(= Amberleyidae Wenz, 1938)

Type genus. – *Eucyclus* Etudes-Deslongchamps, 1860.

Diagnosis. – Conical shell has a simple aperture and simple callus of the inner lip. Protoconch is of archaeogastropod type and the early teleoconch is ornamented with axial ribs to which spiral ribs are added later. Shell wall contains nacre. The family Eucyclidae consists of the Jurassic genera *Eucyclus* (= *Amberleya*), *Eucycloidea* Hudleston, 1887, *Eucyclomphalus* Ammon, 1892, *Riselloidea* Cossmann, 1909, *Trypanotrochus* Cossmann, 1918. To these genera the Triassic genus *Neoeunema* gen. nov. from St. Cassian can be added.

Remarks. – According to Wenz (1938) *Amberleya* Morris & Lycett, 1851 has axial and spiral ornament and *Eucyclus* is dominated by spiral ornament. Knight *et al*. (1960) suggested that both are subgenera of *Amberleya,* without providing evidence for their close relation. Gründel (2004) suggested that Eucyclidae is a synonym of Amberleyidae and of Calliotropidae Hickman & McLean, 1990. But while *Amberleya* and *Eucyclus* may be based on the same Jurassic species or very closely related ones, *Calliotropis* has a sub-recent type species, which species may still be living. As was noted by Gründel (2003b) and repeated by Gründel (2007a), the morphology of the early teleoconch of the type species of *Eucyclus, Turbo ornatus* Sowerby,

Figure 6. All from St. Cassian Formation, Cortina d'Ampezzo. • A – fragmentary shell of cf. *Eunemopsis epaphus* (Laube, 1868) (1.3 mm high shell), loc. Rumerlo (SGPHM, No. 4679). • B – *Eunemopsis dolomitica* Kittl, 1891 with conical shell with apical angle about 60° and flattened whorls has a double keel and basal spiral ribs around the umbilicus (shell 2.2 mm high) (SGPHM, No. 4676). • C – apical shell of *Eunemopsis campense* Zardini, 1978 with protoconch (0.18 mm wide) succeeded by one whorl with axial ornament and spiral ornament in the next whorl. • D – juvenile shell of *Eunemopsis obliquecostata* Zardini, 1978 (as in Fig. 1D, about 1.5 mm high), loc. Campo. • E–I – *Eunemopsis dolomitica* Kittl, 1891. E – shell about 2 mm high. F – apical part of the shell with protoconch (about 0.2 mm wide) (SGPHM, No. 4678). G – adult shell (about 4 mm high) with ridge on the inner lip. H – detail to Fig. 6E, with nacre underlain by inner prismatic structure. I – shell-structure of columns of nacre and a prismatic inner layer as in Fig. 6H.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1819 from the Early Jurassic (Wenz 1938, figs 544, 545), is unknown. This species has been documented as *Amberleya ornata* (Sowerby, 1819) by Hickman & McLean (1990, fig. 38A) from England, but without details of the early ontogenetic shell or data on shell structure.

Gründel (2003b) regarded the type species of *Eucyclus* as another species, *E. obeliscus* Etudes-Deslongchamps, 1860, which is said to resemble *Amberleya.* The later is based on *Terebra nodosa* Buckman from the Middle Jurassic (Wenz 1938, fig. 542), but Knight *et al*. (1960) cited the type species as *A. bathonica* Cox & Arkell, 1950, replacement name for *A. nodosa* Morris & Lycett, 1851, not *Terebra nodosa*. *Amberleya nodosa* is said to differ from *Eucyclus obeliscus* only by uncertain details of the ornament (Gründel 2003b, pl. 4, fig. 7). Koken (1897, fig. 99,1) characterized *Eucyclus ornatus* clearly as conical with angled whorls, with a smooth apical side and spiral ornament on the rounded side and base, and as resembling the Silurian *Eunema* Salter, 1859 in regard to the aperture with indistinct anterior siphon. Hudleston (1888, pl. 2, figs 5a–e) determined similar species from the Inferior Oolite of Dorsetshire as belonging to *Purpurina* (*Eucycloidea*) *bianor* Orbigny and *Purpurina* (*Eucycloidea*) *carinocrenata* Lycett.

When the early whorls of the teleoconch are known and have axial ornament, and the shell contains nacre, the Jurassic genera included in the Eucyclidae grade one into the other and distinction of genera is sometimes quite difficult. *Eucyclus* has rounded whorls and spiral ornament with the conical shell usually higher than wide, as in a slender modern *Ginebis* Taki & Otuka, 1942 and *Bathybembix* Crosse, 1893. Small differences in ornament, shell shape, and shape of aperture among species from the Jurassic have been used to define closely similar genera. *Sertomphalus* Gründel, 2007 was proposed for slender species of *Eucycloidea*, *Trypanotrochus* for a species of *Riselloidea* Cossmann, 1909 with slender triangular shell and finer ornament, *Sadikia* Conti & Monari, 2000 for a short species of *Eucyclus* type with axial ornament, *Gerasimovcylus* Gründel, 2005 for species resembling *Riselloidea* but with an expanded anterior, considered similar to *Turcica* A. Adams, 1854 among the modern species by Kaim (2004). *Biarmatoidella* Gründel, 2003 was created for a more ornamented species of *Riselloidea,* very close in shape to a wide species of *Trypanotrochus*.

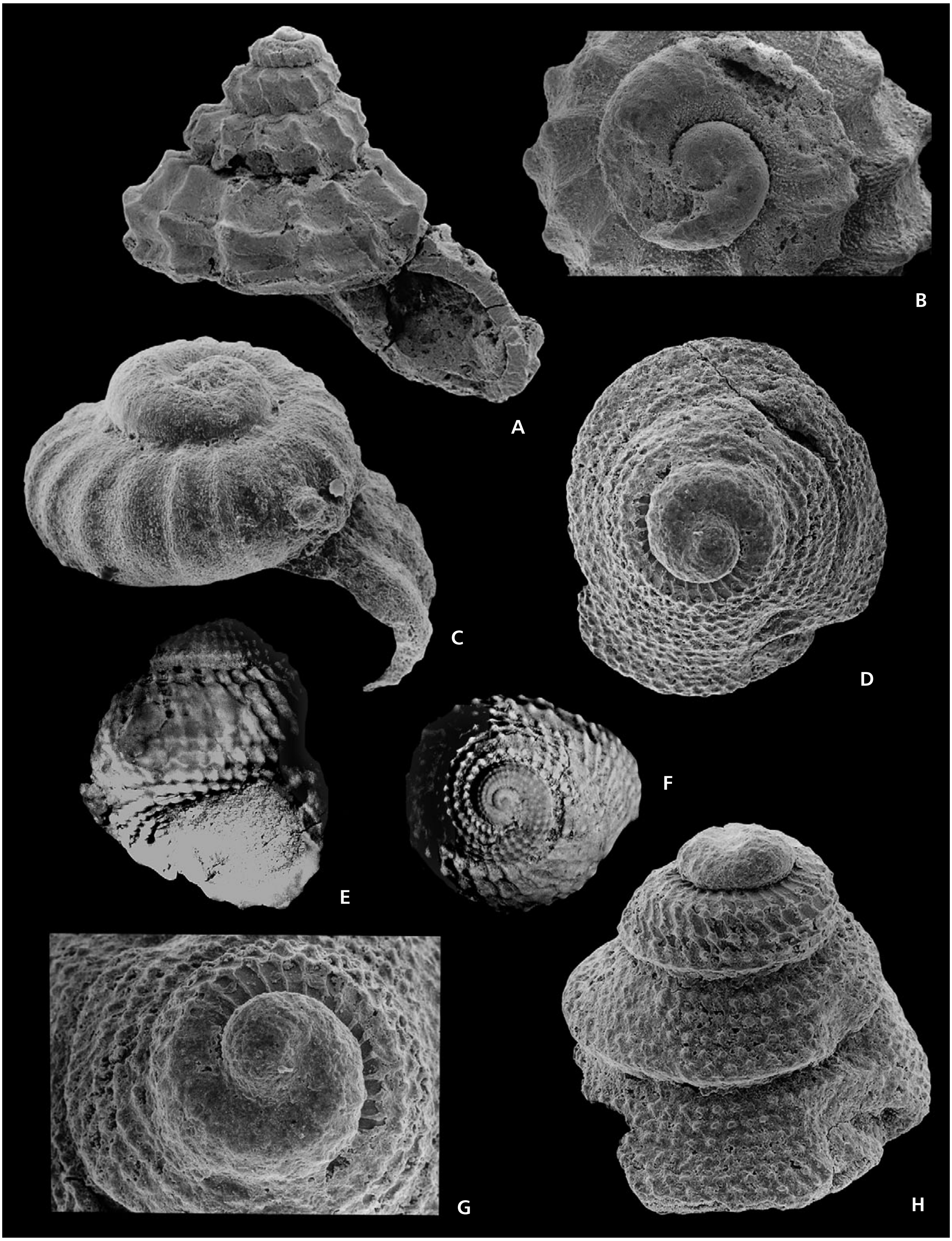
Conti & Monari (2001) discussed the history of the taxonomy of *Eucyclus* and the genera considered to be related to it. Hickman & McLean (1990) included in the Eucyclinae Koken, 1897 the genera *Amberleya*, *Eucyclus*, *Eunemopsis*, *Eucyclomphalus*, *Cirrus* Sowerby 1815, and *Hamusina* Gemmellaro, 1879, the last two of which belong to quite different groups of the Vetigastropoda, the Cirridae Cossmann, 1916 which belong to the Porcellioidea Koken, 1895 (Bandel 1988; Bandel & Frýda 1998, 2004; Frýda 1997; Frýda & Blodgett 1998, 2004; Kiel & Frýda 2004; Frýda & Farrell 2005; Frýda *et al*. 2006, 2008). The tribes Calliotropini and Chilodontini were included into the Eucyclinae with species that occur world-wide. According to Hickman & McLean (1990) a tribe Euyclini Koken, 1897 is composed only of fossil species of the Eucyclidae (proposed as Eucyclinae). During growth of the teleoconch, the Eucyclini change their shell shape from an interrupted peristome (margin of the aperture) in the juvenile stage to a closed one in the adult stage. In case of *Gerasimovcyclus* Gründel, 2005, the circular aperture of the juvenile, in contrast, changes into a pointed one at later growth stages (Gründel & Kaim 2006, fig. 5).

Kano (2008) had a novel approach to that group of the Vetigastropoda that was considered the Eucycloidea. He recognized a similarity in the molecular phylogeny based on mitrochondrial and nuclear gene sequences in a taxon Seguenzioidea containing species, of among others, referred to genera *Calliotropis* Seguenza, 1902, *Ginebis* Taki & Otuka, 1942, *Turcica* A. Adams, 1854, *Seguenzia* Jeffreys, 1876, *Agnathodonta* Cossmann, 1918, *Granata* Cotton, 1957, *Herpetopoma* Pilsbry, 1889, *Adeuomphalus* Seguenza, 1876. This indicates that the groups to which these genera belong have a common ancestor among the Vetigastropoda. In case these can be recognized by characters of the shell, a time can be suggested at which that ancestor to that group Seguenzioidea had evolved and separated from the other nacreous Vetigastropoda. A stem group representative could be suspected to have lived during the Triassic some 240 Ma ago, or even earlier. Bouchet *et al.* (2005) also suggested that the Eucyclidae belong to the Seguenzioidea and are not Trochoidea, following advice from Warén *et al*. (2003).

Genus *Eucyclus* Eudes-Deslongchamps, 1860

Type species. – *Eucyclus obeliscus* Eudes-Deslongchamps, 1860 from the Pliensbachian of France is the

Figure 7. All from St. Cassian Formation at Cortina d'Ampezzo. • A, B – *Pseudoclanculus nodosus* (Kittl, 1891). A – juvenile shell (3 mm wide). B – apical part of the same shell as in Fig. 7A (protoconch about 0.2 mm wide) and first whorl of the teleoconch with axial ribs and background with fine tubercles, loc. Campo (SGPHM, No. 4681). • C – juvenile shell of *Pseudoclanculus cassianus* (Wissmann, 1841) with first whorl of the teleoconch ornamented by about 16 axial ribs (shell about 0.5 mm wide). • D–H – *Rumerloella cancellata* (Münster, 1841). D – seen from the apex with initially spiral ornament of the early teleoconch and only later axial elements (G, H same shell). E – shell (6 mm high) with apex in F (coll. NHM Wien 1992/108). G – embryonic whorl (about 0.25 mm wide), on first teleoconch whorl pattern of axial lines connected to spiral tubercles. H – side view (shell almost 1 mm high).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type (Knight *et al.* 1960, Conti & Monari 2001), while it is *Turbo ornatus* Sowerby, 1819 from the middle Jurassic of England according to Wenz (1938, fig. 544).

Diagnosis. – Shell has a high spire with more than 10 rounded whorls, ornamented with two spiral keels forming angles, to which nodules are added. It is up to 40 mm high and more than 30 mm wide. Upper keel lies on the middle of the whorl, separating a ramp from a convex lower part and the lower keel with smaller nodes. Rounded base has no umbilicus and is ornamented by spiral ribs. Aperture is circular and vertical (Conti & Monari 2001, figs 6.13–17).

Remarks. – *Eucyclus ornatus* (Sowerby, 1819) from the mid-Jurassic of Europe and Morocco has convex whorls ornamented of two angles, which are also spiral keels that bear tubercles or short axial ribs. An upper ramp on the early teleoconch has axial ribs and a spiral rib. The inner lip is straight and thickened. The base has an ornament of granulated spiral ribs (Conti & Monari 2001, figs 6.6–12). *Eucyclus juliae* (Orbigny, 1853) with slender conical shell, 42 mm high and 21 mm wide, has a keeled angle on the edge to the rounded base, ornament of nodular spiral ribs on the whorl sides, and many spiral ribs on the base (Gründel 2007c, pl. 3, figs 5, 6). According to this author this species may be the same as *Eucyclus obelisus*. *Eucyclus murchisoni* (Münster, 1844) from Europe and Morocco is similar in ornament and size (30 mm high, 20 mm wide) with about 10 whorls with two angles, with area between them concave but not as angular as *E. juliae*. The smooth sutural ramp is connected to a convex lower part with spiral ribs and a lower keel with smaller nodes. The rounded base has no umbilicus and is ornamented by spiral ribs. The aperture is circular and vertical (Conti & Monari 2001, figs 6.13–17). *Eucyclus alpinus* Stoliczka, 1861 has ornament of spiral ribs with tubercles all over its rounded whorls (Szabo 2008, fig. 762). The early ontogenetic shell as well as shell structure is unknown, so there is some doubt about the taxonomic place, as there is also in the other species assigned to this genus, E. *mitterseensis* Szabo, 2008, *E. margaritaceus* (Stoliczka, 1861) and *E. sandrae* Szabo, 2008 from the Hierlatz Limestone of Austria and Hungary (Szabo 2008, figs 73, 74). *E. mitterseensis* has a slender conical shape with sharp angle on the whorls just above the suture, as is characteristic to species suggested to represent the genus *Sertomphalus* Gründel, 2007, based on *Sertomphalus schmodei* Gründel, 2007 from the Pliensbachian of north-western France (Gründel 2007c, pl. 3, figs 1–4), which is either very similar or conspecific with *E. mitterseensis*. *S. schmodei* has the early whorls of the teleoconch bearing axial ornament, but the protoconch is not preserved. *Sertomphalus* resembles *Eucylomphalus,* but the apical angle is smaller, the shell thus higher than wide. *Sertomphalus* species resembles those of *Dimorphotectus* Cossmann, 1918, which differ by having no umbilicus and a fold on the inner lip.

Kaim (2004, fig. 5) determined a species of *Eucyclus* from the Mid-Jurassic of Poland as *Eucycloscala izabellae* Kaim, 2004. Its early ontogenetic shell resembles the juvenile shell from Poland illustrated by Schröder (1995, pl. 1, figs 15, 16) with smooth embryonic shell and evenly ribbed early teleoconch (Fig. 9H, I), as is found in the early ontogenetic shell developed in the living species *Euchelus guttarosea* Dall, 1889. Jurassic *Eucyclus* may have a Triassic ancestor, here described as *Neoeumena* gen. nov., and possibly continue today in *Calliotropis* and related taxa.

Genus *Neoeunema* gen. nov.
Figure 8A–D

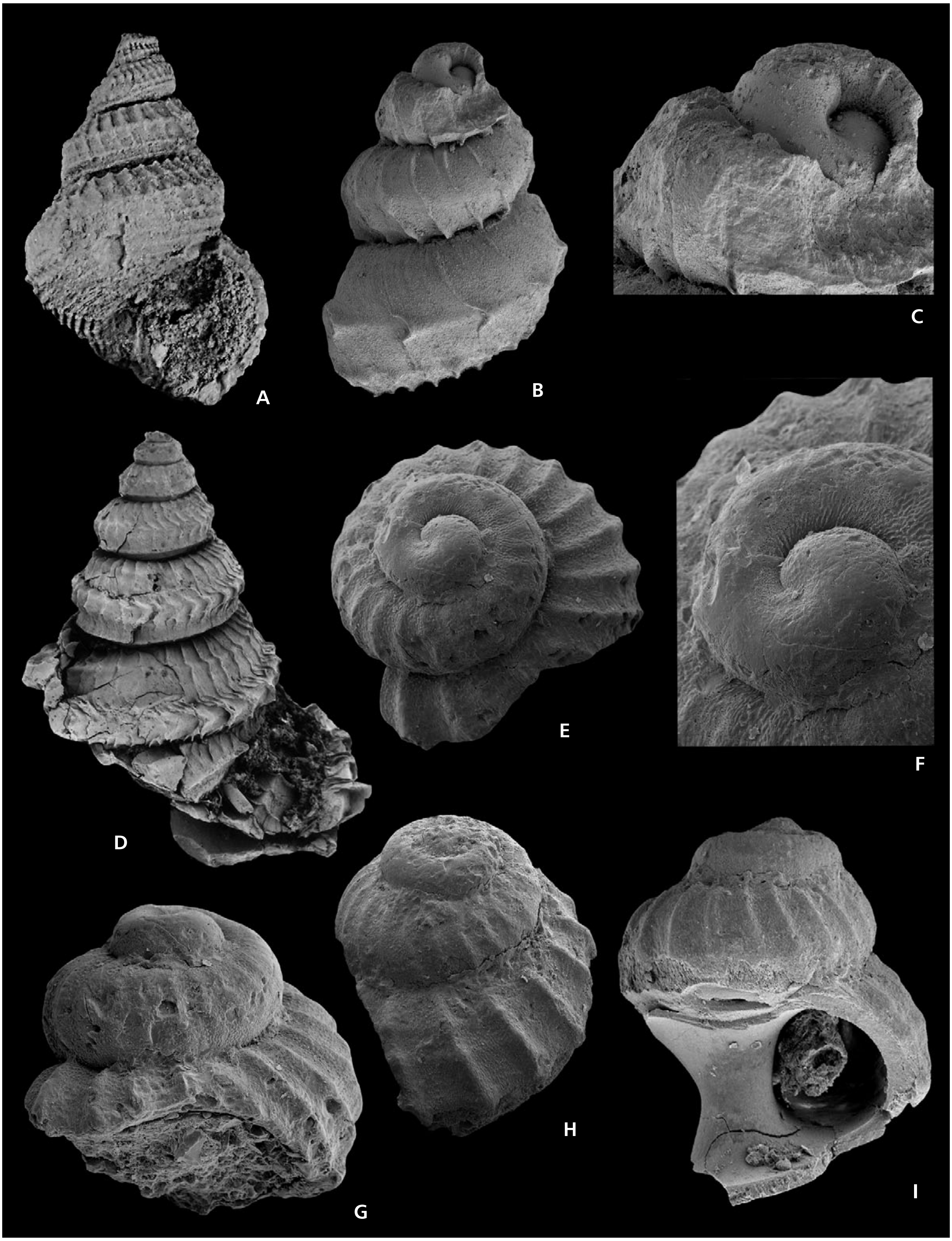
Type species. – *Eunema tyrolensis* Kittl, 1891 from St. Cassian Formation (Bandel 1993, pl. 14, figs 1–3).

Diagnosis. – Conical shell with about 9 whorls is higher than wide. Sutures are distinct and the sutural ramp is inclined and ends in an angle on the otherwise rounded sides of the whorls. Angle at the base of the sutural ramp and the angle around the base are accompanied by a spiral rib, and a third spiral rib lies below the suture. Base has an umbilicus in juveniles and is closed in the adult and is ornamented with spiral ribs.

