

Relationships of Cretaceous Neritimorpha (Gastropoda, Mollusca), with the description of seven new species

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Abstract. Cretaceous Neritimorpha comprise several morphologically, ecologically, and phylogenetically distinct groups. There are three mainly Mesozoic, fully marine groups: the few relict species of *Neritopsis*, the limpets of the Pileolidae, and the widespread neritid *Otostoma*, with its axially ribbed, *Nerita*-shaped shells. The extant marine neritid *Nerita* seems to have had its origin in the Late Cretaceous; the oldest representatives known to us are from the Santonian of South Africa. There are at least four neritimorph groups present in the Cretaceous that independently adapted to brackish and freshwater. In the case of *Mesoneritina* this adaptation took place in the Jurassic, in the case of the Deianiridae in the mid-Cretaceous, in *Schwardtina* at latest in the Santonian, and in *Neritoplica*, which supposedly gave rise to the extant Neritinae, in the Campanian/Maastrichtian. The new species are: *Nerita squiresi*, *Otostoma vidali*, *Neritoplica dockeryi*, *Neritoplica oppenheimi*, *Neritoplica trochispira*, *Mesoneritina ajkaensis*, and *Pileolus ponsi*.

Key words: Gastropoda, Neritimorpha, Cretaceous, phylogeny, taxonomy, new taxa

Introduction

Cretaceous neritimorph gastropods have frequently been described in the literature, most commonly in monographs on entire gastropod faunas. But the taxonomic treatment is often poor: generic names are used in a confusing and inconsistent manner, species may be documented only as drawings which, in the worst case, are idealized, or the species are based on corroded material and/or without a preserved aperture.

The aim of this study is to provide clearly distinctive descriptions for the Cretaceous neritimorph groups, to evaluate their taxonomic position, to document their morphological and ecological ranges, and to discuss their phylogenetic relationships.

Material

One species was collected from deltaic and estuarine sediments near Isona in the Tremp Basin in northern Spain, where the shallow marine Arèn sandstone is interbedded with coal-bearing silts and marls. The Arèn sandstone is of Maastrichtian age (Simo 1986) and the gastropods were previously investigated by Vidal (1921), Bataller (1949), and Kowalke and Bandel (1996). The material is deposited in the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg.

The majority of the species are from the Puimanyons Olisthostrome of the Valcarga Formation exposed in the valley system around Torallola, Toralla and Sensuy near Pobra de Segur in the Tremp basin in northern Spain. Gastropods from this locality have previously been described by Vidal (1921), Bataller (1949), Quintero and Revilla

(1966), Revilla and Quintero (1966), and Calzada (1989), and we are currently revising them (Bandel and Kiel 2000, Kiel and Bandel 2000, 2001a, b, 2002). The age of these sediments is upper Campanian (Simo 1986). The material is deposited in the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg.

Two species are from the Maastrichtian Coon Creek Tongue of the Ripley Formation in Mississippi, USA (Dockery 1993). The locality, its gastropods, and their stratigraphic relations were described in detail by Sohl (1960) and Dockery (1993). The material is deposited in the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg.

One species from the Ajka Coal Formation in Hungary was loaned by the Geological Survey of Hungary in Budapest. These sediments were deposited during the Santonian/Campanian (Bartha 1962, Góczan et al. 1986) and represent coastal swamps (Bandel and Riedel 1994). The material is deposited in the Geological Survey of Hungary, Budapest.

The two South African neritids are from the Umzamba Formation in the Eastern Cape Province. According to Klinger and Kennedy (1980) this formation is of mid-Santonian to early Campanian age. These sediments have been preserved in their place of origin near the former and present shore of the Indian Ocean (Kiel and Bandel 1999). The material is deposited in the South African Museum, Cape Town, South Africa.

One specimen is from a quarry in Laisacker near Neuburg a.d. Donau in southern Germany. These deposits represent reef carbonates and are of lower Tithonian (Upper Jurassic) age (Janicke 1970). The specimen is deposited in the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg.

Systematic palaeontology

Abbreviations: GPIuM = Geologisch-Paläontologisches Institut und Museum, SAM = South African Museum, GSH = Geological Survey of Hungary.

Class Gastropoda Cuvier, 1797

Subclass Neritimorpha Golikov and Starobogatov, 1975

Remarks: The marine species of the Neritimorpha have a characteristic larval shell that has been secreted in addition to the embryonic shell by a planktotrophic larva (Scheltema 1971, Bandel et al. 1997). Mesozoic and modern Neritimorpha can, thus, be recognized by their early ontogenetic shell and differ in this character from all other subclasses of the Gastropoda (Bandel 1982, 1997, 2000a, Bandel et al. 1997). Coiling of the protoconch can be observed from middle Devonian onwards (Heidelberger and Bandel 1999) and has the typical neritimorph shape of a tightly coiled, almost globular shell since Carboniferous time (Bandel 2000a). Members of the superfamily Neritopsoidea Gray, 1847 do not resorb their inner shell walls, while the inner walls are resorbed in the Neritidae Rafinesque, 1815 and Pileolidae Bandel, Gründel and Maxwell, 2000 (Cossmann 1925, Wenz 1938–44).

Key to the Cretaceous neritimorph genera

- A. **Neritopsoidea:** neritoid shells; internal walls of larval and adult shell not dissolved
 - 1. inner lip with a rectangular notch, into which fits a respective projection of the calcareous operculum *Neritopsis*
- B. **Neritoidea:** internal walls of the larval shell dissolved
 - 1. Deianiridae: internal walls of the adult shell not dissolved; rotelliform shell-shape*Deianira* *
 - 2. Pileolidae: internal walls of the adult shell dissolved; limpet-shape; D- or sickle-shaped aperture*Pileolus*
 - 3. Neritidae: internal walls of the adult shell dissolved
 - 3.1. *Nerita*-shaped shells
 - 3.1.1. shell smooth except for collabral growth lines, inner lip without denticles.....*Mesoneritina* *
 - 3.1.2. shell smooth except for collabral growth lines, inner lip with one strong fold, occasionally a few minor ones below*Neritoplica* *
 - 3.1.3. shell spirally sculptured or smooth with collabral growth lines, inner lip with several subequal denticles.....*Nerita*
 - 3.1.4. shell spirally sculptured, inner lip with one strong fold, occasionally few minor ones below*Neritoptyx*
 - 3.1.5. shell with axial ribs on the whorl's upper side and periphery; on the periphery a strongly tuberculate keel may develop; below the periphery the axials are crossed and interrupted by spiral cords, or there are granulated spiral cords only, inner lip with subequal denticles*Ostostoma*
 - 3.1.6. *Hydrobia*-shaped shell*Schwardtina* *

(*) genera that have invaded brackish or freshwater.

