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Valvatiform Gastropoda (Heterostropha and Caenogastropoda) from the Paratethys Basin compared to living relatives, with description of several new genera and species

Klaus Bandel, Hamburg with 17 plates

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Abstract

Many gastropods from the Paratethys during Late Miocene to Early Pliocene had a small and lowly coiled to flat shell. They have often been determined as belonging to the genera Valvata and Planorbis/Gyraulus which in many cases is not correct. The primary objective of this study is to analyze family level characters, provide a revised generic classification compared with living genera, and to describe new species. In previous original description of the species shape and ornament of the protoconch usually had not been studied but especially these characters provide evidence for recognizing their place in the taxonomic system. Some of the fossil species have left coiling mode of the protoconch and resemble species of living Vitrinella. The Vitrinellidae based on that genus are here newly assigned by describing a representative from the Caribbean Sea that is close to the type species of the family and genus. Vitrinella urdunica n. sp. and Tomura aqabaensis n. sp. from the Gulf of Aqaba are described for comparison. Badenian Vitrinellidae such as Cornirostra moesiensis and Vitrinella jekelii n. sp are recognized. The new genera Sarmatorostra, Spiricornirostra are based on Sarmatorostra anistratenkorum n. sp. and Spiricornirostra pantikapaionensis n. sp. from the Sarmatian of Kerch Peninsula. Omalogyra helicinoides of the Omalogyridae with minute shell lived in the Sarmatian of the Paratethys. The Valvatidae from fresh water environment have a characteristic spiral ornament of the protoconch connected to simple growth line pattern on the teleoconch discussed with recent and fossil species of Valvata. Teleoconch whorls are usually rounded, but a keel bearing species lived in a fresh water lake of Rhodes and Kos, and in Lake Pannon in the Pontian of Hungary with Valvata heidemariae. Valvata kamirensis lived in Pliocene lakes across the Paratethys depositional regime from Rhodes to the Carpathian arch. Shape and ornament of the protoconch allow to distinguish species with shell shape as among the Valvatidae to belong in the Hydrobiidae and Planorbidae. Hydrobiidae have a dextral embryonic whorl ornamented with characteristic groove and ridge pattern. Some species have a shape of the shell as among living species of Hauffenia, Islamia, Heraultia and Horatia. The new genus Muellerpalia is based on M. bicinata and includes among others Muellerpalia tabensis n. sp. and M.

striata n. sp.. Graecamnicola from Rhodes is also recognized in the Pontian of Hungary. Jekeliella balatonica is the new type to the genus Jekelia that also includes J. gradata and J. tenuistriata. In case of the new genus Kerchia with K. yurkynensis n. sp. the living environment in a bryozoan reef is distinctive. A transition from lowly coiled shell as in Jekeliella to species with higher shell even close to that of Pyrgula is recognized. The protoconch as in the Planorbidae resembles that of Valvatidae, but differs from them by inclined increments of growth and more rapid whorl expansion. Fuchsogyra n. gen. is based on F. radmanesti and includes F. balatonica n. sp.. Marinescugyra n. gen. is based on M. varians and also includes M. tenuis. Both new genera may represent Basommatophora of the relation of Planorbis, but have a distinct protoconch. Several genera of Planorbidae lived from the Pontian into the Pliocene and their species are difficult to be distinguished from living species as is discussed.

Zusammenfassung

Unter den Schnecken, die während des späten Miozäns und frühen Pliozäns im Ablagerungsraum der Paratethys lebten, haben zahlreiche Arten eine niedrige, kleine und flach aufgewundene Schale. Oft wurden sie den Gattungen Valvata und Planorbis/Gyraulus zugeordnet, was sich in vielen Fällen aber als nicht korrekt erwies. Als vornehmliche Aufgabe dieser Studie werden Merkmale erarbeitet, mit deren Hilfe die Familienzugehörigkeit einer Arte bestimmbar ist. Der Vergleich zu lebenden Arten ermöglicht, es Gattungsmerkmale zu erfassen und neue Arten zu beschreiben. In den in der Literatur vorliegenden Beschreibungen der betreffenden Arten wurden zumeist nicht auf die Gestalt und das Ornament des Protoconches eingegangen. Diese Studie erweist aber, dass ganz besonders die Merkmale des Protoconches eine genauere taxonomische Zuordnung der fossilen Arten ermöglichen. Einige der fossilen Arten besitzen eine links-gewundenen Protoconch und gleichen in ihrer Schalengestalt den Arten der lebenden Vitrinella. Der Vergleich mit der Typusart von Vitrinella aus der Karibischen See ermöglicht, die darauf basierende Familie Vitrinellidae den Heterobranchia zuzuordnen. Vitrinella urdunica n. sp. und Tomura aqabaensis n. sp. von Golf von Aqaba werden neu beschrieben und zudem mit Cornirostra moesiensis und Vitrinella jekelii n. sp. aus dem Miozän in Verbindung gebracht. Der Familie lassen sich zudem die neuen Gattungen Sarmatorostra und Spiricornirostra zuordnen, mit den Typusarten Sarmatorostra anistratenkorum n. sp. und Spiricornirostra pantikapaionensis n. sp. aus dem Sarmat der Halbinsel von Kertsch (Krim). Omalogyra helicinoides mit sehr kleiner Schale und zugehörig den Omalogyridae lebte während des Sarmat im Meer der Paratethys.

Die im Süsswasser lebenden Vertreter der Valvatidae besitzen ein charakteristisches Linien-Muster auf ihrer Embryonalschale verbunden mit einem einfachen Muster der Anwachsstreifung auf Protoconch und Teleoconch. Das wird an Hand rezenter und fossiler Vertreter der Gattung Valvata ausgeführt. Meist sind bei ihnen die Windungen des Teleoconches gerundet, aber ein Kiel tritt bei Valvata heidemariae und Valvata kamirensis auf, die sowohl in Seen des Pliozäns von Rhodos und Kos als auch der Paratethys von Ungarn bis Rumänien lebten. Ein Kiel wird heute noch bei einigen amerikanischen Arten angetroffen. Die Gestalt wie auch das Ornament des Protoconches erlaubt die Unterscheidung von Valvatidae zu Arten mit konvergenter Schale der Hydrobiidae wie auch der Planorbidae. Den Hydrobiidae zugehörige Arten besitzen eine rechtsgewundene Embryonschale mit eigentümlicher Gruben und Wulst- Musterung. Einige fossilen Arten haben die Gestalt rezenter Vertreter der Gattungen Hauffenia, Islamia, Heraultia and Horatia, sind aber nicht bestimmbar, weil die anatomischen Merkmale fehlen. Andere werden der neuen Gattung Muellerpalia zugeordnet, die auf M. bicinata basiert und unter anderem auch Muellerpalia tabensis n. sp. und M. striata n. sp. enthält. Graecamnicola von Rhodos wird auch aus dem Pont von Ungarn nachgewiesen. Jekeliella balatonica dient als Typus der neuen Gattung Jekeliella, die zudem J. gradata und J. tenuistriata enthält. Für die neue Gattung Kerchia mit K. yurkynensis n. sp. ist der Fundort im fossilen Bryozoen- Riff der Halbinsel Kertsch charakteristisch. Ähnlich niedrig gewundene Schalen wie bei Jekeliella sind zu hochgetürmten Schale vom Typus der Gattung Pyrgula mit Übergängen aus dem pliozänen See von Brasov beschrieben, wie ganz generell vielfältige Verbindungen von den vormaligen Seen des Dodekanes zu solchen aus den eigentlichen Becken der Paratethys mit Hilfe der Schnecken belegbar sind.

Der Protoconch der Planorbidae ähnelt jenem der Valvatidae hinsichtlich des Schalenmusters, Planorbidae unterscheidet die geneigte Anwachsstreifung und die rasche Windungszunahme. Den Basommatophora, aber nicht unbedingt der näheren Verwandtschft von *Planorbis*, ist *Fuchsogyra* n. gen. zugehörig, die auf *F. radmanesti* basiert und zudem *F. balatonica* n. sp. enthält. Auch *Marinescugyra* n. gen. die auf *M. varians* begründet ist und auch *M. tenuis* enthält gehört hierher, und beide verbindet die chracteristische Gestalt des Protoconches. Aus den Reihen der Planorbidae lebten die Vertreter mehrer Gattungen in den Seen des Pliozäns der Paratethys und benachbarter Regionen und die Schalen ihrer Arten unterscheiden sich nicht oder wenig von jenen heute lebender Arten.

1 Introduction

The Paratethys consists of a chain of continental basins which formed in a late stage of the alpine orogeny when Afro-Arabia collided into Europe. At first the Paratethys was a marine, northern extension of the Tethys Sea; later, temporary isolation from the sea occurred repeatedly, whether of the entire Paratethys or of individual basins (STEININGER & WESSELY, 2000). During mid-Miocene the sea covered large parts from the Vienna Basin in the West to the Euxinic Basin in the East with connections to the Pacific in the East and the Mediterranean Atlantic to the West. This Badenian Sea was succeeded by a more isolated Sarmatian Sea that extended from the Vienna Basin in the west to the area east of the Caspian Basin to the east, but without or only very restricted contact to the oceans. Near-shore deposits formed close to islands in the Badenian and Sarmatian sea. Species from such an island that had its shore near the village of Soceni in western Romania (JEKELIUS, 1944) and from another one also near Kerch in the eastern Ukraine are described.

