

The new family Nerrhenidae (Neritimorpha, Gastropoda) from the Givetian of Germany

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With 8 figures

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Abstract: Some Devonian gastropods from the Givetian of Sötenich in the Eifel-Mountains and of Villmar at the River Lahn represent members of the Neritimorpha which are neither Cyrtoneritimorpha with openly coiled protoconch nor Cycloneritimorpha like the Neritopsidae. From the latter taxon they are distinguished by having a spirally coiled operculum. The genus *Nerrhena* as well as the newly proposed genus *Hessonia* are placed into the new family Nerrhenidae which is differentiated from the other known families of the Neritimorpha by a spirally coiled protoconch, consisting of few whorls and by an operculum that resembles that of the modern Neritidae.

Zusammenfassung: Einige Gastropoden aus dem Givet von Sötenich in der Eifel und Villmar und der Lahn sind Vertreter der Neritimorpha, die weder den Cyrtoneritimorpha mit offen aufgewundenem Protoconch noch den Neritopsidae unter den Cycloneritimorpha gleichen. Von letzterem Taxon trennt die Gestalt des Operculums. Für die Gattung *Nerrhena* und die neue Gattung *Hessonia* wird die neue Familie Nerrhenidae beschrieben und von den anderen Familien der Neritimorpha abgesetzt. Ihr Protoconch ist bereits spiralig gewunden, aber nicht sehr eng, und ihr Operculum ähnelt jenem der heutigen Neritidae.

Introduction

Within the last decade studies on the anatomy (HASZPRUNAR 1988, 1993) and on the ontogeny of the shell (BANDEL 1982, BANDEL & FRÝDA 1999) corrected the classification of the Neritimorpha GOLIKOV & STAROBOGATOV, 1975 and placed them as independent subclass of the Gastropoda (BANDEL 1997). THIELE (1929), WENZ (1938), KNIGHT et al. (1960) and others had placed them as superfamily of the Archaeogastropoda, mainly due to the shape of their radula. It is arranged in the rhipidogloss mode as is found among the archaeogastropod order Vetigastropoda. Neritoidea representing the modern group of marine Neritimorpha have quite their own mode of early ontogeny (BIGGELAAR & HASZPRUNAR (1996) and also their independent way in producing a larval shell (BANDEL 1982, 1992, BANDEL et al. 1996). A switch in the shape of the larval shell from an openly coiled hook-like one in the Cyrtoneritimorpha BANDEL & FRÝDA, 1999 to the dextrally coiled one of the Cycloneritimorpha BANDEL & FRÝDA, 1999 which include all living neritimorph gastropods apparently occurred within the Devonian (BANDEL & FRÝDA 1999, FRÝDA 1998 a, b, d, FRÝDA 1999). But the internal classification of the Cycloneritimorpha that lived in Devonian and later Paleozoic times is still problematic, and after the Permian Triassic faunal crisis all Cyrtoneritimorpha have apparently become extinct.

Among the Neritimorpha, with their superorder Cycloneritimorpha and order Neritoina RAFINESQUE, 1815, today two marine groups exist, one with only the genus *Neritopsis* GRATELOUP, 1832 in the superfamily Neritopsioidea GRAY, 1847 and the others with several genera and many species in the superfamily Neritoidea RAFINESQUE, 1815. Fossil and recent Neritopsidae GRAY, 1847 and the Carboniferous to Triassic Naticopsidae MILLER, 1889 have a trochispiral shell that is connected to a protoconch in which the inner walls are not dissolved (BANDEL 2000). Their protoconchs appear to be of globular shape and convolutedly coiled as is the case in a *Naticopsis*-like species from the Carboniferous (HERHOLZ 1992) and is recognised in *Naticopsis* MCCOY, 1894 species in the Triassic (SCHWARDT pers. communication). *Naticopsis* from the Early Carboniferous of east Australia has a tightly coiled protoconch (YOO 1994), but the fossil that was analysed does not allow to determine where the protoconch ends and where the teleoconch begins.