Etymology. – The name is derived from the Ordovician *Eunema* but the new genus lived much later (neo).

Remarks. – The difference from *Eucyclus* lies in the sutural ramp. *Neoeunema* has a rib below the suture, and sinuous

Figure 8. A–D – *Neoeunema tyrolensis* (Kittl, 1891) from late Triassic St. Cassian Formation and E–I – *Eucycloidea madagascariensis* sp. nov. from the Mid-Jurassic of SW-Madagascar near Sakaraha (SGPHM, No. 4683). • A – conical shell (about 9 mm high) (coll. NHM Wien 1992/131). • B – juvenile shell with detail of the protoconch (about 0.18 mm wide) in C. Early teleoconch ornamented by thin axial ribs, spiral ornament with spiny keels appears on the third teleoconch whorl (shell about 1.2 mm high) (SGPHM, No. 4682). • D – shell with two lateral keels with gutter-like spines (3.3 mm high). • E – *E. madagascariensis* sp. nov. (0.6 mm wide early teleoconch). • F – protoconch (0.2 mm wide) and early teleoconch with shallow grooves and ridges. • G – side-view as in Fig. 8E (about 0.5 mm high shell) with first and second teleoconch whorls with axial ribs and rounded interspaces with discontinuous wrinkles. • H – axial ribs first spiral ribs initiate on second teleoconch whorl (0.5 mm high shell). • I – about 1 mm high shell with details of shell structure in Fig. 9A.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growth increments, both features are not found in *Eucyclus* species (Szabo 2008, figs 72–76). Species of the genus *Eunema* Salter, 1859 have a turbiniform shell with shallow sinus in the centre of the outer lip of the aperture. This continues as broad spiral ribbon on the whorl, bordered by edges. Ornament has additional spiral ribbons and growth increments. The type to the genus is *Eunema strigillatum* Salter, 1859 from the Middle Ordovician of Quebec (Knight 1941, pl. 41, fig. 1; Knight *et al*. 1960, I 226, fig. 1) and thus lived about 220 Ma before *Neoeunema tyrolensis*.

***Neoeunema tyrolensis* (Kittl, 1891)**

Remarks. – The conical shell consists of about 9 whorls and is 12 mm high and 7 mm wide. The protoconch is smooth and measures about 0.18 mm in diameter (Fig. 8B, C). It has a raised margin and the succeeding teleoconch whorl is rounded and ornamented by narrow, widely spaced axial ribs (Fig. 8B, C). The first two teleoconch whorls have only fine, widely spaced axial ribs and spiral ornament appears as sinus in these ribs at first in the third teleoconch whorl, forming a gutter-like short spine bearing spiral keel. Later whorls are stepped and the suture is deep. Two lateral keels are on the side and a third keel lies below the suture (Fig. 8A, D). The base is rounded, covered by six spiral ribs and has an umbilicus when not fully grown. The adult has a narrow umbilicus covered by the callus of the inner lip. Collabral axial ribs form spines where they cross the spiral ribs. The aperture is vertical and attached lightly to former whorls on the last whorl. The thin outer shell layer is covered by thick inner nacre (Bandel 1993, pl. 14, figs 1–3).

Genus *Eucyclomphalus* Ammon, 1892

Type species. – *Eucyclomphalus cupido* (Orbigny, 1853) (as *Trochus*) from the Lower Jurassic of north western France (Wenz 1938, fig. 369).

Diagnosis. – Conical shell has whorls with almost flat sides separated by a deep suture of triangular section. Periphery is angular and lies at the suture in juvenile whorls, while in later whorls it lies above the suture. Base is convex with wide umbilicus. Ornament is of spiral ribs that bear tubercles on most species. Ornament is present on the lower portions of each whorl and on the base.

Remarks. – The difference between *Eucyclus* and *Eucyclomphalus* is small but most species of *Eucyclus* have more rounded whorls and spiral keels are less tubercle bearing or spiny. Hickman & McLean (1990) included *Eucyclomphalus* in the Eucyclinae, while Wenz (1938) had interpreted it as representative of the Cirridae with dextral shell. Szabo (2008) suggested a place among the Chilodontinae. *Eucyclomphalus* has similar shell shape to be found in some modern Calliotropidae.

Eucyclomphalus nesea (Orbigny, 1853) from the Pliensbachian of France is about 50 mm high and 35 mm wide, with conical shape and ornament of a keel near the suture. Spiral ribs form nodules where they cross axial folds. The convex base has an umbilicus and is ornamented by spiral ribs (Gründel 2007c, pl. 3, figs 7–10). This Jurassic species is extremely similar to the living genus *Bathybembix* Crosse, 1893 as illustrated by Hickman & McLean (1990, fig. 44A) [*B. macdonaldi* (Dall, 1890)]. A similar species to *E. nesea* is present in the Hierlatz Limestone in *Eucyclomphalus hierlatzensis* Ammon, 1892 differing by its wider apical angle and smoother ornament (Szabo 2008, fig. 80).

Eucyclomphalus reminiscencius Kiel & Bandel, 2001 from the Campanian of northern Spain has a tall, conical shell with a strong, spiny keel and a strongly beaded cord below the suture. The shell consists of about 8 angular whorls and is 15 mm high. The early whorls have an apical angle of about 50°. The shell is composed of nacre (Kiel & Bandel 2001, pl. 1, fig. 3). *E. reminescencius* closely resembles the Early Jurassic type species, but the beaded cord below the suture is more strongly developed.

Genus *Trypanotrochus* Cossmann, 1918

Type species. – *Trochus normannicus* Orbigny, 1853 from the Pliensbachium of France (Wenz 1938, fig. 612), by original designation (possibly identical with *Trochus gea* Orbigny, 1853).

Remarks. – The conical shell with flat whorl sides is higher than wide and has an oblique circular aperture and ornament of 3–5 spiral ribs bearing fine nodules. The base bears spiral lines and the umbilicus is surrounded by a spiral ridge. Gründel (2007c, pl. 1, figs 11–18, pl. 2, figs 1–6) described *Trypanotrochus eolus* (Orbigny, 1853), *T. gea*, and an undetermined species with a strong fold on the middle of the inner lip from the Pliensbachian (Jurassic) of France. *T. gea* has a narrow apical angle, consists of 14 whorls, and is 23 mm high and 11 mm wide. *T. latus* Gründel, 2007 has finer ornament, a similar aperture, and a relatively wide apical angle. The early ontogenetic shell has ornament of axial ribs on the first teleoconch whorls, and spiral ribs begin later. Aside from a finer spiral ornament *T. latus* is a relatively broad member of the genus and is very similar to tall species of *Riselloidea,* to which it can be connected by the ornament of the early teleoconch whorls. *Trypanotrochus granuliferus* (Stoliczka, 1861) from the Hierlatz Limestone (Early Jurassic of Austria) has a high conical shell (Szabo 2008, fig. 79). It resembles better-known species of the genus but has neither protoconch nor shell structure preserved.

The shell shape of *Trypanotrochus* is quite similar to that of *Proconulus* Cossmann, 1918 and *Anticonulus* Cossmann, 1918. Axial ornament of the early teleoconch of *T. eolus* resembles that of *Eunemopsis*, *Eucycloscala* or *Eucylus*. Since *T. gea* has a fold in its inner lip and *T. latus* has a simple aperture without fold, these species could be related to the Eunemopsidae as well as the Eucyclidae. While Gründel (2007b) placed *Trypanotrochus* in the Trochidae, the same author at about the same time suggested its placement in the Eucycloscalinae Gründel, 2007 of the Eucyclidae Koken, 1996 (Gründel 2007c). *Trypanotrochus* as documented by Gründel (2007c) resembles *Lischkeia* Fischer, 1879 and *Bathybembix* among modern genera, but with relatively flattened sides of the whorls. The ornament of the early teleoconch in the Early Jurassic species is very similar to that of the modern species. *Trypanotrochus latus* closely resembles *Eucyclus juliae* from the same locality in the Pliensbachian of Normandy in France (Gründel 2007c, pl. 2, fig. 13 and pl. 3, fig. 5).

Genus *Eucycloidea* Hudleston, 1887

Type species. – *Turbo bianor* Orbigny, 1850 from Bajocian of England.

Remarks. – *Eucycloidea bianor* was illustrated by Gründel (1997, pl. 4, figs 1, 2) who determined a related species to represent a definite member of the Vetigastropoda with its shell consisting partly of nacre. *Eucycloidea granulata* (Hébert & Eudes-Deslongchamps, 1860) from the Jurassic of North Germany documents the juvenile shell (Gründel 2000, pl. 3, figs 10, 11). Here the change from the axially ribbed rounded early teleoconch to an angular conical shell is very similar to that observed in the modern *Pagodatrochus* from Aqaba (Fig. 10A–C).

Species of the Jurassic *Eucycloidea* have angled whorls and resembles in shell shape species of *Eucyclus* as well as the modern genus *Lischkeia* Fischer, 1879 with thin shell, and *Perrinia* H. Adams & A. Adams, 1854 with thicker shell. *Perrinia* species have similar ornament with an angulation in the middle of each whorls and spiral ribs dominating over axial ribs.

In *Eucycloidea verrucosa* Gründel, 2000 from the mid Jurassic of North Germany the protoconch is succeeded by rounded first whorls of the teleoconch with ornament of strong axial ribs crossed with fine spiral lines forming irregular rows of fine tubercles (Gründel 2000a, pl. 3, figs 12–16). This early ontogenetic shell closely resembles that described by Schröder (1995, pl. 1, figs 12–14). He also included a fractured shell with the central nacre layer that may belong to *Eucycloidea* or *Riselloidea* (also illustrated here, Fig. 9D–G). The fossil species resembles modern *Lischkeia alwinae* (Lischke, 1871) from the Pacific near Japan or *L. undosa* Kuroda & Kawamura, 1956 from the Philippines.

Eucycloidea madagascariensis sp. nov.

Figures 8E–I, 9A

Diagnosis. – The species is based only on the first three whorls of the shell, and later stages are unknown. The protoconch is smooth and ends in a rim and measures 0.2 mm. First and second teleoconch whorls are ornamented with strong, rounded axial ribs. The first teleoconch whorl has about 20 such rounded axial ribs. The rounded interspaces are covered by fine discontinuous wrinkles. The shell has a central nacreous layer (Figs 8E–I, 9A).

Type material. – The holotype is the specimen in Fig. 8I, deposited together with the other illustrated specimen in the Museum of the Geologisch-Paläontologisches Institut, University Hamburg, registration number SGPH No. 4683. From Lower Early Jurassic deposits just to the west of the town Sakaraha next to the road to the harbor town of Toleara (south western Madagascar) (Luger *et al.* 1994).

Description. – The protoconch has an ornament of rounded grooves and fine ridges (Fig. 8F). The first teleoconch whorl bears rounded axial ribs. On the second whorl two spiral ribs make their appearance (Fig. 8H). The fine pattern present between the ribs consists of wrinkles that follow the growth line pattern and form elongate pits and ridges. This differs from the background pattern of *Eucycloidea* sp. from the Jurassic of Germany, illustrated in Fig. 9D–F. Here the background pattern consists of irregular spiral ornament between the axial ribs, although about the same number of ribs (about 20) is developed on the first teleoconch whorl. The shell structure consists of an outer complex prismatic structure that forms the base to the central nacre, which is organized in stacks in a similar way to that documented in living *Gibbula* (Fig. 9B, C). Behind that zone the nacre is covered with a prismatic layer, which is well developed in *Eucycloidea*. This difference from the growing nacre just behind the shell margin in *Gibbula* is a result of the location of shell fracture quite far behind the aperture of the Jurassic shell. In modern species, nacre is formed only in a narrow zone near the margin of the growing shell. Further within, nacre is covered by prismatic layers.

Remarks. – The juvenile shell of *Eucycloidea madagascariensis* sp. nov. closely resembles that of *Eucycloidea verrucosa*, but has a somewhat narrower apical angle and no angulation on the second and third teleoconch whorl. Early teleoconch whorls have axial ribs and a fine pattern of radial wrinkles. Its protoconch is also smaller (0.2 rather than 0.25 mm across).

Etymology. – This species of *Eucycloidea* is named after its locality, in Madagascar.

Genus *Gerasimovcyclus* Gründel, 2005

Type species. – *Fusus clathratus* Lahusen, 1883 from the Oxfordium (Late Jurassic) of Russia, by original designation. Illustrated as *Turcica clathratus* by Kaim (2004, fig. 11A), by original designation.

Diagnosis. – The genus is based on a conical shell of the *Riselloidea* type of Eucyclidae with the early whorls of the teleoconch with rounded aperture but in later whorls the presence of a short, narrow anterior canal. *Gerasimovcyclus* apparently differs from *Eucycloidea* by having a deep suture of triangular section between the flattened sides of the teleoconch whorls. It resembles the modern *Turcica* H. Adams & A. Adams, 1854 in its conical shell shape, its ornament of beaded spiral ribs, and its flattened whorl sides and a well impressed suture, but *Turcica* species have a circular aperture.

Remarks. – In *Gerasimovcyclus clathratus*, the first and second teleoconch whorls are ornamented with strong, rounded axial ribs. The rounded interspaces are covered by fine, discontinuous wrinkles. Three species from the mid-Jurassic of Poland, *Turcica gerasimovi* Kaim, 2004, *T. ogrodzieniecensis* Kaim, 2004, and *T. wareni* Kaim, 2004 have been referred here. The first two, according to the description of *Gerasimovcyclus lorioli* by Gründel & Kaim (2006) can be placed in this genus with a Jurassic type species, as was suggested by Gründel (2005a). However, *Turcica wareni* Kaim, 2004 is here excluded from *Gerasimovcyclus* and is placed in *Pseudoturcica* gen. nov. The diagnosis of *Gerasimovcyclus,* according to which the first teleoconch whorl has axial ribs, as is characteristic of the Eucyclidae in general, does not apply to *T. wareni*.

Gerasimovcyclus mittai Gründel, 2005 from the Russian Jurassic does not have the protoconch and ornament of the first whorl preserved and, therefore, could also belong to *Pseudoturcica* gen. nov. defined below. *Gerasimovcyclus triplicatus* (Martin, 1862) hardly differs from a *Trypanotrochus broesamleni* Gründel, 2007 and *Eucycloscala brunhuberi* (Schnittmann, 1966) documented from the Sinemurian (Early Jurassic) of southern Germany (Gründel 2007b, pl. 2, figs 2, 3, pl. 3, fig. 1). It also does not have the early ontogenetic shell preserved. *Gerasimovcyclus* is very similar in shape to some living species of *Calliotropis* such as *C. actinophora* (Dall, 1890), living off-shore from Florida (Fig. 16D), and *C. glyptus* (Watson, 1879) from Australia (Poppe *et al*. 2006).

Genus *Riselloidea* Cossmann, 1909

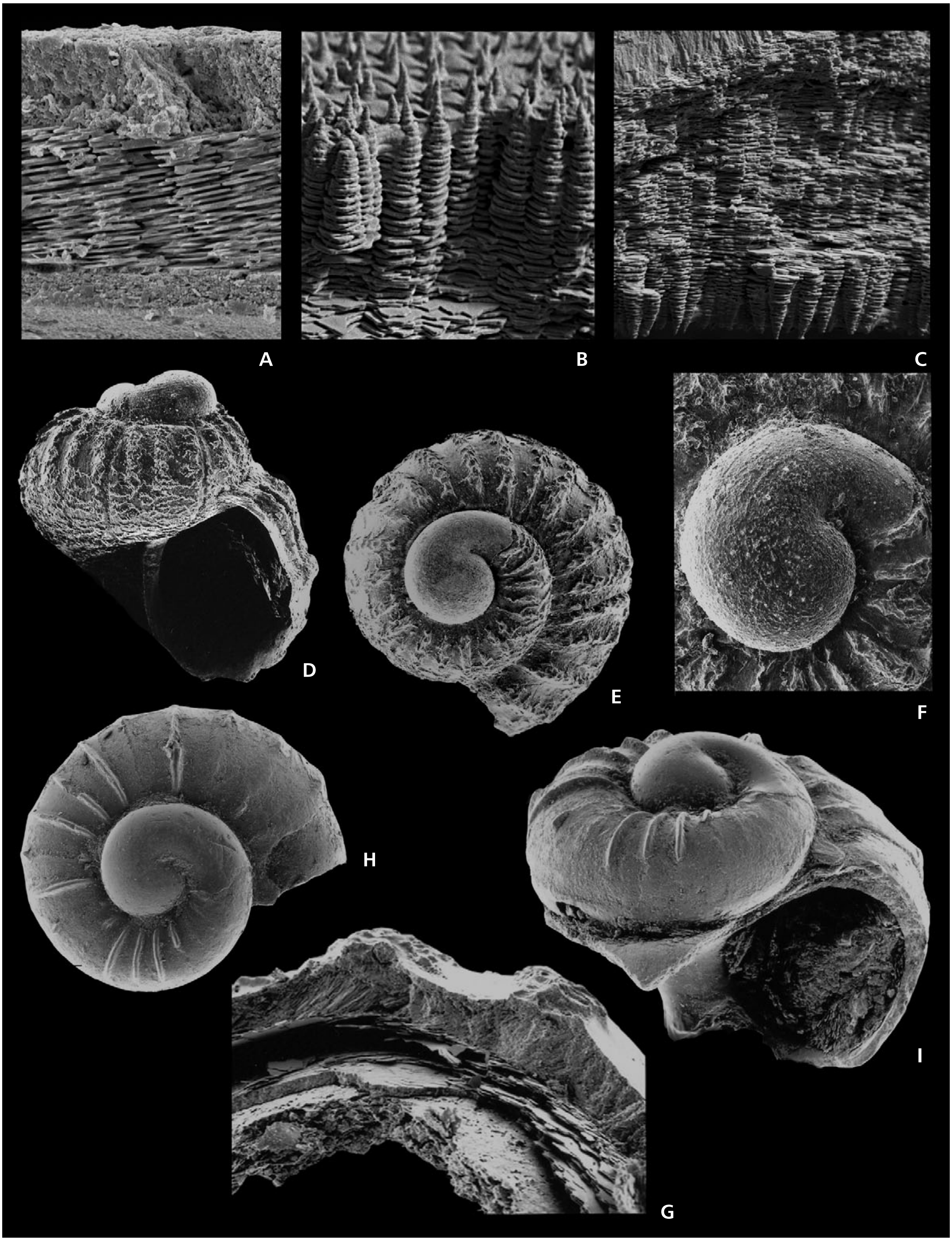
Risellopsis Cossmann, 1908, junior homonym of *Risellopsis* Kesteven, 1902; renamed *Riselloidea* Cossmann, 1909

Type species. – *Risellopsis subdisjuncta* Cossmann, 1908 (Wenz 1938, fig. 552), Jurassic of northern France.

Diagnosis. – Trochiform conical shell has a weakly convex base and whorls with flattened sides and a peripheral angle that lies above the suture. Ornament is of few spiral ribs on the sides and spiral ribs on the base, crossed by collabral axial ribs that may form nodes when they cross the spiral ribs. Base has an open umbilicus in young specimens, but later a callus of the inner lip fills it partially or totally. Plane of the aperture is inclined to the axis of coiling.