The Sarmatian Sea evolved into a chain of brackish lakes during the Late Miocene of which Lake Pannon is the most western one. The depositional environment of Lake Pannon during the Pontian was characterized by MÜLLER (19890), and its development was analyzed by KORPAS-HODI (1983) and CZISZER et al. (2008). Accordingly, Lake Pannon existed as brackish lake from the Late Miocene to the earliest Pliocene and was isolated from the Sarmatian Sea which continued existence further to the east. The lake reached its largest areal extent at ca. 9.5 ma (MAGYAR et al., 1999) and received sediments from the north, northwest, and west which filled it by the end of the Miocene. During about the Messinian period in the Mediterranean region Lake Pannon developed into individual lakes which in part had a quite similar fauna to that which lived contemporaneously and during the Pliocene in lakes at Kos and Rhodes of the Dodenkanes and in a lake of the Jordan valley. The fauna from Kos and Rhodes interpreted by WILLMANN (1981) resembles an about contemporaneous fauna described by JEKELIUS (1932) from the western Romanian Lake Brasov. The basins on Kos and Rhodes were filled by alluvial and lacustrine sediments predominantly during the Pliocene. They lay to the north and west of mountains which have now largely disappeared, submerged in the Mediterranean Sea.

From marine deposits of the Badenian, marine to brackish deposits of the Sarmatian and fresh water deposits of the Pliocene of different regions of the Paratethys gastropods are described, which have a shell, resembling that of species of *Valvata*. A few species with living representatives are included as well which resemble the fossil species from the Paratethys, and also species from a locality with fresh water gastropods from a lake of Pliocene age from the Jordan Valley is included.

The material of the new species is deposited with the holotypes as no. 4700–4709 in the collection of the Geologisch-Paläontologisches Institut and Museum, Universität Hamburg.

2 Marine Vitrinellidae GRAY, 1840 (= Cornirostridae)

Order Allogastropoda HASZPRUNAR, 1985 Superfamily Valvatoidea GRAY, 1840

The small shell is trochiform to discoidal, variously ornamented with a heterostrophic protoconch that is leftcoiled around the same axis as the dextral teleoconch. The protoconch may have secondarily become planispiral in species with lecithotrophic development and those living in fresh water. The aperture is simple. In living species several features of the anatomy are distinctive. For example the gill and especially the pallial tentacle are characteristic (RATH, 1988). The gill is covered by cilia all over and differs from that of the other gill bearing gastropods. It is usually exposed in front of the aperture, when the animal is active. The osphradium has a unique anatomy and lies on the left side right besides the pallial opening (HASZPRUNAR, 1985, 1988). Also the morphology of the sperm is characteristic (HEALY, 1991).

THIELE (1931) recognized that *Valvata* was distinct from other similar fresh water gastropods and placed it in a superfamily by its own. But, he united Valvatoidea with other groups of his Mesogastropoda (subclass Caenogastropoda Cox, 1960). Later *Valvata* was found to belong in the subclass Heterostropha (= Heterobranchia) and here the order Allogastropoda (HASZPRUNAR, 1985). Heterostropha have been recognized to represent a distinct subclass of the Gastropoda and different from Caenogastropoda since at least middle Paleozoic time (FRÝDA & BLODGETT, 2001; BANDEL, 2002; BANDEL & HEIDELBERGER, 2002). The Valvatidae among them are recognized since the Late Jurassic (BANDEL, 1991).

WENZ (1938) knew only members of the *Valvata* relation forming a superfamily Valvatacea which live in fresh water and are restricted to the Northern Hemisphere. PONDER (1991) found marine relatives living in the sea grass environment of tropical seas, and called them Cornirostridae. Marine species with similar characters of their shell as those noted among the living ones have been recognized in deposits as old as Devonian (BANDEL & HEIDELBERGER, 2002).

Family Vitrinellidae BUSH, 1897 (= Cornirostridae PONDER, 1990)

The small (about 2 mm diameter) depressed trochiform shell is usually smooth with open umbilicus. This "valvatiform" teleoconch has a simple aperture and is connected to a smooth protoconch coiled to the left. It consists of an embryonic and a larval shell which are coiled along the same axis as the dextral teleoconch but turning in the left coil. In case of a lecithotrophic development (eggs are rich in yolk) the left coiled mode becomes obscured. The family Cornirostridae is based on the genus *Cornirostra* that closely resembles the genus *Vitrinella* that is the type genus to the Vitrinellidae.

<u>Remarks</u>: The family Vitrinellidae was based on shell characters by BUSH (1897). It derived its name from the genus *Vitrinella* C.B. ADAMS, 1850 of which *Vitrinella helicoides* C.B. ADAMS, 1850 represents the type. Vitrinellidae with shell shape as in *Vitrinella* can be traced back to at least the Triassic (BANDEL, 1994, 1996). Vitrinellidae cannot be connected with Caenogastropoda, as was suggested by BOUCHET & ROCROI (2005).

The characters of the type species of the genus *Vitrinella* should be used to define the family Vitrinellidae. But usually Vitrinellidae have been interpreted to represent Caenogastropoda. Genera such as *Circulus* and *Teinostoma* have been included, for which family names such as Tornidae SACCO, 1896, or Circulidae FRETTER & GRAHAM, 1962, are available. Characteristic species of both of these families can be traced to the Early Cretaceous (DOCKERY, 1993; KIEL, 2006). Their protoconch is dextral.

PONDER (1990, 1991) assumed that a small gastropod that had been determined as a species of *Microdiscula* is actually closely related to the fresh water species of the genus *Valvata*. PONDER (1990) called a species that has a little higher spire than is present in *Vitrinella, Cornirostra* and found it to resemble *Tomura*. Marine members of this group have been described by PONDER (1990, 1991) and WARÉN et al. (1993). Fossil species belonging here were recognized from the Devonian to Triassic by BANDEL (1991, 1996), BANDEL & HEIDELBERGER (2002), the Jurassic by SCHRÖDER (1995), GRÜNDEL (1998), KAIM (2004), and the Cretaceous by KIEL (2006). The radula of *Cornirostra* is not taenioglossate as that of *Valvata*, but has 9 teeth in each row of which two are identically shaped lateral teeth (PONDER et al., 1998: fig. 15, 179D; WARÉN et al., 1993).

Genus Cornirostra PONDER, 1990

The smooth depressed-trochiform shell has rounded whorls, a simple aperture and an open umbilicus (PONDER et al., 1998, fig.15, 179A–B). The genus is based on *Microdiscula pellucida* LASERON, 1954 from the eastern coast of Australia (PONDER, 1990).

Cornirostra floridana BIELER & MIKKELSEN, 1998 from southern Florida has a shell that is about 2 mm wide and high with a little more than three rounded and smooth whorls and apical angle of about 110°. The base has an open umbilicus and is rounded. The aperture is simple continuous, rounded and oblique. The protoconch consists of 1.2 whorls and measures 0.18 mm in width. Its initial portion is left-coiled and ornamented with a reticulate wrinkle pattern (BIELER & MIKKELSEN, 1998: figs. 1–4). They interpreted the unornamented portion of the protoconch as belonging to a larva.

Cornirostra moesiensis (JEKELIUS, 1944) (Pl. 1/1–8)

Valvata moesiensis from the late Sarmatian of Soceni (JEKELIUS, 1944: pl. 7, figs. 11–14) has a lowly coiled shell that measures about 1 mm in diameter with three whorls. The inner lip is straight and the aperture wide. Newly collected individuals of this species from Soceni and from the marine deposits of Badenian–Sarmatian age at the slope of Cape Takil to the Strait of Kerch near Yurkyne on Kerch Peninsula of the Crimea also display the protoconch (figs. 4, 8). It has a slight twist to the left in the first whorl and planispiral coiling in the short larval shell. The diameter of the protoconch is about 0.15 mm and it consists of 1.2 rounded whorls. Its margin is a little thickened and straight. The total shell consists of up to 3.5 rounded whorls and is a little wider than high (up to 1 mm). The ornament of the teleoconch consists of simple and sometimes quite indistinct growth lines. Whorls are evenly rounded at the base and the umbilicus is narrow.

<u>Remarks</u>: This species may also be the same as *Valvata simplex* of JEKELIUS (1944: pl. 7, figs. 6–9). In the fauna from the Peninsula of Kerch and here near Yurkyne-Bulganak *Cornirostra moesiensis* occurs together with a fauna of almost fully marine character at pre Sarmatian time (fig. 6).

Genus Vitrinella C.B. Adams, 1850

The shell is smooth and rounded, its umbilicus open, wide and with simple rounded margins. The type *Vitrinella helicoidea* C.B. ADAMS, 1850 (WENZ 1938: fig. 1284) is most probably a member of the Valvatoidea and identical or very close in shape to the species illustrated here from the shallow Caribbean Sea at Santa Marta (figs. 9, 10). A similar species was placed with the Allogastropoda by BIELER et al. (1998) determined as *Cornirostra floridana*.

Cornirostra PONDER, 1990 has very similar shell shape as noted in *Vitrinella*, and one could argue that it actually represents a species of the genus *Vitrinella*. But the shell of *Vitrinella* from the Caribbean Sea near Santa Marta (figs. 9, 10) has a lower shell than that of *Cornirostra*, and it is wider than high.

Vitrinella helicoidea from Santa Marta is about 1 mm wide and not as high. Its protoconch has a sinistral embryonic whorl distinguished from the larval shell by growth lines. The protoconch diameter is about 0.15 mm. The embryonic whorl is succeeded by half a larval whorl. Change from left coiling mode to planispiral coiling occurs within the larval part of the protoconch. The aperture of the larval shell is a little widened and clearly distinguished from onset of the teleoconch. With a little more than two whorls of the teleoconch the shell is fully grown. Ornament consists of simple growth lines. The living environment of *V. helicoidea* lies on sandy bottom in the shallow, about 2–5 m deep sea in the bay of Santa Marta and similar bays near it along the Colombian Coast of the Caribbean Sea.

