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Eocene *Melanotarebia* n. g. and its relations among modern Thiaridae (Caenogastropoda: Cerithioidea)

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With 10 figures in the text

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Abstract: Eocene *Melanotarebia* n. g. from fresh water deposits of the coastal swamps of Gant/Hungary represents the oldest known member of the Thiaridae s. s. with an early ontogeny that took place in a brood pouch. Data concerning the morphology of the protoconch confirm a close relation to the Recent genera *Melanoides, Tarebia* and *Sermyla*. Thiaridae, thus, were present in Europe during the Eocene and could have originated here. Consequently migrating routes to Europe from the southeast since Late Miocene may represent a reestablishment of Thiaridae after they had disappeared from the region during the Late Oligocene.

Zusammenfassung: Die Gattung *Melanotarebia* n. g. aus eozänen Süßwasserablagerungen des gegliederten Küstenbereichs von Gant/Ungarn stellt bisher den ältesten Vertreter der Thiaridae s. str. mit einer im Brutbeutel verlaufenden Frühontogenese dar. Protoconchmorphologische Daten belegen eine nahe Verwandtschaft zu den rezenten Gattungen *Melanoides, Tarebia* und *Sermyla*. Die Thiaridae könnten somit ihren Ursprung in Europa haben, so daß bisher vermutete Migrationswege nach Europa aus dem Südosten seit dem späten Miozän auch als Wiederansiedlungen nach ihrem Verschwinden aus dieser Region im späten Oligozän interpretiert werden können.

Introduction

Tarebia from southeastern Asia and pantropical *Melanoides* represent related genera with a rather characteristic and apparently close relation to *Melanotarebia* n. g. from the European Eocene. *Tarebia, Melanoides* and *Sermyla* (Thiaridae s. s.) represent a very interesting group of Gastropoda for ecological, ontogenetical, biogeographical and phylogenetical reasons. Thiaridae are members of the large superfamily Cerithioidea and live within the estuarine environment of the coastal realm as well as in fresh water. Their early ontogeny takes place within a brood pouch that lies within the tissue of the head-foot and is separated from the female genital apparatus

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(STARMÜHLNER 1969). In *Melanoides* the developing eggs are usually not fertilized by a male but represent clones of parthenogenetic individuals and males are extremely rare within a population (HELLER & FARSTAY 1990). In the ontogeny of relatives of *Melanoides* such as species of *Stenomelania* and *Thiara* a fully marine planktotrophic larva may be developed. These genera have several species that spend the early ontogeny in the brood pouch, larval phase in the open sea and benthic life after metamorphosis first within the estuary, later in fresh water of rivers and creeks (BANDEL et al. 1997). In very closely related species of the same genera early ontogeny is totally confined to the brood pouch in which embryos develop and feed and hatch as miniature adults (BANDEL et al. 1997). In this regard the Thiaridae s. s. resemble their fully marine sister group Planaxidae (HOUBRICK 1987, 1988). Even though paleontologists have considered *Melanoides* to occur in the Early Tertiary of Europe (OPPENHEIM 1892) it was later speculated that the genus originated in the East and migrated to Europe during the Late Miocene (TCHERNOV 1975, WILLMANN 1981) and that *Thiara* and its relatives such as *Melanoides* had an origin in the Gondwanian continent and here its Indian and eastern portion (GLAUBRECHT 1996).

Melanoides has been considered a member of the family Thiaridae since their initiation as family of the Cerithioidea by TROSCHEL (1856-1863). They have since been considered in very different ways, in the extreme holding almost all species of cerithioidean characters that live in fresh water and a large number of those living in brackish water (THIELE 1928, WENZ 1938, GLAUBRECHT 1996). But the species and genera to comprise the Thiaridae with the uniting character of the pedal brood pouch in their reevaluation by MORRISON (1954), confirmed by HOUBRICK (1987, 1988), were connected to a more concise frame. Due to this evaluation the fully marine cerithioidean family Planaxidae was recognized to occupy the position of a sister taxon of the Thiaridae sensu strictu. The shape and ornament of the larval shell constructed by the planktotrophic veliger in both groups confirm this interpretation and make its application to fossil species feasible.

