Operculum shape and construction of some fossil Neritimorpha (Gastropoda) compared to those of modern species of the subclass

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ABSTRACT

The calcareous operculum of the Neritimorpha is more often preserved in the fossil record than the operculum of most other Gastropoda that is of purely organic composition. Together with the morphology of the protoconch and the shell structure, operculum shape represents a useful tool for understanding evolution within Neritimorpha. The Devonian Nerrhenidae (Nerrhenoidea) have an operculum with spiral construction resembling that present in the operculum of modern Neritoidea during very young stages of growth. The operculum of the modern and Mesozoic *Neritopsis* resembles that of Triassic relatives of the Cassianopsinae (both Neritopsoidea). The Carboniferous and Permian Naticopsidae (Naticopsoidea) can be connected with species from the Triassic St Cassian Formation. *Hologyra* thus resembles *Naticopsis*. The Triassic Tricolnaticopsidae is distinguished by a quite different operculum. The first Neritoidea are represented by the Triassic Neritariidae and have a similar shape of their operculum, with inner hinge, to that of modern *Neritina*. A strong decline in diversity of Neritimorpha occurred towards the Jurassic, and Neridomidae fam. nov. (Neritoidea) has an operculum as in Triassic Ruganeritaria. Cretaceous Otostomidae n. fam. differs in shell shape from Neritidae, while their operculum resembles that of *Nerita*. The shape of the operculum distinguishes Neritiliidae, Neritidae, Smaragdiidae and Septariidae from each other. The Theodoxidae have their lecithotrophic early ontogeny reflected in the simplified construction of their juvenile operculum.

INTRODUCTION

The opercula of living aquatic Neritimorpha may be divided into four categories based on the construction of their layers (Kano, 2006). The most common form has an outer organic layer and a thin inner calcareous layer as in *Pisulina*, *Neritilia*, *Bathynerita*, *Shinkailepas*, *Theodoxus*, *Smaragdia*, *Neritina* (including its subgenera), *Puperita* and *Septaria* (Suzuki et al., 1991; Kano, 2006). A heavily calcified operculum occurs in *Nerita* and *Neritodryas*. The operculum of *Neritopsis* has a thick outer calcareous layer (Kaim & Sztajner, 2005). Members of the shallow-water Phenacolepadidae exhibit no growth of their post-larval operculum (Kano, 2006).

The Cyrtoneritimorpha of the Paleozoic had a planktotrophic larva with openly coiled larval shell (Bandel, 1997; Bandel & Frýda, 1999; Frýda & Heidelberger, 2003). Some of their species have a teleoconch shape that closely resembles that of the Devonian Plagiothyridae Knight, 1956, but the protoconch is not tightly coiled. An operculum belonging to any species of the Cyrtoneritimorpha is not known.

The taxa of the Neritimorpha, Cycloneritimorpha in which an operculum is known are described below.

For a classification of the Neritimorpha as adopted here, see Table 1.

SYSTEMATIC PART

Superfamily **Nerrhenoidea** Bandel & Heidelberger, 2001

A low conical teleoconch with rounded whorls is connected to a low and spirally arranged protoconch. The operculum has sinistral spiral construction (Bandel & Heidelberger, 2001). The relation of the Nerrhenoidea to other Cycloneritimorpha is still unknown.

Nerrhenidae Bandel & Heidelberger, 2001
Pl. 1 fig. 1

The family is based on *Nerrhena* Heidelberger & Bandel, 1999 from the Mid-Devonian of western Germany. Hessonia Heidelberger, 2001 with Hessonia piligera (Sandberger & Sandberger, 1850-1856) is also included.

The *Natica* - shaped shell with smooth teleoconch has a low apex and consists of about four rapidly increasing whorls. It has a low spirally arranged protoconch with small rounded embryonic whorl of about 0.1 mm in width and rounded conical larval shell that consists of about two whorls (Heidelberger, 2007, fig. 2 K, N). Details of its ornament are still unknown. The inner whorls of the teleoconch are not dissolved. The aperture is orientated in an almost vertical position, has a rounded outer lip and the inner lip expanded to form a callus. The protoconch of *Nerrhena reticulata* Heidel-

Superfamily	**Family**	**Subfamily**	**genus**
Nerrhenoidea	Nerrhenidae		*Nerrhena*
			Hessonia
Neritopsoidea	Neritopsidae	Neritopsinae	*Neritopsis*
		Cassianopsinae	*Cassianopsis*
			Zardiniopsis
		Colubrellopsinae	*Colubrellopsis*
	Fedaiellidae		*Fedaiella*
Naticopsoidea	Naticopsidae	Naticopsinae	*Naticopsis*
			Trachydomia
		Hologyrinae	*Hologyra*
		? Ampezzonaticopsinae	
	Tricolnaticopsidae		*Tricolnaticopsis*
			Pachyomphalus
			Rinaldopsis
	Scalaneritinidae		*Scalaneritina*
			Ladinaticella
			Lancedellopsis
Neritoidea	Neritariidae	Neritariinae	*Neritaria*
			Ruganeritaria
			Dentineritaria
	Neridomidae fam. .nov.		*Neridomus*
	Otostomidae fam. nov.		*Otostoma*
			Lissochilus (? syn. *Gnaszynium)*
			? *Cautochilus*
	Neritiliidae		*Neritilia*
			Pisulina
	Neritidae	Neritinae	*Nerita*
			Puperita
		Velatininae	*Velates*
	Smaragdiidae		*Smaragdia*
	Neritinidae		*Neritina*
	Theodoxidae		*Theodoxus*
	Septariidae		*Septaria*
	Phenacolepadidae		*Phenacolepas*
			Shinkailepas
			Olgasolaris
			Cinnalepeta
Helicinoidea	Helicinidae		*Helicina*
			Pleuropoma
Hydrocenoidea	Hydrocenidae		*Hydrocena*
			? *Schwardtina*

Table 1. Classification of Neritimorpha as adopted here.

berger & Bandel, 1999 has rounded whorls and short conical shape (Heidelberger, 2001: pl. 21 fig. 6; 2007; Bandel & Heidelberger, 2001: figs 6-8; Heidelberger & Bandel, 1999).

The operculum of *Hessonia* consists of a semicircular calcareous plate with spiral construction and a nucleus near to the basal inner lip. The small round nucleus is succeeded by one and a half whorls (Bandel & Heidelberger, 2001: figs 6-7). The inner surface of the operculum is unknown.

The operculum of *Hessonia* differs from that of *Naticopsis* and *Neritopsis* by having a spiral shape as is found among the Neritoidea. The spiral is more regular in Nerrhenidae, with the nucleus in more central position than is usually the case among the species of the Neritoidea. The fully grown operculum of *Hessonia* resembles in its spiral construction the operculum of the early ontogenetic stage of modern *Smaragdia*, *Nerita* and *Neritina* (pl. 3 figs 13-15).

Superfamily **Neritopsoidea** Rafinesque, 1815

The inner walls of the globular shell with protruding spire are not dissolved, as in case of the Neritoidea. The protoconch is coiled and may be smooth or ornamented. The inner lip of the aperture is broad and smooth with a central depression into which the angular inner projection of the operculum is fitted.

The family Neritopsidae is characteristic of the superfamily and based on the living species of *Neritopsis* Grateloup, 1832. Some families with only Triassic representatives such as the Fedaiellidae are included.

Neritopsidae Rafinesque, 1815

Neritopsis has a median depression on the inner lip of its aperture. Into it the quadrangular projection at the side of the operculum that is held next to the inner lip is fitted when the aperture is closed. The teleoconch is ornamented with axial and spiral ribs and the ornament lies in the calcitic outer layer. The umbilical groove of living *Neritopsis* is cleft-like. The whorls of the shell are rounded and the protoconch is smooth.

The family is based on *Neritopsis moniliformis* Grateloup, 1832 from the Tertiary of France, and the very similar *Neritopsis radula* Grateloup, 1832 lives near reefs in the tropical Indo-Pacific.

The calcareous operculum is angular to trapezoidal with two attachment scars of the retractor muscle on the inner surface (Fischer, 1875; Zittel, 1895; Thiele, 1929: fig. 55; Ponder, 1998: fig. 15.71C-D). The outer surface is convex and the inner side concave, with a projection that is angular and fits into a groove present on the inner lip of the aperture (Scott & Kenny, 1998). The margin that fits against the outer lip of the aperture is smooth. Two pits near the columellar margin on the inner side of the operculum indicate the attachment scars of the body muscle. Elongate grooves cover the inner extension. The operculum is solid and mineralized with calcite (Bandel, 2007), and no aragonitic layer has been noted (in contrast to Kaim & Sztajner, 2005). The embryonic operculum of *Neritopsis radula* was documented by Kano (2006), but without specific information on its shape. The operculum of Jurassic and Cretaceous *Neritopsis* is similar to that of modern *Neritopsis* (Kaim & Sztajner, 2005: fig. 1). Jagt & Janssen (1988: pl. 1 figs 3-6, pl. 2 figs 1-4) described opercula of *Neritopsis* extracted from Palaeocene sediments from Limburg Province in Belgium with the same shape.