Vitrinella urdunica n. sp. (Pl. 1/11, 12)

<u>Diagnosis</u>: The shell consists of 2.5 whorls of the teleoconch with fine spiral lines on the first whorl and later only ornament of simple growth lines. The protoconch has a sinistral embryonic part ornament by a fine ridge and groove pattern connected to about one half smooth whorl of the larva ending with a raised margin. The base is rounded with open umbilicus.

<u>Origin of the name, typical ecology and holotype</u>: The species is named according to its occurrence at the shore of the Gulf of Aqaba in Jordan, Arabic "Urdun". It lives in shallow environment of the coral reef and its lagoon. The illustrated specimen represents the type which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4700.

<u>Description</u>: The shell is almost smooth, transparent and opaque colorless. Its size when fully grown is 1.2 mm. The protoconch consists of the left-coiled embryonic whorl with fine ridge and groove pattern succeeded by three quarters of a whorl of larval shell with its outer lip slightly expanded. The protoconch measures about 0.18 mm in diameter.

<u>Remarks</u>: *Vitrinella urdunica* was found by washing the debris collected from at the base of the fringing reef just off the Aqaba Marine Science Station of the University of Jordan. The shell is fresh but animals are dead, so that they probably live on the intertidal platform on top of the reef or within the crevices of the reef.

Vitrinella urdunica differs from *Vitrinella* cf. *helicoidea* by having a very fine spiral ornament of the early teleoconch. *Vitrinella jekelii* has a larger protoconch than *Vitrinella* cf. *helicoidea* and *Vitrinella urdunica*. The Caribbean *Vitrinella helicoidea* (figs. 9, 10) closely resembles *Vitrinella urdunica* from the Gulf of Aqaba (figs. 11, 12). Dimension and shape of the protoconch are almost alike and the teleoconch also consists of about 2.5 whorls.

Vitrinella jekelii n. sp. (Pl. 2/13, 14)

<u>Diagnosis</u>: The shell has the shape of *Vitrinella urdunica* and also resembles that of *Vitrinella helicoidea* but the protoconch is larger with about 0.1 mm wide embryonic whorls and 0.3 mm wide larval shell. The teleoconch has rounded whorls with ornament of growth lines. The base is rounded and has an umbilicus.

<u>Origin of the name, type locality and holotype</u>: The species from the Sarmatian sandy near-shore deposits of Soceni in western Romania. It is called in honor of E. Jekelius who described the gastropods of Soceni in great detail. The illustrated specimen represents the holotype which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4701.

<u>Description</u>: The embryonic shell measures about 0.1 mm across and consists of almost one whorl with its initial part hidden under the larval whorl. The margin of its aperture is marked by begin of growth increments. Shell deposited by the larva consists of 0.7 whorls and is planispiral in coiling mode. It has its aperture thickened and clearly distinguished from the onset of the teleoconch. The protoconch is about 0.3 mm wide. The teleoconch consists of 1.5 whorls, but may represent a juvenile shell, that is not fully grown. It is about 1 mm in width and less high. Whorls are rounded and the suture impressed. The base is rounded with umbilicus simple.

<u>Difference</u>: *Vitrinella* from the Caribbean Sea as well as from the Gulf of Aqaba have a smaller protoconch, with its embryonic part more clearly left-coiled. Otherwise they are very similar in shell shape. The teleoconch of *Vitrinella helicoidea* is like that of *Vitrinella jekelii* while that of *Vitrinella urdunica* has fine spiral ornament on the early teleoconch.

<u>Remarks</u>: The illustrated specimen represents the holotype and comes from the lower beds in the deposits at Soceni (Badenian–Sarmatian) in the Romanian Banat. *Vitrinella jekelii* closely resembles the Triassic *Bandellina* SCHRÖDER, 1995 (BANDEL, 1996: figs. 16, 18) that is also known from the Jurassic (SCHRÖDER, 1995: pl. 7, figs. 9–12; KAIM, 2004: figs. 123A–C, 124A–B). Also *Tomura ambatolafiensis* KIEL, 2006 from the Albian of Madagascar is similar (KIEL, 2006: figs. 7.1–7.5). *V. jekelii* is more lowly coiled than *Hyalogyrina amphorae* WARÉN, CAROZZI & ROCCHINI, 1996 coming from deeper water of the Mediterranean Sea. *H. amphorae* has the protoconch with left-coiled embryonic shell and planispiral larval shell with about 0.25 mm in diameter. The teleoconch consists of less than 2.5 whorls and has only flexuous growth lines as ornament. Its size is about 1.5 mm wide and high. This species had been placed with the Hyalogyrinidae WARÉN & BOUCHET, 1993 a family created to encompass small gastropods with smooth shell and rounded lowly coiled whorls which live associate with sunken driftwood and hydrothermal vents. The family includes the genera *Hyalogyra* and *Hyalogyrina* MARSHALL, 1988. *Vitrinella jekelii* has a different growth line pattern of the teleoconch.

Genus Tomura PILSBRY & MCGINTY, 1945

The type species is *Vitrinella bicaudata* PILSBRY & MCGINTY, 1946 that lives under stones in the intertidal area of southern Florida. Its 1.2 mm wide and 0.8 mm high shell has a relatively large aperture and small umbilicus that is accompanied by an edge (BIELER, et al. 1998). *Tomura* differs from *Cornirostra* by smaller size and by having an edge around the umbilicus (PONDER, 1990). But from the Mediterranean (WARÉN et al., 1993) and from the Japanese Pacific (FUKUDA & YAMASHITA, 1997) includes species with the genus without umbilical edge, which resemble the shape as is de developed in the species from the Gulf of Aqaba which can also be included with *Tomura*.

Tomura aqabaensis n. sp. (Pl. 2/15–18)

<u>Diagnosis</u>: Whorls are rounded with simple continuous margin of the aperture and very little overlap onto each other. The base is concave with wide umbilicus and the apical side almost flat. The protoconch has distinct left-coiling mode with the sinistral embryonic shell with ornament of fine tubercles dips below the larval shell that forms a spiral in a plane and widens more rapidly. Ornament of the teleoconch is only by simple growth lines.

<u>Origin of the name, typical living environment and holotype</u>: The species lives in the fringing reef of the Gulf of Aqaba near Aqaba in shallow water and it is named according to that city. The specimen illustrated in fig. 15 represents the holotype which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4702.

<u>Description</u>: The shell is about 1 mm wide and about 0.4 mm high and consists of about 1.7 rounded whorls of the teleoconch and a protoconch of 1.3 whorls. The apical shell is coiled almost in a plane and the basal side is concave with wide umbilicus in which all whorls are visible. The aperture is oblique and rounded with the inner lip also convex. The initial embryonic portion of the protoconch dips below surface reflecting a sinistral mode of coiling. The diameter of the embryonic shell is about 0.06 mm. Its larval shell widens to a simple rounded aperture with slightly thickened sinuous margin and measures about 0.2 mm in width. The following teleoconch is ornamented by a dense pattern of growth lines which reflect the simple outline of the aperture.

Difference: The shell of *Tomura aqabaensis* is more openly coiled than that of the species of *Vitrinella*.

Genus Sarmatorostra n. gen.

<u>Diagnosis</u>: The teleoconch is as high as wide with rounded simple whorls and round aperture. The protoconch is like that of *Cornirostra* consisting of a slightly left-coiled embryonic whorl and the change from sinistral to planispiral in the larval shell. The type species is *Sarmatorostra anistratenkorum* n. sp. from the Sarmatian of Cap Chrony near Yurkyne.

<u>Origin of the name</u>: This genus is from Sarmatian deposits of the Kerch Peninsula and resembles *Cornirostra*, with the genus name representing a free combination of the name of the Sarmatians which lived in the region some 2000 years ago and the probably related modern gastropod.

<u>Difference</u>: *Sarmatorostra* has a smooth shell in contrast to *Spiricornirostra* and the fully grown shell is a little higher than wide, which contrasts to *Cornirostra* or *Vitrinella* which have the shell wider than high.

Sarmatorostra anistratenkorum n. sp. (Pl. 2/19–24)

<u>Diagnosis</u>: The shell is a little higher than wide and consists of rounded whorls with deep sutures. The protoconch consists of one rounded whorl with slight sinistral orientation at first, but mostly planispiral coiling. The teleoconch has a little more than three whorls with circular diameter open umbilicus and deep sutures.

<u>Origin of the name, typical occurrence and holotype</u>: This *Sarmatorostra* is named for Olga and Vitalyi Anistratenko who took part in the collecting trip on the Crimea. It was extracted from fine sandy Sarmatian deposits from Cape Chrony near Yurkyne. The illustrated specimen in fig. 19 represents the holotype which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4703.

<u>Description</u>: The protoconch consists of one rounded whorl that ends with a slightly raised margin (fig. 23). Its diameter is about 0.25 mm and only the initial part has a slight dip towards the axis of coiling (fig. 22). It, therefore, has a slight left-coiling mode. The aperture of the protoconch is round. Whorls of the teleoconch are coiled in dextral mode and growth is allometric. A shell with three whorls completed is about as wide as high (fig. 20) and with growth of the next 1.5 whorls it changes from higher than wide (fig. 19). When fully grown the shell consists of 4.3 whorls is 1.3 mm wide and slightly higher. The base is evenly rounded and the umbilicus simple and open. The aperture is as wide as high and has circular outline.