Geological background

Near Gant/Hungary fossiliferous outcrops are in a large pit in which bauxite has been mined (SZÖTS 1953). On this bauxite covered by pisolithic iron hydroxidic ore layers deposited in fresh water lakes and coastal swamps as well as in shallow marine environment are intercalated and form a well exposed section. Within the fresh water beds exposed in the lower few meters of the section the common *Melanotarebia distincta* represents a gastropod that closely resembles modern *Melanoides* in shell shape. It occurs here together with *Melanopsis doroghensis* OPPENHEIM, 1892. The outcrops in 1996 exhibited deposits of sediments holding a rich fauna that lived in the coastal swamp, probably that of a mangrove forest and associated ponds and

tidal flats. The outcrops utilized by SZÖTS (1953) are just south of Gant (Hosszuharsztos), just east of the modern quarry (Angerret) and about 3 km to the west (Csakbereny Szölohegy). From two of these SZÖTS published measured sections.

Family Thiaridae

Description: The family unites fresh water to brackish water Cerithioidea with a brood pouch in the head-foot in which egg capsules are deposited until larvae hatch. The shell is conical to slender.

Genus *Melanoides* OLIVIER, 1804

(Figs. 1, 2)

The type is *Nerita tuberculata* MÜLLER, 1774 from the Coromandel Coast of Southern India (Tamil Nadu). The snails with up to 5 cm long shells have a high and slender spire of 10 to 15 whorls which is often decollated. Both, transverse and spiral sculpture are generally present, commonly forming tubercules. *Melanoides tuberculata* is an extremely common tropical fresh water member of the Cerithioidea.

Occurrence: *Melanoides tuberculata* lives in Northern Australia, Arabia and Africa and has spread to the Pacific Islands, southern Europe and Central America. Some of the extant living places have probably been reached due to human activity. The Polynesians for example have spread throughout the islands of Polynesia, Micronesia and Melanesia originally coming from the eastern area of the islands of Southeast Asia. Their ancestral economy was based partly on the crop of Taro (*Colocasia antiquorum* (L.)) that originated in India and is grown under water. Their initial expansion into the Pacific island world some 5000 to 7000 years ago occurred on outrigger canoes and rafts. The Polynesians had pottery to carry enough water for their long journeys. They also carried Taro-roots for which they constructed little ponds with muddy ground which provided the perfect environment for *Melanoides*. The snails taken on the roots or in the drinking water could have founded a whole population starting from a single individual within a short time due to its rapid growth and parthenogenetic nature.

Biology: LIVSHITS & FISHELSON (1983) found males in populations of *Melanoides tuberculata* in Israel. Also according to HELLER & FARSTAY (1990) *M. tuberculata* populations in Israel occasionally contain males. These authors were not able to prove that these males are sexually active, but their presence indicated that from time to time sexual reproduction may occur and mix genetic material within populations now and then.

The anatomy of *M. tuberculata* was analysed by STARMÜHLNER (1969). According to RAMAMOORTHI (1950), BERRY & KADRI (1974), and MULEY (1977, 1978) the epithelium of the brood pouch secretes amoeboid cells which

are ingested by the embryos. Another possibility of embryonic feeding was suggested by DUDGEON (1986) who did not trust these histological studies. DUDGEON had found in individuals from Hong Kong juveniles always present within the brood pouch, but noted hatching only during summer. DUDGEON found that the young leave the brood pouch with 5-6 whorls, and suspected that the developing young may feed within the brood pouch by nurse-eggs or by cannibalism. GLAUBRECHT (1996) suggested that nurse-egg feeding or cannibalism is only a minor feature, but presented no data to prove his assumption. The egg of *Melanoides tuberculata* measures 0.06 mm in diameter (BERRY & KADRI 1973) and is surrouned by an egg capsule measuring 0.15 mm in diameter from which embryos hatch with slightly more than half a whorl of the shell (RIEDEL 1993). During further life in the brood chamber the embryo is said to feed only on particles that are secreted by the walls of the brood chamber. RIEDEL (1993) noted that first crystals of calcium carbonate appear early but form no continuous layer on the first shell whorl. From 1.5 whorls of the shell onward mineralization is continuous. Thus, the first shell whorl may later shrink in size forming a characteristic pattern of folds seen in the first whorl. Shrinking patterns can also be noted in the African species *Melanoides liebrechtsi* (DAUTZENBERG, 1901) (RIEDEL 1993, Pl. 2, fig. 8).