Subfamily **Cassianopsinae** Bandel, 2007
Pl. 1 figs 2-4

The subfamily is based on *Cassianopsis* Bandel, 2007 with species with short shell and the larval shell ornamented by axial ribs. In the case of *Cassianopsis ornata* (Münster, 1841) the shell has reticulate ornament with strong axial ribs, in *C. armata* (Münster, 1841) axial and spiral ornament are equally strong with tubercles where their elements cross each other, and in *C. decussata* (Münster, 1841) the axial ornament is crossed by finer spiral ornament forming nodules. All three species are from the St Cassian Formation (Bandel, 2007: figs 1D-M, figs 2E, G-J). The protoconch of *Neritopsis radula*, in contrast, consists of little more than one whorl, and that of *Neritopsis aqabaensis* Bandel, 2007 has a smooth larval shell added to the embryonic whorl (Bandel, 2007: figs 1A, B, C).

The operculum was recognized by Zittel (1895), who noted it in species from the St Cassian Formation (Rhynchidia of Laube, 1869; Kittl, 1892). Koken (1889) found in the case of *C. armata* that the callus of the inner lip bears impressions of the inner projection of the operculum. He therefore concluded that this resemblance indicated a relationship with modern *Neritopsis*. The operculum of *Cassianopsis* was illustrated from the Triassic of the Hungarian Bakony by Kittl (1901: pl. 2 fig. 9). The outer side of the operculum has a smooth outer basal section, a central nucleus and the outer half bears concentric growth increments that form a semicircle. On the inner side of the operculum two muscle scars are present and a rounded smooth projection that fits into the inner side of the outer lip (Zardini, 1978: pl. 15 figs 12-13). The operculum of *Cassianopsis* resembles that of *Neritopsis subvaricosa* Brösamlen, 1909 from the Jurassic (Kaim & Sztajner, 2005: figs 1A-C), but to a lesser degree that of modern *Neritopsis*, where the smooth part on the outside is much larger and the semicircular outer part has no concentric lines.

Zardiniopsis Bandel, 2007 with an elongate shell is based on *Zardiniopsis subornata* (Münster, 1841). Here ornament of the larval shell is axial and spiral (Bandel, 2007: fig. 2D).

Zardiniopsis has an operculum with the projection on its inner side, but its shape is not known in detail. Perhaps an operculum described by Zardini (1978: pl. 15 fig. 15a-b) from St Cassian Formation belongs here. It has a wide, evenly rounded outer side and an inner side with two deep lateral depressions next to the median lobe (Zardini, 1985: pl. 3 fig. 19). This operculum resembles that of *Cassianopsis*, but is wider and has an ornamented inner side of its inner projection. It also resembles the operculum of modern *Neritopsis*. Like the latter it has a trapezoidal shape with grooves on the inner side towards the inner lip, similar to that illustrated by Knight et al. (1960: fig. 182,9b). In contrast the sides and the outer margin are less rounded.

Subfamily **Colubrellopsinae** Bandel, 2007
Pl. 1 figs 5, 7-10

Colubrellopsis Bandel, 2007 based on *Colubrellopsis acuticostata* (Klipstein, 1843) (Bandel 2007: figs 3A-I, K, L) also has a depression on the inner side of the inner lip, which indicates that the operculum is of the Neritopsis type with a projection on the side that is fitted to the inner lip.


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The operculum that could be fitted into the aperture of *Colubrellopsis* is bulging and rounded on the outer side where it can be fitted to the inner lip of the shell (pl. 1 figs 7-8). The side that would rest near the outer lip of the aperture is flattened and has a nucleus at the center and concentric increments of growth. The inner side of the operculum is concave with rounded bulge on the side that can be fitted in the groove of the inner lip of the aperture, such as shown in the shell of *Colubrellopsis* (pl. 1 fig. 5). The sides of the operculum form wings, connected to each other by the rounded margin that could be fitted to the outer lip of the aperture (pl. 1 figs 9-10). Two triangular attachment scars are present separated from each other by a median ridge.

The operculum attributed to *Colubrellopsis* resembles that of *Hologyra* but has a much more bulging surface on the side where it connects to the inner lip (compare pl. 1 fig. 8 with pl. 2 figs 1,4).

Fedaiellidae Bandel, 2007
Pl. 1 figs 11-12

Fedaiella Kittl, 1894 includes the species *Fedaiella neritacea* (Münster, 1841) and *F. elongata* (Kittl, 1992) from St Cassian Formation. Zittel (1895) recognized that the operculum is of the type found in *Neritopsis*, differing from the spiral one of *Nerita*.

The ovoid operculum has concentric pattern on the outer side and two grooves on the inner side, with rounded lobe where it fits against the inner lip of the shell. Its nucleus lies close to the middle, on the outer side (pl. 1 figs 11-12). Two deep rounded scars are present on its inner surface, close to the side that lies next to the inner lip of the aperture (Zardini, 1978:, pl. 21 figs. 11ab, 13ab). Thee attachment scars of the shell muscle to the operculum are separated from each other by a ridge, which is a continuation of the thick smooth surface of the inner side that lies next to the outer lip of the aperture.

An operculum found in place closing the shell aperture is slightly convex. Increments of growth consist of calcitic needle-like crystallites arranged in such a way that they point towards the outside of the operculum. The slightly eccentric nucleus lies closer to the outer lip than to the inner lip and two depressions diverge from it, running to the corners of the operculum (Bandel, 2007: fig. 4D, E, F; pl. 1 figs 11-12). The inner side of the operculum has a thickened margin and two low depressions that are divided from each other by a central swelling (Zardini, 1978).

Superfamily **Naticopsoidea** Waagen, 1880

The type of the genus is *Naticopsis phillipsii* M'Coy, 1844 from the Lower Carboniferous of Ireland (Knight, 1941; Wenz, 1938: fig. 976). Its shell is large (up to 60 mm high and wide), with more than three whorls, bearing fine collabral ornament. Whorls are smoothly rounded and the adult shell consists primarily of the body whorl. Sutures are deep and the base is simple, without umbilicus. The inner lip is concave and covers the former shell wall in a thick callus layer. The protoconch as well as shell structure of the type species of the genus are unknown.

The Carboniferous genera *Naticopsis* and *Trachydomia* Meek & Worthen, 1866 are included, as well as the Triassic Hologyra with the same type of operculum, and *Ampezzonaticopsis* and *Cortinaticopsis* with similarly ornamented protoconch, although their opercula are not known.