Remarks. – In their description of Jurassic species from Morocco, Conti & Monari (2001) discussed the similarity of *Riselloidea subdisjuncta; Riselloidea biarmata* (Münster 1844); and their genus *Sadikia* Conti & Monari, 2001, which was interpreted as having a similar type of juvenile shell. *Sadikia richensis* Conti & Monari, 2001 is documented by Conti & Monari (2001, figs 10, 15.1–6) as well as *Riselloidea* sp., but both species are not preserved sufficiently well to even document that they represent

Figure 9. A – from Jurassic of Madagascar, B, C – from *Gibbula* living in Canary Islands, D–I – from Jurassic of Germany. • A – shell structure of *Eucycloidea madagascariensis* sp. nov. from the Mid-Jurassic of SW-Madagascar near Sakaraha with prismatic structure on the outer (base) and the inner shell layer, and nacre composing the bulk of the shell wall (detail to Fig. 8I). • B, C – nacre columns on the growth surface just behind the shell margin in *Gibbula* from the Atlantic of La Palma, Canary Islands. B – nacre in growth zone with fractured shell. C – shell fractured documents a similar construction as in Jurassic *Eucycloidea* (Fig. 9A) with outer prismatic structure (upper left) and central nacre. • D–G – *Riselloidea* or *Eucycloidea* sp. from the Pliensbachian (Early Jurassic) of NW-Germany with juvenile shell ornamented by axial ribs and irregular spiral lines composed of tubercles (shell is about 0.6 mm wide) (coll. SMF 56010). E – same shell as D in apical view. Protoconch connected to the early teleoconch with axial ribs and fine spiral rows of tubercles. F – embryonic shell (about 0.25 mm) with ornament of pits, ridges and fine spiral ribs, outer lip curved. G – shell structure with complex prismatic outer layer, thin central nacre and thin inner prismatic layer (upper layer represent shell filling and is no part of the original shell wall). • H, I – *Eucycloscala izabellae* Kaim, 2004 with smooth embryonic shell (0.2 mm wide) and evenly ribbed early teleoconch. H – from above, I – from the side (shell about 0.45 mm wide) (coll. SMF 56009).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members of the Vetigastropoda. *Ooliticia* Cossmann, 1894 has a conical shell that consists of more or less rounded whorls with strong spiral ribs bearing nodules, similar to the short shell with rounded whorls and spiral ornament as in modern species of *Danilia* Brusina, 1865. The base is rounded and has the same ornament of spiral ribs. The aperture is circular and wide with low folds on the anterior inner lip. The type species of *Ooliticia* is *Turbo phillipsi* Morris & Lycett, 1851 from the mid-Jurassic of England (Wenz 1938, fig. 554; Knight *et al*. 1960, fig. 203.2a, b). Szabo (1995) regarded *Ooliticia* as resembling the Triassic genus *Eunemopsis* on the one hand and the living genus *Chilodonta* on the other by having a tooth on the inner lip. Kaim (2004, figs 12, 13) noted similarities to exist between *Ooliticia* and *Turcica*, as can also be noted from the description in Knight *et al*. (1960, fig. 203.2a, b), but neither shell structure nor the early ontogenetic shell are known of *Ooliticia*, so that it is not even certain that the genus is a member of the Vetigastropoda.

In *Riselloidea vaihingensis* Brösamlen, 1909 the protoconch is succeeded by a rounded first teleoconch whorl (Gründel 2003b, pl. 5, fig. 2.5). The morphology of the early shell was confirmed in *R. erratica* (Gründel & Koppka, 2007), which was named *Calliotropis erraticus* by Gründel & Koppka (2007). *Riselloidea erratica* has the first teleoconch whorl almost smooth, and only later axial ribs appear, while the spiral ribs appear on the third whorl. A nodular spiral ribs surrounds the umbilicus. The aperture is circular with a continuous margin (Gründel & Koppka 2007, pl. 1, figs 1–5). *R. erratica* resembles *Turbo heliciformis* Zieten, 1831 from the Pliensbachian of Germany, which was interpreted by these authors as representing the oldest species of *Calliotropis*. However, their species *Calliotropis erraticus* is better placed in the Jurassic genus *Riselloidea* even though the similarity is evident to *Calliotropis glyptus* (Watson, 1879) from deep water off New South Wales, eastern Australia, and *C. infundibulum* (Watson, 1879) from off Maine, eastern North America. *Riselloidea erratica* and *R. heliciformis* differ only in minor details of their ornament from modern *Calliotropis* species, but they are at least 180 Ma older. *Riselloidea bitorquata* (Hébert & Eudes-Deslongchamps, 1860) from the mid-Jurassic, described by Gründel (1997, pl. 3, figs 3–7), and Gründel (1999, pl. 1, figs 1–6; 2003) has a protoconch characteristic of that of the Vetigastropoda. *R. bitorquata* is very similar to *Calliotropis acheronti* Marshall, 1979, living in the south-west Pacific Ocean around New Zealand (Marshall 1979, Vilvens 2007). In *Riselloidea multistriata* (Böckh, 1874), the shape of the protoconch is unknown (Szabo 2008, fig. 77), as is also the case in *R. noszkyi* Szabo, 1995. Both are from early Jurassic Hierlatz Limestone. Kaim (2004) determined *R. bitorquata* as *Calliotropis biarmata* and included in this species also *Riselloidea sauvagei* (Cossmann, 1895). Its juvenile shell with protoconch and first whorl of the teleoconch was documented by Schröder (1995, pl. 1, figs 12, 13, pl. 14, fig. 1) from the Jurassic of northern Germany (Fig. 9D–F). The protoconch is about 0.22 mm wide and is ornamented with two fine spiral ribs and a fine pattern of irregular ridges. It margin has a sinuous outline. The first teleoconch whorl has an ornament of rounded axial ribs with irregular spiral wrinkles crossing their crests.

Riselloidea resembles *Pseudoclanculus* and *Eunemopsis* from the Triassic St. Cassian but has no fold on its inner lip. Modern species of *Lischkeia* can be very similar as well, and they have also similar ornament of their early teleoconch whorls. Thus some species currently referred to *Riselloidea* have similar shape as species of *Lischkeia,* whereas other species with a more conical shape, an angled base, and ornament of axial and spiral ribs resembles modern species of *Calliotropis*.

Trochus biarmatus Münster, 1844 from the Middle Jurassic of Marocco was indentified as *Riselloidea biarmata* by Conti & Monari (2001, figs 6.21–26). This species is 14 mm high with 11 whorls. Its shape is conical, with a rounded base and ornament of three strong, spiny spiral ribs. This *Biarmatoidella* Gründel, 2003 resembles *Riselloidea* but has stronger spiny ornament (Gründel 2003c). Gründel (2000a, pl. 7, figs 1–3) still determined this species as a member of the genus *Riselloidea*. However, the first teleoconch whorl is ornamented with axial ribs in *Biarmatoidella,* while the first teleoconch whorl of *Riselloidea* is described as smooth before axial ribs appear. While Gründel (2003d, pl. 5, figs 4, 5) suggested that *Riselloidea biarmata* belongs in the family Proconulidae, Gründel (2003b) preferred the family Eucyclidae including here *Biarmatoidella* and also *Trochonodus* Nützel *et al.*, 2003. In *Trochonodus* species all spiral ribs have nodes and axial ribs are strong. Obviously the species of the three genera *Riselloidea*, *Biarmatoidella* and *Trochonodus* are difficult to distinguish from each other by a clear set of characters. Kaim (2004) suggested that the Jurassic species of *Riselloidea* should be placed with modern *Calliotropis* Seguenza, 1902. This suggestion was accepted by Gründel (2007c) who included *Biarmatoidella*, *Riselloidea*, and *Trochonodus* in the Calliotropinae Hickman & McLean, 1990. Consequently, Gründel & Koppka (2007) placed two species of *Riselloidea* with *Calliotropis*. Among living species, those included in *Mirachelus* Woodring, 1918 resemble the Jurassic species included in *Biarmatoidella*. *Riselloidea vierowiensis* Gründel, 2000 resembles *Riselloidea biarmata,* but it has no spines and has an ornament of finer spiral ribs (Gründel 2000a, pl. 6, figs 16, 17, 2003d, pl. 5, figs 6, 7). *Biarmatoidella* is suggested here to be a synonym to *Riselloidea* and to be distinct from *Calliotropis,* the type species of which lived at least 175 Ma later.

Family Pseudoturcicidae fam. nov.

Type genus. – *Pseudoturcica* gen. nov.

Diagnosis. – Adult shell resembles that of *Riselloidea* among the Jurassic species while early teleoconch has ornament of a network of zigzagging or branching lines and axial ribs appear later. The family is based on *Pseudoturcica* gen. nov.

Remarks. – Among living species a similar ornament of the early teleoconch is found in *Anxietas* Iredale, 1917, *Sericogyra* Marshall, 1988, and *Thelyssina* Marshall, 1983, all of which are interpreted to be related to *Seguenzia* and to represent Seguenzioidea. They have a radula of the character found among the Seguenziidae, as is documented by Marshall (1988, figs 4, 5, 1991, figs 5, 10). *Asthelys* Quinn, 1987 and *Anxietas* have early teleoconch ornament described as branching dendritic threads. Later whorls, in contrast to those of *Pseudoturcica,* are predominantly smooth. Marshall (1991) introduced a subfamily Asthelysinae, including in it *Asthelys* and *Anxietas.* But also *Sericogyra,* with rounded whorls and spiral ornament, and *Thelyssina* with conical triangular shape, have the protoconch succeeded by a rounded early teleoconch, with the ornament formed by a net of branching lines (Marshall 1983, figs 5D–H, 1988, figs 3E, K, 1991, figs 15, 20).

Genus *Pseudoturcica* gen. nov.

Type species. – *Turcica wareni* Kaim, 2004, as described by Kaim (2004, fig. 13) from the mid-Jurassic of Poland.

Diagnosis. – Shell shape resembles that of *Riselloidea* with conical shape and ornament of axial ribs crossed by spiral ribs. Base is set off by an angulation and is ornamented with mainly spiral ribs. Aperture is simple. The difference to *Riselloidea* or *Eucycloscala* lies in the ornament of the early teleoconch. Here the protoconch is succeeded by the first teleoconch whorl, which is ornamented by fine zigzag lines. The beginning of many axial ribs and few spiral ribs is only on the second or third teleoconch whorl. The fully grown shell resembles that of modern *Turcica*.

Etymology. – The shell in the genus has the shape of a *Turcica* A. Adams, 1854 but characteristic fine zigzag ornament of its early teleoconch in contrast to the axial ribs, thus "pseudo" of *Pseudoturcica*.

Remarks. – *Pseudoturcica wareni* as described by Gründel (2007a, pl. 2, figs 17, 18) from the Early Jurassic of north-eastern Germany differs from *Turcica, Eucycloscala* and *Riselloidea* species in the ornament of the early teleoconch. On the first two whorls a zigzag pattern of fine ribs is present and axial ribs are added only within the second or third whorl. A similar pattern of the juvenile teleoconch was noted by Gründel & Nützel (1998, pl. 2, figs 1–3) on a Pliensbachian species from southern Germany. Gründel (1999, pl. 3, figs 1–7) identified *P. wareni* as Trochoidea gen. and spec. undetermined from the late Early Jurassic of north-eastern Germany, with the inclined zigzag pattern of the first teleoconch whorl well developed. A species determined as *Eucycloscala dunkeri* (Goldfuss, 1844) has a protoconch of 0.27 mm in width, succeeded by rounded trochispiral whorls of the early teleoconch, ornamented by a fine honey-comb pattern, and later also axial ribs. Two spiral ribs appear with beginning of the second teleoconch whorl. The later whorls are angular and more spiral ribs appear (Gründel 2007a, pl. 3, figs 4–7).

Family Chilodontidae Wenz, 1938

Type genus. – *Chilodonta* Etallon, 1859 from the Late Jurassic.

Remarks. – The small and robust shells mostly possess ornament of spiral ribs. Numerous spiral and axial ribs produce reticulate ornament or finely scaly pattern. The adult aperture has teeth on the inner lip as well as on the interior of the outer lip. The first teleoconch whorl is ornamented with axial ribs. Similar ornament is found in Eucycloscalidae, Euchelidae and Pagodatrochidae without teeth on the outer lip of their aperture. The inner lip of Chilodontidae has one or two teeth on the inner side rather than a ridge as in the Eunemopsidae (*Eunemopsis* and *Pseudoclanculus*).

Wenz (1938) included in his Chilodontinae not only the Jurassic genera *Chilodonta* and *Chilodontoidea*, with its subgenus *Wilsoniconcha* Wenz, 1938 (replacement name for *Wilsonia* Hudleston, 1896, preoccupied), but also the Triassic genus *Pseudoclanculus* and the Early Cretaceous genus *Agathodonta.* This was accepted by Gründel (2007c), who added *Odontoturbo*. Hickman & McLean (1990) expanded the Chilodontidae to include living species, but these are here treated in a the family Calliotropidae. *Agathodonta* has a small, solid shell that is higher than wide, with spiral ribs with tubercles. Its outer lip has internal ridges and inner lip has a larger tooth. The type species is from the Early Cretaceous (Cossmann 1918, Wenz 1938, fig. 653, misspelled *Agnathodonta*). Living species of the genus were recognized by Hickman & McLean (1990, fig. 40E). *Agathodonta nortonia* McLean, 1984 resembles the fosssil type species from the Early Cretaceous (McLean 1984). It could also be placed in *Herpetopoma,* but is considered to have more prominent teeth on the inner lip. Another possible position is *Danilia,* which it resembles in shape but differs from it in some characters of the ornament.

Kano *et al*. (2009) classified most genera of Eucyclinae *sensu* Hickman & McLean (1990) in Chilodontidae and Calliotropidae. The two were interpreted as sister tribes or as two subfamilies in Chilodontidae (Bouchet *et al.* 2005, Williams *et al*. 2008). Molecular data indicate that Calliotropidae are more closely related to Seguenziidae than to Chilodontidae. However, the species considered by them to represent Chilodontidae are here considered to belong to the Pagodatrochidae, Turcicidae and Calliotropidae (see below).

Genus *Chilodonta* Etallon, 1859

Type species. – *Chilodonta clathrata* Etallon, 1859 (Cossmann 1918, fig. 71; Wenz 1938, fig. 651).

Remarks. – *Chilodonta* has the rounded conical shell higher than wide, with narrow whorls separated by deep sutures, and large body whorl occupying 60% of shell height. Ornament consists of a reticulate pattern formed by spiral ribs and vertical axial ribs. The base is convex. The rounded aperture has a heavy circular rim and is denticulate on the inner and outer lips; the outer lip forms a varix. *C. clathrata* resembles Late Cretaceous *Chilodonta* as documented by Sohl (1998, pl. 6, figs 1–17) and Kiel & Bandel (2001, pl. 2, figs 3–8). *Chilodonta ilerdensis* (Vidal, 1921) from the Campanian of the Tremp Basin (Spain), the 0.3 mm wide protoconch is surrounded by the first rounded, helical whorls of teleoconch whorl, which has an ornament of axial ribs that are continuous from one suture to the other. The fully grown shell is about 10 mm high and 6 mm wide, consists of six whorls, 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 teeth. It has four teeth on the inner lip, the anterior part has a strong plate. The base bears only spiral cords (Kiel & Bandel 2001, pl. 2, figs 5–8). *Chilodonta crespelli* Bataller, 1959 from the same Campanian locality has a conical shell about 6.5 mm high and wide with four whorls, ornament of keel-like axial ribs and weaker spiral lines, which also cover the base, and a keeled margin. The inner lip, with callus, carries two small, closely spaced teeth and the interior of the outer lip has four teeth (Kiel & Bandel 2001, pl. 2, figs 3, 4).

Chilodonta obliqua Sohl, 1998 from the Late Cretaceous (Maastrichtian) of Puerto Rico is similar to the species from the Campanian of Spain. It differs from them by the presence of wrinkles and tubercles on the callus of the inner lip (Sohl 1998, pl. 6, figs 1–17). Ornament is of spiral ribs forming a rectangular pattern with the axial ribs. The shell is about 8 mm high and 6 mm wide with up to six whorls. The teeth and ridges in the adult aperture are characteristic to the species. *Chilodonta jamaicaensis* Sohl, 1998 has a taller spire (Sohl 1998, pl. 7, figs 1–3, 10) and appears to be closely related to *C. ilerdensis*. The ornament of the first whorl of the teleoconch documented by Sohl (1998) consists of numerous curving axial ribs, with spiral ribs beginning within second teleoconch whorl.

The aperture of *Chilodonta marcaisi* Orbigny, 1842 from the Turonian of the Uchaux Basin is smaller than in the species described above and the anterior inner lip carries only one tooth (Roman & Mazeran 1913). *Chilodonta rudis* Binkhorst, 1861 from the Maastrichtian has four teeth on its inner lip and has fine ornament (Kaunhowen 1897). *Chilodonta geslini* Archiac, 1847, as figured by Weinzettl (1910, pl. 2, figs 16–19) from the Upper Cretaceous of the Czech Republic, differs in having an ornament of more numerous spiral ribs. *Chilodonta ovallei* (Philippi, 1887) from the Maastrichtian of the Quiriquina Formation, Central Chile, is quite large and is ornamented with numerous nodulose spiral ribs (Bandel & Stinnesbeck 2000).

Genus *Wilsoniconcha* Wenz, 1939

Type species. – *Wilsonia liassica* Hudleston, 1896 from the Early Jurassic of England (Hudleston 1895, fig. 13; Cossmann 1918, fig. 79; Wenz 1938, fig. 650).

Remarks. – The shell is somewhat egg-shaped with spiral rows of nodules, and with two teeth on the inner lip. *Wilsoniconcha tora* Gründel, 2007 from the Pliensbachian of France is less rounded but also has allometric growth (Gründel 2007b, pl. 4, fig. 12.4) and closely resembles living *Cidarina cidaris* (Carpenter, 1864) (Hickman & McLean 1990, fig. 44G). *Wilsoniconcha* is transitional to *Chilodonta,* which has teeth also on the inner side of the outer lip.

Genus *Hudledonta* Kiel & Bandel, 2001

Type species. – *Chilodontoidea ooliticia* Hudleston, 1896 from the Bajocian of Dorsetshire (Wenz 1938, fig. 649; Kiel & Bandel 2001).

Remarks. – The small pupoid shell has a high spire and well developed sutures. Ornament consists of spiral and axial ribs forming a reticulate pattern. The last whorl is a little less expanded than former whorls, with rounded aperture that has a short funnel on its upper edge and bears a thickened, continuous callus margin in fully grown individuals. The inner lip has an upper tooth and may be thickened. *Hudledonta nicolae* Kiel & Bandel, 2001 from the Campanian of northern Spain has the protoconch succeeded by a rounded first teleoconch whorl with an ornament of strong axial ribs. The concave whorl-sides are sculptured with five beaded spirals per whorl, there is no axial ornamentation. The trochiform shell consists of seven whorls. The aperture is circular with one tooth at the base of the inner lip. The shell is 9 mm high, 7 mm wide, and exhibits allometric growth, with the early whorls forming an apical angle of about 70° which lowers to about 40° on the last one (Kiel & Bandel 2001, pl. 2, figs 1, 2).

Sohl (1987) interpreted the Jurassic *Hudledonta* (= *Chilodontoidea*) and *Wilsoniconcha* as well as the predominantly Cretaceous *Chilodonta* Étallon, 1859, *Calliomphalus* and *Planolateralus* Sohl, 1960 as composing a large portion of the Mesozoic Trochidae, which mostly became extinct during the transition from the Cretaceous to the Tertiary. This discontinuity of the group was shown to be erroneous (Kiel & Bandel 2001).

Genus *Denticulabrum* Sohl, 1998

Type species. – *Denticulabrum laevigatum* Sohl, 1998 from the Maastrichtian of Jamaica.

Remarks. – *D. laevigatum* with a conical shell of seven whorls and 6.5 mm in width and height. It apical angle changes from wider in the early teleoconch to narrower in the later teleoconch. The shell has flat sides ornamented by spiral ribs and a nodular ribbon below the suture. The oblique aperture has a channel separated from the anterior part of the aperture by a plate and ridges on the interior of the inner and outer lips. The protoconch is succeeded by a rounded early teleoconch whorl bearing axial ribs and only later the spiral ornament begins and whorls become more flattened (Sohl 1998, pl. 15, figs 1–9). *D. duckettsensis* Sohl 1998 has more numerous spiral ribs than *D. laevigatum* (Sohl 1998, pl. 16, figs 1–3, 5, 6, pl. 17, figs 1–10). Sohl (1998) suggested that *Denticulabrum* is derived from *Discotectus* Favre, 1913 by modification of the aperture, but the early ornament of the teleoconch of *Discotectus* consists of spiral ribs, indicating a different place within the Vetigastropoda.

Family Pagodatrochidae fam. nov.

Type genus. – *Pagodatrochus* Herbert, 1889.

Diagnosis. – Small shell is higher than wide with flattened apex and a conical teleoconch with angular whorls. Protoconch is surrounded by a round first teleoconch whorl with simple axial ribs. On the second teleoconch whorl, trochispiral shape begins and whorls become angular due to the appearance of strong spiral ribs. Rounded base has open umbilicus and aperture is circular, and closed by an organic operculum with central nucleus (Herbert 1998, figs 1a–f, figs 2a, b, fig. 3, figs 4a–c). The radula has four pairs of lateral teeth (Herbert 1989, fig. 5), and the early teleoconch has ornament of axial ribs.

Remarks. – The living species of the genus *Pagodatrochus* from the Indian Ocean closely resembles *Eucycloidea* from the Jurassic in teleoconch characters, while the early ontogenetic shell is flat and more resembles that of some species of *Eucycloscala* such as *E. elegans* (Fig. 2D–F).