Superfamily Neritopsoidea Gray, 1847

Family Neritopsidae Gray, 1847

Genus *Neritopsis* Grateloup, 1832

Type species: *Nerita radula* Linné, 1758, Recent, from the Indo-Pacific.

Diagnosis: The neritoid shell has beaded spiral sculpture, and its columella has a squarish embayment into which fits a thick, calcareous, white operculum (Abbott 1974).

Neritopsis ilerdensis Vidal, 1921

Pl. I, Figs 1–3

1921 *Neritopsis ilerdensis* Vidal: 101, Pl. 6, Figs 1, 2.

Material: Ten specimens from the Campanian of Torallola, north-eastern Spain (figured GPIuM Type. Kat. No. 4001).

Description: The shell has a low but erect spire with rapid increase in whorl width and with three whorls of the teleoconch separated by a deep suture. Its last whorl is globular with evenly convex flanks. The aperture has a rounded outer lip and a convex inner lip and columella. The inner lip is moderately thickened, forming a concave callus band, and has a quadrangular depression at the middle of its columellar edge. Sculpture consists of about 30 spiral cords that are intersected by fine collabral growth increments. The umbilicus is closed up to a narrow slit. The figured shell is the largest available, and is 14 mm high and wide, the smallest specimen is 6.5 mm wide and 7 mm high.

Remarks: The Recent *Neritopsis radula* is larger (about 20 mm high), has fewer spiral cords and a less developed inner lip-callus. Of the Late Cretaceous *Neritopsis ornata* Orbigny, 1842 only the backside was figured by d'Orbigny (1842: pl. 176, figs 8–10), thus its placement within *Neritopsis* cannot be confirmed. However, that species has a lower spire than *Neritopsis ilerdensis* described here. *Neritopsis tanohatensis* Kase, 1984 from the Aptian of Japan differs from *Neritopsis ilerdensis* by having broader and less numerous spiral cords and by its lower spire. Kase (1984: 83–84) provided an extensive list of Mesozoic species belonging to *Neritopsis*.

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Remarks: Six genera are recognized among the Late Cretaceous Neritidae: *Nerita* Linné, 1758, *Ostostoma* d'Archiac, 1859, *Mesoneritina* Yen, 1946, *Neritoplica* Oppenheim, 1892, *Neritoptyx* Oppenheim, 1892, and *Schwardtina* Bandel and Riedel, 1994. From all except the last one, species are described herein. For diagnostic differences between these genera, see the “key to the Cretaceous neritimorph genera” given above.

Genus *Nerita* Linné, 1758

Type species: *Nerita peloronta* Linné, 1758, by subsequent designation (Montfort 1810), Recent, from the Caribbean Sea.

Description: The outline of the shell is oval to globular with a low spire. The sculpture consists of weakly to strongly developed spiral lines or ridges. The callus of the inner lip may show ridges and tubercles or may be smooth. Its columellar edge has few more or less well developed denticles, the interior of the outer lip may be smooth or crenulated. All internal walls are dissolved and the shell consists of a calcitic outer layer and an aragonitic inner layer.

Remarks: Squires (1993) introduced the subgenus *Nerita (Bajanerita)* Squires, 1993 based on a species from the Late Cretaceous of Punta Banda in northwestern Baja California, Mexico. But the type species of *Bajanerita* shows a strong columellar fold and it must thus be considered a synonym of *Neritoplica* (Kiel and Aranda-Manteca 2002).

Seven Late Cretaceous species are considered by us to belong to *Nerita*. Two of them are spirally sculptured, the others are smooth. The oldest spirally sculptured species is *Nerita umzambiensis* Woods, 1906 from the Santonian/Campanian Umzamba Formation in South Africa. The next oldest is *Nerita gemmata* Pethö, 1906 from the Maastrichtian of the Fruska Gora Mountains in Serbia (Pethö 1906: 126, textfig. 3). The spirals of *N. gemmata* are stronger and have stronger tubercles than in *Nerita umzambiensis* and it has only four denticles on the inner lip. The drawings of *Nerita cingulata* Reuss, 1854 provided by Reuss (1854: pl. 29, fig. 6a, b) and Weinzettl (1910: pl. 3, fig. 10) both show a *Nerita*-like shell but neither author figured the aperture. This species could also represent a member of *Neritopsis*.

The oldest smooth species is *Nerita kaffraria* Woods, 1906 from the Santonian/Campanian Umzamba Formation in South Africa. It has six denticles on the columellar edge of the inner lip with the central ones being stronger than the outer ones; the inside of the outer lip shows many fine denticles. Their exact number remains uncertain but there are certainly more than six. A very similar or perhaps identical species was described as *Nerita subcompacta* Trechmann, (1927: 35, pl. 4, figs 34–35) from Jamaica. According to the description *N. subcompacta* has a smooth surface with irregular growth lines, and the columellar edge bears six denticles of which the central ones are the strongest. The drawing, however, is not very meaningful. Trechmann (1927) was somewhat uncertain about the age of this species and tentatively suggested “Middle Senonian”. It is thus of similar age and similar shape to *N. umzambiensis*. These species are likely to be conspecific. This would indicate that Cretaceous species had a similar wide distribution to modern Indopacific species of the genus *Nerita*, which in some cases ranges from Hawaii in the East to the shores of East Africa in the West, and from Jordan in the North to Australia in the South (Abbott and Dance 1982, own obs.).

Two species occur in the Campanian of Torallola, northern Spain. *Nerita* cf. *bergadana* Vidal, 1921 differs from *N. kaffraria* by the possession of eight denticles on the columellar edge of the inner lip that are arranged into two groups of four denticles each, with a slightly larger interspace between the two groups than between the denticles of each group; the interior of the outer lip is smooth. The newly introduced *N. squiresi* has six denticles on the columellar edge, and they are arranged into two groups as in *N. cf. bergadana* but the interior of the outer lip bears six equally sized denticles while *N. cf. bergadana* has a smooth keel here.