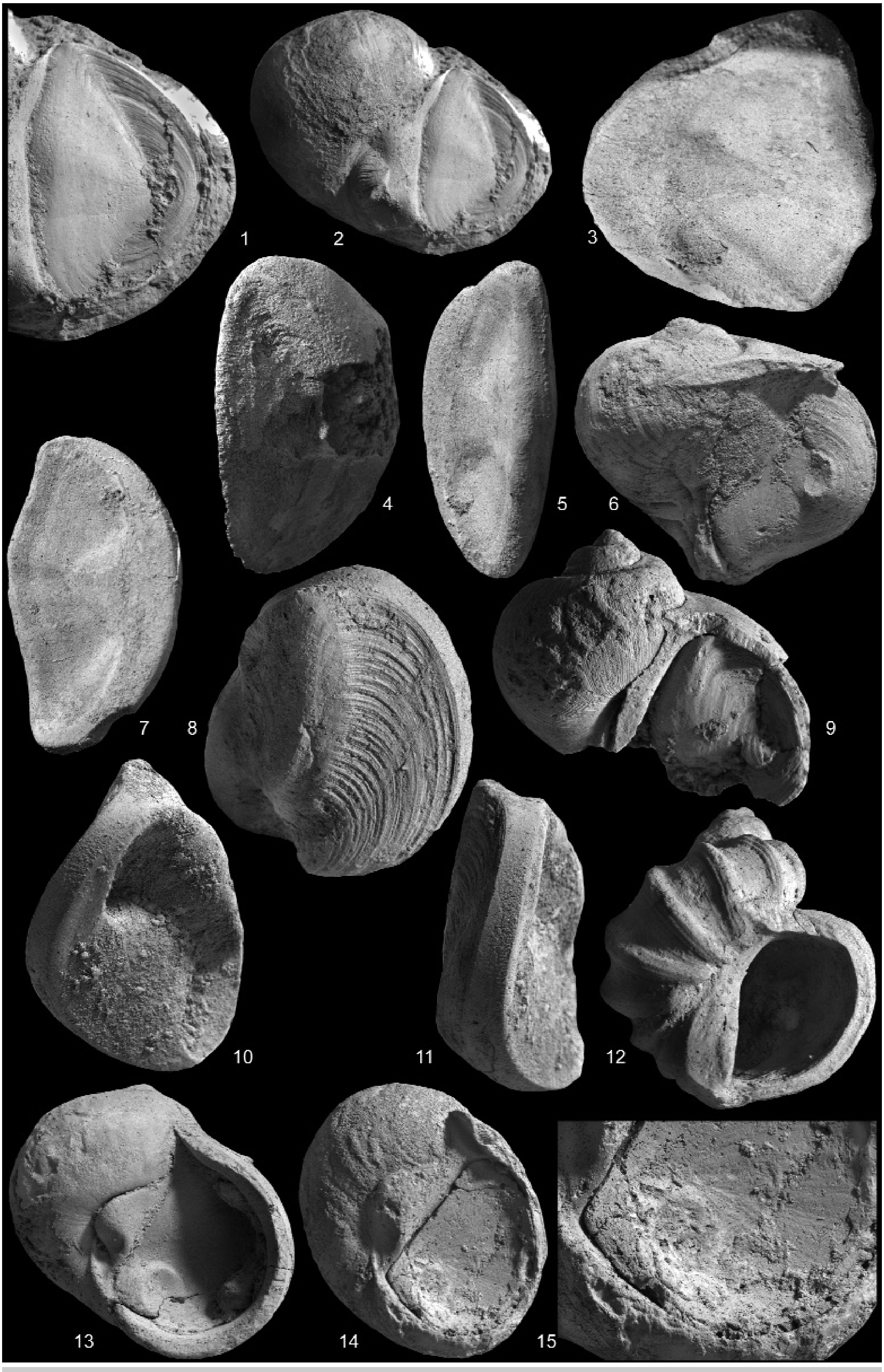
Species with a smooth larval shell as in the Naticopsidae, as they have been defined by Nützel et al. (2007), have not been recognized connected to an operculum. The Carboniferous to Permian Trachyspiridae Nützel, Frýda, Yancey & Anderson, 2007 can be included with the Naticopsoidea.

Naticopsidae Waagen, 1880

Included are species with large shell, thick walls, and mainly Paleozoic occurrence. *Naticopsis* M'Coy, 1844 is the type genus. The protoconch of Naticopsidae has sinuous ornament. The subfamily Ampezzonaticopsinae Bandel, 2007 from the Triassic is included.

PLATE 1

Figs 1-13. **Fig.1**. The middle Devonian *Hessonia piligera* (Sandberger & Sandberger, 1865) with the operculum in original position, of spiral construction. (from Bandel & Heidelberger 2001). The shell is 3.3 mm high and 3.8 mm wide. **Fig. 2**. *Cassianopsis armata* (Münster, 1841) from the Triassic St Cassian with shell 5 mm wide, with the operculum, also in fig.3. **Fig. 3**. Same as in fig. 2 but seen at different angle with the smooth bulging part of the operculum towards the inner lip and the outer half with concentric growth increments well visible. **Fig. 4**. The about 2 mm high shell of *Cassianopis armata* shows the groove on its inner lip, into which the operculum is fitted. The shell is 1.8 mm high. **Fig. 5**. *Colubrellopsis acuticostata* (Klipstein, 1843) with 5 mm high shell and the inner lip with a wide groove in which the projection of the operculum, as in fig. 8, could be fitted. **Fig. 6**. *Fedaiella elongata* (Münster, 1841) from St Cassian Formation probably had an operculum of quite similar shape to that of *Fedaiella neritacea*, with the inner lobe fitting into a wide groove on the inner lip. The shell is about 3 mm high. **Fig. 7**. The side view with the rounded projection on the inner flank of an operculum of the type as in *Cassianopsis*, or *Colubrellopsis*. Different views of the same operculum with greatest diameter of about 0.8 mm are in figs 7-9. **Fig. 8**. View of the same operculum as in figs 7,9 with rounded outer side and bulging projection that fits into the groove of the inner lip of the shell as seen in fig. 4 and fig. 5. **Fig. 9**. The inner side of the type of operculum as in figs 7-8,10 with the ridge between the attachment scars and the inner projection, that is fitted into the groove of the inner lip of the aperture. **Fig. 10**. The inner side with scars and inner lobe accompanied by two rounded marginal depressions as seen in fig. 8 from the outside. **Fig. 11**. The operculum of *Fedaiella neritacea* (Münster, 1841) from St Cassian, Late Triassic of the Italian Alps. Detail of fig. 12. **Fig. 12**. The operculum is still in place in *Fedaiella neritacea* with a shell about 22 mm high. The operculum has concentric growth increments around a nucleus in almost median position. **Fig. 13**. Detail of the operculum of *Hologyra cassiana* (Wissmann, 1841), the shell shown on pl. 2 fig. 6.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An operculum was described connected to smooth *Naticopsis*-like shells of species from the Mississippian, which have not been recognized with preserved protoconch (Gordon & Yochelson, 1982a, b), and connected to Pennsylvanian *Trachydomia* with characteristic ornament and teleoconch shape (Linsley et al., 1989). The operculum called *Hypodema* Koninck, 1853, consists on its outer side of a shield-shaped triangle connected to a rounded part with concentric growth lines, with their centre present at the point of the triangle (Knight, 1941: pl. 83 figs 5a-g). Knight (1941) suggested that *Hypodema* represents the operculum of a *Naticopsis* like those occurring in the same beds of the Early Carboniferous of Visé in Belgium, as described by Koninck (1853).

Kittl (1892) compared the operculum of the Carboniferous *Naticopsis* that was described by Koninck (1853) with the Triassic operculum of *Hologyra cassiana* from the St Cassian Formation. Cossmann (1925: pl. 9 fig. 13) suggested that the Carboniferous *Naticopsis* is related to the species from the St Cassian Formation with similar opercula.

The operculum that was suggested to belong to *Trachydomia* from the Pennsylvanian Finis Shale of Texas measures about 2.5 mm in greatest diameter (Linsley et al., 1989). On its outer side is an almost central nucleus with oval outline and widely spaced concentric growth increments around it. From the nucleus two lines run to the inner edge. An inner triangular part with weaker concentric growth increments that lay next to the inner lip of the aperture is thus differentiated from the outer rounded part with growth increments more strongly developed, which was in position on the inner side of the outer lip. On the inner surface of the operculum the part that lay close to the inner lip of the aperture of the shell has two rounded depressions which represent the muscle scars and a smooth thick outer part with evenly rounded surface that lay next to the inner side of the outer lip. The operculum is thus subdivided into a part with the rounded ovoid muscle scars and a smooth outer part (Linsley et al., 1989: figs 2-3). The Pennsylvanian operculum that was attributed to *Trachydomia* closely resembles that of *Hologyra* from the St Cassian (Zardini, 1978: pl. 21 figs 5-13; Bandel, 2007: figs 8A-C; pl. 1 fig. 13, pl. 2 figs 1-7, 9).

Subfamily **Hologyrinae** Bandel, 2007
Pl. 1 fig. 13; pl. 2 figs 1-7, 9

The subfamily is based on the genus *Hologyra* Koken, 1892 that was redefined from the St Cassian Formation (Bandel, 2007). *Hologyra cassiana* (Wissmann, 1841) from the St Cassian Formation has a solid teleoconch with a ridge in the umbilical groove, and an ornamented protoconch with a median chevron on its larval shell.

The operculum of *Hologyra* is calcareous, with an angular side fitting against the inner lip and a rounded smooth and thick side fitting against the outer lip of the aperture of the shell. The outer surface of the operculum bears on its inner triangular portion straight increments of growth and on its semicircular outer part rounded concentric growth lines. The nucleus lies at the apex of the triangular part (Bandel, 2007: figs 8A, B, C; pl. 2 figs 1,4). On the inner side of the operculum two attachment scars with a rounded and triangular margin are separated from each other by a median ridge (Zardini, 1978: pl. 21 figs. 5-7; pl. 2 figs 3, 5, 7).

The preservation of the operculum indicates that it is constructed of calcitic material and it has a darker colour than the shell. Its semicircular shape matches perfectly with the aperture and the inner side fits with the concave curvature of the inner lip. The nucleus lies eccentrically, near the middle but towards the outer lip. Increments of growth follow the outline of the outer lip and end in a triangular inner zone or continue here as more weakly developed straight growth lines.