Ontogeny: Practically every grown individual of an aquarium-population contained embryos in its brood pouch. Their number is high and clearly related to the size of the maternal animal. The eggs of *Melanoides tuberculata* are surrounded by a clear transparent egg capsule and are uncleaved when they leave the genital tract and enter the brood chamber of the head-foot situated behind the head in the "neck" of *Melanoides*. Each egg is surrounded

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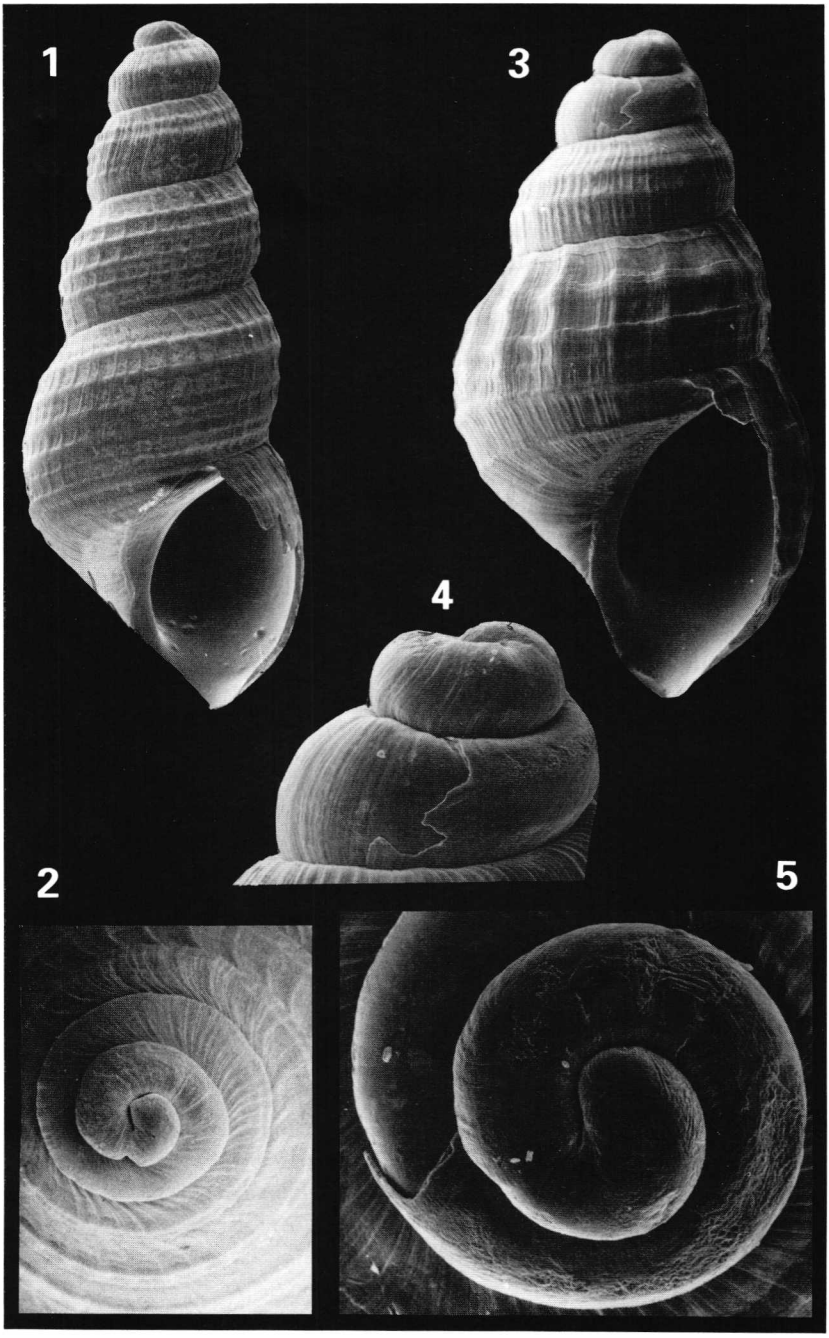
Figs. 1-5

1. Juvenile specimen of *Melanoides tuberculata* (MÜLLER, 1774) from Rarotonga (Cook Isl.). It measures 3.06 mm in length.
2. Apical view of the initial whorls of the same specimen as in Figure 1 with characteristic pattern of foulds in the first 1.5 whorls indicating an irregular calcification and later shrinking of the shell. The first whorl measures 0.22 mm in diameter.
3. Juvenile specimen of *Tarebia granifera* LAMARCK, 1822 from Lovina (Bali) measuring 1.43 mm in length.
4. Lateral view of the apex of the same specimen as in Figure 3 measuring 0.23 mm in height. The protoconch is terminated by a fractured sinusigera. Note the onset of deviating sculpture of the early teleoconch.
5. Protoconch of the same specimen as in Figure 3 in apical view. It measures 0.26 mm in diameter.