Squires and Saul (2001: 49, figs 3.1–5) described a neritid as *Otostoma sharonae* Squires and Saul, 2001 from the Campanian/Maastrichtian of southern California. This species is smooth except for fine collabral growth lines and thus belongs to *Nerita* rather than the strongly ribbed genus *Otostoma*. *Nerita sharonae* strongly resembles *N. squiresi* from the Campanian of Spain but differs slightly in size, in the height of the spire, and in its denticles on the columellar edge, which are equally distributed and not arranged into groups.

In the Maastrichtian of Paita in northern Peru occurs *N. jayanca* Olsson, 1944 which has four or five denticles on its inner lip, and the inside of the outer lip is crenulated (Olsson 1944: 67, Pl. 9, figs 6, 7).

Nerita umzambiensis Woods, 1906
Pl. I, Figs 4–5

1906 *Nerita umzambiensis* Woods: 311, Pl. 37, Figs 14, 15.
1930 *Nerita umzambiensis* Woods – Rennie: 209, Pl. 24, Figs 6, 7.

Material: Three specimens from the Santonian/Campanian Umzamba Formation in south-eastern South Africa (figured SAM-PCP 18135).

Description: The thick semi-ovate shell is wider than high and has a low, flattened spire. The last whorl is large, inflated, and somewhat flattened posteriorly and rounded anteriorly. The aperture is nearly semicircular with a rounded outer lip. The inner lip is slightly convex and its columellar edge shows six subequal denticles of which the basal one is slightly smaller than the others. The shell surface is ornamented by a reticulate pattern of collabral growth lines crossed by numerous spiral cords. The figured shell is 18 mm high and 19 mm wide, the smallest shell is 15 mm high and 17 mm wide.

Remarks: The specimens figured by Woods (1906) and Rennie (1930) all have a corroded outer side, which makes them appear smooth. A better preserved specimen collected by us shows typical *Nerita*-like spiral sculpture. But even in their corroded stage, they can clearly be distinguished from the smooth *Nerita kaffraria* (Woods 1906) from the same outcrop. That species has a flat top and an angular periphery, while *Nerita umzambiensis* has a somewhat elevated spire and a rounded periphery without angulation.

Nerita kaffraria Woods, 1906
Pl. I, Figs 6–7

1906 *Nerita kaffraria* Woods: 311, Pl. 37, Fig. 16
1930 *Nerita kaffraria* Woods – Rennie: 209, Pl. 24, Fig. 5

Material: Four specimens from the Santonian/Campanian of the Umzamba Formation in south-eastern South Africa (figured SAM-PCP 18136).

Description: The shell is semi-globular with an indistinct, flat spire. Its last whorl is very large, inflated, and has the posterior part flattened, the median part convex and rounded, and the anterior part somewhat produced. The aperture is large and rounded with a thin outer lip and a smooth inner lip. The latter is smooth, nearly flat and depressed below the level of the outer lip. Its inner margin is rather coarsely denticulate. The six apertural denticles are arranged in two groups of three denticles with a slightly larger interspace between the groups than between the denticles of each group. One individual shows an exterior color pattern, which consist of two spiral bands of dark maculations on a light grey background. The figured shell is 10 mm high and 16 mm wide, the smallest specimen is 7 mm high and 9 mm wide.

Remarks: Differences from other Late Cretaceous species of *Nerita* are outlined in the “Remarks” on *Nerita*.

Nerita cf. *bergadana* Vidal, 1921
Pl. I, Figs 8–10

1921 *Nerita bergadana* Vidal, Pl. 6, Figs 15, 16
1948 *Nerita bergadana* Vidal – Bataller: 32, Fig. 489

Material: One specimen from the Campanian of Torallola, north-eastern Spain (GPIuM Type Kat. Nr. 4003).

Description: The smooth neritiform shell has a flat spire and consists of about three teleoconch whorls. The inner lip is callus-covered and the columellar edge bears eight denticles which are arranged into two groups of four denticles each, with a slightly larger interspace between the groups than between the denticles of each group. The outer denticles are smaller than the inner ones. The interior of the outer lip shows a smooth keel. The shell is 17 mm high and 20 mm wide.

Remarks: Nothing is known about the dentition of the columellar edge of the specimens described by Vidal (1921), thus its assignment to that species remains tentative. Differences from other Late Cretaceous species of *Nerita* are outlined in the “Remarks” of *Nerita*.

Nerita squiresi n. sp.
Pl. I, Figs 11–13

Holotype: GPIuM Type Kat. Nr. 4002, figured on Pl. I, Figs. 11–13.

Paratypes: GPIuM Type Kat. Nr. 4018, 4019.

Type locality and strata: The Campanian marls of the Puimanyons Olisthostrome exposed in the

valley system around Torallos, Toralla and Sensui in the vicinity of Poble de Segur, north-eastern Spain.

Etymology: Named after Richard Squires, Northridge, USA, who is working on fossil molluscs from the Pacific slope of North America.

Material: Three specimens from the type locality.

Diagnosis: This *Nerita* has a slightly erect spire, six denticles on the columellar edge which are arranged into two groups with three denticles each, and there are six equally sized denticles on the interior of the outer lip.

Description: The neritiform shell consists of about two whorls that increase in size rapidly. The spire is little erect and the whorls are smooth except for fine collabral growth lines. The callus on the inner lip is squarish and smooth. The columellar edge is slightly convex and bears six denticles of which the basal one is smaller than the others. They are arranged in two groups with three denticles each, having a slightly larger interspace between the groups than between the denticles of each group. The interior of the outer lip shows six equally sized denticles. The holotype is 10 mm high and 11 mm wide, the two paratypes are 11 mm high and 12 mm wide, and 10 mm high and wide respectively.

Remarks: This species appears very closely related to *N. sharonae* (Squires and Saul 2001), it differs only by having a slightly erect spire, by being smaller (*N. sharonae* growth up to 19 mm in height), and by having the denticles on the columellar edge arranged into two groups, while they are equally distributed in *N. sharonae*. Differences from other Late Cretaceous species of *Nerita* are outlined in the “Remarks” on *Nerita*.

Genus *Otostoma* d’Archiac, 1859

Type species: *Nerita rugosa* Hoenighaus, 1830, by subsequent designation (Douville 1904). Squires and Saul (1993) have extensively discussed the nomenclatural history of the type species of *Otostoma*.