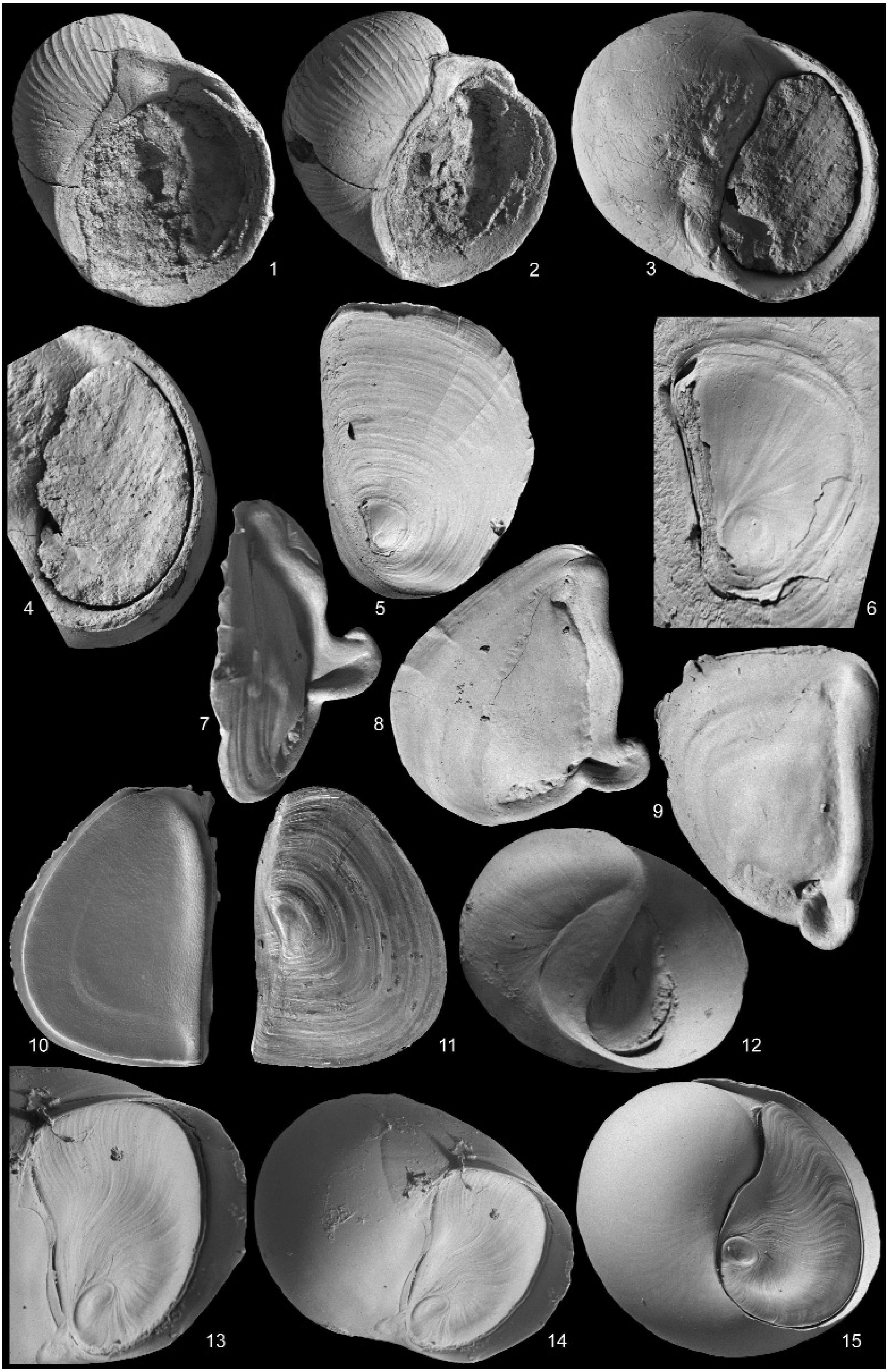
The operculum of a *Hologyra cassiana* from the St Cassian was illustrated by Cossmann (1925: pl. 9 fig. 27) with the growth lines indicated on the outer surface.

Tricolnaticopsidae Bandel, 2007
Pl. 2 figs 8, 10-12

The elongate shell has an aperture with convex inner lip, and the taxon is based on *Tricolnaticopsis* Bandel, 2007 with type species *Tricolnaticopsis striatulus* (Münster, 1841). It has rounded, smooth whorls and the spire is relatively high. *Pachyomphalus* Böhm, 1895 includes *Pachyomphalus angus-*

PLATE 2

Figs 1-15. All shells are from the St Cassian Formation, Italian Alps, Cortina d'Ampezzo, Early Carnian age, upper Triassic. **Fig. 1**. *Hologyra cassiana* (Wissmann, 1841) with the operculum still in place, detail of fig. 2. **Fig. 2**. *Hologyra cassiana* with the operculum in place and the shell about 10 mm high. **Fig. 3**. Operculum of the type as in *Hologyra* with about 3 mm in largest diameter. Different views in fig.4, 5, 7. Here the inner side is seen at angle so that the grooves of the attachment scars are seen as triangular impressions. **Fig. 4**. The pattern on the outer side is with central nucleus (in erosion pit) and concentric growth lines towards the rounded outer side that is fitted to the outer lip, and smooth about triangular inner portion. **Fig. 5**. The inner margin of the operculum that is in contact with the inner lip is rounded and smooth, and its inner surface has two attachment pits. **Fig. 6**. The shell about 2 mm high of a juvenile *Hologyra cassiana* (Wissmann, 1841) has the nucleus on the outer surface of the operculum. **Fig. 7**. Inner surface of the operculum with two rounded attachment scars of the shell muscle. **Fig. 8**. Outer surface of the operculum that may belong to *Pachyomphalus*, different views also in fig. 5-6, with greatest diameter about 1.5 mm. The nucleus lies marginal and growth lines are concentric, but only present on part of the surface. **Fig. 9**. *Fedaiella* as in pl. 1 fig. 6 with about 5 mm wide shell. **Fig. 10**. The inner surface of the same operculum as in figs 8 and 11 with deep muscle attachment pits and rounded outer and weakly convex inner margin. The inner margin fits with a concave inner lip. The operculum that would fit the aperture of *Pachyomphalus* Böhm, 1895 or *Scalaneritina* Bandel, 2007 is 1.5 mm high, also seen in figs 8, 11. **Fig. 11**. The margin of the operculum is flattened and thick. Same operculum as in figs 4-5. **Fig. 12**. The 4 mm high shell of *Scalaneritina triadica* (Kittl, 1892) has an aperture that would fit with an operculum as in figs 8, 10, 11. **Fig. 13**. *Ruganeritaria subovata* (Münster, 1841) with 3 mm high shell has its aperture sealed by an operculum with nucleus in the anterior inner corner of the aperture. **Fig. 14**. *Ruganeritaria subovata* with 5 mm high shell, operculum detail in fig. 15. **Fig. 15**. The spiral nucleus of the operculum of *Ruganeritaria* lies in the inner anterior corner and is round, resembling more that of modern *Neritilia* (pl. 3 fig. 5) than the more oval one of modern *Smaragdia* (pl.4 figs 5-7).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tus (Münster, 1841) and *P. uhligi* (Kittl, 1892) from the St Cassian Formation; it has rounded whorls with a relatively short spire. *Rinaldopsis* Bandel, 2007, with type species *Rinaldopsis ampezzana* Bandel, 2007, has a flat callus plate on its inner lip.

An oval, bean-shaped operculum that can be fitted into the aperture of Pachyomphalus has two depressions on its inner surface (pl. 2 fig. 10). The two pits on the inner surface represent the attachment scars of the shell muscle and are separated by a broad ridge, dividing it into two unequal fields (Zardini, 1978: pl. 21 figs 12a-b). Concentric increments of uneven thickness feature on the convex outer surface of the operculum. The eccentric nucleus lies near its outer edge and the side that lies next to the inner lip forms a low sinus (pl. 2 fig. 8). The smooth margins of the thick operculum are flattened (pl. 2 fig. 11). The best fit would be with the aperture of Pachyomphalus with a convex inner lip (Bandel, 2007: fig. 9C,G), but it could also be fitted into the aperture of *Scalaneritina* (pl. 3 fig. 12).

An operculum of similar shape with drop-shaped outline has been documented from the Carboniferous of the USA (Missouri) by Knight (1933), but without indication as to which species it may belong. This could indicate that relatives of the Tricolnaticopsidae lived in the Mississippian of North America. The group did apparently not continue into the Jurassic.

Scalaneritinidae Bandel, 2007
Pl. 3 figs 1-2

The shell is ornamented by axial ribs and the inner lip is concave. The inner whorls of the shell are not dissolved. In case of *Scalaneritina* Bandel, 2007, including Scalaneritina triadica (Kittl, 1892), the shell has a pointed conical shape (pl. 2 fig. 12). In *Ladinaticella* Bandel, 2007, with type species *Ladinaticella muensteriana* (Orbigny, 1849), the shell is shorter and *Lancedellopsis* Bandel, 2007, with type species *Lancedellopsis inaequiplicata* (Klipstein, 1843), has a low shape and a rounded tooth on the upper inner side of the inner lip (Bandel 2007: figs 10-11).