Figs. 1-5 (Legend see p. 686)

by some clear yolk which can be devoured by the early embryo once it has formed a first functional digestive system. In it the embryo develops in a normal way up to the stage in which the shell has about the size of the initial part seen on the protoconch forming slightly more than half a whorl. The foot shows two statocysts with statolites and the head bears a short simple velum.

With all this completed the embryo hatches from its egg capsule and swims within the liquid of the brood chamber. It deviates from such veligers that hatch to the open sea, as found in the closely related *Stenomelania punctata* LAMARCK, 1822 in that the animal can not retract into its shell (BANDEL et al. 1997). The muscle seems to be a little weak and the animal somewhat too large to be contained within the shell. It differs from free swimming larvae in the same stage of development by being filled with yolk rich cells, found everywhere in the foot, the velum, the head and the mantle. Thus, the embryo appears clumsy and cannot withdraw into its shell. Cilia only rotate it within the brood pouch liquid and the foot can not crawl as would be the case in the free veliger when it gets ready for metamorphosis. Tentacles and eyes develop as the veliger grows, even though the velum does not develop a true velar shape since it is so much filled with yolk rich cells. The food appears to be represented by the numerous cells that float in the brood pouch liquid and which are produced by the brood pouch walls as was suggested by STARMÜHLNER (1969).

Metamorphosis occurs with about 1.5 whorls completed. Afterwards the shell becomes fully mineralized, the retractor muscle becomes functional and feeding is now by buccal mass with a radula. The animal now withdraws into its shell and can pull back for quite a way, closing the aperture with the operculum. The animal remains within the brood pouch until it has five to six whorls completed. There are many embryos that do not develop into functional animals, but disintegrate becoming part of the food ingested by the developing embryos in the pouch.

Geological history: It is assumed that *Melanoides* appeared in Europe only in the Pliocene where it also occurs in Hungary (KROLOPP 1976). According to WILLMANN (1981) *Melanoides tuberculata* and rather close varieties or species occurred in lakes of Pliocene age on the islands of Kos and Rhodos (Greece). In the Near East *Melanoides* appeared in the Pliocene as well (BLANCKENHORN & OPPENHEIM 1927, TCHERNOV 1973, 1975). Representatives of *Melanoides* did not live in the lakes and rivers that have formed after the sea had withdrawn from the Pannonian planes during the Mid-Miocene, but it appeared in Hungary later in the Pliocene (KROLOPP 1976). In Africa *Melanoides* also migrated across the continent at about the same time reaching Lake Turkana (WILLIAMSON 1981).

Genus *Tarebia* H. & A. Adams 1854

(Figs. 3-5)

The type is *Melania semigranosa* von dem Busch, 1842 from China and south-eastern Asia. The shell is wider than that of *Melanoides tuberculata* and ornament consists of regular spiral ribs and axial ribs that form a cancellate pattern. There are up to 15 whorls and the shell may be up to 4 cm high. The operculum is paucispiral with excentric nucleus. Morrison (1954) noted a brood pouch in members of this genus. Glaubrecht (1996) studied the protoconch of *Tarebia granifera* Lamarck, 1822 and described the brood pouch that resembles that of *Melanoides tuberculata*, and in which the embryos develop until hatching as miniature adults with 4.5 whorls completed. The anatomy and shell was described in detail by Abbott (1952), the radula is illustrated by Starmühlner (1976, 1984) and Glaubrecht (1996). Bandel & Riedel (in prep.) noted that the midriver area of the Kawasan river in Cebu is characterized by *Tarebia* H. & A. Adams, 1854 and *Melanoides* Olivier, 1804. *Tarebia* feeds on rock surfaces, grazing plant covers from them. Its biozone abruptly ends where the Neritidae Rafinesque, 1815 with a similar feeding strategy come in. *Melanoides*, in contrast, feeds on soft bottom substrates which are only marginally exploited by the Neritidae and thus can be found in the lower reaches of the river as well, down to the uppermost estuarine influence, but in lesser numbers of individuals.