From Ordovician to Devonian times neritimorphs formed an openly coiled shell during embryonic and larval life and switched to normal helicospiral coiling when changing from planktic to benthic life. They, thus, have a hook-like protoconch which places them in an independent superorder Cyrtoneritimorpha. While they appear to have been the only neritimorphs present in Ordovician and Silurian time (FRÝDA 1998a, b, 1999), during the

Devonian coiled protoconchs are found (HEIDELBERGER & BANDEL 1999) connected to shells which appear to belong to the Neritimorpha. While their relation appears to have developed into the Mesozoic and Cenozoic Neritopsoidea and Neritoidea only few species that belong to the Cyrtoneritimorpha survived to the late Permian to become extinct then (FRÝDA 1998a, b, 1999; BANDEL & FRÝDA 1999).

The ontogeny of the Neritimorpha is more complex than that of the Archaeogastropoda since it includes a stage of a planktotrophic larva. The split-off between ontogenies leading to the Neritimorpha on one side and the Archaeogastropoda on the other side occurred at a very early stage in gastropod evolution, probably during late Cambrian or early Ordovician time (BANDEL & FRÝDA 1999, BANDEL 2000, FRÝDA 1999). The idea of THIELE (1929), WENZ (1938) repeated by PONDER & LINDBERG (1997) about a sister-group-relationship between *Patella* and *Nerita* is correct, but these sisters lived about 500 Million years ago.

Systematic part

Subclass: Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Description: Marine Neritimorpha originally have a planktotrophic development as pelagic veliger larva. The veliger hatches from the egg case with embryonic shell that resembles an egg with its upper portion cut off obliquely (BANDEL 1982).

Difference: Archaeogastropoda do not have a planktotrophic larva, and Caenogastropoda as well as Heterostropha differ anatomically, for example regarding the radula that is not rhipidoglossate and the ctenidium that is not feather-like.

Order Cycloneritimorpha BANDEL & FRÝDA, 1999

Description: To the embryonic shell during the larval stage a convolutedly coiled shell is added. The teleoconch has usually a lowly helicoidal shape, is rarely limpet-like, and usually has an outer calcitic and an inner argagonitic mineral shell layer, rarely only an aragonitic layer. The latter is of crossed lamellar structure. The operculum is calcified.

Difference: The larval shell of the Cyrtoneritimorpha is openly coiled and not spirally coiled as that of the Cycloneritimorpha.

Superfamily Nerrhenoidea n. superfam.

Diagnosis: The naticoid teleoconch is connected to a low and spirally arranged protoconch. The mineralized operculum has a sinistral spiral construction. The superfamily is based on the family Nerrhenidae.

Difference: The operculum of the Neritopsoidea RAFINESQUE, 1815 is not spirally arranged as that of the Nerrhenoidea, and the inner walls of the shell are not dissolved in the larval shell as well as in the teleoconch as is the case in the Neritoidea RAFINESQUE, 1815. Neritopsoidea are characterised by retaining their inner walls and not resorbing them as is the case in the Neritoidea (WENZ 1938). But their calcareous operculum is not spirally arranged as in the Mesozoic and modern Neritidae and the mid-Devonian Nerrhenidae. A similar protoconch may be noted in some members of *Naticopsis* from the Carboniferous and on some members belonging to *Platyceras*, CONRAD, 1840, *Praenatica* PERNER, 1903 and *Dalejeconcha* FRÝDA, 1998 from the Devonian (pers. comm. Jiří Frýda).

Family Nerrhenidae n. fam.

Diagnosis: The shell has ovoid to naticoid shape and consists of about four whorls. The small embryonic whorl is evenly rounded and continues into an unornamented helicoidally coiled larval shell that may consist of up to two whorls. The protoconch and early teleoconch form an only slightly elevated spire and the last whorl occupies more than two thirds of total shell height. The sutures are distinct and the umbilicus may be narrowly open or closed. The aperture is wide, rounded, oriented parallel or slightly oblique to the shell axis. The outer and inner lip are simple, and the later is thickened by a callus. The operculum is calcareous and paucispiral and may be fitted in a groove that may be present on the inner side of the adult aperture.

The type genus: *Nerrhena* HEIDELBERGER & BANDEL, 1999 from the Eifel mountains (Sötenich) is based on *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999 (Pl. 1, Figs. 1-5), and HEIDELBERGER & BANDEL (1999, Pl. 2, Figs. 10-12). The operculum is known from *Hessonia* that is considered to belong here.