Lancedellopsis has a thin operculum of calcareous, probably calcitic composition that is preserved in one individual, and it appears to have some kind of projection on its apical side and a smooth surface on the larger basal side. The operculum is partly crushed (pl. 3 figs 1-2). It was thin and in that regard similar to the operculum of *Ruganeritaria* Bandel, 2007. However, in contrast to the latter genus, its growth line pattern is not preserved (Bandel, 2007: fig. 11E).

Superfamily **Neritoidea** Rafinesque, 1815

In the species belonging to this superfamily the inner shell walls are dissolved. Their operculum is usually of spiral construction. The larval shell may be ornamented with axial ribs in Neritariidae, with weak axial pattern in Neridomidae Fam. nov., with spiral ribs in Neritiliidae and it may be smooth or with very fine narrow axial lines in Neritidae, Neritinidae, Smaragdiidae, Septariidae and Phenocolepadidae.

Neritariidae Wenz, 1938

The protoconch has ornamented larval whorls, teeth on the inner side of the inner lip of the teleoconch, and an operculum resembling that of *Neritina*.

Subfamily **Neritariinae** Wenz, 1938
Pl. 2, Figs 13-15

The shell is globular in shape, and the protoconch has ornament of its larval whorls consisting of undulating axial ribs (Bandel, 2007: figs 12C, I, 13A, B, J-L). Teeth on the inner lip are small in *Neritaria* Koken, 1892, with type species *Neritaria mandelslohi* (Klipstein, 1843). *Ruganeritaria* Bandel, 2007, with type species *Ruganeritaria subovata* (Münster, 1841), has the inner lip resembling that of *Neritaria* but a wrinkled teleoconch surface. In case of *Dentineritaria* Bandel, 2007, with type species *Dentineritaria neritina* (Münster, 1841), a tooth lies on the inner lip in a central posi-

PLATE 3

Figs 1-15. **Fig.1**. *Lancedellopsis inaequiplicata* (Klipstein, 1843) with 2.5 mm high shell and the thin operculum in place but fractured into small shards. **Fig. 2**. *Lancedellopsis* as in fig. 1 also shows the thin operculum broken into small shards. St Cassian Formation, Late Triassic. **Fig. 3**. *Neridomus* sp. from the Mid Jurassic of Madagascar with the operculum in place. The shell is 1.3 mm high. **Fig. 4**. *Neridomus* as in fig.3 but documented at slightly different angle has preserved the spiral nucleus in the anterior corner of the aperture. The shell is from near Sakaraha in the SW of Madagascar. **Fig. 5**. The 1.3 mm long operculum of *Neritilia* from Bali (Indonesia) has a basal nucleus on the inner side, with concentric growth increments. **Fig. 6**. Detail of the nucleus of *Neritilia* from Bali (fig. 5) with spiral ornament on the round embryonic part and ornament forming a wider and more open spiral on the semicircular larval part. **Fig. 7**. The operculum of *Neritilia* from Bali seen from the side with the inner surface and the spoon-like projection of the hinge on the inner side. **Fig. 8**. The inner side of the operculum of *Neritilia*, as in fig. 7, with a hinge that consists of a marginal ridge and a spoon-like projection. **Fig. 9**. The muscle scar is seen on the inner side of the operculum of *Neritilia* next to the spoon-like projection on the anterior surface. **Fig. 10**. The inner side of the operculum of *Pleuropoma* as in fig. 11 with elongate ridge on its inner side. The snail lives on land. **Fig. 11**. The operculum of *Pleuropoma* is 2.5 mm wide and has concentric growth around a central nucleus that lies close to the inner margin on its outer side. Lizard Island, NE Australia. **Fig. 12**. 2.2 mm high shell of *Neritilia* from Bali with operculum in place. **Fig. 13**. The operculum of a fully grown larva of *Smaragdia* has a spiral growth pattern on the embryonic part, and sinuous growth increments on the part produced during larval life. The 0.5 mm high shell is depicted in fig. 14. **Fig. 14**. The fully grown larval shell of *Smaragdia* from the plankton of the Gulf of Aqaba. **Fig. 15**. The early larva of *Smaragdia* has an operculum with spiral construction that resembles that of the Devonian *Hessonia* Heidelberger, 2001 (pl. 1 fig.1) and that of the Triassic *Ruganeritaria* (pl. 2 fig.13).

tion. Its large protoconch has straight (orthocline) axial ornament.

The operculum is preserved in place in several individuals of *Ruganeritaria subovata*, usually crushed, since it is relatively thin. The operculum has a concentric construction and is hinged into the shell, aided by a tooth or ridge on the inner side of the inner lip. The operculum fits with its straight inner margin to the straight edge of the inner lip. Its centre of growth lies close to the basal inner lip (pl.2 figs 13-15). Beginning from the spiral nucleus, growth lines fan out towards the outer, rounded margin, showing that growth was along the inner lip and faster towards the apex than towards the umbilicus. The inner edge of the operculum is hinged into the groove formed by the tooth on the inner lip and the basal margin of that lip. A tooth on the inner side of the operculum has not been documented, but may be present (Bandel, 2007: figs 12J,L). The growth of the operculum resembles that of the operculum of modern *Neritina*.

Neritaria mandelslohi has an operculum that resembles that of *Ruganeritaria*, but it is preserved only in fragments.

Neridomidae fam. nov.

Pl. 2 figs 13-15

Diagnostic characters. — The round shell has a smooth surface with smooth inner lip. The protoconch is globular with low axial ribs ornamenting its larval shell. The operculum resembles that of the Neritariidae or Neritinidae. The family is based on the genus *Neridomus* Morris & Lycett, 1851 with type species from the Middle Jurassic.

Differences. — *Neridomus* has a protoconch shaped as in *Nerita*, but contrasting by the ornament of the larval shell (own data). Here axial ribs are present, whereas *Nerita* has fine straight axial lines. *Neritilia* differs by having the protoconch attached to the teleoconch in an inclined position and the ornament of its larval shell may consist of rounded spiral ribs. *Neritaria* differs from *Neridomus* by having the inner lip connected to a tooth, and the ornament of the larval shell is stronger.

Neridomus Morris & Lycett, 1851

Pl. 3 figs 3-4

The shell is globular and smooth, with a simple aperture (Cossmann, 1925). The inner lip has a callus pad and its edge against the aperture is convex and smooth or wavy. The callus ends before it reaches the base and the margin of the outer lip of the aperture. The calcitic outer layer is very thin and the thick inner layer consists of crossed lamellar structure with lamellae in one direction arranged according to the aperture. The genotype is Nerita hemisphaerica Morris & Lycett, 1851 from the Middle Jurassic of England (Hudleston, 1884: pl. 9 figs. 4-6; 1894: pl. 28 figs 11-12; Cox & Arkell, 1950; Gründel, 1975: fig. 4; Gründel, 2001).

Neridomus sp. from the Middle Jurassic of Madagascar has a round smooth shell with a semicircular aperture (Pl. 3, Fig. 3; own data). Its protoconch with almost three convolute whorls and a size of 0.6 mm has a fine ornament of low axial ribs on the larval whorls. The teleoconch is smooth and the inner lip of the aperture has a callus pad on the umbilical area and an indistinct depression below it. The outer margin of this groove connects to the edge of the outer lip. The shell structure is of a thin calcitic layer and a thick aragonitic crossed-lamellar layer. The inner walls of the shell become dissolved during shell growth. The species from Madagascar is quite similar to *Neridomus mais* (Buvignier, 1843) from the Oxfordian of Poland (Gründel & Kaim, 2006: fig. 11). *Neridomus* spp. lived in a shallow marine environment probably representing an estuary (Bandel, 2006).

Otostomidae fam. nov.

Pl. 2 figs 13-15

Diagnostic characters. — The rounded shell with depressed spire is close in shape to that of *Nerita*, but the ornament is dominated by axial ribs. The ornament consists of axial ribs above the periphery and spiral and axial elements below it. The half-moon-shaped aperture is provided with an expanded and thickened inner lip. The callus of the inner lip is flat and wide. Its inner edge can have about equal-sized tubercles, but may also be smooth. The shell has a relatively thick outer calcitic layer and an inner aragonitic layer of crossed-lamellar structure, just as in the Neritidae. The protoconch is globular with several whorls and ornamented by straight (orthocline) low axial ribs on its larval whorls. The calcareous operculum has one inner marginal tooth. The family is based on *Otostoma* Archiac, 1859, with teeth on the inner lip.