Ontogeny: In *Tarebia granifera* each egg is surrounded by a spherical egg capsule which is not much larger than the actual egg. Veligers hatch with well developed statocysts after 0.75 whorls are completed. The shell is fully calcified. Veligers with 1.2 whorls have a larval hook and can withdraw into their shell and close the aperture with the operculum. With 1.75 whorls the embryos are fully metamorphosed measuring about 0.26 mm in diameter. The velum is lost and the embryos have an adult heart, a functional mantle cavity, operculate foot, tentacles and eyes on their base. Food is taken up from material secreted from the brood sac, and it enters through the mouth into the brightly red intestine and after digestion is expelled through the anus that lies on the mantle edge. Even though the little snail in the brood pouch after two shell whorls seems a quite normal miniatur adult, it remains within the maternal shelter until five whorls are completed.

Differences in the ontogeny of *Melanoides* and *Tarebia*: The difference lies in the early ontogenetic shell formation. In contrast to that of *Melanoides* the veliger of *Tarebia* hatches from its egg capsule with a fully calcified shell. Also the shell formed during veliger stage in the brood pouch is fully mineralized. Thus, the early shell is not shrinking during metamorphosis as can be observed in *Melanoides*. In *Tarebia* metamorphosis is terminated with 1.75 whorls indicated by a strong sinusigera notch. This is absent in *Melanoides*. In the latter the adult shell becomes visible by a regular calcification after 1.5 whorls.

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

(Figs. 6, 7)

The type is *Melania mitra* Dunker = *Sermyla tornatella* (Lea, 1850). *Sermyla riqueti* (Grateloup, 1840) is a synonym. The individuals from the type locality near Bombay in India live in brackish water of estuaries, as is the case in the individuals that Bandel & Riedel (in prep.) found in Argao/Cebu (Philippines) and Lovina/Bali (Indonesia). The anatomy was described by Pace (1973), but the embryonic shells remained undescribed. As analysed by Bandel & Riedel (in prep.) the young held in the brood pouch hatch as miniature adults. There are usually juveniles found within the brood pouch of fully grown individuals just as is the case in *Melanoides tuberculata*. The living environment differs since it is typically estuarine with the adults prefering brackish water and not fresh water for their habitat.

Protoconch-morphology: The protoconch consists of 1.25 whorls measuring 0.3 mm in diameter. The embryonic shell of 0.75 whorls measures 0.22 mm. The non spiral part measures 0.14 mm across. The surface of the embryonic shell is formed by a pattern of wrinkles as forms when the non-mineralized shell shrinks in size before becoming fixed in shape by a mineral layer from below. A thickened rim of the embryo's aperture indicates the point of hatching from the egg capsule within the brood pouch. After that, mineralization became regular and a well developed sinusigera terminated the protoconch.

Differences: The early ontogeny of *Sermyla* sp. from Bali and Cebu differs from that of *Melanoides* by having a well developed sinusigera characterizing the terminus of the larval stage within the brood pouch, and by having a fully mineralized shell when metamorphosis occurs. Thus, it is intermediate between *Tarebia* with fully mineralized embryonic and larval shell and