Diagnosis: According to Pethö (1906), the *Nerita*-shaped shell has a depressed spire and rapidly expanding whorls. The ornament consists of axial ribs above the periphery, below the periphery the axial ribs may be broken or crenulated, and they eventually die out before reaching the base. The periphery itself may be developed as an angulation or as a strongly tuberculated keel. The semi-lunular aperture is provided with an expanded and thickened inner lip which bears strong subequal denticles on its columellar edge.

Remarks: There have been different opinions regarding the validity of subgeneric divisions within *Otostoma*. Cossmann (1925), Wenz (1938–44), and Knight et al. (1960) considered *Corsania* Vidal, 1917 a synonym of *Otostoma*, while Bataller (1949) and Cushing Woods and Saul (1986) regarded *Corsania* as full genus. It was introduced for species which have the axial ribs raised when they cross the peripheral edge and the basal edge, and end before passing onto the base. The subgenus *Otostoma* (*Otostoma*) would be used for species that are more rounded in shell

shape and without a peripheral keel. However, in the case of *Otostoma divaricata* (d'Orbigny, 1842) described below, the younger growth stages could be considered to represent a species of *Otostoma* s.str., while later stages have changed into *O. (Corsania)* (see Pl. II, Figs 4–6). Thus, *O. (Corsania)* represents only a late adult growth stage of *Otostoma* s.str. Therefore we follow Cossmann (1925), Wenz (1938–44), and Knight et al. (1960) and consider *Corsania* a junior synonym of *Otostoma*.

Damesia Holzapfel, 1888 was introduced as a genus within the Neritidae, and was considered a subgenus of *Otostoma* by Wenz (1938–44). However, Dockery (1993) illustrated the sinistrally coiled protoconch of *Damesia* and thus showed that *Damesia* represents a *Nerita*-shaped allogastropod and belongs to the subclass Heterostropha.

Still problematic is the position of *Lyosoma* White, 1880, which is based on some poorly preserved specimens from the Jurassic of Utah, USA. Zittel (1882) and Fischer (1880–1887) treated *Lyosoma* as a synonym of *Otostoma*, while it was listed as a subgenus of *Otostoma* by Wenz (1938–1844). According to Sohl (1965) its smooth inner lip represents the diagnostic difference from *Otostoma* sensu strictu. However, this could be a preservation artifact. Pethö (1906) pointed out that the resorption of the inner walls has never been investigated in species of *Lyosoma* and left its systematic position open.

Otostoma divaricata (d'Orbigny, 1847)

Pl. II, Figs 1–6, 10–11

1847 *Nerita divaricata* d'Orbigny: Figs 43–44

1906 *Nerita (Otostoma) divaricata* d'Orbigny – Pethö: 127, Pl. 9, Figs 11–17

Material: 30 specimens from the Campanian of Torallola, north-eastern Spain (figured GPIuM Type Kat. Nr. 4004–4007, 4009).

Description: The thick-walled, neritiform shell is as wide as high, and consists of about three whorls of the teleoconch. The periphery as well as the sides are rounded. Sculpture consists of fine axial ribs which increase in size with shell growth. The late whorls have fine collabral ribs between the larger ones and the ribs often turn into blunt tubercles on the shoulder of the whorls. Granular spirals are present only on the lower half of the whorls. The callus of the inner lip is flat and slightly concave toward its anterior portion, covering much of the flattened base. The denticles on the straight or slightly convex columellar edge vary in number from seven to ten and decrease in size from the centre to the margins. The specimen illustrated in Pl. 2, Figs 1–3 is 13 mm high and wide, the largest specimen is 16 mm high.

Remarks: *Otostoma marcouana* (Cragin, 1895) from the Albian of Texas is quite similar to *O. divaricata* but the American species appears to have stronger spiral cords on its base (see Akers and Akers 1997: 51, fig. 30). The Indian *Otostoma coralina* (Stoliczka, 1868) from the

Campanian of the Trichinopoly Group is also similar but differs in having a lower spire (see Bandel 2000b: 72, pl. 1, fig. 6). *Otostoma vidali* n. sp. described below differs by having a peripheral ridge and bifurcating axial ribs.

Otostoma vidali n. sp.

Pl. II, Figs 7–9

1966 *Nerita* cf. *douvillei* Vidal – Quintero and Revilla: 47, Pl. 7, Figs 3–5

Holotype: GPIuM Type Kat. Nr. 4008, illustrated on Pl. II, Figs 7–9.

Paratype: GPIuM Type Kat. Nr. 4020.

Type locality and strata: The Campanian marls of the Puimanyons Olisthostrome exposed in the valley system around Toralloa, Toralla and Sensui in the vicinity of Poble de Segur, north-eastern Spain.

Etymology: In honour of Luis Mariano Vidal who described many gastropods from the Cretaceous of Catalonia.

Material: 15 specimens from the type locality.

Diagnosis: The neritiform shell has an angular whorl periphery, and is sculptured by axial ribs that bifurcate below the angulation. The inner lip is almost straight and has six to eight subequal denticles.

Description: The thick-walled neritiform shell consists of about four whorls of the teleoconch. The early teleoconch whorls are ornamented by fine axial ribs and show a peripheral angulation. On later whorls the ribs become stronger above the periphery, and bifurcate below. The aperture is D-shaped, its columellar edge is almost straight and shows six to eight denticles. The callus of the inner lip is often depressed on its lower side. The holotype is 12 mm wide and 10 mm high, the paratype is 18 mm high and 20 mm wide.

Remarks: *O. douvillei* described by Vidal (1917) from the lower Cretaceous of Montsech (northern Spain) differs from *O. vidali* n. sp. by having the crests of the ribs elevated above the spire. The Mexican *O. allisoni* (Saul and Squires, 1997) differs from *O. vidali* by having finer sculpture, and *O. divaricata* from the Spanish Campanian has rounded whorl in contrast to the angular ones of *O. vidali* n. sp.

Genus *Neritoplica* Oppenheim, 1892

Type species: *Neritina uniplicata* Sowerby, 1823 (= *Neritina globulus* Deshayes, 1824), by subsequent designation (Wenz 1929: 2895), from the upper Paleocene of the Paris Basin.

Diagnosis: The smooth neritid shell has an oblique, semicircular aperture that has a strong fold on the apical side of the columellar edge of the inner lip that continues into the shell's interior. Some weak denticles may be present below (Oppenheim 1892).