Differences. — Otostomidae fam. nov. resembles the Neritidae in regard to the shape of the shell, the construction of the shell wall and the characters of the aperture. They differ from the latter by the ornament of their adult as well as that of the larval shell. Also their occurrence in the geological record ranges well into the Jurassic, while Neritidae existed from the Late Cretaceous onward.

The type species of *Otostoma* with rapidly expanding whorls and a ridge-bearing corner is *Nerita rugosa* Hoeninghaus, 1865 from the Maastrichtian of Europe. The family also includes *Lissochilus* Zittel, 1882 with a smooth edge to the inner lip. A juvenile of *Lissochilus* may be represented by *Gnaszynium* Kaim, 2004. *Cautochilus* Gründel, 2004, with three teeth on the inner lip, could also belong here. Otostomidae are common in Late Cretaceous near-shore deposits of warm seas (Saul & Squires, 1997; Bandel & Kiel, 2003).

The operculum of *Otostoma* was documented by Jagt & Kiel (2007: figs 1-2). It resembles that of *Nerita* and *Neritina*, with a strong projection at the inner side next to the anterior columellar lip. The nucleus on the outer side of the operculum is located at the lower side close to the columellar margin.

Neritiliidae Schepman, 1908
Pl. 3 figs 5-9, 12

The shell is small, rounded and smooth, with a semicircular oblique aperture. In case of *Neritilia* the inner lip has a narrow callus with smooth columellar margin, while in *Pisulina* the callus forms a projection into the aperture. The family is based on *Neritilia* Martens, 1879, which has species in estuarine regions of warm seas. *Pisulina* Nevill & Nevill, 1869 belongs here and lives in cavities in caves and reefs of the Indo-Pacific Ocean (Kano & Kase, 2000; 2002; Kano et al., 2003). The globular larval shell lies inclined in the teleoconch. In *Neritilia* as well as *Pisulina* species with a free larval stage the larval shell is ornamented by spiral lines on its final whorl (Bandel & Riedel, 1998: figs 6A-B; Sasaki, 1998: fig. 78g,h; Kano & Kase, 2000: fig. 10; 2002; 2003; Kano et al., 2001). *Neritilia* lives in estuarine environments, mostly in places bordering continuously freshwater conditions (Bandel & Riedel, 1998; Bandel & Kowalke, 1999). The genotype is *Neritina rubida* Pease, 1865 from Tahiti.

The operculum of *Neritilia* has a marginal ridge extending from its inner side next to the inner lip and one hinge projection (pl.3 figs 7-9). Next to the spoon-like projection of the hinge an attachment scar of the shell muscle is developed. No ridge crosses the outer surface (Thiele, 1929, Starmühlner, 1993: pl. 7 fig. 37; Bandel, 2001: fig. 306; pl. 3 fig. 5). The outer side is of concentric construction, and there is a spiral nucleus near the basal corner next to the inner lip (Kano et al., 2003: fig. 5; Kano, 2006: fig. 3B,O; pl. 3 fig. 6). The larval operculum of *Neritilia rubida* has several spirals.

Pisulina has a small shell with a thick wall, and is of globular to obliquely ovate shape with a robust quadrangular projection on its inner lip. The teleoconch consists of less than four whorls and its inner walls are dissolved. The thin operculum is semicircular with an expanded ridge near the base of the inner margin of its inner surface and a smooth outer surface (Kano, 2006: fig. 3O). Kano & Kase (2000) noted that the operculum of *Pisulina* has few spirals, is calcified on its interior surface, and bears an apophysis without peg. Its nucleus lies near the centre and not on the inner side as in the other Neritiliidae.

Neritidae Rafinesque, 1815

The inner walls of the protoconch are dissolved as are the inner walls of the teleoconch. The shell is solid with an ornament of spiral ribs, more rarely axial ribs, or smooth. A thick outer calcitic layer is connected to a solid inner aragonitic layer composed of crossed-lamellar structure (Bandel, 1990, 1990; Sasaki, 2001). The protoconch has strongly convolute whorls with a shiny smooth surface and ornament of fine straight lines only (Robertson, 1971; Bandel 1982, 2001: figs 225-226; pl. 3 figs 14-15). The genus *Nerita* Linnaeus, 1758, on which the family is based, has species that live on hard substrates in tropical seas (Abbott & Dance, 1982). The genus can be traced with little change back to the Late Cretaceous (Santonian) (Bandel & Kiel, 2003), and no member of the family has been recognized to occur at earlier times.

Subfamily **Neritinae** Rafinesque, 1815
Pl. 4 figs 1-4

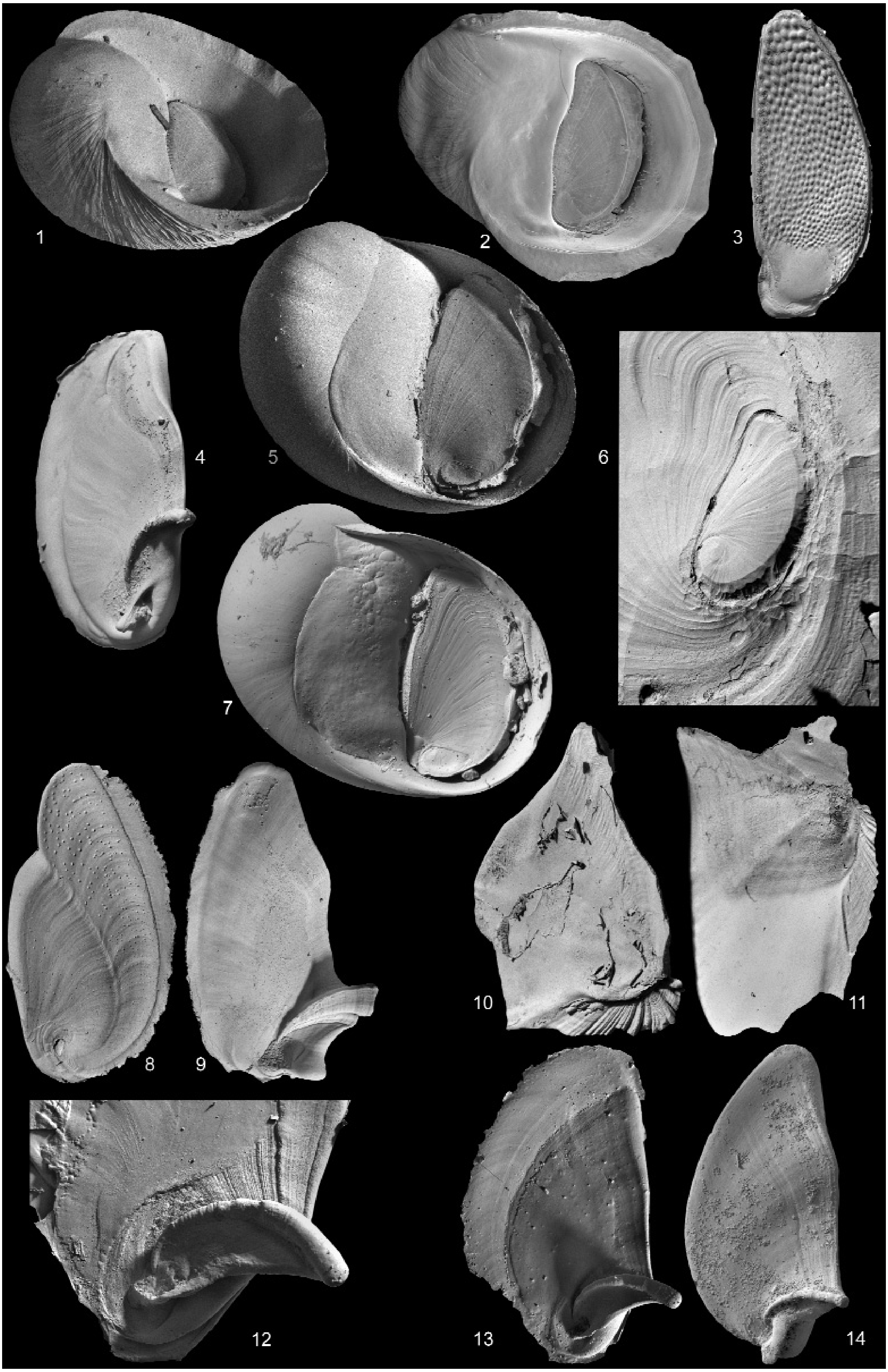
The oval to globular shell has a low spire with all internal walls dissolved. The initial whorl of the protoconch is only partly visible and displays the growth lines present in the embryonic shell. The globule-like larval shell is smooth with very fine and sharp axial lines. It is coiled in a strongly convolute manner and all inner whorls are dissolved (Bandel, 1982: pl. 21 figs 3,5). The callus of the inner lip of the teleoconch forms a flat shelf that may be smooth or have wrinkles and tubercles on its edge. The outer lip may bear ridges on its inner side. Ornament and teeth of the margin of the aperture appear during shell growth and juveniles have a more simple inner lip (pl. 4 figs 1-2).