Difference: Plagiothyridae KNIGHT, 1956 are based on the middle Devonian *Plagiothyra* WHIDBORNE, 1892 and include *Dirachis* WHIDBORNE, 1891 and *Littorinides* KNIGHT, 1937. They have at least one distinct columellar tooth on their inner lip which distinguish them from the Nerrhenidae that have no such feature, but rather a smooth columellar lip. The operculum and the protoconch of members of the Plagiothyridae are still unknown.

Remarks: Nerrhenidae hold the genera *Nerrhena*, and the new *Hessonia*. Whether *Paffrathopsis* FRÝDA, 1999 and *Natirhenia* HEIDELBERGER, 2001 belong here is not known, since the protoconch and the operculum of these are still unknown. KNIGHT et al. (1960) did not offer more characteristics to the family Plagiothyridae than a neritoid shell shape and the presence of one or several columellar teeth. WENZ (1939) had placed *Plagiothyra*, as well as *Dirhachis* and *Littorinides* in the Cyclonematidae MILLER, 1889 of the Trochonematoidea ZITTEL, 1895. This family and superfamily are now problematic taxa. Naticopsidae have an operculum like the Neritopsidae and unlike the spiral one of the Nerrhenidae (see below).

Genus *Nerrhena* HEIDELBERGER & BANDEL, 1999 Fig. 1-5

Description: *Nerrhena* is described by the diagnosis of the family. The ornament of the shell consists of spiral ribs which are crossed by collabral axial ribs forming a rhomboid pattern with each other. The genus is based on *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999.

Remarks: According to the description in HEIDELBERGER & BANDEL (1999, Pl. 2, Figs. 10-12) the turbiniform shell with convex whorls and only little elevated apex is ornamented by eight spiral ribs which are crossed by collabral ribs forming pattern of rhombs with each other. The convex base is not umbilicate, and the aperture is large. The first two whorls forming the protoconch are smooth and rounded.

Difference: *Nerrhena* differs from *Hessonia* by having a strongly ornamented shell.

Genus *Hessonia* n. g.

Derivatio nominis: The name is derived from Hessen, the state in central Germany in which the fossils have been found.

Diagnosis: The smooth, anomphalous shell is naticiform with low apex and about four rapidly increasing whorls. Only indistinct growth lines are present as ornament, and there is no umbilicus. The shell is smooth, and sutures are distinct. The oval aperture is angulated posteriorly, and its inner lip is also angular where its columellar part begins. While the parietal part is thin, the columellar portion of the inner lip is thickened by callus. The operculum has a small round nucleus, and one and a half whorls succeeding it. Its nucleus lies off centre towards the columellar lip, and its margin with the inner lip forms an angle that fits with the angle present here. Its spire consists of a flattened inner band and an inclined outer band.

Genotype: *Natica piligera* SANDBERGER & SANDBERGER, 1850-56 from Villmar (Lahn Syncline).

Stratum typicum: Middle Devonian, Givetian.

Remarks: The Pragian *Krasopea glabra* FRÝDA & BANDEL, 1997 has a columellar groove suggesting the presence of an operculum. But its protoconch is of archaeogastropod-type (FRÝDA & BANDEL 1997, Pl. 3, Figs. 6-7). In *Dalejeconcha* FRÝDA, 1998 from the uppermost Emsian teleoconch shape resembles that of *Hessonia*, but protoconch and operculum are unknown. Similar shells are found in *Umbonellina* KOKEN, 1925 from the late Ordovician and *Tychonia* KONINCK, 1881 from the early Carboniferous, but in both cases nothing more than teleoconch shape are known.

Hessonia piligera (SANDBERGER & SANDBERGER,
1850-1856) Fig. 6-8

non 1844 *Natica antiqua*. – GOLDFUSS, p. 117, Pl. 199, Figs. 2a, b.

1850-1856 *Natica piligera*. – SANDBERGER & SANDBERGER, p. 235, Pl. 6, Figs. 6, 6a-c.

1891 *Natica antiqua*. – WHIDBORNE, p. 193, Pl. 19, Figs. 2, 2a.

1895 *Turbonitella piligera*. – HOLZAPFEL, p. 197, Pl. 14, Figs. 4, 5.

1922 *Turbonitella piligera*. – PAECKELMANN, p. 41.

Diagnosis: The description of the genus fully applies to this species.