Genus Spiricornirostra n. gen

<u>Diagnosis</u>: This shell with shape of a *Cornirostra* has ornament of fine spiral lines. The genus is based on *Spiricornirostra panticapaionensis* from the Sarmatian beds at the cliffs of Cape Takil near Zavitne south of Kerch.

Spiricornirostra pantikapaionensis differs from Cornirostra by having a fine spiral ornament.

Spiricornirostra pantikapaionensis n. sp. (Pl. 3/25–31)

<u>Diagnosis</u>: Shell shape is like that of *Cornirostra* but with fine ornament of spiral lines on the teleoconch. The protoconch of about one and a quarter whorls has only sinistral coiling mode in its initial portion, and is plane in coiling in its later portion. The species occurs in the Sarmatian deposits of the cliffs to Cape Takil south of Zavitne south of Kerch.

<u>Origin of the name, typical occurrence and holotype</u>: The shell with shape as in *Cornirostra* has an ornament of spiral lines thus indicated in the name *Spircornirostra* and it comes from Kerch which used to be the ancient Greek Pantikapaion. The typical sediment is sandy and exposed as Cape Takil near Zavitne and Cape Chrony near Yurkyne. The holotype is the specimen of fig. 26 from Yurkyne, Kerch Peninsula. The holotype is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4704.

<u>Description</u>: The shell consists of a little more than three whorls and is about 1.3 mm wide and 1.1 mm high. Whorls are evenly rounded and the aperture is circular with slightly less curving inner lip. The umbilicus is wide and open, is relatively wider in the first whorl and a little narrower in the last whorls. The protoconch consists of a little more than one whorl with diameter of about 0.25 mm with the initial part rounded and dipping in direction of the axis of coiling. While this first part has a tendency to sinistral coiling, later coiling mode is planispiral. Protoconch margin is turned up and is surface is smooth. The teleoconch is distinguished from the protoconch by stronger growth lines and after about a quarter of a whorl by the appearance of fine spiral lines. The spiral ornament is well preserved on two whorls of the teleoconch, while in the third and last whorl growth line pattern is more prominent.

3 Omalogyridae G.O. SARS, 1878

Superfamily Omalogyroidea G.O. SARS, 1878

This superfamily of the Heterobranchia holds the Omalogyridae and the Triassic Stuoraxidae BANDEL, 1994 (BOUCHET & ROCROI 2005).

FRETTER (1948) and FRETTER & GRAHAM (1962) recognized that *Omalogyra* resembles opisthobranchs, and HEALY (1990) found the sperm to be of the heterobranch type, so they were placed with the Allogastropoda Haszprunar, 1985. PONDER & DE KEYZER (1998) placed here *Omalogyra* and *Ammonicera* VAYSSIÉRE, 1893 and considered the family to represent an own superfamily Omalogyroidea. BAEUMLER et al. (2008) analyzed the anatomy of *Omalogyra atomus* and found an affinity to the Heterobranchia (= Heterostropha) but not to the Architectonicidae among them which sometimes have a similar, but larger shell.

Family Omalogyridae G.O. SARS, 1878

Here extremely small lowly coiled gastropods are included with planispiral shell and size below one mm.

<u>Remarks</u>: They are often difficult to determine, and their taxonomy may be quite confused. Among the marine gastropods for example *Omalogyra* JEFFREYS, 1860, *Skeneopsis* IREDALE, 1915, and *Ammonicera* from the European Atlantic coast look almost alike. Their shell is minute, disk-like in shape and they are difficult to keep apart. *Ammonicera rota* (FORBES & HANLEY, 1850) is very similar to *O. atomus* but even smaller when fully grown (0.5 mm according to GRAHAM, 1988: fig. 111). BIELER & MIKKELSON (1998) reviewed the American species and compared them with the European types.

Genus Omalogyra JEFFREYS, 1860

The tiny (usually less than 2 mm in diameter) marine snails with disc-like shell have a reduced radula (BAEUMLER et al., 2008: figs. 2E, F). The flatly coiled teleoconch is connected to a planorboid protoconch (BANDEL, 1988).

<u>Remarks</u>: *Omalogyra* from the Pannonian of Soceni was interpreted to represent a species of *Valvata*. This *Valvata helicinoides* was described by JEKELIUS (1944, pl. 43, figs. 1–3) and is documented below (fig. 30) along with the same species from Sarmatian deposits of the Crimea (Kerch region).

Omalogyra helicinoides (STOLICZKA, 1862) (Pl. 3/32–37; Pl. 4/38–39)

The shell is a minute disc with about 2.5 whorls, of which the first is represented by the protoconch. The embryonic whorl is planispiral and measures about 0.2 mm in diameter. Its surface is wrinkled and of relatively coarse ornament when compared with the teleoconch. The aperture of the teleoconch is almost straight and distinct, with the teleoconch ornamented predominantly with growth lines. The shell measures only about 1 mm in diameter when fully grown.

Difference: Omalogyra helicinoides differs from O. atomus by minute details of the ornament of the protoconch.

<u>Remarks</u>: JEKELIUS (1944: pl. 43, figs. 1–3) placed *Omalogyra* in the genus *Valvata* as *Valvata helicoides* STOLICZKA, 1862 characterizing it as small shell that is coiled in one plane with round whorls only touching each other. A spiral rib is present on the apical as well as the umbilical side. The later is a little more concave than the former.

Omalogyra atomus (PHILIPPI, 1841) from the Atlantic has whorls of the planispiral shell almost circular in section and the red brown shell is about 1 mm wide and 0.5 mm high. At the coast of the Bretagne near Roscoff the small snail is found on the green alga *Ulva* on which it feeds (own observations). The minute shell consists of about three whorls that lie in one plane and the teleoconch has irregular fine growth increments. The protoconch consists only of the embryonic shell, so that life history of this species from more than about 10 million years back was probably as described by FRETTER (1948) from the species living in the North Sea now. The protoconch consists only of the embryonic shell and was described by SLEURS (1985) and BANDEL (1988: pl. 4, fig. 4). It differs from that of *Ammonicera* by having no ornament, while *A. fischeriana* (MONTEROSATO, 1869) from the Mediterranean Sea has spiral grooves (BANDEL, 1988: pl. 5, fig. 4).

4 Valvatidae GRAY, 1840 (= Valvatidae THOMPSON, 1840)

According to WENZ (1938) *Valvata* and relation have usually a small to very small thin shell that is lowly trochispiral to plane in shape with open umbilicus with few rounded whorls that may be smooth or bear spiral lines or more rarely spiral ribs. The aperture is round and thin and closed by a multi-spiral round operculum with central nucleus. According to RIEDEL (1993) and BANDEL & RIEDEL (1994) the protoconch consists of a planispiral whorl with characteristic ornament of spiral ribs and crossing collabral lines. The characteristic genus is *Valvata*.

The Valvatoidea of the fresh water developed alongside the Planorbidae, which may have a quite similar shell. Their history also ranges back in time for about 150 million years into the Late Jurassic (WENZ & ZILCH, 1960; BANDEL & RIEDEL, 1994). The protoconch distinguishes them quite well from other small species with planispiral shell (BANDEL, 1991; RIEDEL, 1993; HADZISCE et al., 1976). Even though Planorbidae are also members of the subclass Heterostropha (= Heterobranchia) among the Gastropoda, they belong to a different branch. The Basommatophora appear to have evolved from the Allogastropoda latest at Triassic time (BANDEL, 1996). During the Jurassic both groups, Valvatoidea and Planorboidea (Basommatophora), become distinct from each other and well recognizable.

RIEDEL (1993) documented that the protoconch as found in Valvata and Planorbis/Gyraulus has similar spiral ornament, but differs in detail. Both are distinguished by ornament of fine spiral lines which have growth increments crossing (compare figs. 47-48 with figs. 183-184). This pattern differs from that of other fresh water gastropods with similar shell and similar shape of the protoconch. During formation of the first shell the embryo of Valvatidae differs strongly from that of the Planorbidae. Planorbis, like the Basommatophora in general, has the shell secreting mantle tissue concentrated in a groove (shell gland) until the embryo has absorbed the yolk of the egg capsule. Only afterwards the tissue of the mantle is evaginated (everted from pit-like shape) to cover the visceral mass. During this process the embryonic shell is secreted rapidly (BANDEL, 1982, and here references). The embryo of Valvata, in contrast, has no shell gland that grows in a groove (invaginated) but the mantle tissue remains on the surface of the visceral mass and begins to cover it during growth. Here shell formation occurs prior or during the process of yolk uptake by the embryo. The earliest shell thus formed differs in its composition and shape from the shell secreted by detached mantle tissue. It begins to be calcified very early and the mantle edge holds to the shell on its outside while the margin of it is free (RIEDEL, 1993: figs. 1-3). This change is reflected in the embryonic shell of Valvata. The primary shell is seen as cap-like initial and wrinkled shell portion succeeded by ornamented shell with growth increments (figs. 47, 48). Only the secondary shell produced when shell and mantle have separated from each other has the spiral ornament.

Genus Valvata MÜLLER, 1774

WENZ (1938, fig. 1320) based the genus on the lowly trochispiral *Valvata cristata* MÜLLER, 1774 with smooth rounded whorls from Middle Europe. According to GRAHAM (1988) the genotype is *Nerita piscinalis* MÜLLER, 1774, a species with higher shell.

The Valvata species living in Europe differ in shell shape, with the planispiral Valvata cristata about 3 mm in size, with Valvata naticina MENKE, 1845 that has a low shell and rounded whorls, Valvata piscinalis with the shell about as wide as high (up to 5 mm) but of quite variable shape, Valvata pulchella STUDER, 1820, also quite variable regarding shell shape and less tightly coiled as V. naticina and up to 4 mm in size. Shell shape regarding size and more or less trochispiral coiling within each species is rather variable and all European species have rounded whorls. The common Valvata tricarinata from the United States, in contrast, has three spiral keels. It

resembles fossil species from the Paratethys such as Valvata kamirensis and Valvata heidemariae described below.