Remarks: The newly described *N. oppenheimi* from the Campanian of Spain differs from all other members of *Neritoplica* known to us by its sharp peripheral keel. The

second new species, *N. dockeryi* from the Coffee Sand Formation in Tennessee, USA, shows almost convolute coiling and is globular in shape. The third new species described herein, *N. trochispira*, is very similar to *Neritina loganensis* Erickson, 1974 from the Maastrichtian of the Fox Hill Formation in North Dakota (Erickson 1974: 163, pl. 14, figs 7–9). This author pointed out that the upper denticle on the columellar edge of the inner lip is stronger than the lower two, thus, that species most probably belongs to *Neritoplica*. It resembles *N. trochispira* in general shape and even has a similar sinus in the left margin of the inner lip callus, but it appears to have a broader spire and the lower two denticles on the columellar edge are stronger. Additionally, *Neritoplica loganensis* has a straight columellar edge, while that of *N. trochispira* is slightly concave. According to Erickson (1974) *N. loganensis* resembles *Neritoplica pisum* (Meek, 1873) from the Turonian of Coalville in Utah, USA, which has four columellar denticles, of which the uppermost is the strongest. A poorly preserved Albian/Cenomanian species from Austria was described as *Neritoplica* sp. by Kollmann (1982: pl. 6, figs 77–78). It appears to have only one columellar denticle and the whorls seem subsuturally constricted. In contrast to the species discussed so far, *N. matheroni* Oppenheim, 1895 has a blunt spire and well-rounded whorls (Kowalke and Bandel 1996: pl. 1, fig. 2).

Neritoplica dockeryi n. sp.
Pl. II, Figs 12–14

?1993 *Neritina* sp. Dockery: 44, Pl. 4, Figs 3–4

Holotype: GPIuM Type Kat. Nr. 4010, illustrated on Pl. II, Figs 12–14.

Type locality and strata: The Coon Creek Tongue of the Ripley Formation, Union County Lake, Mississippi, USA, Early Maastrichtian.

Etymology: Named for David T. Dockery III who described many of the fossil gastropods of Mississippi and who helped to collect this species.

Material: One specimen from the type locality.

Diagnosis: This *Neritoplica* is tightly coiled, globular, and shows one columellar plate in a posterior position and one minor fold at the base of the columella.

Description: The globular neritid shell is very tightly coiled, almost convolute, and is smooth on its outer side. The columella is concave, has one plate in posterior position, is smooth below, and has a minor fold at its base. The shell is pale brown and shows three dark-brown spiral stripes and irregular white splotches. The holotype is 13 mm high and has a diameter of 12 mm.

Remarks: Dockery (1993: 44) described two specimens to have a non-denticulate columellar edge. Since his specimens are from the same locality as our individual, show the same tight coiling and the same colour pattern, we consider them to represent the same species. For diagnostic characters see the “Remarks” about *Neritoplica*, above.

Neritoplica oppenheimeri n. sp.
Pl. II, Figs 15–17

Holotype: GPIuM Type Kat. Nr. 4011, illustrated on Pl. II, Figs 15–17.

Type locality and strata: The Campanian marls of the Puimanyons Olisthostrome exposed in the valley system around Torallola, Toralla and Sensui in the vicinity of Pobra de Segur, north-eastern Spain.

Etymology: Named in honour of Paul Oppenheim, for his excellent work on Cretaceous and Tertiary neritid gastropods.

Material: 13 specimens from the type locality.

Diagnosis: The smooth neritiform shell has a peripheral keel which disappears on the last half whorl. The columellar edge of the inner lip has one strong fold in an apical position and is otherwise smooth.

Description: The spherical shell consists of the protoconch and about three whorls of the teleoconch, which increase in width quite rapidly. The spire is low and there is a peripheral keel which disappears on the last half whorl. Ornament consists of fine growth lines, one specimen shows a colour pattern of irregular, small white spots on a brown background. The inner lip is formed by a broad, flattened callus with a columellar edge bearing one large plication on its apical portion. The holotype is 10 mm high and 11 mm wide, the largest specimen is 12 mm high and 13 mm wide.

Remarks: For diagnostic characters see the “Remarks” about *Neritoplica*, above.

Neritoplica trochispira n. sp.
Pl. II, Fig. 18

Holotype: GPIuM Type Kat. Nr. 4012, illustrated on Pl. II, Fig. 18.

Type locality and strata: The Campanian marls of the Puimanyons Olisthostrome exposed in the valley system around Toralloa, Toralla and Sensui in the vicinity of Pobra de Segur, north-eastern Spain.

Etymology: Named according to its trochiform spire.

Material: One specimen from the type locality.

Diagnosis: The smooth neritiform shell has a trochiform spire and well-rounded whorls. The smooth inner lip callus bears one strong apical fold on the slightly concave columellar edge and two minor denticles below.

Description: The teleoconch consists of about three volutions which increase rapidly in size. The spire is trochiform and the body whorl is sculptured with fine, transverse growth lines. The inner lip callus is smooth, the columellar edge is slightly concave and possesses a strong denticle on its apical side, and two minor denticles below it. The shell is 7 mm high.

Remarks: For diagnostic characters see the “Remarks” about *Neritoplica*, above.

Genus *Neritoptyx* Oppenheim, 1892

Type species: *Nerita goldfussi* Keferstein, 1829 (non Zekeli, 1852), by original designation (Oppenheim 1892: 773, pl. 36, fig. 5), from the Gosau Formation, Austria.

Diagnosis: The neritiform shell is ornamented by spiral ribs crossed by collabral growth elements in a regular way, and there is one fold on the columellar edge of the inner lip (Oppenheim 1892).

Remarks: Cossmann (1925) as well as Wenz (1938–44) considered the type species of *Neritoptyx*, *Nerita goldfussi*, to be a species of *Neritopsis*. This is not the case, as Kowalke and Bandel (1996) pointed out that *Neritoptyx* dissolves its internal wall and is, therefore, a member of the Neritidae.

Neritoptyx reticulirata (Dockery, 1993)

Pl. II, Figs 19–20

1993 *Nerita reticulirata* Dockery: 43, Pl. 1, Figs 18–20; Pl. 2, Figs 1–2.

Material: Ten specimens from the Campanian Coffee Sand member of the Ripley Formation, USA (figured GPIuM Type Kat. Nr. 4013–4014).