Genus *Pagodatrochus* Herbert, 1989

Type species. – *Minolia variabilis* H. Adams, 1873 from the Persian Gulf, by original designation. This species was also noted in the Red Sea by Yaron (1979) and has been described in detail by Herbert (1989).

Remarks. – The shell is characterized by a strong change in ornament during ontogeny. Following the protoconch, an inflated rounded first teleoconch whorl has ornament of strong axial ribs and is almost planispiral. In the second whorl, trochospiral coiling begins, along with spiral ornament, with one spiral cord forming an angulation. Later ornament is formed by cancellate ribs. The base is inflated with an umbilicus and a simple, vertical, circular aperture. The spire outline is stepped. The species was encountered living on the shallow reef platform of the Gulf of Aqaba at Aqaba. The shell has turbiniform shape when young, becoming elongate to pagodiform with growth (Fig. 10A–C).

***Pagodatrochus variabilis* (H. Adams, 1873)**
Figure 10

Remarks. – Specimens were found living in the shallow lagoon between beach and reef near the Marine Station at Aqaba. The apex is flattened and the teleoconch has up to 6.5 almost tubular whorls. Sutures are impressed and the periphery lies at mid whorl. Sculpture consists of spiral ribs and axial folds, with two prominent spiral ribs at the periphery. The base is convex with a deep umbilicus and the aperture is almost circular. The operculum has a central nucleus, concentric construction and is organic in composition. The protoconch is less than 0.2 high and more than 0.15 mm in diameter. Its margin is thickened and ornament consists of very fine spiral ribs. The first teleoconch whorl is inflated and coiled in a plan, and only the second whorl changes to trochospiral coiling, with ornament consisting of sharp, straight axial ribs with only very fine growth increments between them. In the second whorl a spiral rib appears that forms an upper angulation, and a little later also several smaller spiral ribs are formed on the angulation around the base. These ribs become more dominant over the axial ones, with the one highest on the whorl the strongest, and those on the basal angulation variable in number. Ornament varies between individuals. The spiral rib surrounding the umbilicus develops either axial folds or rounded tubercles.

The structure of the shell consists of an outer layer with acicular, somewhat spherulitic biocrystals of aragonitic composition. Transition to the nacreous layer is sharp and nacre tablets are of the normal type in arrangement of stacks of coins. Growth-zones on the margin of the aperture are well marked with the nacreous zone ending with begin of a thin inner prismatic layer.

The radula (Fig. 10D–G) has the central tooth accompanied by four pairs of lateral teeth, all of which have several cusps on the cutting edge. The central tooth is longer than wide, with wide rounded base, narrow middle area, and wide cutting edge with five cusps. Its anterior part is accompanied by lamellae, on which the margins of the cutting edges of the inner pair of lateral teeth can be rested when the radula is folded. The lateral teeth are elongate with strongly bent median part. Their margins overlap each other and have a strong cusp on their cutting edge accompanied by 2–3 inner and 3–4 outer cusps. Neighbouring teeth fit into grooves next to a median ridge. The marginal teeth are slender. More than 20 are present on each side of the radula, all with spoon-like top with narrow cusps on the margins. The innermost pair of marginal teeth has a wide base on which the base of the outer lateral tooth may be fitted.

Pagodatrochus variabilis from Aqaba has similar radula characters to specimens from the coast of South Africa described by Herbert (1989, fig. 5). The radula resembles that of *Turcica caffea* (Gabb, 1865) from California (Hickman & McLean 1990, fig. 43C) regarding shape of the central and lateral teeth, and the presence of four pairs of lateral teeth. A transitional innermost marginal tooth as in *Pagodatrochus* is documented in case of *Calliotropis hataii* Rehder & Ladd, 1973 (Hickman & McLean 1990, fig. 47H), but *C. hataii* has only three pairs of lateral teeth. Herbert (1989) suggested that the radula places *Pagodatrochus* near the Gibbulinae. However, no similar radula or shell to that of *Pagodatrochus* can be noted among the species of the Gibbulinae studied by Hickman & McLean (1990, fig. 58), whereas the radula of *Turcica* has a similar central zone. The radula of several species of the Gibbulinae from the Mediterranean Sea and the Pacific was studied (own data) and confirm the data presented by Hickman & McLean (1990). The early ontogenetic shell of the first teleoconch whorls does not agree with any member of the Gibbulinae (compare Bandel 1982, Beck 1995). Neither the ornament of the first teleoconch whorls, bearing spiral ribs, nor the trochispiral mode of coiling agree, while those of Triassic Eucycloscalidae are closely similar.

Family Turcicidae fam. nov.

Type genus. – *Turcica* H. Adams & A. Adams, 1854.

Diagnosis. – Shell of conical shape, ornamented with spiral ribs with tubercles. Folds are present on the inner lip in the circular aperture. The protoconch is succeeded by early teleoconch with prominent axial ribs. Shell composition includes an inner nacreous layer. The central field of teeth of the radula has four lateral teeth (nine teeth).

Remarks. – *Turcica* had been proposed by Habe (1976) as type genus to the Turcininae, but without diagnosis. The family also includes *Lischkeia* Fischer, 1879. Most species of *Turcica* have a thick shell wall, whereas the similar *Lischkeia* Fischer, 1879 has a thin shell; both live in the Pacific. Similar shape is found in *Mirachelus* Woodring, 1928 and *Solariella* Dall, 1919 and *Danilia* Brusina, 1865. Preliminarily included is also *Perrinia* H. Adams & A. Adams, 1854.

Genus *Turcica* H. Adams & A. Adams, 1854

Type species. – *Turcica monilifera* Adams, 1854 from the Pacific.

Remarks. – The shell has a conical shape, with whorls ornamented with spiral ribs with tubercles. Two folds are present on the inner lip in the circular aperture. The spiral rib just above the periphery is stronger than the others (Wenz 1938, fig. 566; Hickman & McLean 1990, fig. 40A). The protoconch is succeeded by early teleoconch with prominent axial ribs. Shell composition includes a thick inner nacreous layer. The central row of teeth of the radula has four lateral teeth. Most species of *Turcica* have a

Figure 10. *Pagodatrochus variabilis* (H. Adams, 1873) from the Gulf of Aqaba. • A – 2.2 mm high shell with flattened apex, first spiral ribs on second whorl and organic operculum with spiral construction (SGPHM, No. 4684). • B – apical whorls with 0.18 mm wide protoconch surrounded by first teleoconch whorl with simple axial ornament. • C – protoconch (0.18 mm wide) is ornamented by fine spiral ribs and has outer lip of the aperture thickened. • D–G – radula. D – median row of the radula with central tooth accompanied by four pairs of lateral teeth, all of which have the cutting edge with several cusps. E – anterior part of radula ribbon with the 9 teeth of the central row forming a line with overlap of their bases and more than 20 marginal teeth on each side with spoon-like top with narrow cusps on the margins (0.2 mm in width). F – teeth of the side of the radula with marginal teeth forming interconnected rows with the base of the innermost pair connected to the base of the outer lateral pair by groove and ridge. G – half row with central tooth longer than wide and wide rounded base, narrow middle and wide cutting edge with five cusps. Bases of teeth of the central zone fitted with their base. Marginal teeth more elongate in shape.


A
B
C
D
E
F
G

thick shell wall, whereas the similar *Lischkeia* Fischer, 1879 has a thin shell; both live in the Pacific. Similar shape is found in *Mirachelus* Woodring, 1928 and related genera from the Caribbean Sea.

Kano *et al*. (2009), analyzing *Turcica coreensis* Pease, 1860, noted that molecular data indicate that *Turcica* and the Calliotropidae are more closely related to Seguenziidae than to Chilodontidae. Characters discriminating the Chilodontidae from the Calliotropidae include a smaller and thicker shell and the presence of teeth on the apertural inner lip and a thickened outer lip (Hickman & McLean 1990). *Turcica monilifera* Adams, 1854 from Australia, has a relatively thick shell with ornament of granulose spiral ribs (Fig. 15A–C). The radula of *Turcica caffea* (Gabb, 1865) from California was illustrated by Hickman (1984, fig. 15B) and Hickman & McLean (1990, figs 43B, C, F). It has nine teeth in the central field, contrasting to that of *Euchelus, Calliotropis* and *Hybochelus,* which have seven teeth in the central field and long, and thin marginal teeth (Hickman & McLean 1990, figs 43A, D, fig. 47).

Genus *Lischkeia* Fischer, 1879

Type species. – *Trochus moniliferus* Lamarck, 1816 from the eastern Pacific (according to Kano *et al.* 2009).

Remarks. – Species of *Lischkeia* have the callus of the inner lip rounded and with central groove (Wenz 1938, fig. 569; Hickman & McLean 1990, fig. 44E). *L. monilifera* closely resembles *L. imperialis* (Dall, 1881) from the Strait of Florida (Fig. 11I) with a thin shell 50 mm high, with more than five whorls, its sutures deep and the umbilicus covered (Wenz 1938, fig. 567; Abbott 1974, fig. 262; Quinn 1979, figs 29, 30). Ornament consists of blunt nodules on the periphery of the whorl and a further row with smaller nodules lies above the angulation around the flattened base, which lacks an umbilicus. The juvenile shell of *L. imperialis* has a rounded, smooth protoconch succeeded by ornament of simple axial ribs on the first teleoconch whorl and the later appearance of spiral ribs. The juvenile shell (illustrated in Fig. 11I) is about 3.5 mm high.

Kaim (2004, figs 5–7) placed Jurassic species from Poland that resemble *Lischkeia imperialis* and *L. alwinae* (Lischke, 1871) in the genus *Eucycloscala*, but their shape and ornament more closely resembles those of living *Lischkeia* than those of Triassic *Eucycloscala* species. Kano *et al*. (2009) noted that molecular data indicate that *Lischkeia* is close to the Calliotropidae. They analyzed *Lischkeia imperialis* and *Turcica coreensis* Pease, 1860, both with relatively thin shell, one or two teeth on their inner lip and slightly thickened outer lip.

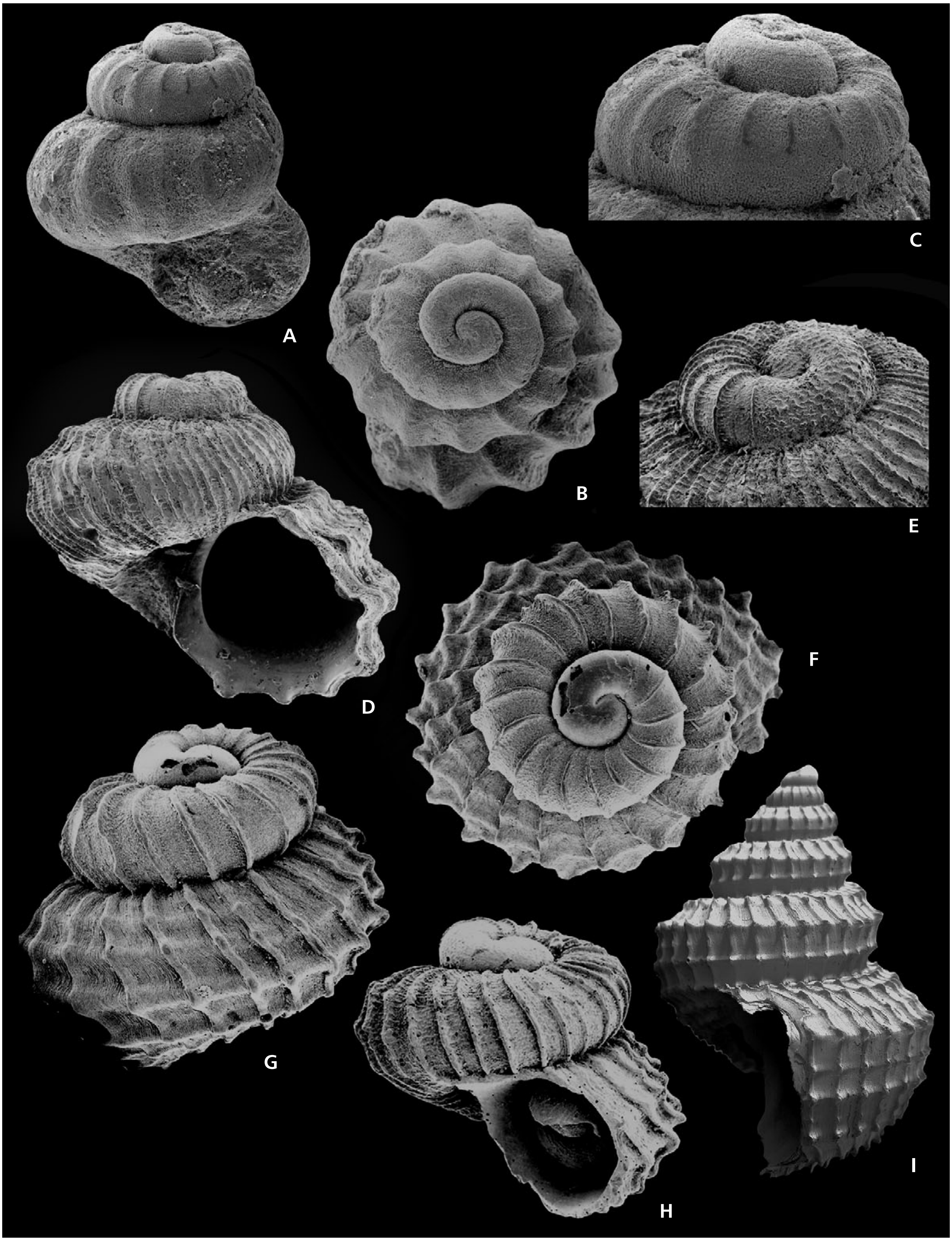
Genus *Mirachelus* Woodring, 1928

Type species. – *Euchelus* (*Mirachelus*) *corbis* (Dall, 1889) from the Caribbean Sea (Wenz 1938, fig. 575; Abbott 1974, fig. 259; Quinn 1979, figs 35, 36, 1991b).

Remarks. – The small conical shell has a flattened base and ornament of straight axial and spiral ribs crossing each other, forming a regular pattern of rectangles. *Mirachelus guttarosea* Dall, 1889 is about 5 mm high and wide and the shell consists of about five rounded whorls. Its aperture is circular and the inner lip bears two teeth (Abbott 1974, fig. 258; Quinn 1979, figs 37, 38). Juvenile shells that probably belong to *M. guttarosea* from the Gulf of Mexico near Yucatan have a protoconch of about 0.28 mm in diameter with an upturned straight margin of its aperture. It is ornamented with axial wrinkles in a spiral arrangement (Fig. 11D, E). The evenly convex, trochispiral first teleoconch whorl is ornamented with strong narrow axial ribs with fine spiral wrinkles between them. Spiral ornament begins on the second whorl and continues to the last whorl. While in the juvenile shell the convex base has a narrow umbilicus surrounded by a spiral rib, the umbilicus is closed in the fully grown shell. The juvenile shells of *M. guttarosea* from the Gulf of Mexico resemble those of *Euchelus* from the Indonesian region in shape and ornament (Fig. 11F–H).

The radula of *Mirachelus clinocnemus* Quinn, 1979 has a central tooth with a triangular cutting edge and marginal lamellae on its narrow anterior part, resembling that of *Euchelus*. But in contrast to the radula of *Euchelus,* with

Figure 11. A–C – *Lanascala cassiana* Bandel, 1992 from St. Cassian Formation of Cortina d'Ampezzo (coll. NHM Wien No. 1992/209), D–I – juvenile shells of living species of *Mirachelus* and *Euchelus*. • A – juvenile shell with early teleoconch ornamented by rounded axial ribs and a fine pattern of wrinkles (shell about 1 mm high). B – apical part with the embryonic shell ornamented by fine spiral lines (shell about 0.8 mm wide). C – detail of the embryonic whorl with ornament of spiral lines (about 0.2 mm wide). • D, E – *Mirachelus guttarosea* (Dall, 1889) from the shallow Gulf of Mexico at Yucatan. D – juvenile shell (about 1 mm high) with transition from the regular axial ribs of the first teleoconch whorl to later of nodular spiral ribs. E – protoconch of the same shell (0.28 mm wide) with ornament and thickened aperture. • F, G – *Euchelus* cf. *atratus* (Gmelin, 1791) from Satonda, Indonesia. F – protoconch (about 0.22 mm wide) with ornament of pits and ridges. G – same juvenile shell (0.8 mm wide) with regular axial ornament of first teleoconch whorl. • H – juvenile shell with transition of the regular axial ribs on the first teleoconch whorl to cross-rib pattern of the later shell (shell about 0.7 mm high). • I – juvenile shell of *Lischkeia imperialis* (Dall, 1881) from the shelf of the south-eastern US (off Cape Kennedy) with ornament of simple axial ribs on the first whorl of the teleoconch and later appearance of spiral ribs (shell about 3.5 mm high) (SGPHM, No. 4685).



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three pairs of lateral teeth, *M. clinocnemus* has four pairs with a triangular, serrated cutting edge (Quinn 1979, fig. 89). The shell of *M. clinocnemus* resembles that of *M. corbis.* Wenz (1938) interpreted *Mirachelus* as a subgenus of *Euchelus,* but that cannot be accepted because of the difference in the number of lateral teeth in the radula: three pairs in *Euchelus* and four in *Mirachelus*. *Mirachelus* resembles the Jurassic *Biarmatoidella biarmata* (Münster, 1844) and *B. lorioli* (Greppin, 1898) (Gründel 2003c, pl. 6, figs 5–10) in shell shape.

Genus *Solaricida* Dall, 1919

Type species. – *Solariella hondoensis* Dall, 1919 living near Japan, was considered a synonym to *Calliotropis* by Wenz (1938).

Remarks. – *Solaricida infundibulum* (Watson, 1879) lives in the Northern Atlantic as well as the southern Pacific around New Zealand (Marshall 1979, figs 4E–G). Its radula has four lateral teeth (Marshall 1979, figs 9C–F). Here the central tooth has lateral wings forming a hood next to the cutting edge. The lateral teeth consist of an inner, larger pair and an outer, smaller pair. The protoconch of *Solaricida* cf. *calatha* (Dall, 1927) from the deep shelf off northern Florida is smooth and well rounded and is about 0.35 mm in diameter. The first teleoconch whorl has simple, straight axial ribs, and only later spiral ornament appears and becomes dominant. Similar species were described by Quinn (1979) from off Florida (Fig. 16G). Here the margin of the aperture is straight and a little uplifted. The first, inflated teleoconch whorl has an ornament of strong axial ribs and a few weak spiral ribs on a background of fine collabral rows of tubercles. The axial ribs dominate from the second teleoconch whorl and the spiral rib above the suture changes to form an angulation, which on the third whorl is a ribbon crossed by the axial ribs, forming nodules. On the fourth teleoconch whorl axial ribs are strong on the upper whorl, weak further down, but still form nodules with the spiral keel. The dominant ornament is now formed by many spiral ribs, which also cover the base.

Calliotropis or *Solaricida actinophora* (Dall, 1890) from the American Atlantic shelf, determined according to Quinn (1979, figs 21, 22), has a smooth, inflated protoconch almost 0.6 mm wide and a straight, raised margin. The inflated first teleoconch whorl has axial ribs at first, and three fine spiral ribs make their appearance on the third whorl (Fig. 16D). The background is covered by fine spirally elongated tubercles on smooth surface. On the second whorl the lower of the spiral ribs form a keel on which the axial ribs form spine-like angulations. This ornament results in a narrow shoulder, a flattened side and an angulation around the base.