Description: The globular, smooth shell measures 3,3 mm in height and 3,8 mm in width. Its pleural angle is about 105°. The spire is low but pointed and conical and the last whorl occupies more than two thirds of total shell height. Four whorls are present with convexly rounded sides. They are separated by deep and distinct sutures. There is no umbilicus. The aperture is wide with a well arched outer lip that begins at the median periphery of the preceding whorl. On the inner lip the parietal portion is convex and bears two

Fig. 1. *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999; Wachtberg (Sötenich; Eifel, Cürten strata); lateral view, oblique. Holotype: SMF XII/3449.

Fig. 2. *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999; Wachtberg (Sötenich; Eifel, Cürten strata); same specimen as in Fig. 1, apical view.

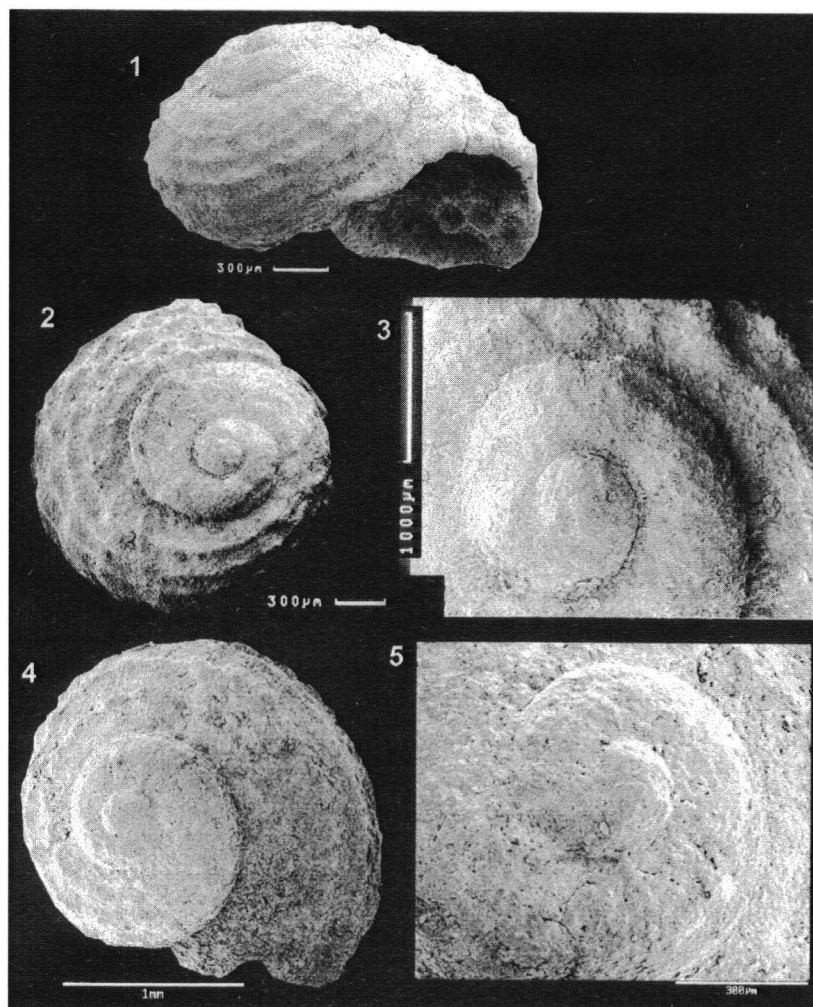


Fig. 3. *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999; Wachtberg (Sötenich; Eifel, Cürten strata); same specimen as in Fig. 1, apical view, detail of the preserved protoconch.

Fig. 4. *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999; Wachtberg (Sötenich; Eifel, Cürten strata); apical view. Paratype: SMF XII/3461.

Fig. 5. *Nerrhena reticulata* HEIDELBERGER & BANDEL, 1999; Wachtberg (Sötenich; Eifel, Cürten strata); same specimen as in Fig. 4, apical view, detail of the preserved protoconch.