The operculum is calcareous and usually carries a projection on its inner side next to the anterior inner lip. Here the muscle of the snail is attached. This projection consists of a flattened branch extending to the side and is supported by a basal thickening and connected to a lateral ridge (Starmühlner 1993: pl. 6 figs 22-25; pl. 4 fig. 4). Below the ridge a muscle scar is present (Sasaki, 2001: fig. 4). The operculum of the larva ready to metamorphose consists of an embryonic part succeeded by a paucispiral larval part (Kano, 2006: fig.3). The type genus of the subfamily is *Nerita* Linné, 1758, with type species *Nerita peloronta* Linnaeus, 1758 from the Caribbean Sea (Wenz, 1938).

Puperita Gray, 1857 lives in tidal pools and has a smooth shell. The operculum of *Puperita pupa* (Linnaeus, 1767) is smooth on its outer surface and is composed of a well ordered layer of prismatic calcite crystallites (own obervations). The hinge-like structure on the inner side next to the anterior inner lip has the shape of a cow-horn with a knob-like end and the ridge also ends in a similar knob (Russell, 1941). It is not connected to a muscle scar (Bandel, 2001).

Subfamily **Velatininae** Bandel, 2001

The large teleoconch with limpet-like shape has a flattened base with rounded corners. Its apex lies in a posterior position oriented sideways. The protoconch is egg-shaped, 0.5 mm high and about 0.4 mm wide with strongly convolute larval shell ornamented by fine sharp collabral lines (Bandel 2001: figs 273-274). The juvenile shell has a low spire and only later is the shell transformed to a limpet-like shape. Juvenile growth stages end after formation of about 1.5 whorls of the teleoconch. Adult shells grow to a size of 10 to 12 cm in width, and consist of three or a little more whorls of the teleoconch. In this large shell the spire is largely concealed by succeeding whorls and glazed over. All the shell interior, including that of the embryonic and larval shell, forms a single cavity with all internal walls dissolved. On the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base the callus of the inner lip extend into a convex plate. It forms a crescent-shaped rim around the narrow aperture, which has a narrow channeled upper portion and teeth on its inner edge.

The operculum of *Velates* was described by Cossmann (1925) as resembling that of *Nerita*, but it has not been illustrated.

Smaragdiidae Baker, 1923
Pl. 3 figs 13-15, pl. 4 figs 5-7

The outer calcitic shell layer is relatively thick compared to the small and relatively thin shell. Species of *Smaragdia* live on seagrass. The shell is glossy, rounded to oval in shape, with oblique aperture with inner lip callus rounded, thick and convex, sometimes with a depression near the umbilical region. The edge of the inner lip is quite variable. There may be hardly any tooth on it, or there may be up to 8 teeth present. Sometimes they are well developed, especially the basal and most apical tooth. The protoconch is like that in *Nerita* (pl. 3 figs 13-15).

The family is based on *Smaragdia* Issel, 1869, with the type species *Smaragdia viridis* (Linnaeus, 1758) from the Mediterranean Sea. The genus can be traced back to the mid-Miocene. The larval shell is very similar to that of *Nerita* (Bandel et al., 1997), but the Smaragdiidae are considered to represent an independent family related to the Neritidae, but with characteristic mode of life on seagrass, and distinct shape of its operculum. In contrast to Neritinidae, *Smaragdia* lives in the sea distant from the influence of fresh water and has a thicker outer calcitic layer of its shell.

The spiral operculum is thick and has fine radial striations. It bears a single tooth on its inner side. Its growth is by accretion, predominantly along its anterior (columellar) edge, which is partly buried in the foot of the animal (Holthuis, 1995). Accretion occurs along the entire length of the inner edge (pl. 4 figs 5-7). An extension projects into the musculature of the dorsal foot and arises from the left anterior region of the inner surface of the operculum. The operculum is made of two layers and is calcitic in mineral structure, as was confirmed in case of *Smaragdia viridis* from the Caribbean Sea (own data). Shell addition is along the thick margin by simple crystalline aggregates, which appear not well ordered on the growth surface and are prismatic when fractured.

Neritinidae Poey, 1852
Pl. 4 figs 8-9

Neritinidae spend their benthic life under estuarine and freshwater conditions. The hatched embryo usually has a larval life as a plankton-feeding veliger in the open sea. Metamorphosis occurs on the shore under the influence of fresh water (Bandel & Riedel, 1994). The teleoconch has a thin calcitic outer layer and a solid inner aragonitic layer. It is usually smooth, rarely with spines, and the inner lip of the aperture forms a callus-covered flattened shelf and an inner edge to the aperture that commonly bears one large tooth in its upper half, accompanied by small teeth below and above.

The operculum has a hinge with two appendages (pegs), one of which is ridge-like, and the muscle scar lies outside of the hinge (Starmühlner, 1976: pl. 8 figs 48-61, pl. 10 figs 80-91, pl. 12 figs 113-128; Starmühlner, 1993: pl. 6 figs 26-29, pl. 7 figs 31-33; Bandel, 2001: figs 67, 74, 79; pl. 4 fig.9). The operculum of *Neritina gagates* Lamarck, 1822 is semicircular in outline with polished external surface and fine fan-like growth lines. The nucleus lies on the inner margin. The hinge consists of a double peg with rounded thickened top and the inner surface is smooth. Hinges of different species of *Neritina* Lamarck, 1816 may be quite variable in their shape, as has been checked in case of *Neritina turrita* (Gmelin, 1791). Commonly a shallow groove lies on the exterior surface of the operculum of *Neritina coronata* (Leach, 1815) and a corresponding low ridge on the inner side ends in the hinge teeth (Bandel, 2001: fig. 74). Differences in hinge construction are more related to growth stages of individuals than to the species (Bandel, 2001).

PLATE 4

Figs 1-14. **Fig. 1**. Juvenile shell of *Nerita orbignyana* Récluz, 1842 with 2.7 mm high shell from the Gulf of Aqaba with the operculum as in the adult. **Fig. 2**. Juvenile *Nerita orbignyana* from Aqaba with a shell about 2 mm high and open spiral ornament which is later in life more coated by external deposits and displays a marginally ornamented rim. **Fig. 3**. The operculum of *Nerita histrio* Linnaeus, 1758 from Bali has its outer surface coated by a callussed smooth shield over the nucleus and by rounded granules on most of the surface. The operculum measures a maximum of 5 mm in diameter. **Fig. 4**. The operculum of *Nerita histrio* as in fig. 3 from Bali seen from its inner side with the two ridges that form the hinge with curved main tooth and adjacent muscle scar. **Fig. 5**. *Smaragdia* from Aqaba with 2.5 mm high shell and operculum in place, with detail of the nucleus in fig. 6. **Fig. 6**. Detail of the nucleus of *Smaragdia* (fig. 5) with the initial operculum formed by the embryo before hatching round and the larval operculum more elongate, as seen in pl. 3 fig. 15. **Fig. 7**. The operculum of *Smaragdia* about 3 mm high is in place and closely resembles that of Jurassic *Neridomus* (pl. 3 figs. 3-4). **Fig. 8**. The operculum of *Neritina corona* (Linnaeus, 1758) from Bali, seen from the outside and characteristically divided into zones, of which the outermost is an organic lamella, the median has a thin cover with granules added from the outside and the inner zone is smooth. The operculum is 4 mm in maximal diameter. **Fig. 9**. Operculum of *Neritina* as in fig. 8 from Bali with the solid hinge teeth and the muscle scar at their base. **Fig. 10**. The inner side of the operculum of *Septaria porcellana* (Linnaeus, 1758) from Bali, with margin as well as hinge reduced and without apparent function. The diameter is 7 mm. **Fig. 11**. The outer side of the operculum of *Septaria porcellana* from Bali, of similar size but the outer margin of different shape to that in fig. 10. **Fig. 12**. The inner side of the operculum of *Theodoxus* from the Sea of Asov (Black Sea) with the characteristic single hinge tooth as in the *T. fluviatilis* group. Detail of fig. 13. **Fig. 13**. The same operculum of *Theodoxus* as in fig. 12, measuring 3 mm in maximum diameter. **Fig. 14**. The operculum of *Theodoxus jordani* from Jordan is 2.5 mm in maximum diameter and has two hinge teeth.