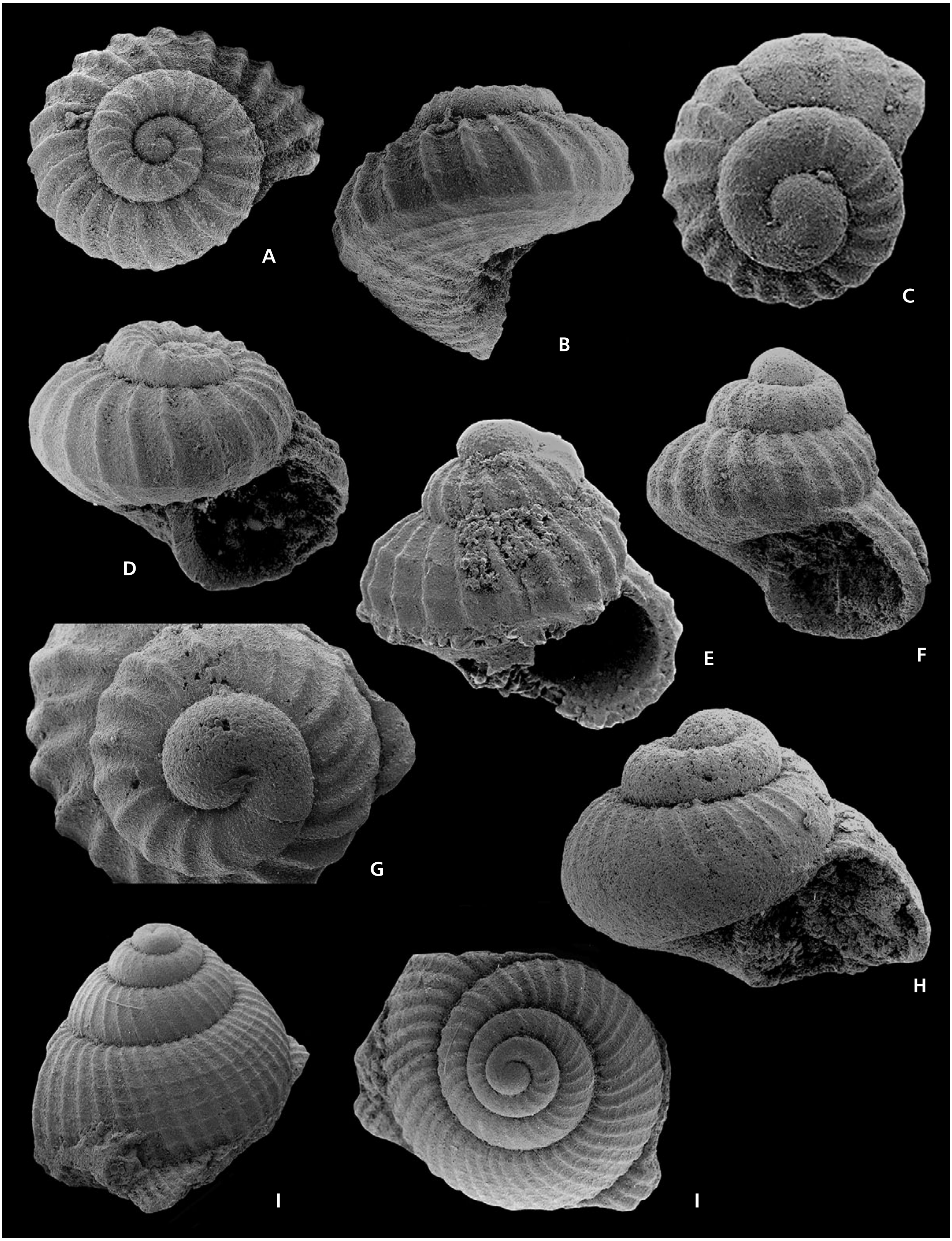
Genus *Danilia* Brusina, 1865

Type species. – *Monodonta tinei* Calcara, 1839, which lives in the Mediterranean (Wenz 1938, fig. 572; Graham 1988, fig. 30; Hickman & McLean 1990, fig. 40H).

Remarks. – *Danilia* has the conical shell higher than wide (up to 14 mm) with about seven whorls. It is ornamented with spiral ribs crossed by collabral ribs, forming tubercles where they cross. The base is rounded, the aperture circular, thickened and the inner lip in fully grown shells has a prominent tooth. *D. tinei* has a sharply pointed conical shell with ornament of a regular array of tubercles arranged in spiral ribs, and a convex base without an umbilicus. The early teleoconch differs from the adult teleoconch (Fig. 13A–C). Here the inflated protoconch about 0.25 mm in diameter has a fine pattern of grooves surrounded by ridges and some fine spiral lines (Fig. 13C). The first teleoconch whorl is inflated and ornamented with about 15 prominent, narrow axial ribs. The space between the ribs is crossed by numerous fine undulating spiral lines (Fig. 13A, B). Strong spiral ribs begin on the second teleoconch whorl and tubercular ornament begins in the third whorl, characterizing the following whorls to the large, rounded last whorl.

Danilia also contains species in which the inner lip of the aperture is without a ridge or tooth, such as *Danilia wiseri* Calcara, 1842 (= *Putzeysia wiseri*) from the Canary Islands. This species has a shell resembling that in Fig. 13A–C but

Figure 12. From the Paleocene of Faxe, Danmark. • A–D represent *Danilia faxensis* (Ravn, 1933) (SGPHM, No. 4686). A – apical view of shell in side view in Fig. 12B. Protoconch is surrounded by one whorl with axial ribs before spiral lines make their appearance (1 mm wide shell). The base has spiral lines and spiral ribs insert on the second whorl of the teleoconch. C – a 0.8 mm wide shell with axial ornament has 0.25 mm wide smooth and rounded protoconch. D – juvenile shell with plane whorl around protoconch (1.2 mm wide). • E–G – *Danilia quadricostata* (Ravn, 1833) (SGPHM, No. 4687). E – protoconch exposed above first teleoconch whorl (1.4 mm high shell). Spiral ornament insertion resembles *Lischkeia* (Fig. 11I). F – juvenile shell (about 1 mm high) with smooth inner lip and begin of spiral ribs on the second teleoconch whorl. G – apical view with protoconch (0.22 mm wide) with straight outer lip and first half whorl of teleoconch with axial ribs to which later spiral ribs are added. • H–J – juvenile shell of *Danilia fenestrata* (Ravn, 1933) (SGPHM, No. 4688). H – shell with evenly rounded whorls (about 1 mm wide). I – ornament changes from axial ribs in the first teleoconch whorl to a regular pattern of axial ribs crossed by fine spiral ribs resembling the pattern in cf. *Brookula* (Fig. 14D, E) from the tropical Pacific (shell about 1.6 mm high). J – same shell in apical view (about 1.5 mm wide) with first teleoconch whorl with smooth axial ribs, on the second whorls spiral lines are added.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without tubercles in rows, instead having axial ribs. *Euchelus hummelincki* Moolenbeek & Faber, 1989 (= *Euchelus guttarosea* Dall, 1889 in Quinn 1979, figs 37, 38) from the Caribbean Sea has a shorter shell. The radula of *Danilia eucheliformis* (Nomaru & Hatai, 1940) was described by Beck (1995, pl. 53, figs 4–6). The central tooth has a triangular base with a narrow anterior part and a large triangular cutting edge with smaller cusps on the sides. The four pairs of lateral teeth are elongate, with a similar triangular cutting edge. The inner pair is the shortest, the outer two the longest. The transition to the elongate marginal teeth is not well marked but the teeth of the central zone are shorter than the slender teeth of the marginal zones. The radula of *Danilia insperata* Beu & Climo, 1974, a species from the temperate Southwest Pacific resembling the Mediterranean type species in size and ornament (about 13 mm high), has also nine teeth in the central field (Beu & Climo 1974). Thiele (1931) also suggested the presence of four pairs of lateral teeth in *Danilia* (*i.e.* 4 + 1 + 4). Beu & Climo (1974) discussed the similarity of *D. insperata* to other species of the genus, including *D. tinei,* and the probable existence of species of the genus since the Cretaceous.

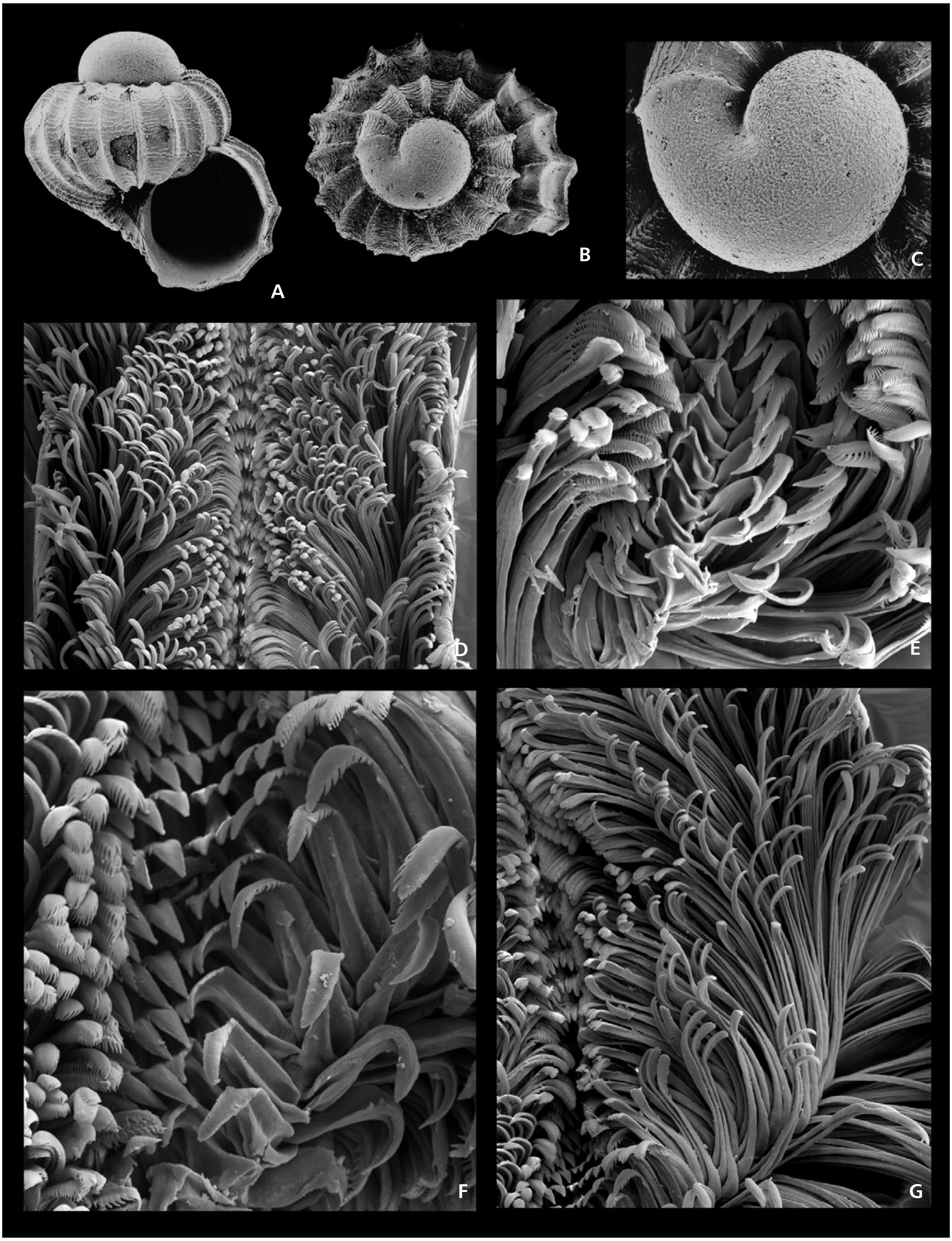
Danilia kosslerae Kiel & Bandel, 2001 from the Campanian of the Tremp Basin resembles *D. tinei* with its high-conical shell and less rounded whorls. It is sculptured with four rows of tubercles formed by short gutter-like spines. The aperture is thickened by a varix and the inner lip bears one strong and one minor tooth. The base is convex and the shell about 10 mm high and eight mm wide (Kiel & Bandel 2001, pl. 2, figs 9–11). *Danilia kosslerae* may represent the oldest *Danilia* species known to date.

From the Danian (Early Paleocene) of Danmark at Faxe, Ravn (1933) described three species belonging to the genus *Danilia*. Their shell shape resembles that of *Danilia tinei*, but shell size is smaller and closer to that of *Brookula* Iredale, 1912 or *Aequispiratella* Finlay, 1924 as described by Tsuchida & Hori (1996) and Hasegawa (2006) from Japan or *Mirachelus* and *Antillachelus* from the southern East Coast of North America (Abbott 1974). *Danilia faxensis* Ravn, 1933 from the early Paleocene (Danian) of Faxe was named as *Monodonta* (*Danilia*) *faxensis* by Ravn (1933, pl. 2, fig. 4). It has five whorls and is turbiniform, reaching 4.5 mm in height and 3.2 mm in width. The suture is distinct, the protoconch smooth, the first teleoconch whorls are ornamented with straight axial ribs and later a few spiral ribs are added, dominating on the base. The last whorl has no umbilicus. The shell is higher than wide and the base is convex and ornamented by spiral ribs. The studied specimens (Fig. 12A–D) are juvenile shells, and here the umbilicus is open. The protoconch is about 0.25 mm wide and its margin is simple and straight. About 18 axial ribs are present on the first teleoconch whorl. Their number increase down the shell, with about 20 on the second whorl. Spiral ornament becomes more evident on this whorl as well but is dominant only on the base. A similar succession of ornamental patterns is seen in modern *Perrinia* species from Aqaba (Fig. 15D, E) as is the case in *Cidarina cidaris* Carpenter, 1864 and *Danilia* sp. from the southern US-East coast shelf.

Danilia quadricordata Ravn, 1933, named by Ravn (1933, pl. 2, fig. 5) as *Monodonta* (*Danilia*) *quadricordata* from the Paleocene of Faxe, has a turbiniform shell with five whorls, about 5 mm high and 4 mm wide, with whorls separated from each other by a deep suture. It differs from *Danilia faxensis* by having two spiral ribs appearing quite rapidly on the first teleoconch whorl. The juvenile shells studied here (Fig. 12E–G) may belong to this species. It has an embryonic shell about 0.22 mm in diameter, a first teleoconch whorl with about 17 axial ribs and about the same number on the second whorl, with two spirals quite distinctly present. The aperture is circular with a flattened inner lip, and the umbilicus is almost closed. The early teleoconch of *Danilia quadricordata* resembles that of *Perrinia,* while later whorls of the latter genus are more angular. *Calliotropis* (*Solaricida*) *actinophora* (Fig. 16D) from deep coral reefs of the North American shelf is especially similar to *D. quadricordata*.

Danilia fenestrata Ravn, 1933, which also was placed by Ravn (1933, pl. 2, fig. 8) in *Monodonta,* resembles modern species of *Lischkeia.* This species from the Paleocene of Faxe is ornamented with a rectangular pattern of axial ribs, to which regular spiral ribs are added on the third teleoconch whorl. In general ornament of the first teleoconch whorl it resembles *D. quadricordata* and *D. faxensis* but has a shallower suture. The shell consists of up to five whorls, is 3.2 mm high and 2.4 mm wide, and has rounded whorls. The protoconch is about 0.3 mm in width and lies in the top of the first teleoconch whorls (Fig. 12H–J). Its inflated whorls end with a straight margin

Figure 13. A–C – juvenile shell of *Danilia tinei* (Calcara, 1839) from Pliocene deposits of SE France near the Mediterranean Sea (SGPHM, No. 4689), D–G – radula of *Euchelus asper* (Gmelin, 1791) from the Indian Ocean near Pondicherry, south eastern India. • A – early teleoconch ornament with sharp axial ribs and fine spiral wrinkles (shell 0.6 mm high and wide). • B – apical view of the same shell with adult type ornament initiating on the second teleoconch whorl. • C – protoconch of the same shell with fine pits and ridges and spiral ribs (embryonic shell 0.25 mm wide). • D – radula with 7 short teeth of the central zone almost hidden under the numerous elongate marginal teeth on both sides of it (about 0.6 mm wide). • E – transition from the teeth of the central zone to those of the margin, the inner of which have comb-like teeth at their ends. • F – half of the central row field exposed near the base of the figure. Central tooth with triangular pointed cutting edge that is continuous into a hood on the margin. Three pairs of continuously larger lateral teeth have similar cutting edge. • G – marginal zone with numerous teeth with long, thin stalks and brush-like margins.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that is not thickened. The first teleoconch whorl is strongly ornamented, with about 20 curving axial ribs, a slow appearance of spiral ribs in the second teleoconch whorl, and a rectangular pattern of spiral and axial ribs formed on the third whorl.

Danilia faxensis resembles species of *Mirachelus*, *Calliotropis* or *Cidarina* among modern genera in having a conical shape with rounded whorls and pattern formed by axial and spiral ribs. Similar ornament of axial ribs crossed by fine spiral ribs is noted in cf. *Brookula* Iredale 1912 or *Aequispirella* Finlay, 1924 from near Satonda of the Indonesian Islands (Fig. 14D, E). *Eucycloscala ultima*, *Danilia quadricordata, Danilia fenestrata* and *Danilia faxensis* lived within the zone of a former deep-water coral reef in water well below the wave base (Bernecker & Weidlich 1990). Nowadays on the deep shelf of the North American East coast, species with similar ornament of their early ontogenetic shell can be found within a similar environment, along with members of the Seguenziidae. From the Seguenziidae the species of the Paleocene from Faxe differ by having the axial ribs of the first teleoconch whorl not connected to a large spiral rib. Shell structure of the fossil species can no longer be determined, as was documented when the genus *Maxwellella* was proposed (Bandel 1999), based on *Scissurella annulata* Ravn, 1933. The original shell material of crossed lamellar structure in *Maxwellella* and of nacre in *Danilia* and *Eucycloscala ultima* has been transformed into chalk – that is, very fine-grained calcite granules preserving the original shell shape and ornament.

Genus *Perrinia* H. Adams & A. Adams, 1854

Type genus. – *Monodonta angulifera* A. Adams, 1853 (Wenz 1938, figs 570, 571; Herbert 1996, figs 18, 19) that lives off Japan.

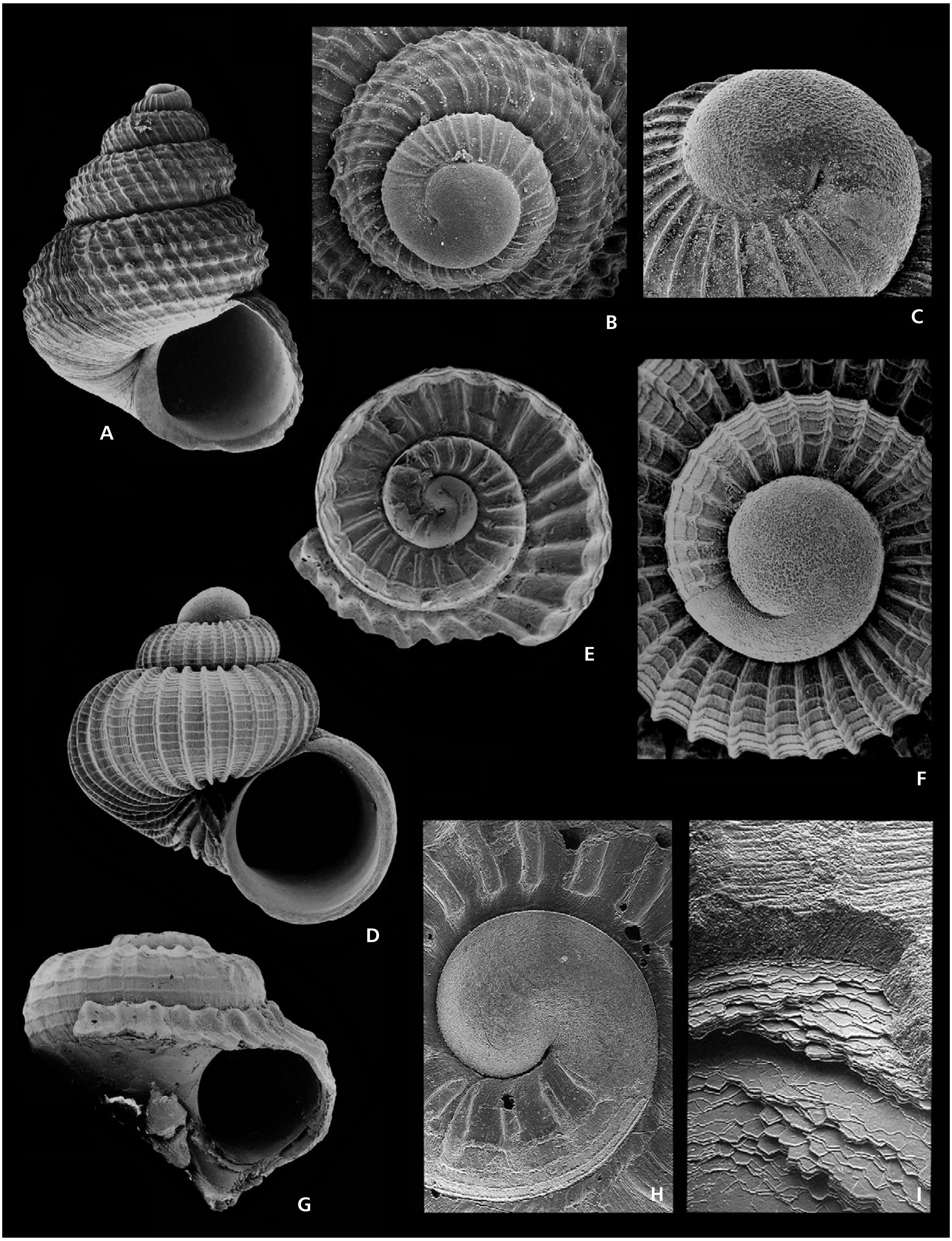
Remarks. – *Perrinia* has a small shell, has a high spire and axially ornamented early teleoconch. Later ornament is by axial ribs crossed by strong spiral ones, forming nodules where they cross (Fig. 15D, E). The conical shell with a solid wall is higher than wide, with about seven whorls, about 7 mm high. It has flattened whorls, an angulation formed by a coarser spiral rib, and a flattened base without an umbilicus. The peribasal angulation remains just above the suture. The aperture is circular with a tooth on the anterior half of the inner lip, and the interior of the outer lip has ridges. Ornament is of spiral ribs, consisting of nodules that unite into elongate ridges on the broad axial ribs.