Valvata cristata MÜLLER, 1774 (Pl. 4/40–46)

The shell has a maximum diameter of about 3 mm. All three whorls coil in one plane with the apical side of the shell flattened to weakly concave and the base with wide umbilicus. Whorls meet only at their periphery and the aperture is circular (GLÖER & MEIER-BROOK, 1998). The protoconch has a slight twist to sinistral coiling and consists of about one whorl with 0.3 mm in diameter (figs. 41–42, 46). Its ornament consists of fine spiral lines and its end is usually documented by a stronger appearance of growth lines. Species that are like *Valvata cristata* may be recognized as far back as the Miocene of the Paratethys Basin. From the living individual is can be observed that the eggs are contained in vase shaped capsules. Juveniles hatch after about one month of development.

The embryonic shell of *V. cristata* resembles that of *Valvata piscinalis* (FALNIOWSKI 1990: fig. 95–96, 99), but ornament differs in details and also from that of *V. pulchella*.

V. pulchella has a maximum diameter of about 5 mm and is maximally 3 mm high (GLÖER & MEIER-BROOK, 1998). The shell consists of up to 4 whorls which are well rounded and have a low trochospiral shape. The first whorls are planer in coiling than the body whorl. Member of this species from Poland have a protoconch very similar to that of *Valvata piscinalis* in shape but not in details of the ornament (FALNIOWSKI, 1990: figs. 90–94, 100–101).

Valvata piscinalis (MÜLLER, 1774) (Pl. 4/47–49)

V. piscinalis is a common European species with its shell about as high as wide, with rounded whorls and dull apex (CLELAND, 1954; GRAHAM, 1988: fig. 53). Its juvenile shell is quite flatly coiled so that is resembles the shell of *Valvata pulchella* at that stage of growth (GLÖER & MEIER-BROOK, 1998). Maximum diameter may vary as well as the maximal shell height. Ornament consists of lines of growth and the final whorl may become relatively narrow. The umbilicus is narrow, but whorls are rounded and do not overlap much onto each other. The eggs are laid in spherical capsules measuring 1–2 mm across. Each capsule contains several greenish eggs which develop for two to four weeks until crawling juveniles hatch (FRETTER & GRAHAM, 1962; GRAHAM, 1988). The protoconch consists of 1.5 whorls and is ornamented by spiral lines with curving grooves with bridges at growth increments (FALNIOWSKI, 1990: figs. 85–89, 98). Shells of freshly hatched juveniles from North Germany presented in figs. 47–48 have the primary initial shell cap well distinguished from the ornamented and growth increment bearing secondary embryonic shell.

A very similar species of *Valvata piscinalis* also lived in the lakes on Rhodes and Kos during the Late Miocene and Pliocene disguised under the name *Valvata skhiadica* BUKOWSKI, 1895. This *V. skhiadica* was also called *Valvata monachorum* BUKOWSKI, 1895 and *Valvata aberrans* BUKOWSKI, 1895 (WILLMANN, 1981: fig. 22). Own observations on individuals from the Istrios Formation in Rhodes also show a resemblance to the living *Valvata pulchella*. The shell is solid, up to 2.8 mm high and 3.8 mm wide. The first whorls are almost planispiral, later whorls rounded with inclined base. The umbilicus is open and spiral lines surround it, while the shell is otherwise smooth. JEKELIUS (1932: pl. 5, figs. 16–27) and WENZ (1942) determined *Valvata piscinalis* also from Dacian and Levantinian deposits of Rumania with the shell as variable in shape as was noted for living individuals. This is evidence for very little change in the species regarding shell shape at least for the last 3 to 4 million years.

Valvata hellenica TOURNOUER, 1877 (Pl. 4/49–51)

The shell has low trochispiral shape, with variable shell height. *V. hellenica* from the Pliocene Salakos Formation of Rhodes has the ornament of its embryonic whorl very close to that of a modern *Valvata*. According to WILLMANN (1981: pl. 3, figs. 8–17) it also occurs in the Kritika Formation in Kos and Rhodes with synonyms *Valvata kupensis* Neumayr, 1880, and *Valvata agaea* Neumayr, 1880. The fossil *Valvata gregaria* BUKOWSKI, 1895 from the Istrios Formation in Rhodes is lowly coiled with first whorls planispiral and later whorls lowly trochispiral, close to the living *Valvata cristata*.

Valvata saulcyi BOURGUIGNAT, 1853 (Pl. 5/52–54)

Valvata saulcyi BOURGUIGNAT, 1853 has a trochiform shell that consists of three whorls with a little more than 2 mm in diameter. SCHÜTT (1988: pl. 3, fig. 26) described a variety with upstanding embryonic shell portion from the Pliocene of the Orontes valley as *Valvata saulcyi pliocaenica*. The modern *Valvata saulcyi* lives in springs in Jordan. According to HOROWITZ (1979) the species lived in subrecent Lake Hula (to the north of Lake Tiberias) and the ancient lakes of the Ubeidiya and Erk el Ahmar Formations. SCHÜTT (1983) suggested that this species represents the replacement to *Valvata piscinalis* in the area of Syria and south of it. TCHERNOV (1975: pl. 1, fig. 4) suggested that *V. saulcyi* represents the only species that lived throughout the Neogene and Pleistocene of the Levant and it had been determined as *Valvata cristata* by BLANCKENHORN (1897). The species is encountered in the deposits of the late Pliocene lake of the Al Qarn Formation in the northern Jordan Valley of Jordan (BANDEL & SHINAQ, 2003) (figs. 52–53).

Valvata naticina MENKE, 1845 (Pl. 5/55–56)

The shell has maximum diameter of about 5.5 mm and is 4.5 mm high (GLÖER & MEIER-BROOK, 1998). *N. naticina* from the river Oder the shell consists of 3.5 whorls, is almost globular and rather solid with narrow umbilicus. The aperture is almost round and closed by an operculum with of 3.5 whorls (own observations). It was also collected from Lacul Razim in eastern Rumania, a lagoon near the delta of the Danube into the Black Sea. Here the protoconch is large and ornamented by spiral lines with rows of pit between them as documented by FALNIOWSKI (1990: figs. 97, 102–103).

In Lake Ochrid *Valvata hirsutecostata* and *Valvata rhabdodonta* are interpreted to represent a closely related endemic pair of species (RADOMAN, 1973). The subgenus *Valvata (Liratina)* LINDHOLM, 1906 has the type *Valvata baicalensis* GERSTFELDT living in Lake Baikal. The shell is lowly conical in shape, almost flat with spiral ribs and keels. It is a member of a group of species endemic to Lake Baikal. Here the embryonic whorl is larger due to a more yolk-rich embryonic development in the cold water of that lake.

Among the species that have been described as *Valvata* from the late Miocene and the Pliocene, *Valvata wenzi* PAPP, 1953 according to PAPP (1953: pl. 4, figs. 4–5) is represented by an endemic species from Eichkogel of the Pontian of the Vienna Basin (STOJASPAL, 1989). *Valvata cobalcescui* BRUSINA, 1885 according to WENZ (1942: pl. 10, figs. 120–121) from the Levantin of Romania consists of 3.5 whorls and is rounded with simple, oblique aperture. Its protoconch is unknown and its place in the genus *Valvata* as well. It is very similar in shape to *Valvata crusitensis* FONTANNES, 1886 that occurs in the Levantin of Rumania (WENZ, 1942: pl. 10, figs. 122–126) but has a smaller inclination of the aperture (PANA & ANDREESCU, 1981: pl. 67, figs. 12–19). Here also the protoconch needs to be known to be able to decide whether these species represent valvatids or belong to the Caenogastropoda.

Valvata soceni JEKELIUS, 1944 has a 1.2 mm wide and high shell that consist of the protoconch and three round whorls (JEKELIUS, 1944: pl. 43, figs. 11–13). HARZHAUSER et al. (2002) found this species also in the Vienna Basin (St. Margarethen), stating that the protoconch is smooth and of rounded shape. It resembles *Valvata obusaeformis* LÖRENTHEY, 1902 but is smaller. It is of similar size but with higher shell as *Valvata minima* FUCHS, 1877, *Valvata banatica* (BRUSINA, 1902) and *Valvata kupensis* FUCHS, 1870 (FUCHS, 1870b: pl. 22, figs. 23–25). *Valvata minima* FUCHS, 1877 is a Sarmatian species from Soceni with its shell with three whorls and only 1.2 mm in diameter and 1 mm in height (JEKELIUS, 1944: pl. 7, fig. 10). The whorls are round and smooth, the umbilicus deep. The species has its origin in Greece (FUCHS, 1877). *Valvata minima* FUCHS, 1877 lived in Lake Pannon during the time of *Congeria ungulacaprae* (Pontian) (KORPAS-HODI, 1983).