Diagnosis: A *Neritoptyx* with the first two whorls of the teleoconch smooth, then starts a sculpture of 20 or more spiral cords and fine axial growth laminae. The spire is low but erect, and the inner lip of the aperture bears one columellar fold.

Description: The shells have a smooth protoconch and a strongly lirate teleoconch with a single denticle on the upper part of the inner lip. The protoconch is spherical and consists of several whorls overlapping each other strongly and measures about 0.15 mm in diameter. The early teleoconch is almost smooth, apart from fine, closely spaced growth laminations. A first spiral lira is present here but is covered by the succeeding whorl. Spiral lirae appear abruptly after two smooth whorls. These lirae number 20 or more in the adult and form a reticulate pattern with fine simple growth laminae crossing them. The aperture is semicircular and the inner lip bears a columellar fold. The figured shells are 4 mm high.

Remarks: This American species resembles the type species but differs by lacking spiral sculpture on the first two whorls of the teleoconch. The French *Neritoptyx renauxiana* (d'Orbigny, 1842: pl. 176, figs 5–7) differs by having a more roundish aperture.

Genus *Mesoneritina* Yen, 1946

Type species: *Neritella nebrascensis* Meek & Hayden, 1861, by original designation, from the early Cretaceous of Nebraska, USA.

Diagnosis: “Shell of small size, moderately thick, with a small but slightly raised spire and rapidly dilated body whorl. Whorls smooth except for weak growth lines and scarcely convex, marked by irregular zigzag colour

patterns. Aperture broadly ovate, outer lip thin, columellar area nearly flat, well defined, thickened, and smooth, with a blunt and almost straight edge.” (Yen 1946: 7).

Remarks: *Mesoneritina* differs from *Neritina* by its smooth columellar edge of the inner lip, while *Neritina* has denticles there. *Neritoplica* differs from *Mesoneritina* by its strong fold on the columellar edge of the inner lip.

Mesoneritina ajkaensis n. sp.

Pl. III, Figs 1–6

Holotype: K 2948A, GSH, Budapest, figured on Pl. III, Figs 1–3.

Paratype: K 2948B, GSH, Budapest, figured on Pl. III, Figs 4–6.

Type locality and strata: The Ajka Coal Formation in the Csingertal, near Ajka (Bakony Mountains), Hungary.

Etymology: Named after the Ajka Mountains in Hungary, where this species was found.

Material: Two specimens collected by M. Hantken, were loaned by the Geological Survey of Hungary.

Diagnosis: This *Mesoneritina* is wider than high, has a thin and narrow callus pad on its inner lip, the columellar edge of the inner lip is straight and has well-rounded apical and basal margins, and the interior of the outer lip is smooth.

Description: The low-spined neritid shell has little more than two rapidly expanding whorls, a smooth surface, and has color patterns of zigzag stripes and spiral lines. The aperture is almost quadrangular with a rounded outer side, has a narrow callus pad with a smooth and straight columellar edge on the inner lip, and a simple outer lip. The holotype is 6 mm wide, the paratype is 4.5 mm wide.

Remarks: *Mesoneritina subhercynica* (Mertin, 1939) from the “lower Senonian“ of Quedlinburg near the Harz Mountains in Germany (Mertin 1939: 197, pl. 4, figs 3a–c) differs by having a narrower aperture with a much larger callus pad on the inner lip.

Family Pileolidae Bandel, Gründel and Maxwell, 2000

Remarks: This family contains limpets with more or less well developed radial sculpture, a subcentral apex and a basal plate which has a relatively small, more or less D-shaped aperture (Bandel, Gründel and Maxwell 2000). The Neogene to Recent neritimorph limpet family Phenacolepadidae differs by having the inner lip totally reduced (see Scott and Kenny 1998, Bandel 2001). In the *Septaria* group of the Neritidae the shell is usually smooth and the aperture is very wide in contrast to the narrow ones of the Pileolidae (Bandel 2001).

Genus *Pileolus* Sowerby, 1823

Type species: *Pileolus plicatus* Sowerby, 1823, by original designation, from the Bathonian of England.

Diagnosis: A limpet-shaped shell with subcentral apex, radial sculpture and a D-shaped aperture.

Remarks: A steinkern of a *Pileolus* specimen from the Upper Jurassic of Laisacker, Germany is documented here on Pl. III, Fig. 10. It shows that the protoconch of *Pileolus* had dissolved internal walls. This feature is characteristic for members of the Neritoidea and confirms the placement of *Pileolus* within this superfamily.

Pileolus ponsi n. sp.
Pl. III, Figs 7–9

Holotype: GPIuM Type Kat. Nr. 4016, illustrated on Pl. III, Figs 7–9.

Type locality and strata: The Campanian marls of the Puimanyons Olisthostrome exposed in the valley system around Toralloa, Toralla and Sensui in the vicinity of Pobla de Segur, north-eastern Spain.

Etymology: Named after Jose Maria Pons from the Universitat Autonomia de Catalonia who introduced us to the Tremp Basin and the locality of Torallola.

Material: One specimen from the type locality.

Diagnosis: This *Pileolus* has numerous subequal ridges on its base perpendicular to the aperture and two ridges parallel to the aperture. The aperture is narrow and sickle-shaped, and located near the edge of the base. The radial ribs on the shell's outer side are prominent and their interspaces are each about three times as wide as one rib.

Description: The small limpet has a circular base, a smooth, dome-shaped apex, and eleven almost equally strong radial ribs on the outer side of its shell. The narrow, sickle-shaped aperture has nine denticles on the inner lip: a central one and two rows of four denticles on each of its side. The remaining base has nine ribs at right angles to the aperture, and two ribs parallel to it, with a space between them next to the central tooth on the inner lip. The holotype has a diameter of 6.5 mm and is 3.5 mm high.

Family Deianiridae Wenz, 1938

Remarks: Oppenheim (1892) was the first to propose that *Deianira* should constitute its own family but did not provide a name. Wenz (1938–1844) therefore coined the family Dejaniridae, a spelling which later was corrected by Knight et al. (1960) to Deianiridae. Oppenheim (1892) suggested a systematic position of this taxon intermediate between Neritoidea and Helicinoidea. Pethö (1906) discussed *Deianira* according to his examinations of *D. bicarinata* (Zekeli) and *D. hörnesi* Stoliczka from the Gosau Formation in the northern Alps. He noted that these differ from the Neritidae in having a non-hollow inner space in the shell. He thus concluded that *Deianira* should be excluded from the Neritimorpha and placed near the Amphibolidae (Archaeopulmonata). Cossmann (1925) adopted this treatment. But Wenz (1938–4844) followed Oppenheim's (1892) placement and stated that the shape of the operculum places the genera related to *Dejanira*

within the Neritoidea. Bandel and Riedel (1994) demonstrated that the protoconch of *Deianira* has dissolved inner walls and is quite similar in shape to that of *Nerita* or *Neritina*. They also showed that *Deianira* in fact has the columella dissolved, but fully grown specimens fill much of their internal shell lumen with shell material. The Deianiridae is here placed within the Neritoidea.