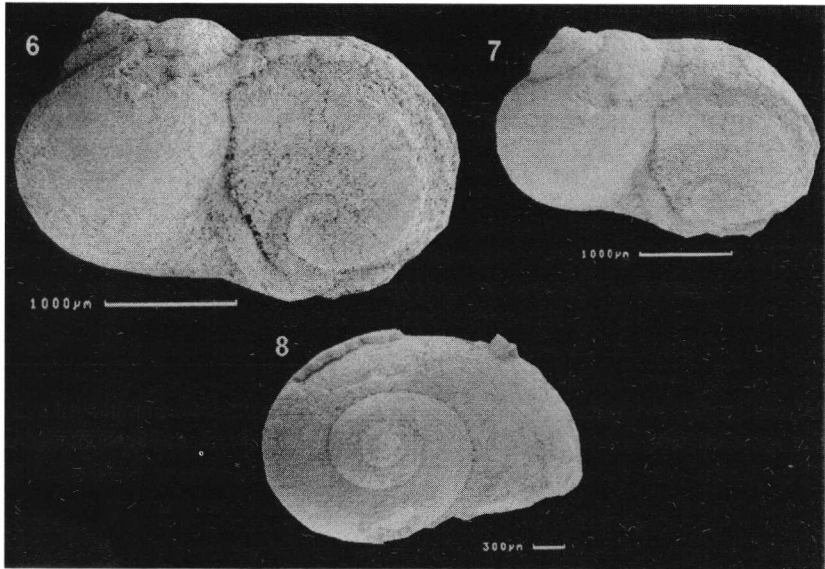


Fig. 6. *Hessonia piligera* (SANDBERGER & SANDBERGER, 1850-56) n. g.; Villmar, Bodensteiner Lay (Lahn syncline, Massenkalk); apertural view with operculum in situ. SMF XII/3435

Fig. 7. *Hessonia piligera* (SANDBERGER & SANDBERGER, 1850-56) n. g.; Villmar, Bodensteiner Lay (Lahn syncline, Massenkalk); same specimen as in Fig. 6, apertural view, slightly oblique.

Fig. 8. *Hessonia piligera* (SANDBERGER & SANDBERGER, 1850-56) n. g.; Villmar, Bodensteiner Lay (Lahn syncline, Massenkalk); same specimen as in Fig. 6, apical view.

grooves at its ends into which the edges of the operculum are fitted, and the columellar part is thickened by callus. The operculum measures 1.95 mm in height and 1.58 mm in width. It is sinistrally coiled. Its nucleus is positioned in the lower left third of the apertural opening, and it consists of one and a half whorls. Its outer surface is a plane accompanied by an inclined flank on the outside with an angulation between both.

Remarks: The protoconch of *Hessonia piligera* is not well preserved, but appears to be dextrally coiled and is interpreted to resemble that of

Nerrhenia. The calcareous operculum preserved in place is a rather lucky coincidence which rarely occurs in fossil gastropods. Another specimen from Villmar with the operculum still in place is present in the SANDBERGER Collection at the Hessisches Landesamt in Wiesbaden. But here its ornament is not recognizable. HOLZAPFEL (1995) had already illustrated an operculum connected to *Hessonia piligera* from Finnentrop (Sauerland, Germany) which appears to be similar to the one described here. Also WHITEAVES (1885-98) mentioned the occurrence of a paucispiral operculum in connection to a naticopsid specimen from the Devonian Guelph limestone of Ontario, but did not illustrate it.

The operculum of *Naticopsis* in place was figured by MCCOY (1844, Pl. 3, Fig. 9) and described by MEEK & WORTHEN (1866). It has been illustrated again by WENZ (1938, Fig. 978) and KNIGHT et al. (1960, Fig. 181, 7). It has concentric growth lines on the outside and trapezoidal shape on the inside. The actual specimen with preserved operculum mentioned by KNIGHT (1941) can not be located in the MCCOY collection of the Earth Science Museum in Dublin. It resembles somewhat the operculum of *Neritopsis* that has a symmetrical trapeziform shape (KNIGHT et al. 1960, Figs. 8, 9). The operculum of *Hessonia piligera* differs from that of *Neritopsis* by having a spiral shape as is found among the Neritioidea. But in *Nerita* and relation the side of the operculum that lies next to the inner lip is usually straight and does not form two angulations on its inner edge as in *Hessonia*. Opercula of turbidinid archaeogastropods usually have concentrically oriented spirals as have also been noted in some opercula of Paleozoic gastropods like *Omphalocirrus* by LINSLEY (1978), *Oriostoma* and *Cyclostoma* by YOCHELSON & LINSLEY (1972) and *Australonema* by HORNY (1998).