Valvata gradata FUCHS, 1870 from the Pannonian of the Vienna Basin has the protoconch with almost two smooth whorls, while the teleoconch is ornamented by 3–6 spiral ribs (JEKELIUS; 1944: pl. 43, figs. 14–20; HARZHAUSER & KOWALKE, 2002). *Valvata pseudoadeorbis* SINZOV, 1880 from the Sarmatian of St. Margarethen closely resembles *Valvata simplex, Valvata minima*, and *Valvata moesiensis* (JEKELIUS, 1944: pl. 7). The species from St. Margarethen is *Valvata* with characteristic protoconch (HARZHAUSER & KOWALKE, 2002: pl. 9, figs. 6, 7, 12). The shell consists of up to 3 whorls measures 1 mm in width and is less high. The aperture is round, the umbilicus wide and ornament is only of growth lines. They distinguish *Valvata sarmatica sulekiana* BRUSINA, 1874 according to WENZ (1942: pl. 11, figs. 136–138) from the Dacian and Levantin of Romania has the shell consisting of 3.5 whorls and is rounded low with shallow sutures, resembles *Valvata adeorboides* FUCHS, 1870 from the Pontian.

Valvata heidemariae WILLMANN, 1981 (Pl. 5/60–63)

The planispiral shell measures about 2.2 mm with 3.2 whorls. A keel lies on the edge of the apical side and another one around the wide umbilicus on the basal side. The last part of the fully grown shell deviates a little from planispiral coiling towards the base. The protoconch is planispiral and about 0.4 mm in diameter with the characteristic ornament of fine spiral ribs.

<u>Remarks</u>: A valvatid with angular teleoconch quite similar to that of *Valvata heidemariae* from the Pliocene lake deposits of Kos (Vokasia Formation) is found in the Pontian sediments of Varpalota in Hungary. The species was described by WILLMANN (1981: fig. 56) and it is very similar to the specimen from Varpalota near Lake Balaton. Apparently the species lived from the Hungarian plane to the southeastern margin of the Paratethys in Kos.

Valvata kamirensis WILLMANN, 1981 (= ? Valvata eugeniae NEUMAYR, 1875) (Pl. 6/64–68)

The 2.6 mm wide shell is about as high and lived in the Pliocene lake that existed in Rhodos during the deposition of Salakos Formation. WILLMANN (1981: figs. 42–43) found this species to be quite variable in shape and with smooth embryonic shell. Actually the protoconch has a fine dense spiral ornament, not quite characteristic of *Valvata*, but still close to it. It is similar to the ornament found in *Valvata heidemariae* but still finer. In difference to *Valvata heidemariae* the shell is larger and higher and there are three spiral keels on it. But WILLMANN (1981) noted that individuals from the Salakos Formation in Rhodes are quite variable in shape and also ornament of the shell. The more or less planispiral shell has three spiral keels is up to 2.6 mm wide with 2.75 whorls. PAPP (1953, 1955) noted this species from the Pliocene lake deposits of Rhodes as well.

A similar species from NW Anatolia was described as *Valvata kavusani* SCHÜTT, 1984 with ornament of one to three spiral lines. SCHÜTT suggested that it differs from the species of Rhodes, without indicating which character actually differs from *Valvata kamirensis* (SCHÜTT & KAVUSAN, 1984: fig. 2).

Valvata kamirensis WILLMANN, 1981 also resembles *Valvata eugeniae* NEUMAYR, 1875 in shape, variability and size. *Valvata eugeniae* lived at about at the same time in the vicinity of the Carpathian arch (compare JEKELIUS, 1932: pl. 6, figs. 1–41) when *Valvata kamirensis* lived in the lake that occupied the southern margin of the Paratethys Basin which has since become the Island of Rhodes (WILLMANN, 1981: figs. 42–43). In case the protoconch of *V. eugeniae* becomes known and has spiral ornament, this species name would have priority over *V. kamirensis*.

Among the living species of *Valvata* the common species of the area around the Great Lakes in North America represented by *Valvata tricarinata* SAY, 1817 (figs. 57–59) has keels, even more strongly developed than in *V. kamirensis*, and one more than in *Valvata heidemariae*. Its protoconch has the characteristic shape and ornament of *Valvata* (fig. 59). *Valvata eugeniae* from the Pliocene Lake Brasov is quite variable in shape and JEKELIUS (1932: pl. 6, figs. 1–41) differentiated several subgenera. This variability is reflected by quite a range of morphologies noted in *Valvata tricarinata* from the USA (BAKER, 1928).

5 Valvatiform Hydrobioidea (Pl. 6/69–81)

Several species living in freshwater or slightly brackish environment have convergent shell shape with *Valvata* but belong to a quite different group of gastropods. BODON et al. (2001) documented convincingly that low valvatiform Hydrobioidea with small shell that have a flat or low spire and rounded whorls, more or less wide umbilicus, and less than 4 whorls. They may belong to a number of anatomically quite distinct genera but have convergent shell shape. A number of species of that type live around the Mediterranean Sea with distinct and sometimes geographically relatively limited areas of occurrence.

Fossil species resembling these small valvatiform modern species are difficult to be determined and connected to modern species with similar shell shape. It will not even be safe to include the fossil species in any of the recognized genera. Migrations can have occurred at about Messinian time about 5 ma ago. During that period the Mediterranean Sea had lost most of its water and dried up to a large extent. Fresh water lakes and rivers in the Mediterranean Basin offered quite different migration paths than those as found today. Connections across this basin were possible. A migration path for small invertebrates of the fresh water for example coming from the river Nile to ponds, lakes and rivers in the Paratethys Basin can be reconstructed. Within the Paratethys Basin changes of distribution of living environments for aquatic animals continued after the Mediterranean Basin

became flooded again by water from the Atlantic. It is, therefore, difficult, if not impossible to trace migration paths that have opened and closed here since Messinian time.

Hauffenia POLLONERA, 1898 is restricted to the area of Slovenia and near it, and the quite similar *Islamia* RADOMAN, 1973 distributed from the Iberian Peninsula around the Mediterranean to Jordan, with somewhat spotty distribution (BODON et al., 2001). Among living species the anatomy is the most important characters besides the shape of the shell. The mode of development of *Horatia* BOURGUIGNAT, 1887, *Islamia*, and *Hauffenia* is from yolk-rich eggs. Young snails hatch crawling with a shell of about 1.5 whorls, trochispiral coiling mode and ornament by small pits and ridges in irregular orientation or arranged to form spiral ribs (BINDER, 1967). In case of such spiral ornament convergence is not only among the species of hydrobiid relation but approaches shapes as found among Valvatidae. The latter usually have an ornament of the embryonic shell consisting of spiral ridges, but in contrast to the Hydrobioidea have planispiral whorls of the protoconch.

The small species from the Pontian of Kötese at the shore of Lake Balaton belongs to the Hydrobioidea and is characterized by the beaten ornament of its embryonic shell (figs. 69–70). When compared with living species it could be determined as a species of *Heraultia* BODON, MANGANELLI & GUISTI, 2001 as described by BODON et al. (2001). A very similar shell from the Pannonian deposits of Soceni has a similar, but not the same shape and ornament (figs. 71–72). It cannot be decided whether it represents the same or another species than that from Pontian of Kötese. The similar individuals from Tihany at Lake Balaton (figs. 73–74) has the same type of protoconch with pit and ridge ornament as found among the modern species but also as found in those species here described under *Muellerpalia* with usually spirally ornamented teleoconch. These species could be fitted into the description of *Islamia* as in BODON et al. (2001) when a little less planispiral and it would also have the ornament of hammered surface of the protoconch (fine groove and ridge pattern).

From the Pliocene of the Jordan Valley (fig. 77) a cf. *Horatia* has the same shape as that of the Pannonian of Lake Balaton region. Especially a species from the Pontian of the eastern margin of Lake Balaton is quite the same as that having lived in the Al Qarn Lake in the Jordan Valley, by all features of the shell. Characteristic is also the detachment of the body whorl. This is seen in specimen of the sand pit near Papkesi close to the eastern end of Lake Balaton (figs. 77–81).

Genus Muellerpalia n. gen.

<u>Diagnosis</u>: The small shell (about 1.2 mm in diameter) is flat planispiral and composed of four whorls with slow and regular increase in diameter. The apical shell surface is plane. Ornament may consist of a median apical keel and spiral ribs, but whorls may also be smooth. Whorls are round and separated by deep sutures. Growth increments may be strong. They reflect a simple almost vertical aperture. The base is concave with the umbilicus surrounded by a sharp keel. The aperture is round with continuous margin. The protoconch is raised above surface and consists of one whorl with rounded diameter and about 0.2 mm in diameter. Its ornament consists of a more or less well developed groove and ridge pattern. The genus is based on *Planorbis bicinata* FUCHS, 1870 described from Tihany by FUCHS (1870b: pl. 21, figs. 7–9).

<u>Differences</u>: When fully grown *Muellerpalia* has about half the size of *Graecamnicola* but resembles it in shape and ornament. From *Islamia* as in BODON et al. (2001) the species of *Muellerpalia* differ by having more planispiral shape and often the spiral ornament is distinct while the fine groove and ridge pattern of the protoconch is similar.

<u>Derivatio nominis</u>: The genus is called in honor of Dr. Müller-Pal who introduced me to the Pontian deposits and its fossil-rich localities around the Lake Balaton and who has worked with the fossils and stratigraphy of these strata.

Muellerpalia bicinata (FUCHS, 1870) (Pl. 7/82–85)

The small shell (about 1.2 mm in diameter) has a flat planispiral apical side, rounded margin and a deeply concave base. It is composed of up to 3.5 whorls with slow and regular increase in diameter. The protoconch consists of 1.5 rounded whorls which are raised somewhat above surface. It measures about 0.22 mm in diameter and is ornamented by a coarse net pattern of ridges and grooves which disappears on the last part of the embryonic shell. Here growth lines are fine and regular. The teleoconch is clearly marked by strong growth lines at its initial part. They continue in a regular pattern up to the margin of the fully grown shell. On the second half of the first whorl a spiral keel begins. Another one is present on the base of the side forming a corner. The wide umbilicus that exposes all whorls of the shell is surrounded by a corner that forms a keel. Ornament is variable

among individuals and keels may be developed more or less. Whorls are rounded, even so in the basal corner, and are separated by distinct sutures. The rounded aperture bears a continuous margin and has almost vertical, slightly inclined orientation (FUCHS, 1870b). Strong growth increments and deviation from planispiral coiling marks the fully grown shell.