Theodoxidae Bandel, 2001
Pl. 4 figs 12-14

The family consists of species that live in freshwater lakes and more rarely in rivers, and have done so for more than 60 million years, hatching from their egg cases as crawling young with only the embryonic shell. The adult shell closely resembles that of *Neritina*, but in contrast to Neritinidae the ontogeny of Theodoxidae is without a planktotrophic larva (ref. in Bandel, 1982). The genus is based on *Theodoxus* Montfort, 1810, with its genotype *Theodoxus fluviatilis* (Linnaeus, 1758) living in fresh water. The genus has been present in Europe since the Paleocene (Bandel 2001: figs. 222-223), when it was represented by *Theodoxus fabulus* (Briart & Cornet, 1887).

The operculum closely resembles that of *Neritina*, has a D-shape, with internal ridge that may be accompanied by a knob that represents a projection that is almost vertical. Ridge and knob provide an articulation of the operculum with the shell muscle and columellar lip (pl. 4 figs 12-15).

Theodoxus fluviatilis has the peg of the operculum markedly reduced and lives in Western Europe and in western North Africa (Brown, 1980), while *T. jordani* (Sowerby, 1832) has a slender peg well developed and occurs in SW Asia. The operculum is provided with a ridge and a peg representing a solid structure and the inner side of the columellar margin as illustrated by Dagan (1971: pl. 2 figs 1-2). Bandel (2001) analysed the operculum of more than 200 individuals of *T. jordani* and found it to be of rather uniform construction regarding the ridge and peg forming the hinge on its inner side.

Bodon & Giovanelli (1995: figs 1-22) demonstrated that the ridge on the inner side of the operculum in the case of *Theodoxus danubialis* is less wide and less spoon-shaped, as is that of *T. fluviatilis*. Both have only a ridge without an additional peg. Rust (1997: fig. 10) found within a single population of late Neogene *Theodoxus* from Thessalonica in Greece that the opercular projection graded from individuals without a second peg as in modern *T. fluviatilis* to individuals with a peg as in modern *T. jordani*. Jekelius (1932) noticed similar variation in opercular construction in the case of *T. semiplicatus* from the Pliocene of Romania and Roth (1984) observed similar variation and a broad morphological spectrum in the case of living *T. jordani* from the Levant.

The embryonic portion is paucispiral, reflecting hatching from the egg case as crawling young (Kano, 2006).

Septariidae Jousseaume, 1894
Pl. 4 figs 10-11

The limpet-like septariids have a narrow septum that separates the body portion with the foot from the visceral mass. The symmetrical cap-like shell has a protoconch that has the same characters as the protoconch of Neritina (Bandel & Riedel, 1998: figs 4,7; Bandel, 2001: figs. 264,266). The genus has the type species *Septaria borbonica* (Bory de St Vincent, 1803) and includes about 13 species (Haynes, 1994) all from the tropical Pacific Ocean.

At first the teleoconch including the operculum is *Neritina*-like, but soon afterwards the outer lip and the outer margin of the inner shelf of the inner lip fuse with each other to form one margin of the sandal-shaped shell. In the limpet form the operculum no longer forms a semicircular plate but is of angular outline and it no longer functions to close the shell (Starmühlner, 1969; 1976: pl. 14 figs 150-157; 1993: pl. 7 figs 34-36; Bandel 2001: fig. 84). In the fully grown individuals the operculum lies between visceral mass and the surface of the foot, buried in its top. It lies in a pocket between shell and foot, and is of quadrate shape with nucleus in marginal position. It has no apparent function. Starmühlner (1976) described the opercula of three species of *Septaria*, and Starmühlner (1993) those of two more, all of which have a thin outer margin and a ridge on the margin. This ridge is the median rib present on the operculum of *Neritina* (Thiele 1929). *Septaria porcellana* (Linnaeus, 1758) has a thin and brittle operculum when fully grown (pl. 4 figs 10-11), while that of *S. borbonica* is much more solid at about the same stage of life (Bandel, 2001).

Remarks. — Septariidae appear to represent a relatively young group having been derived from Neritinidae, and they occur only in the Pacific realm (Haynes 1994, 2001). Like the Neritinidae they live in an estuarine environment, have pelagic and planktotrophic larvae and can migrate upstream into fresh water. There is no indication of their having entered the Atlantic Ocean area including the Caribbean Sea.

Phenacolepadidae Pilsbry, 1895

In this shallow conical limpet-shell no trace of an inner lip or of inner walls is present and also the larval shell has totally dissolved inner whorls and is open to the cup-like teleoconch. The shell is predominantly aragonitic with crossed lamellar structure. The protoconch resembles that of *Nerita* and lies inclined in the apex of the cap-like teleoconch (Bandel 1982: pl. 21 figs 7-8; own data). Most species are of small size. The family is based on *Phenacolepas* Pilsbry, 1891 and species of the group live in very shallow tropical water to deep sea around volcanic hot springs.

The operculum is vestigial and was described by Fretter (1984) as having a rudimentary hinge. The operculum of the deep-water species of *Shinkailepas* and *Olgasolaris* is partly not mineralized (Okutani et al., 1989; Beck, 1992). The opercula with their size reduced resemble those of *Septaria* (Sasaki, 2001), while the operculum of the just metamorphosed juvenile resembles that of juveniles of other Neritioidea with planktotrophic larva (Kano, 2006: fig. 3,D). *Cinnalepeta pulchella* does not further increase the size of the operculum during further growth but it is retained on the foot of the adult (Kano, 2006).

Superfamily **Helicinoidea** Férrussac, 1822

Here are included species living on land and breathing with a lung, which usually have a calcareous operculum and characteristic neritimorph radula (Troschel, 1861).

Helicinidae Férrussac, 1822
Pl. 3 figs 10-11

The family contains terrestrial Neritimorpha that are found in temperate to tropical climates, mostly among leaf litter in moist forests (Thompson, 1980). They usually have a low, rounded shell. The embryo hatches when the shell is between 0.5 to 1 mm in diameter and has a uniform embryonic shell that connects to the teleoconch without intermediate larval shell (Richling, 2004, own data). Adult shells may have quite different shapes, but usually with low spire and rounded aperture connected to a callus of the inner lip. The margin of the aperture in fully grown individuals often expands. The shell has only very thin and lamellar calcite crystallites in its thin periostracal layer and consists predominantly of an aragonitic layer with crossed lamellar structure (own data).

The operculum has a concentric structure with eccentric nucleus (Thiele, 1929; Wenz, 1938; Thompson, 1980; Scott & Kenny, 1998: figs 15,77; Richling, 2004). Its shape is semispherical to rhombohedra-like with eccentric nucleus on the outer side (pl. 3 fig. 11) and a ridge on the inner side next to the position on the inner lip (pl. 3 fig. 10).

The illustrated operculum (pl. 3 figs 10-11) belongs to *Pleuropoma* Möllendorf, 1893 from Lizard Island, northwestern Australian. The animals live on the bark of trees in dense forest as well as among the litter below. The operculum may seal the aperture perfectly and is composed of two layers. The inner is corneous and the outer calcareous, not composed of a single layer of calcitic crystallites as assumed by Suzuki et al. (1992), but rather of sheets of calcite crystallites wrapped in organic material and deposited in layers on top of each other.

The operculum of *Pleuropoma* resembles that of *Helicina* as was documented by Richling (2004). She noted that the operculum of *Helicina* is concentric and consists of an inner horny plate attached to the foot and another calcareous plate. The horny plate projects beyond the margin of the calcareous plate, which may be quite thin.

Superfamily **Hydrocenoidea** Troschel, 1856

This group of small lung bearing land snails was identified by Troschel (1861) as belonging to the Rhipidoglossa and here near the Neritomorpha due to the shape of the radula.

Hydrocenidae Troschel, 1856

The small shell is conical with about three rounded whorls of the teleoconch, usually measuring only a few mm and with inner walls dissolved. Its shell wall consists predominantly of aragonitic material with crossed lamellar structure (Suzuki et al. 1991). The exclusively terrestrial snails inhabit mainly limestone outcrops and other calcium-rich substrates in the tropics and subtropics. Their embryos develop within an egg capsule and hatch crawling. The protoconch is rounded (Bandel 2001: figs 308-315), about 0.4 mm in size, consists only of the embryonic whorl. It may be ornamented by spiral ribs. The operculum is thin and of semicircular shape with a finger-like projection on its inner side (Scott & Kenny, 1998: figs 15, 76B-C). The type genus is *Hydrocena* Pfeiffer, 1847.

According to molecular data Hydrocenidae are on the evolutionary branch of the Neritoidea and not that of the Neritopsoidea (Kano et al., 2002), and they represent an independent branch of terrestrial Neritimorpha, while the Helicinidae are closer to the Neritiliidae. Molecular data are in accordance with the suggestion of Bandel & Riedel (1994) that the Cretaceous *Schwardtina* may be related to the Hydrocenidae and that the family arose during the Mesozoic.

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