Böhm (1900: 194, text-fig. 6, pl. 5, figs 8, 8a) introduced *Myagrostoma* Böhm, 1900 for *Myagrostoma plexum* Böhm, 1900 from the Late Cretaceous of Syria, which he placed within the Neritidae. Wenz (1938–1844: 419, fig. 1021) followed this treatment. Böhm compared this species with *Deianira*, which has a similar shape and a similar dentition of the inner lip but differs by lacking the cancellate sculpture of *Myagrostoma*. He also compared it with the Triassic to Jurassic *Lissochilus* Pethö, 1882, which has similar sculpture but lacks columellar dentition. *Myagrostoma* possibly represents a deianirid with cancellate sculpture.

Genus *Deianira* Stoliczka, 1859

Type species: *Rotella bicarinata* Zekeli, 1852, by original designation, from the “Edelbachgraben” near Gosau in Austria (Bandel and Riedel 1994).

Diagnosis: The teleoconch is of rotelliform shape, broader than high, with 3–4 dextral whorls, bordered by a carina. The spire is depressed or dome-shaped, the base is convex and there is no umbilicus. The aperture has an almost egg-shaped outline and is obliquely oriented and notched at the carina, with one or more columellar plaits. The protoconch is convolutely coiled, sculptured by axial ridges and its inner walls are resorbed (Bandel and Riedel 1994).

Deianira matheroni Vidal, 1874
Pl. III, Figs 11–13

1874 *Deianira matheroni* Vidal, Pl. 3, Fig. 18

Description: The rotelliform shell has a slightly elevated spire comprising three whorls, sculptured by oblique growth lines only. There are two peripheral ridges with a deep groove in between, the lower keel is the stronger one. The base is conical and smooth, the inner lip callus is very thick, the columellar edge possesses a strong apical fold and one minor one near the base. The figured specimen is 10 mm high and 13 mm wide.

Material: Six specimens from the Maastrichtian Arèn Sandstone near Isona in the Tremp basin in north-eastern Spain (figured GPIuM Type Kat. Nr. 4017).

Discussion

Only a few species of *Neritopsis* are known from the Cretaceous and they show a morphological range that is only slightly broader than today (Kase 1984). According to Wenz (1938–1944) and Kase (1984) the genus had its

heyday in the Jurassic. Kase (1984) discussed the neritopids *Hayamia* and *Neritopsis* (*Hayamiella*) which were still present with a few species in the mid-Cretaceous, but seem to have disappeared in the Late Cretaceous. Also *Neritopsis* apparently had declined to a few relicts that time, but managed to survive until today.

The Pileolidae represent a distinct later Mesozoic family of neritoid limpets. Since the extant neritoid limpets of the Phenacolepadidae and the group related to *Septaria* all have a different morphology and cannot be derived from the Pileolidae, that group is considered extinct (Wenz 1938–1944, Sohl 1987, Bandel 2001). Species of the Pileolidae were most abundant in the Tethyan carbonate facies and are considered to have inhabited tropical lagoons (Sohl 1987, Mustafa and Bandel 1992).

Among the Neritidae, *Otostoma* is the most common genus in the Tethyan realm from the Aptian to the end of the Cretaceous. *Otostoma* shows a broad morphological range of form from well-rounded forms such as *O. divaricata* to those with a strong angulation formed by a heavily tuberculated peripheral ridge such as *O. japonica*. There are transitional forms between these two extremes so that the use of subgeneric divisions based on the peripheral keel appears inappropriate.

Among the seven Late Cretaceous species of *Nerita*, smooth-shelled species (five) are far more common than spirally sculptured ones (two). This is in contrast to the Recent conditions where spirally sculptured forms far outnumber the only smooth species *Nerita polita*. The earliest known species representing both ornamentation types which we were able to confirm occur in the Santonian of South Africa – an ancestor has not yet been identified. Bandel (2001) suggested that the smooth *Nerita polita* could actually belong in a separate genus *Dontostoma* Herrmannsen, 1847. However, new material of that species from Madagascar documented that spiral ornament is present in races or varieties of *N. polita*.

Neritoplica-like shell are well-known from the Cretaceous. The earliest report of *Neritoplica* from a brackish environment is from the Maastrichtian (Kowalke and Bandel 1996). Oppenheim (1892) considered *Neritoplica* to be related to *Deianira*, which inhabited marine to brackish water, and to the fully marine *Neritoptyx*, due to the strong columellar fold which is characteristic of these genera. No records of *Deianira* or *Neritoptyx* from strata younger or older than the Cretaceous are known to us. *Neritoplica* itself was regarded by Oppenheim (1892) as ancestral to the extant brackish to freshwater genus *Neritina*. Oppenheim (1892) stated that no extant member of *Neritina* has a strong columellar fold like *Neritoplica*. This is only partly correct, as certain members of *Neritina* show a strong apical denticle on the columella (Bandel 2001). These denticles however, are not developed as spiral columellar folds that wind around the columella as in *Neritoplica*. This observation supports Oppenheim's (1892) interpretations regarding the phylogeny of *Neritoplica* and *Neritina*, and is followed here.

Mesoneritina has a smooth columella and has lived in brackish water since the Jurassic (Yen 1946). Following

Oppenheim's (1892) interpretation that extant *Neritina* is derived from *Neritoplica*, *Mesoneritina* represents an independent radiation into the brackish environment. The phylogenetic relationships of the *Hydrobia*-shaped neritid *Schwardtina*, from the brackish environment of the Ajka Coal Formation (Santonian/Campanian) in Hungary are still unclear (Bandel and Riedel 1994).