Among the gastropods of the Middle Devonian of the "Rheinisches Schiefergebirge" quite a number of species have a neritiform or naticiform shell that consist of about four well rounded whorls that embrace each other more or less strongly (HEIDELBERGER 2001). Usually the shell consists of the teleoconch only, and the protoconch is not preserved or damaged, but in fragments appears to consist of more than one spirally coiled whorl. The aperture is usually wide with a well rounded outer lip and a concave inner lip. Quite a number of newly or redescribed genera and species show these or similar teleoconch features (HEIDELBERGER 2001). Among these are ? *Naticopsis* (*Naticopsis*) *efossa* (GOLDFUSS), ? *Naticopsis* (*Naticopsis*) *macrostoma* (SANDBERGER & SANDBERGER), *Naticopsis* (*Naticopsis*) *convoluta* HEIDELBERGER, *Paffrathopsis subcostata* (ARCHIAC & VERNEUIL), *Paffrathopsis lirata* (SANDBERGER & SANDBERGER), *Paffrathia lotzi* FRÝDA, *Paffrathia aarica* HEIDELBERGER, *Turbonitella ussheri* (WHIDBORNE), *Basiplanus baldus* HEIDELBERGER, *Naticonoda priouri* HEIDELBERGER, *Naticonoda elegans* HEIDELBERGER, *Natirhenia margaritifera* (ARCHIAC &

VERNEUIL), *Spiranodus quadrilineatus* HEIDELBERGER, *Lotzia schaeferkaldi* HEIDELBERGER, *Nerrhenia aequistriata* (KIRCHNER) and *Hessonia germana* HEIDELBERGER. Many of them have been described under the generic name *Natica* by authors like ARCHIAC & VERNEUIL (1842), GOLDFUSS (1844), SANDBERGER & SANDBERGER (1850-56), HOLZAPFEL (1895), KIRCHNER (1915) and PAECKELMANN (1922). But *Natica* belongs to a group of gastropods that make their first appearance within the Cretaceous (BANDEL & RIEDEL 1994, BANDEL 1993, 2000) and have nothing to do with these Devonian species of similar shell shape. This had been recognized earlier, and WENZ (1938) as well as KNIGHT et al. (1960) grouped all these Devonian species with the Carboniferous *Naticopsis* MCCOY, 1844. In case of *Hessonia* and *Nerrhenia* we can document that *Naticopsis* is not the correct relation to these. The protoconch of Triassic species of *Naticopsis* resembles that of *Neritopsis* (BANDEL 1992, BANDEL & FRÝDA 1999), but the type of this genus is not of Triassic but of Carboniferous age.

Conclusions:

Nerrhenia and *Hessonia* represent a characteristic group of gastropods that have lived within the tropical environment of reefs and reef-lagoons in the mid Devonian. It is quite probable that with time and based on better preserved material there will be other species and genera joining these two genera and the family Nerrhenidae. A superfamily status for these mid-Devonian gastropods is needed, because they can neither be fitted into the neritopsids nor the neritids and their relatives. Neritopsoidea are very richly diversified in the Triassic and from that time we know that the trapezoidal operculum is characteristic as well (ZARDINI 1978). Neritoidea are present from the Triassic onwards (BANDEL 2000), and they clearly differ in regard to their tightly coiled protoconch and also the internal dissolution of shell walls, both not developed in the Nerrhenioidea. Regarding the operculum the shape resembles that of some Neritoidea, for example in the family Neritiliidae SCHEPMAN, 1908 and here the genus *Pisulina* NEVILL & NEVILL, 1869. Here the operculum has more than one spiral whorl, while all other Neritidae have less than one whorl in their operculum (KANO & KASE 2000). *Pisulina* in contrast to all other modern species has a quadrangular median ridge on its columellar edge of the inner lip, accompanied by a depression anteriorly and posteriorly. This may represent a very ancient feature of the Cycloneritomorpha, already present in a similar way in *Hessonia* from the mid-Devonian. Most of the neritimorphs from the Carboniferous and Permian are still incompletely known as is their transition into the Triassic.

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