The radula of *Perrinia stellata* A. Adams, 1864 is not known, but shell shape resembles that of *Turcica* species, for example *Turcica maculata* (Brazier, 1877) from occurring near Australia. The genus *Perrinia* was not treated by Hickman & McLean (1990), while Wenz (1938, fig. 570) placed it close to *Danilia* and *Lischkeia,* which it resembles in shape and ornament. *Perrinia stellata* from Aqaba confirms this position by having the first teleoconch whorls with axial ribs. The small shell from the Gulf of Aqaba has a high spire and an axially ornamented early teleoconch, later ornament with axial ribs crossed by strong spiral ones, forming nodules where they cross. *P. stellata* was reported from sand near corals in Safaga by Zuschin *et al*. (2009, pl. 9, figs 5–7). They treated the species as a member of the Trochidae, Trochinae together with *Pagodatrochus*. *P. stellata* was also recognized from the Red Sea by Bosch *et al*. (1995, fig. 28) and Rusmore-Villaume (2008). *Perrinia angulifera* from Japan has a small conical shell with flattened whorls bearing spiral ribs, of which the median one has pointed nodules and fine axial ribs, with circular aperture that has a shallow anterior gutter, an inner lip with a low tooth. Juvenile shells from the Great Barrier Reef at Lizard Island may belong to *Perrinia elisa* (Gould, 1849) but could also be *Turcica maculata* Brazier, 1877 (Fig. 15A–C). Here the first teleoconch half-whorl is ornamented with axial ribs and fine, irregular spiral lines, and on the following whorls the spiral ornament becomes dominant. The protoconch has ornament of wrinkles and a thick apertural margin, and is 0.3 mm across.

Family Calliotropidae Hickman & McLean, 1990

Type genus. – *Calliotropis* Seguenza, 1903.

Figure 14. A–C – *Danilia* sp. from off-shore Cape Kennedy, Florida, at about 400 m of depth on the shelf (SGPHM, No. 4691), D, E – *Brookula* Iredale, 1912 or *Aequispirella* Finlay, 1924 living near Satonda Island (Indonesia) (SGPHM, No. 4692), F–I – *Calliomphalus paucispirilus* Sohl, 1964 from the Late Campanian of Mississippi, USA (SGPHM, No. 4693). • A – has a conical shell of about 2.2 mm in height, with the protoconch in Fig. 14B, C. Ornament consists of node bearing spiral ribs on the sides and spiral ribs on the rounded base. • B – early teleoconch is ornamented with axial ribs, while spiral ribs appear later. • C – protoconch (0.27 mm in diameter) with ornament of small pits and outer lip straight and thickened. • D – circular aperture and ornament of regular axial ribs and fine spiral ribs (shell 1.2 mm high) with protoconch in Fig. 14E with fine pit and ridge ornament (0.22 mm wide). • F – apex has a stair-step spire of the shell with the first teleoconch whorl with radial ribs, spiral ribs inserting change ornament into nodular spiral cords (shell about 1 mm wide). • G – side view of juvenile shell (0.9 mm wide) with change of ornament from axial ribs to spiral lines and spiral rows of tubercles. • H – protoconch (about 0.25 mm in diameter) with indistinct spiral ribs, fine tubercles and thickened curving margin of the aperture. • I – shell-structure of *C. paucispirilus* from Campanian with outer prismatic layer underlain by nacreous layer.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Remarks. – Ornament of the whorls is by axial and spiral ribs that form a wide net and may have tubercles where they cross each other. The central tooth of the radula has a wide base and lamellar margins that accompany the narrow anterior cutting edge. It is accompanied by three pairs of lateral teeth (Thiele 1931). Genera contained are, among other, *Calliotropis*, *Bathybembix* Crosse, 1893, *Cidarina* Dall, 1909, *Ginebis* Taki & Otuka, 1942, and perhaps *Calliomphalus* Cossmann, 1888, which is based on a type species from the Eocene (Hickman & McLean 1990, McLean 1996). The shell of *Lamellitrochus* Quinn, 1991 closely resembles *Calliomphalus* and it belongs in the Calliotropidae according to the organization of its radula. The shape of the radula connects *Euchelus* Philippi, 1847 to the family, even though its shell walls are thick. Some fossil species from the Late Cretaceous included in *Calliotropis* have a thick shell. Kiel & Bandel (2001), therefore, recognized only the Eucyclini and Chilodontini and placed *Calliotropis* and *Cidarina* in the Chilodontidae. Bouchet *et al.* (2005) suggested a subfamily Calliotropinae to be placed in the Chilodontidae, representing a part of the Seguenzioidea. This later approach is based on the data of Kano (2008) according to which *Calliotropis*, *Ginebis* and *Turcica* form a group of interrelated genera, with a sister group that includes *Seguenzia*.

Genus *Calliotropis* Seguenza, 1903

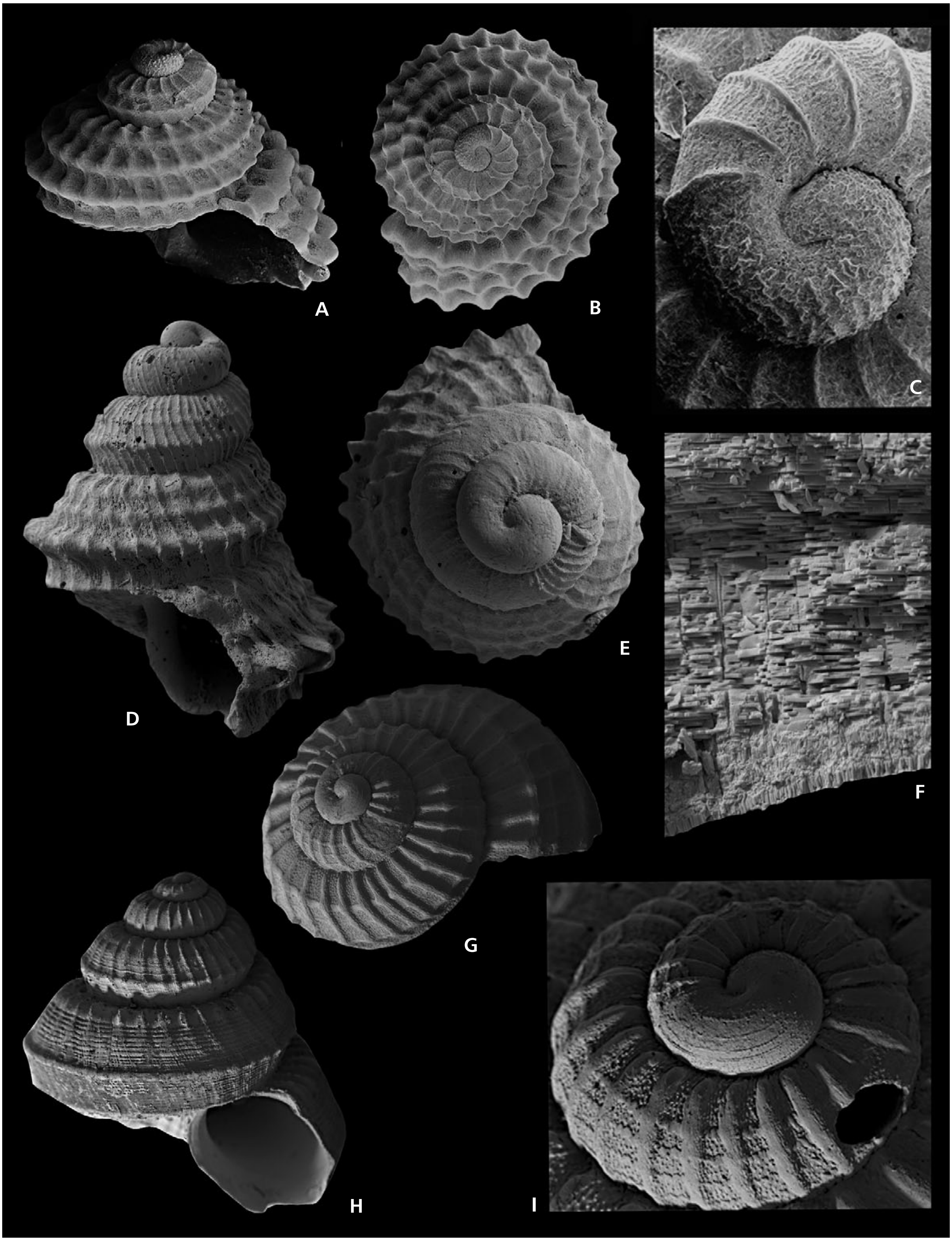
Type species. – *Calliotropis ottoi* (Philippi, 1844) (Wenz 1938, fig. 568; Quinn 1979, figs 5, 6; Kaim 2004) and this species has been recognized as still living on the shelf of the eastern Atlantic Ocean near New England in the Northern Atlantic.

Remarks. – Calliotropidae is based on *Calliotropis* from the Pleistocene of Italy, thus the Mediterranean Sea. It has a thin, conical shell with flattened whorl sides and a wide open umbilicus. Ornament consists of small, spirally arranged beads, and the aperture is oblique and angular. The spiral cord around the basal angulation is stronger than the others in most species and the umbilicus is conical. The aperture has a rounded other lip and a straight inner lip that may or may not carry a tooth on its anterior end. An individual determined as *Calliotropis ottoi* by Quinn (1979, figs 5, 6) resembles living species *Lamellitrochus lamellosus* as well as Cretaceous *Calliomphalus* species in size and ornament.

The radula of *Calliotropis hataii* Rehder & Ladd, 1973 from Hawaii has the central field with seven teeth and elongate narrow marginal teeth (Hickman & McLean 1990, fig. 47A, D, H). The central tooth is elongate with a narrow, triangular, pointed, serrated cutting edge and lateral lamellae (hood) (Thiele 1931). Three pairs of lateral teeth are similar in shape, linked to each other with their bases, and with a long, pointed, serrated cutting edge. The innermost pair of marginal teeth has a wide lamellar base and reduced anterior part and connects to the marginal zone (Hickman 1984, fig. 19C). The radula of *Calliotropis regalis* (Verrill & Smith, 1880) from the US East Coast, *C. glyptus* (Watson, 1879) from Australia and *C. acherontis* Marshall, 1979 have similar teeth (Marshall 1979, figs 9a–c; Hickman 1981, fig. 15A; Hickman & McLean 1990, fig. 47B, C, E, F, I). The shell of *C. glyptus* is thin and up to 20 mm high and 24 mm wide, and the last whorl has four or five spiral ribs between the suture and the periphery. The upper cords bear larger, rounded beads and the bottom two bear smaller ones. The base is convex, with 4-6 very closely beaded ribs and a wide umbilicus with its margin beaded. The inner lip is simple and the interior shell layer is nacre. *Calliotropis eucheloides* Marshall, 1979 from the Pacific has a tubercle at the base of the inner lip, a character that differentiates it from the Atlantic, species which do not have such a tooth.

Calliotropis seguris Kiel & Bandel, 2001 from the Campanian of Northern Spain resembles the living *Calliotropis* species in shell shape but has thick, solid walls. *C. seguris* is a 10 mm high and slightly less wide, with a conical shell with flattened flanks, and with two tubercle-covered ridges on the early whorls and three on the last whorl. The base is ornamented by many spiral lines and is pierced by an umbilicus with a toothed margin (Kiel & Bandel 2001, pl. 1, figs 4, 5). *Calliotropis torallolensis* Kiel & Bandel, 2001 is distinguished from *C. seguris* by the beaded umbilical margin and more strongly transverse growth lines. The shell is 13 mm high, 9 mm wide and has an apical angle of about 65° (Kiel & Bandel 2001, pl. 1, fig. 7). *Calliotropis nilssoni* (Münster) described by Müller

Figure 15. A–C – *Perrinia elisa* (Gould, 1849) or *Turcica maculata* Brazier, 1877 from Lizard Island, Great Barrier Reef, Australia, D–F – juvenile shell of *Perrinia stellata* (A. Adams, 1864) from the Red Sea at Aqaba (SGPHM, No. 4694), G–I – *Lamellitrochus lamellosus* (Verrill & Smith, 1880) from the about 150 m deep shelf off-shore Key West of Florida SGPHM, No. 4695). • A – juvenile shell (about 1.2 mm wide). • B –apex of same shell with the first halve teleoconch whorl with axial ribs and fine irregular spiral lines, while on later whorls spiral ornament dominates. • C – protoconch with ornament of wrinkles and thickened margin of its aperture (0.3 mm wide). • D –juvenile shell with first teleoconch whorl with axial ribs, later two spiral ribs and characteristic ornament of granular spiral ribs on third whorl (1.5 mm high). • E – protoconch continuous into a first teleoconch whorl with axial ribs and spiral ribs later (shell about 0.7 mm wide). • F – shell wall broken with central layer of nacre. • G – apical shell with detail in Fig. 15I. • H – shell about 3.5 mm wide and similar to that of *Calliotropis ottoi* Philippi, 1844. • I – protoconch with spiral ornament (0.3 mm in diameter) and first teleoconch whorl with coarse axial and fine spiral ribs.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(1848) from the Vaals Greensands near Aachen in western Germany, is very similar in shape but has stronger tubercles.

Genus *Bathybembix* Crosse, 1893

Type species. – *Bathybembix aeola* Watson, 1879 from Japan.

Remarks. – The conical shell has a keel above the suture, flat upper whorls and triangular-section groove at the suture, a rounded base with spiral ribs, and the umbilicus is closed in adults (Hickman & McLean 1990, figs 44a, b). Species occur in the Pacific from Japan to the Americas (McLean 1996, fig. 1.5A). *Bathybembix macdonaldi* (Dall, 1890) from the Pacific near Chile is a little higher than wide, while *B. bairdii* (Dall, 1889) is as high as wide, although they both have similar ornament (Hickman & McLean 1990, figs 44A, B). *Bathybembix* was considered as subgenus to *Calliotropis* by Thiele (1931) who regarded *C. imperialis* Dall, 1881 as a typical representative. Its radula was described by Troschel & Thiele (1866–1893), determined as of *Turcica imperialis.* The same species was determined as *Lischkeia (Turcicula) imperialis* by Wenz (1938, fig. 567). The central tooth of the radula is accompanied by three pairs of lateral teeth in *B. bairdii*. The shell wall is thin, nacreous, and is up to 50 mm high. The radula of *Bathybembix macdonaldi* has the characteristic central tooth with lamellae on the sides of the central cutting edge, three pairs of lateral teeth and many elongate marginal teeth (McLean & Andrade 1982, figs 6, 7). *Ginebis* Taki & Otuka, 1942 from Japan is commonly considered a subgenus of *Bathybembix.* It has a conical shell, a little higher than wide, with simple aperture, two ribs forming angulations on the flattened flank, and a rounded base. The upper of the spiral cords bears strong folds, the lower one fine tubercles. The base has spiral ornament (Hickman & McLean 1990, fig. 44d). *Ginebis argenteonitens* (Lischke, 1892) closely resembles *Bathybembix* in shape and composition. It also resembles Jurassic *Eucyclus,* which lived 150 Ma before.

Genus *Cidarina* Dall, 1909

Type species. – *Cidarina cidaris* (Carpenter, 1864), California.

Remarks. – The conical shell that is as high as wide (about 30 mm) with about 6 rounded whorls ornamented on the sides with spiral ribs bearing nodes, and spiral ribs on the rounded base (Hickman & McLean 1990, fig. 44g; McLean 1996, fig. 1.5B). Early whorls are flat-sided with three strongly nodular spiral ribs; later whorls are rounded and have more numerous spiral ribs. Spiral ribs are present also on the rounded base, which lacks an umbilicus. The central tooth of the radula is accompanied by three pairs of lateral teeth. Very similar in shape to the Pacific *Cidarina* is *Danilia* sp. from the American East Coast off the Carolinas and Florida (Fig. 14A–C).

Genus *Calliomphalus* Cossmann, 1888

Type species. – *Turbo squamulosus* Lamarck, 1804 from the Eocene of the Paris Basin (Cossmann 1915, pl. 10, figs 1–5; Wenz 1938, fig. 741).

Remarks. – The trochiform shell has weakly convex whorls and deep sutures. The shell wall has a nacreous inner layer (Fig. 14I). Ornament is of beaded or tubercle-bearing spiral ribs crossed by collabral ribs. The base is striated and the wide umbilicus is surrounded by a ridge bearing nodes. The aperture is circular or nearly so. Since *Calliomphalus* is based on a fossil species its radula is unknown. *Calliomphalus squamulosus* has a shell of about 35 mm in height and width, while the Cretaceous species are much smaller reaching only a maximum size of about 10 mm.

Calliomphalus americanus Wade, 1926 (Sohl 1960, pl. 5, figs 1–10) and *Calliomphalus nudus* Sohl, 1960 differ by the number of spiral elements in their sculpture (Sohl 1960, pl. 5, figs 32, 33). Both species are from the Maastrichtian Ripley Formation. *Calliomphalus paucispirilus* Sohl, 1964 from the Late Campanian of Mississippi has a stepped spire with a flat ramp below the suture, ornamented with nodular spiral cords. It is about 8 mm in height and 10 mm in width is fully grown. The protoconch, 0.25 mm in diameter, is ornamented by three fine spiral ribs and fine tubercles and has a thickened curving margin of the aperture (Fig. 14H). The first teleoconch whorl is rounded and ornamented with narrow rounded axial ribs (Fig. 14F). Spiral ribs become prominent on the second teleoconch whorl, and in the third whorl a spiral row of nodules if formed below the suture and the peripheral angulation becomes prominent (Dockery 1993, pl. 3, figs 5–7; Fig. 14F, G). The exterior shell layer is of prismatic structure while the inner layer is nacreous and may be underlain by a prismatic layer again (Fig. 14I).

The trochiform shell of *Calliomphalus tuberculosus* Sohl, 1964 is 7 mm wide and high, with a nodular surface. The umbilicus is narrow and surrounded by a spiral row of nodes. The protoconch is 0.25 mm wide and rounded, and the early teleoconch is ornamented with axial ribs and also rapidly develops spiral ribs (Dockery 1993, pl. 3, figs 1–4). About 10 species of *Calliomphalus* have been recognized from the Late Cretaceous deposits of the Gulf and Atlantic coast of the USA (Dockery 1993).

Genus *Planolateralus* Sohl, 1960

Type species. – *Calliomphalus argenteus* Wade, 1926 from the Campanian and Maastrichtian of USA (Sohl 1960, pl. 5, figs 19, 23–25).

Remarks. – *C. argenteus* and *C. tuberculosus* were included in the genus and are characterized by having more flattened whorls, a basal keel and more beaded ornament than is found in *C.* (*Calliomphalus*). *Planolateralus decoris* Sohl, 1960 occurs in the Maastrichtian Ripley Formation of the south-eastern USA as well as in beds of the same age of Mexico (Perrilliat *et al*. 2000, figs 5.3–5). Sohl (1998, pl. 8, figs 6.8–12) documented *Planolateralus hanoverensis* Sohl, 1998 from the Campanian of Jamaica, which also has the axial ornament of the first teleoconch whorl preserved.