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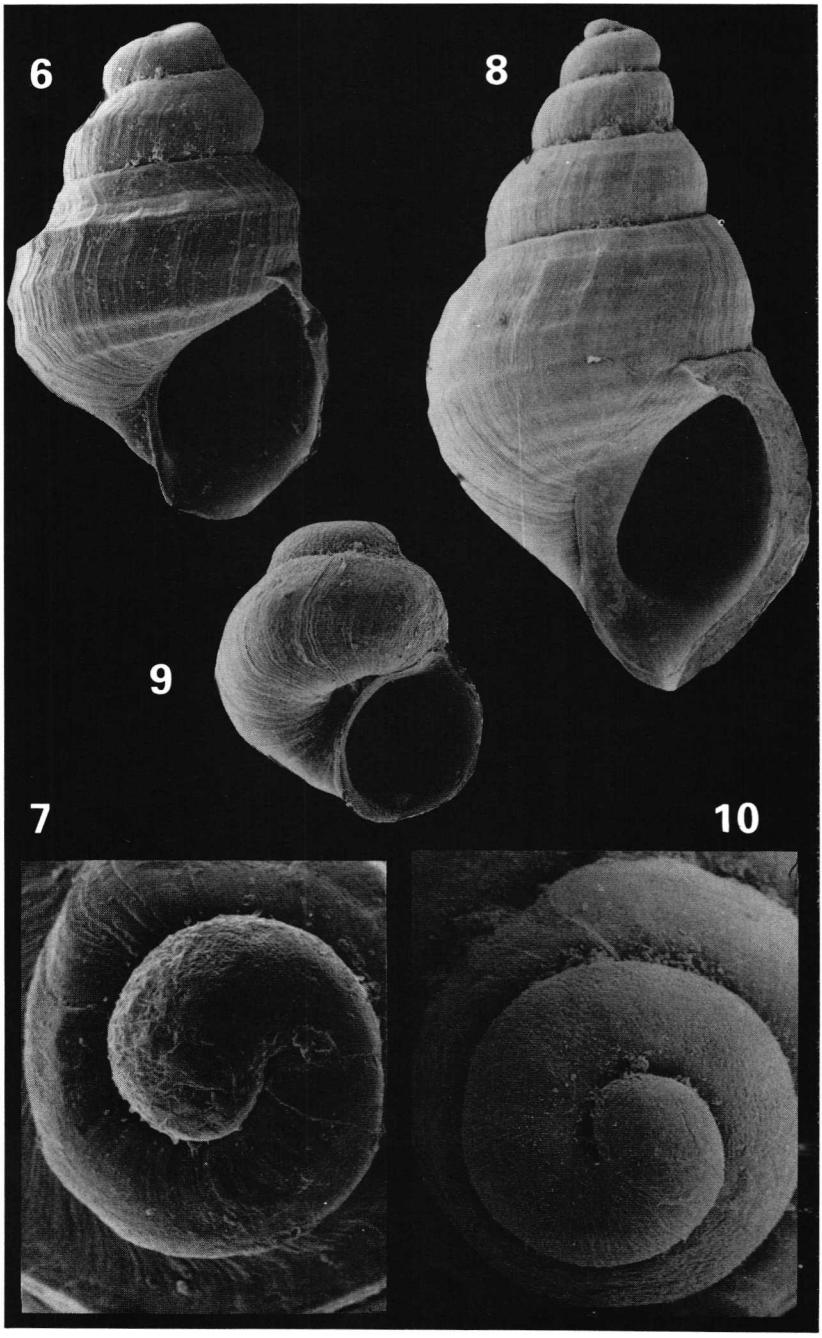
Figs. 6-10

6. Early ontogenetic shell of *Sermyla* sp. from Lovina (Bali). The specimen measures 0.97 mm in length.
7. Protoconch of the same specimen as in Figure 6 measuring 0.3 mm in diameter. The embryonic shell is characterized by a wrinkled surface.
8. Juvenile specimen of *Melanotarebia distincta* (Zittel, 1862) from the Eocene of Gant (Hungary). It measures 1.84 mm in length.
9. Early ontogenetic shell of *M. distincta* measuring 0.47 mm in length. The protoconch with a wrinkled surface is terminated by a sinusigera.
10. Apical view of the protoconch of the same specimen as in Figure 8 measuring 0.39 mm in diameter.



Figs. 6-10 (Legend see p. 690)

Melanoides where mineralization of the shell occurs only after metamorphosis from the larval to crawling stage.

Genus *Melanotarebia* n. g.

(Figs. 8-10)

Type species: *Melania distincta* ZITTEL, 1862 from the Eocene Upper-Nummulite-Formation of Hungary

Derivatio nominis: Combination of the thiarid names *Melanoides* and *Tarebia* to characterize similarities regarding protoconch- and teleoconch-characters.

Diagnosis: The slender, turreted shell is up to 1 cm high. Adult shells are decollate with about six whorls preserved. The highly variable sculpture consists of more or less prominent spiral and axial ribs forming a reticulate pattern and rows of tubercules in their cross-points. The protoconch consists of two wrinkled whorls terminated by a sinusigeral notch.