This scenario indicates that members of the Neritoidea invaded the brackish and freshwater environment at least four times during the Mesozoic: *Mesoneritina* lived there already in the Jurassic (Yen 1946), the Deianiridae probably invaded brackish water in the Albian/Cenomanian (Kollmann 1982), the *Hydrobia*-shaped *Schwardtina* is known from a brackish environment of Santonian/Campanian age (Bandel and Riedel 1994), and *Neritoplica* gave rise to the extant Neritinae in the Maastrichtian (Oppenheim 1892, Kowalke and Bandel 1996).

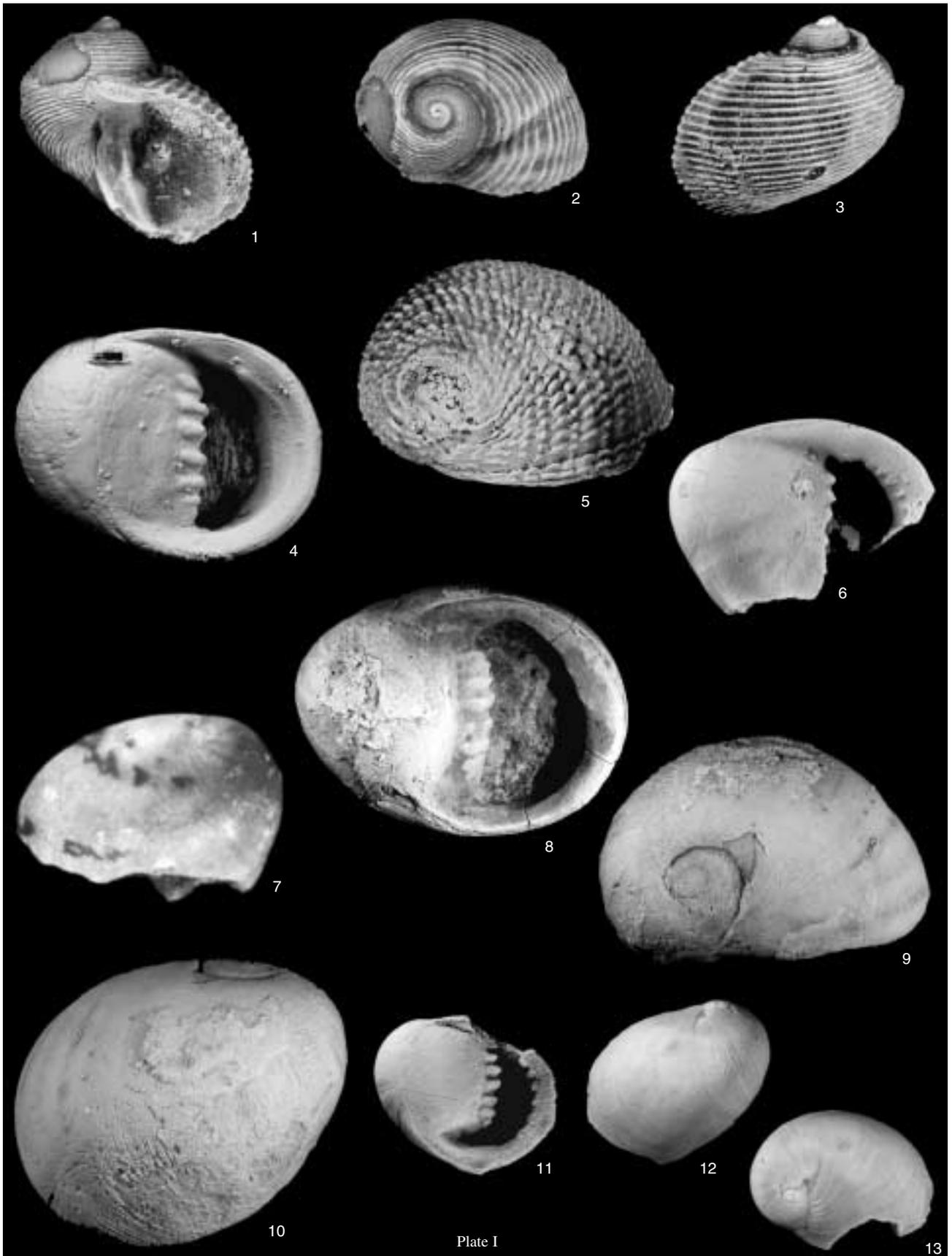
Acknowledgements. We would like to thank David T. Dockery, Jackson, who helped during the field-trip in Mississippi, USA; Jose M. Pons, Barcelona, for his introduction to the localities in the Tremp basin in northern Spain; David Herbert, Richard Kilburn, Pietermaritzburg, and Herbert Klinger, Cape Town, for their help during the fieldwork in South Africa; all our colleagues who helped to collect in the Tremp basin; and Alan Beu, Lower Hutt and Frank Riedel, Berlin, for their critical and helpful reviews of the paper. Financial support was granted by the University of Hamburg.

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Handling editor: Jiří Frýda



All figures $\times 3$.

1–3 *Neritopsis ilerdensis* Vidal, 1921; 4–5 *Nerita umzambiensis* Woods, 1906; 6–7 *Nerita kaffraria* Woods, 1906; 8–10 *Nerita* cf. *bergadana* (Vidal, 1921); 11–13 *Nerita squiresi* n. sp., holotype



All figures $\times 3$ except where indicated otherwise.

1–6 *Otostoma divaricata* (d’Orbigny, 1847); 1–3 three views on a juvenile shell; 4–6 ventral views on three specimens showing ontogenetic changes in the sculpture;

7–9 *Otostoma vidali* n. sp., holotype; 10–11 *Otostoma divaricata* (d’Orbigny, 1847), cross-section showing that the internal walls are mostly dissolved; 10 – $\times 4$; 11 – $\times 15$; 12–14 *Neritoplica dockeryi* n. sp., holotype; 15–17 *Neritoplica oppenheimeri* n. sp., holotype; 18 *Neritoplica trochispira* n. sp., holotype; $\times 6$; 19–20 *Neritoptyx reticulirata* (Dockery, 1993); $\times 10$



1-6 *Mesoneritina ajkaensis* n. sp.; all figures $\times 10$; 1-3 holotype, 4-6 paratype;
7-9 *Pileolus ponsi* n. sp., holotype; $\times 8$; 10 Steinkern of a protoconch of a Jurassic *Pileolus* from Kehlheim, Germany, showing that the internal walls of the protoconch are dissolved, $\times 40$; 11-13 *Deianira matheroni* Vidal, 1874; $\times 4$