Sohl (1960) interpreted *Calliomphalus* and *Planolateralus* as representing members of Angariidae, as had been suggested by Cossmann (1915). A relation with the Jurassic *Metriomphalus* Cossmann, 1915 was suggested, and that genus has been thought related to *Amphitrochus* Cossmann, 1907. Recently the later has been described as member of the Nododelphinulinae Cox, 1960 of the Turbinidae by Gründel (2009a). *Amphitrochus* has the first teleoconch whorl ornamented with spiral ribs and thus differs from the Calliotropidae, which have axial ornament. The similar genus *Metriomphalus,* with a Jurassic type species, has ornament of the first teleoconch whorl of one or several strong spiral ribs, and axial ribs may or may not be present (Gründel 2009b, pls 1, 2) and Gründel suggested its relation to the Angariinae. The Cretaceous *Calliomphalus and Planolateralus* species with early ornament of axial ribs (Fig. 14F; Dockery 1993, pl. 1, figs 1–7) thus more properly can be considered related to the modern Calliotropidae and the Mesozoic Eucyclidae than to the Nododelphinulinae. Cretaceous species of the Ripley Formation lived on muddy sediment in a quiet, fully marine environment in front of a delta system resembling that of the modern Mississippi in the Gulf of Mexico (Dockery 1993).

The shell of living genus *Lamellitrochus* Quinn, 1991 resembles that of *Calliomphalus* and its radula has been documented (Quinn 1991a, figs 28–36). Quinn interpreted the genus as belonging to the Solariellinae, which can be doubted because of the shape of the early teleoconch as well as the arrangement and shape of radula teeth. The similarity of the shell to the fossil *Calliomphalus* is such that *Lamellitrochus* could also be interpreted as representing living species of that genus. *Lamellitrochus lamellosus* (Verrill & Smith, 1880) has a number of similar relatives, or it represents a species with a somewhat variable shell, all of which have the same protoconch with ornament of distinct spiral ribs (Fig. 15G, I). The shell is smaller than 10 mm and whorls are angular with a row of tubercles below the suture, a peripheral keel, and the base has a wide umbilicus. The aperture is circular and oblique. Quinn (1991a, figs 28–35) illustrated the radula, and counted four pairs of lateral teeth. This cannot be confirmed from the only reasonably well documented radula that is determined to have been extracted from *Lamellitrochus lamellosus*. Here three pairs of lateral teeth can be recognized (Quinn 1991a, figs 28, 29).

Genus *Euchelus* Philippi, 1847

Type species. – *Trochus quadricarinatus* Holten, 1802 with a rounded shell from the tropical Pacific (Wenz, 1938, fig. 573).

Remarks. – The solid shell is turbinate with rounded whorls ornamented by spiral beaded ribs, the base has an umbilicus or it is closed. Shell sides are rounded or flattened and some species have a peribasal angulation. The outer lip is thickened and ridged on its inner side; the inner lip has a tooth on its base. The protoconch is succeeded by the first teleoconch whorl with ornament of axial ribs. *Euchelus* has a shell with exterior characters resembling those of the Chilodontidae, but has fewer teeth on the inner lip and no or small teeth on the inner side of the outer lip. The early ontogenetic shell succeeding the protoconch is ornamented with sharp axial ribs (Fig. 11F–H). Most species of *Euchelus* live in relatively shallow water and are small with a thick shell that has a central layer of nacre.

Euchelus atratus (Gmelin, 1791) collected in the intertidal zone of south eastern Australia has an ovate shell with a thick, predominantly nacreous wall, with axial and spiral sculpture producing a beaded ornament. The aperture is nearly circular with an anterior tooth on the inner lip and crenulated interior of the outer lip. Juvenile shells of the *E. atratus* from near Satonda of the Indonesian Archipelago are shown (Fig. 11F, G). *Euchelus scrobiculatus* Pilsbry, 1889 has cancellate ornament, a thick shell wall, and a circular aperture with teeth on the interior of the inner and outer lips. *Euchelus asper* (Gmelin, 1791) has a shell up to 30 mm high and wide and is covered with beaded ridges, including three or four prominent ones. A tooth lies on the callus of the inner lip near its lower end.

The radula of *Euchelus asper* (Gmelin, 1791) collected near Pondicherry in southern India has three lateral teeth (Fig. 13D–G). Its shell closely resembles the type *Euchelus quadricariatus* (Holten, 1802) (Wenz 1938, fig. 573), which occurs in the same region. The arrangement of the teeth in the radula of *E. asper* is similar as in *Calliotropis* and *Euchelus* as documented by Hickman & McLean (1990, fig. 43D) in case of *E. atratus*. The central tooth has a triangular pointed cutting edge that extends at the margins to a hood surrounding the anterior part of the tooth

(Fig. 13E). Its widened base has rounded posterior margins and continues in the central supporting ridge of the tooth (Fig. 13F). It resembles the central tooth of *Calliotropis regalis* (Verrill & Smith, 1888) as documented by Hickman & McLean (1990, fig. 47E). In *Euchelus atratus* the central tooth is accompanied by three pairs of lateral teeth of which the outermost is the largest, and all are of similar shape (Fig. 13D–F). Numerous marginal teeth are long thin, and form brush-like margins of the radula ribbon (Fig. 13G).

A species determined as *Mirachelus galapagensis* McLean, 1669 resembles *Perrinia elisa* (Gould, 1849), which lives in the Pacific near the Philippines. McLean (1969) presented a drawing of the radula with a central tooth with lamellar extensions on the cutting edge and three pairs of lateral teeth and noted that it resembles the radula of *Euchelus* as described by Thiele (1924). *Herpetopoma* Pilsbry, 1889 based on *Herpetopoma scabriuscula* A. Adams & Angas, 1867 from Australia (Wenz 1938, fig. 576; Hickman & McLean 1990, fig. 40B) was considered a subgenus to *Euchelus* by Thiele (1928) and Wenz (1938). The conical shell of about 10–20 mm high, with rounded whorls and strong spiral ribs all over, has a circular aperture and two teeth on the inner lip.

Genus *Ilerdus* Calzada, 1989

Type species. – *Trochus melgari* Bataller, 1949 from the Campanian of northern Spain (Kiel & Bandel 2001, pl. 1, figs 6, 10, 13).

Remarks. – *Ilerdus* has a conical shell that is higher than wide, bears axial and spiral sculpture, and has incised sutures. The margin of the aperture lies in one plane and the inner lip carries an anterior tooth (Calzada 1989). The first teleoconch whorl is rounded and ornamented with strong axial ribs. The protoconch of *I. melgari* is 0.4 mm across. On the second, more flattened whorl the ribs develop strong tubercles on their upper and lower ends. The adult shell with eight whorls has an ornament of four nodule-bearing spiral keels, and is about 16 mm high and 13 mm wide, with a smooth, flat base and no umbilicus. A nacreous layer is present. The same is the case in *Ilerdus pyrenaeus* Kiel & Bandel, 2001 from the same locality. It has a high, trochiform spire with about five whorls with flattened sides, sculptured with beaded spiral ribs that increase in number during growth from 3 to 8. Its protoconch is 0.23 mm wide, and the early teleoconch whorls are ornamented with axial ribs, which later turn into cords resembling string-of-pearls. The shell is 10 mm high, 8 mm wide (Kiel & Bandel 2001, pl. 1, figs 8, 9, 11, 12). The species lived on hard substrates near the shore of the tropical Tethys Ocean. The shell of *Ilerdus* species resembles those of *Biarmatoidella* species as defined by Gründel (2003c) from the mid Jurassic of Germany. *Ilerdus melgari* most closely resembles the grown shell of Jurassic *Biarmatoidella lorioli* (Greppin, 1898), of which the early shell is not known well (Gründel 2003c, pl. 6, figs 9, 10).

Superfamily Seguenzioidea Verrill, 1884

Type genus. – *Seguenzia* Jeffreys, 1876.

Diagnosis. – Shell is small and with nacreous inner layer and the radula has a central field with central tooth accompanied by a single pair of lateral teeth and few marginal teeth. Included are Seguenziidae with shell slit, as well as Ancistrobasidae fam. nov. without shell slit.

Remarks. – The superfamily has been defined regarding characters of the shell, anatomy, and radula (Quinn 1983, 1987, 1991a, b, c). Thiele (1931) noted that the radula of *Basilissa* Watson, 1879, *Seguenzia* Jeffreys, 1886 and *Guttula* Schepman, 1908 has only three teeth in the central field and relatively few marginal teeth but considered these to belong to the Margaritinae of the Trochidae. Quinn (1983, figs 39–48) assembled drawings of the radula of different species of Seguenzioidea and noted that all resemble each other as had been noted earlier by Schepman (1908) and confirmed by Marshall (1983, 1988, 1991). The central tooth is flanked by a single pair or lateral teeth succeeded by up to 12 pairs of marginal teeth. The range of the superfamily Seguenzioidea was greatly enlarged by Kano (2008) and Kano *et al*. (2009) based on molecular data. They included also Calliotropidae and Chilodontidae with genera such as *Danilia, Euchelus, Granata, Herpetopoma* and *Hybochelus*. Including studies by various authors they thus united the Seguenziidae Verrill, 1884, Chilodontidae Wenz, 1938, Calliotropidae Hickman & McLean, 1990 and Cataegidae McLean & Quinn, 1987 within the Seguenzioidea including here several hundred species with a wide range of body size and different morphologies of shell and construction of their radula.

Family Seguenziidae Verrill, 1884

Diagnosis. – Seguenziidae are here interpreted to hold species with the shell character of species of *Seguenzia* Jeffreys, 1876. Their shell has a narrow deep posterior lobe, giving rise to a selenizone, and a wide anterior lobe on the outer lip of the aperture. Shell composition and ornament of the first teleoconch resembles that of *Ancistrobasis,* which lacks a posterior slit. The protoconch of *Seguenzia* has a characteristic shape and structure as usually found among Vetigastropoda (Bandel 1982). The succeeding early teleoconch has a characteristic ornament of strong, narrow axial ribs and one strong spiral rib that initiates on the outer lip of the protoconch (Bandel 1979, 2009; Quinn 1983, figs 25–27; Marshall 1983, figs 2, 3).

Remarks. – Wenz (1938) suggested that genera as *Seguenzia* Jeffreys, 1876, *Basilissa* Watson, 1879 and *Guttula* Schepman, 1908 are closely related to *Calliotropis, Lischkeia*, *Turcicula*, *Bathybembix* and *Ginebris*. Marshall (1979) noted that the protoconch in all these is succeeded by first teleoconch with axial ornament and later complex axial ornament.

Quinn (1983) included within the Seguenziidae also species with characters of the shell as in other groups of the Vetigastropoda with a nacreous shell, but differing from them by having internal fertilization and a radula with a central tooth accompanied only by one pair of lateral teeth and the number of marginal teeth restricted to 4 to 12 pairs. According to Thiele (1931) the radula of *Seguenzia* has a roundish central tooth with a serrated cutting edge, accompanied by a single pair of lateral teeth with wide cutting edge, and a few marginal teeth with pointed apices, as confirmed by Bandel (1979, pl. 3, fig. 8; 2009, pl. 9, figs 127–129) and Hickman (1980). The number of the marginal teeth varies among species. This rhipidoglossate radula with relatively few teeth in each row may resemble the taenioglossate radula of the Caenogastropoda with 7 teeth in a transverse row, as documented in case of *Seguenzia* and *Ancistrobasis* Dall, 1889 by Marshall (1983, 1991).

Thiele (1931) and Wenz (1938) followed Watson (1897) and placed *Seguenzia* and *Basilissa* in the Trochidae, subfamily Margaritinae. Abbott (1974) preferred to include *Margarites* Gray, 1847 as well as *Seguenzia*in the Stomatellinae, whereas Quinn (1979) preferred the Solariellidae. The independent status of Seguenziidae and its place among the Vetigastropoda as proposed by Quinn (1983) was confirmed by Sasaki (1998) and supported by molecular analysis of *Seguenzia* and several other genera by Kano (2008). They confirm Seguenziidae as a member of the Vetigastropoda, represented by *Seguenzia*, *Hadroconus* Quinn, 1987 and *Fluxinella* Marshall, 1983, related to Eucyclinae and also *Adeuomphalus* Seguenza, 1876 among some of the deep-sea Vetigastrooda (Kano *et al*. 2009). They supported the trochoid ancestry of the family suggested by Quinn (1983).

Genus *Seguenzia* Jeffreys, 1876

Type species. – *Seguenzia monocingulata* (Seguenza, 1876) from the Atlantic Ocean.

Remarks. – The shell has a deep sinus in the apical portion of its outer lip. This sinus below the suture appears in the third whorl (Bandel 1979, pl. 1, figs 2, 4; 2009, pl. 8, figs 113, 114) and not immediately after the termination of the protoconch as was assumed by Quinn (1983, figs 25–29). Species have been described by Keen (1971), McLean (1981), Quinn (1983, figs 1, 2, 1987, 1991), Marshall (1983, figs 1–3, 1988, 1991), Warén (1992), Okutani (2000), Hasegawa (2001, pl. 1, figs K–N; 2005, figs 5E, F). The shell is composed predominantly of nacre and the protoconch is that of the Vetigastropoda (Bandel 1979) as was confirmed in *Seguenzia mirabilis* Okutani, 1964 from Japan by Sasaki (1998, fig. 66; 2008, figs 4A, B).

Seguenzia carinata Jeffreys, 1876, as identified in Abbott (1974), was determined as *Seguenzia hapala* Woodring, 1928 by Quinn (1983) from the deeper North Amercan shelf near Florida of the Atlantic. It has a 0.3 mm-wide protoconch ornamented with irregular fine ridges and with a simple thickened margin of the outer lip. The teleoconch whorls have a spiral rib forming a keel on the upper flank, a second spiral rib that comes to lie in or next to the suture, and a third forming an angulation around the base. These keels are crossed by axial ribs of which those between first and second keel are more widely spaced than those above and below. Axial ribs reflect the formation of a slit only on the third whorl. On the fifth whorl, the ornament of axial ribs becomes indistinct and the last whorl has growth lines and three keel-like spiral ribs. The outer lip of the aperture has a deep and relatively wide apical sinus, a central concave lobe with the spiral keels forming its margin, a short well rounded short lobe below, and a third lobe between outer lip and inner lips at the posterior end. The inner lip forms a plate that extends into the interior (Bandel 1979, 2009).

Carenzia Quinn, 1983 is founded on *Seguenzia carinata* as determined by Quinn (1983, fig. 4). It has a conical shell with almost plane sides, with one low median keel as ornament, and is wider than high. Its aperture is angular with a narrow anterior sinus on the inner lip. The shell has a slit that forms a selenizone with the growth increments documenting a deep sinus (Quinn 1983, fig. 18). Marshall (1983, figs 4K–O; 1991, figs 144–163) described some additional species of *Carenzia* from the South Pacific. Of these, some have rather weak axial ribs in the first teleoconch whorl, but in general shell shape they resembles the species of *Quinnia* Marshall, 1988, which are smoother and species of *Ancistrobasis,* which are more strongly ornamented. *Quinnia* (= *Seguenziella* Marshall, 1893) from New Zealand is also common in other parts of the South Pacific (Marshall 1991, figs 164–178). *Quinnia* differs from *Carenzia* by its ornament predominantly of spiral ribs and keels and the first teleoconch whorl as in *Carenzia* and *Seguenzia*.

Family Ancistrobasidae fam. nov.

Type genus. – *Ancistrobasis* Dall, 1889.

Diagnosis. – Small conical shell with about five whorls has flattened sides and a conical umbilicus. Almost vertical aperture has a straight inner lip and rounded outer lip with thickened margin. Protoconch is smooth or ornamented by fine granular ridges. Teleoconch whorls increase their diameter very regularly and also change their ornament in a regular way. First whorl has two spiral ribs and regular collabral axial ribs. With increasing whorl diameter, spiral ribs may be added and axial ribs increase in size, in *Ancistrobasis,* or ornament decreases and the shell is almost smooth, as in *Thelyssa* Bayer, 1971, *Calliobasis* Marshall, 1983 and *Seguenziella* Marshall, 1983. Final margin of aperture on fully grown shell is thickened and upturned on the outer and inner lip. Radula resembles that of *Seguenzia* with a central tooth accompanied by one pair of lateral teeth and a few marginal teeth.

Remarks. – The type species of *Ancistrobasis*, *Basilissa costulata* Watson, 1879 from the Strait of Florida, was described by Abbott (1974, fig. 241) and Quinn (1979, figs 85, 86). *Ancistrobasis reticulata* (Phillippi, 1844) is similar with a conical shell with flattened sides and conical umbilicus (Quinn 1983; Warén 1991, fig. 1A) (Fig. 16A–C). It consists of almost five teleoconch whorls and has an almost vertical aperture with straight inner lip and rounded outer lip. The protoconch is 0.35 mm wide with fine granular ridges as ornament. Marshall (1991, figs 31–60) described several species from the Pacific with similar ornament and the radula resembling that of *Seguenzia*.

Marshall (1991) suggested placing *Ancistrobasis* and the very similar *Calliobasis* together with *Basilissa* Watson, 1879 and the very similar *Basilissopsis* Dautzenberger & Fischer, 1897 and *Carenzia* Quinn, 1983 in tribe Fluxinellini. But while most of the species placed in the Fluxinellini have the characteristic early teleoconch ornament consisting of a spiral rib crossed by axial folds, the name-giving *Fluxinella* Marshall, 1983 is here almost smooth (Marshall 1991, figs 91–120), including the type species, *Fluxinella lepida* Marshall, 1983. *F. lepida* has a radula resembling that of *Seguenzia* (Marshall 1983, figs 6, 8M–O).

Basilissa, with type species *Basilissa superba* Watson, 1879 from the Pacific Ocean (Okutani 1982), has a shell that is lower than wide, with conical shape and straight sides, and the first teleoconch whorl has an ornament of spiral keels only, and axial ornament come later (Marshall 1991, fig. 143). *Halystes* Marshall, 1988 based on *H. chimaera* Marshall, 1988 from the South Pacific has the conical shell with fine spiral ornament and rounded whorls. The early teleoconch has the same ornament as in *Seguenzia* but later ornament is quite different (Marshall 1988, figs 2F–J). The radula also resembles that of *Seguenzia,* with the central tooth accompanied by one pair of broad lateral teeth and a few marginal teeth. *Halystes* demonstrates that the shell in this group of Seguenzioidea has the characteristic early ontogenetic whorls, while the later teleoconch is quite different in shape and ornament, with simple rounded whorls and fine spiral ribs. *Guttula* Schepman, 1908 has a simple shell almost free of ornament, with smooth, rounded whorls, quite different from those of *Seguenzia*. The type species is *Guttula sibogae* Schepman, 1908 from the Pacific and Indian Oceans (Quinn 1983, figs 10, 11). In the similar genus *Sericogyra* Marshall, 1988, fine branching and curving lines ornament the first teleoconch whorl (Marshall 1988, figs 3E, K). *S. metallica* Marshall, 1988 has the shell composed of rounded whorls with the nacre shining through the surface layer. Such smooth species with a radula as in *Seguenzia* have been placed in the subfamily Guttulinae Goryachev, 1987.

Problematic recent and fossil planispiral species resembling *Adeuomphalus*

Genus *Adeuomphalus* Seguenza, 1876

Type species. – *Adeuomphalus ammoniformis* Seguenza, 1876 from the Pliocene of Sicily, Italy.

Remarks. – It is a shell that is smaller than three mm in diameter and is almost planispiral, with a concave apex and base. The protoconch is about 0.2 mm in diameter and succeeding early teleoconch whorls are ornamented with axial ribs crossed by a spiral keel. The aperture is circular with a thin edge. The operculum is transparent and multispiral with a central nucleus (Warén 1991, fig. 14F). *A. ammoniformis* has a very similar living representative which had been interpreted as a member of the Vetigastropoda by Nofroni & Sciubba (1985). The species lives in depths of 300–900 m in the Mediterranean Sea. The shell is covered with very regular collabral ribs crossed by one fold forming the angle of the aperture. The radula is as in *Seguenzia* with three marginal pairs of teeth (Kano *et al*. 2009, fig. 6). They discussed the place in the system of *Adeuomphalus* and speculated that the fossil record of Seguenzioidea dates back to the Middle Triassic, some 240 Ma ago, as they assumed was suggested by Hickman & McLean (1990). To them the extinct family Eucyclidae Koken, 1897 was the only recognized Triassic representative of the superfamily. They noted that the taxonomic diversity increased in the Middle and Late Jurassic, around 150–170 Ma ago, as was apparently indirectly extracted from Knight *et al*. (1960). To them Seguenzioidea are represented by Jurassic members of Chilodontidae, Calliotropidae and also skeneimorph *Eudaronia*. Kano *et al*. (2009) noted that *Adeuom-*

phalus resembles *Eudaronia* and *Palazzia* in having planispiral shell shape with concave apex and nearly vertical aperture (Warén 1991, Rex 2002), but their systematic position still remains unresolved. The first known appearances of Seguenziidae were much later, in the Late Cretaceous (assumed by Hickman 1998) and Cenozoic (documented by Marshall 1983), but their apparent absence in older sediments was attributed by Kano *et al*. (2009) to difficulties in determining phylogenetic positions of fossils solely by shell characters. Williams *et al*. (2008) estimated the divergence of Seguenzioidea from Scissurellidae, Lepetodrilidae, Fissurellidae to have taken place 124–221 Ma ago, based on molecular data derived from various Vetigastropoda and confirmed by Williams *et al*. (2010).