Differences: *Melanotarebia* n. g. differs from *Thiara, Tarebia* and *Sermyla* by having two whorls of the protoconch with a wrinkled surface. Thus, the shell was not fully mineralized before metamorphosis occurred, as is the case in modern *Melanoides*. *Melanotarebia* differs from this genus in having a well developed sinusigeral notch indicating the terminus of the larval stage within the brood pouch, similar as is seen in modern *Tarebia*.

Species *Melanotarebia distincta* (ZITTEL, 1862)

Description: ZITTEL (1862) described the teleoconch well. The initial whorl measures 0.26 mm in maximal diameter. The whole protoconch of two whorls measuring 0.39 mm in diameter is characterized by a wrinkled surface. This indicates that the larval shell was not continuously mineralized during its formation. Mineralization occurred later after metamorphosis and fixed the shell causing the shrunken and wrinkled shape of the surface. The protoconch is terminated by a prominent sinusigeral notch after two whorls are completed.

Remarks: SZÖTS (1953, Pl. 2, figs. 52, 53) illustrated this species from Gant that looks rather similar to *Melanoides* and *Tarebia*. KECSKEMETY-KÖRMENDY (1972. Pl. 2. Fig. 9) calls a very similar shell from the Mid-Eocene fresh water deposits of the Dorog Basin in Hungary *Melania distincta*. The former generic name *Melania* LAMARCK, 1799 is a synonym of *Thiara* BOLTEN, 1798 and can not be applied. The ontogeny of *Melanotarebia* mediates between that of *Melanoides* and *Tarebia*. This and the considerably large diameter of the first whorl, that is not found in Thiaridae like *Stenomelania* and *Thiara* with planktotrophic veligers, make it obvious that the early ontogeny took place in a brood pouch up to several whorls. The difference to a direkt development outside a brood pouch is reflected in the shrunken surface of the post-embryonic shell. In free direct development incomplete mineralization may only occur during the intracapsular stage of the embryogeny and not after

hatching. Eocene European *Melanotarebia* could well be a direct precursor of recent thiarids with brood pouch development and young hatching with several whorls completed.

Discussion and conclusions

Melanoides tuberculata had a potential ancestor in the fossil *Melanotarebia distincta* from the European Eocene. The protoconch indicates that the rather specific ontogeny found among the modern Thiaridae like *Melanoides*, *Tarebia* and *Sermyla* had been employed by the fossil species that lived in fresh water lakes along the coast of the Tethys Ocean in Hungary during the Eocene. It is to be expected that strategies as found among *Stenomelania* and *Thiara* with planktotrophic veligers were also present at that time but still have to be discovered. Thiaridae may have become extinct in Europe afterwards, but very similar shells to *Melanoides* are known from lake deposits of the Oligocene of Spain. Among the fresh water gastropods in Miocene time like in Pannonian Basin, Mainz Basin or Steinheim lake *Melanoides* and similar shells are not known. Post-Oligocene extinction of the Thiaridae in Europe and a later reestablishment from emigrants coming from the southeast remains quite possible. But it is an established fact that among the many fresh water gastropods that lived in the lakes and rivers of the Paratethys during Middle and Late Miocene *Melanoides* and other Thiaridae (s. s.) are not known, while *Melanoides tuberculata* lived in lakes and streams of that area and further to the East during the Pliocene/Pleistocene.

Eocene *Melanotarebia* appears to be the oldest known member of the Thiaridae (s. s.) with an early ontogeny that took place within a brood pouch. This is in accordance with the occurrence of its sister taxon, the marine Planaxidae, which are also documented since the Middle Eocene (Cossmann 1886-1913, Houbrick 1987, Lozouet & Maestrati 1994). The genera *Juramelanoides* Bandel. 1991 and *Juramelanatria* Bandel, 1991 from fresh water deposits of the Early Cretaceous of the French Jura are characterized by smooth embryonic whorls that indicate a direct mode of development without an intercalation of a (lecithotrophic) larva (Bandel 1991). It remains unclear whether they were ancestors of the Thiaridae or represent an independent group of fresh water gastropods of the cerithiimorph relation. There are plenty of such groups known and there is ample convergence of shell shapes. The rich and extremely well preserved fresh water gastropods of the Late Cretaceous Ajka-fauna contain quite a few species of Cerithioidea but not a single one that could be related to the Thiaridae (Bandel & Riedel 1994).

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