<u>Differences</u>: The embryonic whorl has strong growth lines it its early portion, which become more irregular near the aperture of the fully grown shell, as is also the case in *Muellerpalia carinata*. In contrast to *Muellerpalia bicincta* with one keel on the upper side of the shell of *Muellerpalia varians* has here two keels. The margin the shell of *Muellerpalia bicincta* has a rounded lower keel and is widest near the corner to the base, while the corner to the base of the other species is evenly rounded. *Muellerpalia simplex* has no spiral ornament.

FUCHS (1870b: pl. 21, figs. 7–9) described *M. bicinata* as member of *Valvata* from the Pontian of Tihany at the Balaton Lake in Hungary. Individuals from this locality were used here as well to describe this species in more detail to distinguish it from the other rather similar species of *Muellerpalia* from other localities nearby but different stratigraphical levels in the Pontian deposits.

Muellerpalia carinata (FUCHS, 1870) (Pl. 7/86–89)

The shell has a flattened apical side and a concave basal side and a rounded margin. A median keel on the upper side and another one in the middle of the basal side are present. The teleoconch consists of about three whorls. The embryonic shell consists of about 1.5 whorls with diameter of about 0.27 mm, is rather flat and rounded with distinct dextral coiling mode. The first whorl of the protoconch is ornamented by a groove and ridge pattern which does not continue onto its last half whorl that is smooth. Begin of the teleoconch is indicated by the appearance of strong growth lines which cover the shell to the aperture. Final growth lines in fully grown shells are a little stronger and of more irregular size. The median keel initiates within the first whorl of the teleoconch and continues to the outer lip. The aperture is as wide as high and of almost round shape with the keels forming weak irregularities. Shell size is about 1.2 mm in diameter and 0.25 mm in shell height. The base is concave and displays all whorls with succeeding whorls just covering the basal keel behind their suture.

<u>Remarks</u>: FUCHS (1870b: pl. 21, figs. 10–12) described this flatly coiled species from Tihany as *Valvata carinata*. Accordingly it consists of few whorls, measures 1.2 mm in diameter and has sides with a corner. Otherwise shape is rounded except for one keel on the apical side. A wide umbilicus and round aperture are present. Transition exists, apparently, from the smooth *Valvata debilis* FUCHS, 1870 to *Valvata simplex* FUCHS, 1870 which may or may not have a keel around the umbilicus, to *Valvata bicinata* FUCHS, 1870 with keel around the umbilicus as well as one keel on the apical side, which may disappear in older shell portions, and to *Valvata carinata* with acute sides.

From Radmanesti GILLET & MARINESCU (1971: pl. 19, figs. 24, 25) noted this species to be rare. They called it *Valvata* (*Valvata*) *carinata* with a keel on the top and one surrounding the umbilicus.

Muellerpalia varians (FUCHS, 1870) (Pl. 8/90–94)

Diagnostic characters: The shell has a flat apical side, a concave basal side and a rounded margin. Two spiral keels feature the apical shell side, one in the middle and one near the shoulder. The base also carries a keel. The teleoconch consists of almost 3.5 whorls and the protoconch has 1.5 whorls with 0.25 mm in diameter. The first whorl is ornamented by a groove and ridge pattern which does not continue onto the last half whorl of the embryonic shell which is smooth. Begin of the teleoconch is evident by the appearance of strong growth lines. Such lines are present on the whole shell and are stronger and more irregular in size in the last whorl of the shell. The median keel initiates within the first whorl of the teleoconch and continues to the outer lip. The aperture is as wide as high and of almost round shape with the keels forming weak irregularities. Shell measures about 1.2 mm in diameter and 0.25 mm in height. The base is concave and displays all whorls with succeeding whorls just hiding the basal keel behind their suture.

Muellerpalia varians was collected by MÜLLER-PAL from the Pontian of the shore of Lake Balaton at the railroad station of Kötese documents that *Planorbis* was not the right choice, but also not *Valvata* as had been

suggested later on. The protoconch has the ridge and groove pattern as is characteristic for hydrobioid species. The species also found in Tihany and Köbanya.

The umbilicus is open and surrounded by a keel in *Valvata sibinensis* NEUMAYR, 1875. According to WENZ (1942: pl. 11, figs. 132–135) it is from the Levantin of Romania. Its shell is low trochiform and consists of 3.5 whorls which have a median keel. Since the protoconch is unknown its exact relation cannot be decided.

Muellerpalia simplex (FUCHS, 1870) (Pl. 8/95–98)

The shell in size and general shape resembles that of *Muellerpalia varians* or *Muellerpalia carinata*, but has no ornament of keels.

M. simplex from Tihany was described as belonging to *Valvata* by FUCHS (1870b: pl. 21, figs. 4–6) with simple flattened shell with no keels. In size and shape it is like *Muellerpalia bicinata* and it has the rounded sides as *Muellerpalia carinata* which differ by having an acute side in the first case and by ornament in the second case. According to FUCHS (1870b) the shell consists of four whorls and is 1.5 mm in diameter with rounded shape of its whorls, wide umbilicus and round aperture. Individuals of this species are from the locality at Tihany with transitional specimens to *M. bicinata*. It is also present in the fauna from Köbanya and Tab.

The species described as *Valvata simplex* by JEKELIUS (1944: pl. 7, figs. 6–9) from Soceni also belongs here. The almost planispiral shell also measures 1.5 mm in diameter, is low with whorls having rounded diameter and smooth, wide umbilicus. *Valvata simplex* has also been recognized by BRUSINA (1902) from Slavonia.

Valvata debilis as described species by FUCHS (1870b: pl. 21, figs. 1–3) together with the three similar species of *Muellerpalia* has a more rapid increase in shell diameter. It probably represents a small species of the Planorbidae. *Valvata (Valvata) oecsensis* SOOS, 1934 as illustrated by SCHLICKUM (1978) from the Pontian of Öcs was also described by BARTHA (1959: pl. 4, figs. 7–9) as *Valvata simplex oecsensis*. It has a flat shell with median apical keel. The protoconch is unknown and thus relation to *Muellerpalia* in doubt.

Muellerpalia tabensis n. sp. (Pl. 8/101; Pl. 9/102–103)

<u>Diagnostic characters</u>: The small shell (about 1 mm in diameter) has a flat planispiral apical side with only the protoconch forming a rounded median elevation. The base is deeply concave with two spiral keels. A third spiral keel forms the corner on the apical side. The shell has three whorls with slow and regular increase in diameter. The protoconch consists of 1.5 rounded whorls with 0.3 mm in diameter and ornament of strong net-like pattern of ridges and grooves on the first whorl. The teleoconch closely resembles that of *Muellerpalia carinata*.

<u>Holotype and origin of the name</u>: The specimen in fig. 102 represents the holotype from the locality at Tab, as described by STRAUSZ (1942). The name is chosen accordingly. The holotype is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4705.

<u>Differences</u>: *Muellerpalia tabensis* resembles the other species of this genus in shape, size and protoconch, but has the apical spiral keel near the margin and two spiral keels around the umbilicus. Characteristic individuals have a flat apical side on the whorls of the teleoconch.

<u>Remarks</u>: The periostracal layer of *Muellerpalia tabensis* has a pattern of fine crystals as found in "frost flowers" of ice on glass. As similar character is also present on varieties of *Muellerpalia simplex* into which *M. tabensis* grades in shell shape. Such "frost flower-like" crystallites are known otherwise from the calcitic thin outer layer of Neritimorpha (BANDEL, 2007) as present in species of *Nertina* or *Theodoxus*. This pattern indicates that the outermost layer of the otherwise aragonitic shell in *Muellerpalia* contained some calcite that grew as thin sheet into the periostracal layer during mineralization of the shell.

Muellerpalia striata n. sp. (Pl. 9/104–107)

<u>Diagnostic characters</u>: The small about 1.2 mm wide shell has a flat planispiral apical side, rounded margin, and a deeply concave base. It is composed of up to 3.5 whorls with slow and regular increase in diameter. Only the whorls of the protoconch are rounded. Those of the teleoconch are flattened on the apical side and next to the wide umbilicus. Ornament consists of seven spiral keels, the apical one lies near the corner to the side, five keels

are on the side of which the basal one forms the corner to the base, and one keel surrounds the umbilicus. Growth lines are regular and form a pattern of elongate rectangles with the spiral ribs. The aperture is round with the spiral ribs not seen on its inner side. Its orientation is slightly inclined to the axis of coiling.

<u>Holotype, origin of the name and stratigraphical position</u>: The individual of fig. 104 is the holotype, and the name is due to the spirally ribbed ornament (*striata*). The type locality is Balatonkenese Csittenyhegy at the Lake Balaton, Hungary. The stratigraphical position lies in Pontian deposits of Lake Pannon. The holotype is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4706.

<u>Description</u>: The shell with 3.3 whorls is about 1.5 mm is diameter (width) and 0.4 mm high with angular shape of the whorls. The margin of the aperture is almost detached from the whorls and coiling mode is dextral with flat apical side and wide and concave basal side.

<u>Difference</u>: *Muellerpalia striata* has the relatively flattest shell of the species of *Muellerpalia* described here. It was found only at Balatonkenese Csittenyhegy and appear to have no transitional species to the others.