Genus *Heterodiscohelix* gen. nov.

Type species. – *Discohelix bandeli* Schröder, 1995 from the Early Cretaceous, Valanginian of central Poland.

Diagnosis. – Teleoconch has the character of the Mediterranean *Adeuomphalus*, but bears a protoconch that consists of more than one whorl, has the earliest part of the shell left-coiled (sinistral) and is later planispiral. The embryonic whorl ends with first growth lines and almost one quarter of a whorl is larval shell.

Etymology. – The shell resembles that of *Adeuomphalus* but bears a sinistral embryonic shell connected to a short planispiral larval shell, documenting that it is a member of the Heterostropha. The name is a combination of Hetero and *Discohelix*.

Remarks. – The genus is based on *Discohelix bandeli* Schröder, 1995 from the Early Cretaceous, Valanginian of central Poland that was transferred to *Adeuomphalus* by Kaim (2004, fig. 3C, D). A closer look at the protoconch of *Discohelix bandeli* indicates that it is a member of the Heterostropha (Schröder 1995, pl. 1, figs 1–4; Fig. 16F, G). Kaim (2004, figs 2C, D) suggested placing *Discohelix bandeli* in *Adeuomphalus* and to interpret that genus as related to the Jurassic *Discohelix* Dunker, 1848. However, *Discohelix bandeli* is neither the oldest known species of *Adeuomphalus,* as was stated by Kano *et al.* (2009), nor can it be considered to represent a member of *Discohelix.* In contrast to *Heterodiscohelix bandeli* the Jurassic genus *Discohelix* belongs to the Vetigastropoda (Bandel 1988).

Genus *Discohelix* Dunker, 1848

Type species. – *Discohelix calculiformis* Dunker, 1847 from the Early Jurassic of Hainberg near Göttingen, Germany.

Remarks. – Discohelicidae Schröder, 1995 are based on *Discohelix*, which has a planispiral disc-like shell that is commonly quadrangular and whorl diameter increases slowly. The protoconch as well as the nacreous shell structure is as in the Trochidae. Ornament is of fine spiral and axial lines and few axial folds present only on the periphery in many species. The early teleoconch is smooth or has fine spiral lines as ornament and axial ribs, and the strong peripheral spiral rib may appear later (Bandel 1988, Schröder 1995). Discohelicidae can best be interpreted utilizing the description by Gründel (2005b, figs 1–3) of the type species, *D. calculiformis* Dunker, 1847, confirming Schröder (1995). The locality was determined as of Pliensbachian age by Gründel (2005b) (not from the Late Triassic of Germany as assumed by Kaim 2004).

Species of *Discohelix* from the Jurassic have flat shells coiled in a plane as in *Adeuomphalus*, but their early teleoconch is smooth in most species. A juvenile shell with the first teleoconch whorl having a series of varix-like axial ribs (Schröder 1995, pl. 1, figs 5–8) was determined as *Discohelix* sp. from the Callovian of Poland. It represents the juvenile shell of a member of the Vetigastropoda that with later growth ceases planispiral coiling and changes its shell shape. It was found to belong to *Torallochus lukoviensis* Kaim, 2004 (Kaim 2004, figs 4A, B), a species of *Torallochus* Kiel & Bandel, 2002 that has a flat juvenile shell and later pupoid shape.

Genus *Levihelix* Gründel, 2000

Type species. – *Levihelix pusilla* Gründel, 2000 from the mid-Jurassic of Poland (Gründel 2000, pl. 2, figs 7–12).

Remarks. – Gründel (2005b) in a discussion about the systematic place of the Discohelicidae among the Vetigastropoda transferred *Levihelix* to *Eudaronia* Cotton, 1945, as had been suggested by Kaim (2004). The protoconch of *Levihelix pusilla* Gründel, 2000 was illustrated by Gründel (2000, pl. 2, fig. 10) and Kaim (2004, fig. 2B) as *Eudaronia pusilla* (Gründel, 2000). But this species represents a member of the Allogastropoda Haszprunar, 1985 (Heterostropha), with a protoconch of weakly heterostrophic shape due to lecithotrophic embryonic development. Gründel (2005b) tentatively suggested a place of the Mid-Jurassic *Levihelix pusilla* in the Skeneidae Thiele, 1929 and in subfamily Eudaroniinae Gründel, 2004. This taxon had been introduced by Gründel (2004a) to hold *Eudaronia*, *Adeuomphalus* and *Palazzia* based on living types, and the Jurassic genus *Levihelix*.

Levihelix does not have an axially ribbed early teleoconch, while it is ribbed in *Heterodiscohelix bandeli* and *Palazzia prisca* Gründel, 2007. But since *H. bandeli* and *Levihelix pusilla* do not have a protoconch characteristic of the Vetigastropoda, the Eudaroniinae represent a problematic taxon and need not be reconsidered here.

Eudaronia Cotton, 1945 has a similar planispiral shell to that of *Adeuomphalus,* but with a smooth surface and no ornament of ribs. Its type species, *Cyclostrema (Daronia) jaffaensis* Verco, 1909 from deep water of South Australia, has an atypical rhipidoglossate radula. Warén (1991, fig. 14) demonstrated that the embryonic shell is smooth and characteristic of Vetigastropoda, and described with *Eudaronia aperta* (Sykes, 1935), a species that lives from the Mediterranean to Norway in deep water. Modern species of *Eudaronia,* as member of the Vetigastropoda, are thus not related to the Jurassic fossils interpreted as belonging to that genus.

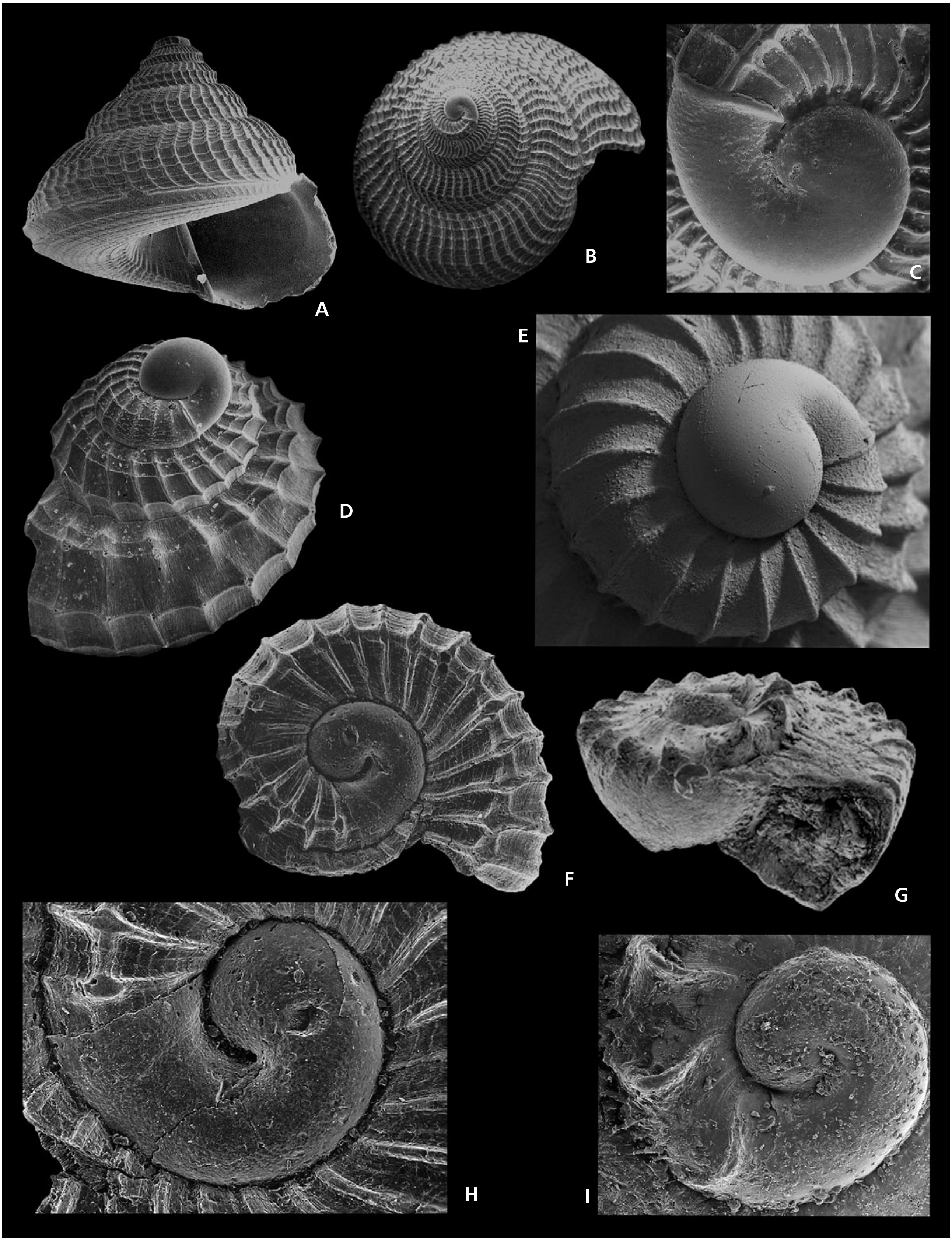
Palazzia prisca Gründel, 2007 is a Jurassic fossil (Gründel 2007a, pl. 3, figs 15–17). *Palazzia* Warén, 1991 is based on a small gastropod living in the Mediterranean Sea, originally named *Omalogyra ausonia* Palazzi, 1988. It has the characteristic protoconch of a member of the Vetigastropoda (Warén 1991, fig. 18). *Palazzia prisca* has rounded whorls, about 0.8 mm in width and consisting of 1.8 teleoconch whorls ornamented by axial ribs that branch at the rounded whorl side. The protoconch measures about 0.2 mm and is smooth. It appears to resemble that of type species of *Palazzia*, which differs by having a fine pitted teleoconch surface, while that of fossil species from the Early Jurassic of north-eastern Germany is smooth between ribs.

Conclusions

Triassic species of *Eucycloscala, Ampezzotrochus, Eunemopsis, Pseudoclanculus, Sabrinella, Microcheilus, Neoeunema* and *Lanascala* demonstrate that the Eucycloidea branch of the Vetigastropoda was quite diverse about 220 Ma years ago. Sixteen different species belonging in the Eucycloidea lived in the reef environment of the tropical Tethys Ocean, and are present in St. Cassian Formation of the Dolomites in the Alps of northern Italy. Only two comparable species live in the modern coral reef in the Red Sea, in the Gulf of Aqaba, belonging to *Perrinia* and *Pagodatrochus*. Shell morphology of members of the superfamily in case of *Eucycloscala, Neoeunema* and *Lanascala* continued across the Triassic-Jurassic faunal crisis and continuation lies in genera such as *Eucyclus, Eucycloidea*, and *Riselloidea*, some of which have shell shape that is difficult to distinguish from that of living genera. Most of these are known from sediments of more or less carbonate-rich muddy substrates that formed in shallow to moderately deep shelf regions within relatively warm sea in Europe. A species of *Eucycloidea* from Madagascar lived on soft bottom in the shallow southern Tethys Ocean in a similar environment (Bandel 2006). As a characteristic late Mesozoic group, the species around *Chilodonta* evolved with special features of their aperture. It appears that during the Cretaceous, most of them lived among pebbles and hard substrates near the shore in relatively warm environment and it is not quite safe to assume that they have living representatives, although they are perhaps represented by *Agathodonta* and *Visayaseguenzia*. Among the living members of the superfamily Eucycloidea genera can be grouped according to their radula. In case of the Pagodatrochidae and Turcicidae the radula has four pairs of lateral teeth, including genera such as *Pagodatrochus, Danilia* and *Turcica*. In the Calliotropidae, with genera *Calliotropis, Cidarina*, and *Euchelus* the radula has three pairs of lateral teeth. The genera within the two families merge shell characters, and tracing them across time into the Cretaceous makes it difficult to distinguish between, for example fossil *Calliomphalus* and living *Lamellitrochus*. Species with thick shell such as belonging to *Euchelus* appear to live mainly in warm shallow water, and most species of deeper water of the same Calliotropidae have a thin shell. Deep-water coral reefs appear to have as diverse a fauna as that living near the edge of the slope to the deep sea off the coast of the Carolinas and Florida, and this appears to have been similar as far back as the Paleocene, exemplified with the fauna of the deep-water reef at Faxe in Danmark.

The paleontological record provides evidence for a view according to which superfamily Seguenzioidea is better interpreted in a more restricted way than suggested by Bouchet *et al.* (2005) and Kano *et al*. (2009). Species

Figure 16. A–C – *Ancistrobasis reticulata* (Phillippi, 1844) from off-shore Cape Kennedy, Florida and about 400 m depth (SGPHM, No. 4696). • D – *Calliotropis actinophora* (Dall, 1890) from the deep shelf off-shore Cape Kennedy, Florida at about 50 m depth (SGPHM, No. 4697). • E – *Calliotropis* cf. *calatha* (Dall, 1927) from the deep shelf off-shore Cape Kennedy, Florida (SGPHM, No. 4698). • F, G – *Heterodiscohelix bandeli* (Schröder, 1995) from the Valanginian of Poland. • H, I – *Torallochus lukovensis* Kaim, 2004 from the Mid Jurassic (Bajocian) of Poland. • A – conical shell with flattened sides and base with conical umbilicus, ornament is with spiral ribs connected to axial ones (shell is about 4 mm wide). • B – apical view of shell ornamented with a spiral keel at first (Fig. 16C) and later spiral ribs connected to axial ribs. • C – protoconch (0.35 mm wide) with raised margin. • D – *Calliotropis actinophora* with large rounded protoconch (more than 0.5 mm), first teleoconch whorl with axial ribs to which some spiral lines are added. • E – smooth protoconch of *Calliotropis* cf. *calatha* (about 0.35 mm in diameter) and first teleoconch whorl with straight axial ribs. • F – juvenile shell of *Heterodiscohelix bandeli* with ornament of the teleoconch as in *Adeuomphalus* and heterostrophic protoconch as in Fig. 16G (shell 0.6 mm wide) (coll. SMF 56001). • G – protoconch in detail with more than one whorl and apex twisted in sinistral way below whorls surface (0.22 mm in diameter). • H – juvenile shell of *Torallochus lukovensis* (shell 0.6 mm wide). Early teleoconch with several varix-like axial ribs. • I – detail to Fig. 16H with protoconch (0.27 mm wide) with the outer lip thickened and sinuous (coll. SMF 56004).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belonging to the stem group of the Seguenziidae may have lived side-by-side with stem group Chilodontidae, Pagodatrochidae, Turcicidae and Calliotropidae in the tropical reef of the Tethys Ocean, together with many representatives of quite different groups of the Vetigastropoda (Bandel 1993, 2009). Quinn (1983, 1991) suggested that the Seguenziidae-Seguenzioidea evolved from Trochoidea, perhaps during the Cretaceous, from stem Vetigastropoda. This would place their origin at about 100 Ma ago. But if the Seguenzioidea are interpreted as suggested by Kano (2008) the ancestral species of this superfamily as well those of the Trochoidea would have lived before the time of deposition of St. Cassian Formation, more than 220 Ma ago. At that time, taxa that may be considered related to stem group taxa of Trochoidea in these tropical reefs were quite diverse, as were those here interpreted to be stem group taxa of the Seguenzioidea in the broad sense (Eucycloidea). The suggestion by Salvini-Plawen & Haszprunar (1987) to insert between Vetigastropoda and Caenogastropoda an independent order Seguenziina, which was adopted as suborder of the order Vetigastropoda by Marshall (1988, 1991), also cannot be supported. The results of Williams *et al*. (2008, 2010) according to which a separate branch of the Vetigastropoda including the Seguenzioidea can be distinguished from another one including the Trochoidea is supported by the paleontological evidence. These branches were distinct from each other as early as the time of deposition of Triassic St. Cassian Formation 220 Ma ago.

Summary

Subclass Archaeogastropoda
Order Vetigastropoda

Superfamily Eucycloidea Koken, 1897
Family Eucycloscalidae Gründel, 2007
  Genus *Eucycloscala* Cossmann, 1895
  Genus *Ampezzotrochus* Bandel, 1993
Family Sabrinellidae fam. nov.
  Genus *Sabrinella* Bandel, 1993
  Genus *Microcheilus* Kittl, 1894
Family Eunemopsidae fam. nov.
  Genus *Eunemopsis* Kittl, 1991
  Genus *Pseudoclanculus* Cossmann, 1918
Family Lanascalidae Bandel, 1992
  Genus *Lanascala* Bandel, 1992
Family Eucyclidae Koken, 1896
  Genus *Eucyclus* Etudes-Deslongchamps, 1860
  Genus *Neoeunema* gen. nov.
  Genus *Eucyclomphalus* Ammon, 1892
  Genus *Trypanotrochus* Cossmann, 1918
  Genus *Eucycloidea* Hudleston, 1887
  Genus *Gerasimovcyclus* Gründel, 2005
  Genus *Riselloidea* Cossmann, 1909
  Genus *Biarmatoidella* Gründel, 2003
Family Pseudoturcididae fam. nov.
  Genus *Pseudoturcica* gen. nov.
Family Chilodontidae Wenz, 1938
  Genus *Chilodonta* Etallon, 1859
  Genus *Wilsoniconcha* Wenz, 1939
  Genus *Hudledonta* Kiel & Bandel, 2001
  Genus *Denticulabrum* Sohl, 1998
Family Pagodatrochidae fam. nov.
  Genus *Pagodatrochus* Herbert, 1889
Family Turcicidae fam. nov. (?Euchelidae??)
  Genus *Turcica* H. Adams & A. Adams. 1854
  Genus *Lischkeia* Fischer, 1879
  Genus *Mirachelus* Woodring, 1928
  Genus *Solaricida* Dall, 1919
  Genus *Danilia* Brusina, 1865
  Genus *Perrinia* H. Adams & A. Adams, 1854
Family Calliotropidae Hickman & McLean, 1990
  Genus *Calliotropis* Seguenza, 1903
  Genus *Bathybembix* Crosse, 1893
  Genus *Cidarina* Dall, 1909
  Genus *Calliomphalus* Cossmann, 1888
  Genus *Planolateralus* Sohl, 1960
  Genus *Euchelus* Philippi, 1847
  Genus *Ilerdus* Calzada, 1989

Superfamily Seguenzioidea Verrill, 1884
Family Seguenziidae Verrill, 1884
  Genus *Seguenzia* Jeffreys, 1876
Family Ancistrobasidae fam. nov.
  Genus *Ancistrobasis* Dall, 1889

Problematic recent and fossil planispiral species resembling *Adeuomphalus*
  Genus *Adeuomphalus* Seguenza, 1876 (possibly Seguenzioidea)
  Genus *Heterodiscohelix* gen. nov. (member of Allogastropoda)
  Genus *Levihelix* Gründel, 2000 (member of Allogastropoda)
Family Discohelicidae Schröder, 1995 (member of Vetigastropoda)
  Genus *Discohelix* Dunker, 1848

Acknowledgments

Material from the St. Cassian Formation was collected by the author (aided by his students) during several trips in the region of Cortina d'Ampezzo with localities pointed out by the late Rinaldo Zardini, and also some of the studied material was provides by him. Living species have been collected at several tips, the last ones at the Marine Science Station at the Gulf of Aqaba helped by Tariq Al-Najjar. Ivonne Milker helped in documenting the material with the scanning electronic microscope. Plates were assembled by my wife Mike van Spaendonk-Bandel. I like to thank Alan Beu and Bruce Marshall for their thoughtful reviews of the manuscript. Material has been assembled in several scientific projects largely funded by DFG (German Science Foundation). To all these persons and to other colleagues and friends I want to express my sincere thanks.

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