Genus *Graecamnicola* WILLMANN, 1981 (Pl. 9/108–110; Pl. 11/130–134)

The shell of the type to the genus is flatly coiled and consists of 3.5 whorls about 3 mm in diameter and 1.3 mm in height. The umbilicus is wide and the apical face plane. Ornament consists of spiral keels crossed by collabral growth increments. The aperture is a weakly oblique.

The genus is based on a species with planispiral shell with two keels *Graecamnicola euomphalus* (FUCHS, 1877) by WILLMANN (1981: fig. 71). Due to the small sized protoconch WILLMANN (1981) renamed *Valvata euomphalus* into *Graecamnicola*. It differs from *Valvata* by having a trochispiral und smooth protoconch and is therefore interpreted to represents a member of the Hydrobiidae of the Caenogastropoda. Willmann interpreted this species to be closely related to the more conical *Valvata graeca* FUCHS, 1877, and placed the later also into his genus *Graecamnicola*.

Individuals with about the same characters of their shell as those from Salakos Formation of Rhodes are also found in the Pontian deposits of Köbanya Ujhegy near the Balaton Lake, as is documented in figs. 108–110 from Köbanya and figs. 130–134 from Salakos Formation of Rhodes. The smooth protoconch of the specimen from the Pliocene of Rhodes measures about 0.5 mm in diameter and is a little larger than that of the Balaton region, where it measures about 0.4 mm. Also shell size of the fully grown individuals differs by about one third, with 2 mm in the Pannonian Lake and 3 mm in the lake on Rhodes.

Genus Jekeliella n. gen.

<u>Diagnosis</u>: The shell is trochiform and about as high as wide, rarely a little higher than wide. Ornament consists of spiral ribs and keels. The protoconch consists of one rounded whorls in dextral coiling mode that is ornamented by a groove and ridge pattern or is smooth. The type species is *Valvata balatonica* ROLLE, 1861 from the Pontian of Tihany at Lake Balaton as described by FUCHS (1870b).

<u>Derivatio nominis</u>: The genus is called in honor of Erich Jekelius who described many gastropods from the Romanian region of the Paratethys in a very detailed way.

Jekeliella balatonica (ROLLE, 1861) (Pl. 9/111–114)

The shell is about as wide as high (2 mm) and has pointed conical shape. About six whorls compose the shell with rounded whorls and deep sutures. The first whorl is smooth, the second has growth increments and later ones are ornamented with 4–5 sharp spiral ribs. The base has spiral lines and the umbilicus is narrow. The aperture is round (FUCHS, 1870b). The protoconch is typical of that found among fresh water Hydrobiidae with the first whorl smooth or granular ornament with about 0.3 mm in width representing the whorl produced by the developing embryo before detachment of the mantle from the shell. About another halve whorl with growth lines is added before the young hatches from its egg case. The specimens are from the locality Varpalota near Lake Balaton, and here from Pontian strata.

<u>Remarks</u>: Specimen which are a little higher than wide could be determined as *Pseudamnicola margaritata* as described by JEKELIUS (1932) from Lake Brasov, Romania. MÜLLER (1989) recognized that *Valvata balatonica* may not represent a member of the genus *Valvata*. This suspicion was confirmed when the protoconch of material, that was partly collected by him, partly collected by us when he guided us, was studied. The protoconch is dextrally coiled and thus differs from that of *Valvata*, but it has a shape as is found among Hydrobiidae. *Valvata balatonica* ROLLE, 1861 resembles *Valvata gradata* FUCHS, 1870, and *Valvata tenuistriata* FUCHS, 1870 in shape and the character of the protoconch. *Pseudamnicola bithynoides* JEKELIUS, 1932 resembles the species illustrated by MÜLLER (1989: pl. 6, fig. 9) as "*Valvata*" balatonica from Tihany.

Jekeliella gradata (FUCHS, 1870) (Pl. 10/115–119)

The shell of about 2 mm in width is lowly conical in shape consisting of about 4.5 whorls. It varies in height. Early whorls of the teleoconch are stair-like, while the last whorl is more rounded. The shoulder is flattened and sides are rounded. The umbilicus is conical and deep and may vary in width among individuals. The aperture has a slightly oblique plane, round shape and continuous margin (FUCHS, 1870b). First whorl of the protoconch is well rounded with dextral-coil and ornament of pustules. It measures about 0.3 mm across. On the final portion of the embryonic shell growth line pattern predominates. When about 1.5 whorls are present initiation of the ornament consisting of spiral ribs documents the beginning of the teleoconch. Spiral ribs near the shoulder are strongest, 9 to 10 weaker spiral ribs are on the side and one lies on the shoulder.

JEKELIUS (1944) described a species with very similar shell from Soceni as *Valvata* (*Cincinna*) gradata (FUCHS, 1870). It had originally been described as *Valvata* by FUCHS (1870b) from Tihany and Kup (Hungary) and was accepted as such by BRUSINA (1902) and WENZ (1928). Individuals with 3–6 spiral ribs were noted by JEKELIUS (1944: pl. 43, figs. 14–17). They have flattened shoulder than a more rounded variety that was called *Valvata* gradata globulosa (JEKELIUS 1944: pl. 43, figs. 18–20). Jekelius noted the similarity and transitions between both forms. Strangely he did not compare these with species determined by him (JEKELIUS, 1932) as *Valvata* and *Pseudamnicola* from the Lake Brasov, even though they are similar in ornament and size as well as in their variability of shell shape and ornament.

Valvata (Cincinna) obtusaeformis LÖRENTHEY, 1911 was recorded by STOJASPAL (1989: pl. 1, fig. 3) as simple rounded species, also illustrated by PAPP (1953: pl. 3, figs. 20–22) and PAPP (1985: pl. 3, fig. 20) from the Pontian of the Vienna Basin. The similar *Valvata (Cincinna) subgradata* LÖRENTHEY, 1902 was recorded by STOJASPAL (1989), also illustrated by PAPP (1953: pl. 5, fig. 1) from the Pontian of the Vienna Basin.

Jekeliella tenuistriata (FUCHS, 1870) (Pl. 10/120–125)

The shell is up to 4 mm high and a little less wide with globular shape and about 4.5 rounded whorls. While the first whorls are smooth later ones have a spiral keel at the corner to the shoulder, show strong collabral increments of growth and very delicate spiral striation. The last whorl increases relatively in height and has no spiral keel and well rounded sides. The aperture is round and the umbilicus narrow. The protoconch is rounded and consists of almost 1.5 whorls with about 0.2 to 0.3 mm in diameter. The first whorl has a hammered pattern of shallow grooves surrounded by fine ridges. The last part of the embryonic shell has only growth lines, which increase in density when the teleoconch begins. The spiral keel on the corner inserts in the second part of the first whorl of the teleoconch. The second whorl of the teleoconch has a flattened shoulder, while the body whorl of the shell is evenly rounded and without shoulder. Shell growth, thus, is allometric. First teleoconch whorl is rounded, second and part of third whorl is shouldered and the body whorl is rounded again with rounded base. End of shell growth is indicated by a thickened margin of the aperture and by dense growth lines.

MÜLLER (1989: pl. 7, fig. 3) characterized *Valvata tenuistriata* FUCHS, 1870 as having rounded whorls with deep sutures and a shell that is about as high as wide with ornament of many fine spiral ribs. FUCHS (1870b: pl. 21, figs. 19–20) described this species from Tihany. Very similar is *Valvata variabilis* FUCHS as described by GILLET & MARINESCU (1971: pl. 18, figs. 25–31, pl. 19, figs. 1–7) but its shell is smooth. *Valvata adeorboides* FUCHS, 1870 according to MÜLLER (1989, pl. 7, figs 4–5) has indistinct sutures and tight coiling in a low shell. FUCHS (1870a: pl. 14, figs. 5–7) described this species from Radmanesti in western Romania as 3 mm in diameter and 2 mm in height consisting of four whorls. The whorls are rounded, smooth and the umbilicus in narrow. The round aperture is inclined.

Also *Valvata semigradata* PAVLOVIC, 1928 according to PAVLOVIC (1928: pl. 14, figs. 23–25) is similar but its protoconch is unknown. PAVLOVIC (1928) also noted two species with higher shell shape from the Pontian near Beograd in Serbia, as were noted by JEKELIUS (1932) from Lake Brasov in Romania. Also the trochispiral

Valvata gradata FUCHS, 1870 as illustrated by BARTHA (1956) from the fauna of Tab is one of these. According to BASCH (1990) the Croatian Pontian contains *Valvata balatonica* ROLLE, 1861, *Valvata tenuistriata* FUCHS, 1870, both species probably not belonging to *Valvata*, and a number of other species of doubtful *Valvata* with rounded flat shell. MÜLLER (1989: pl. 6, fig. 9) illustrated from the Balaton region *Valvata balatonica* (= *Pseudamnicola* of JEKELIUS, 1932), *Valvata tenuistrata* (= as *Valvata balatonica* but finer spiral lines) (MÜLLER, 1989: pl. 7, fig. 3), *Valvata simplex* (with flat shell) (MÜLLER, 1989: pl. 7, figs. 1–2), *Valvata adeorboides* FUCHS, 1870 (with little higher shell) (MÜLLER, 1989: pl. 7, figs. 4–5) which according to in FUCHS (1870a) it is rounded and low.

Jekeliella dombovarensis n. sp. (Pl. 11/126–129)

<u>Diagnosis</u>: The shell consists of a smooth rounded and trochispiral protoconch of 1.5 whorls and added to them a teleoconch consisting of 2.5 whorls. Here the shoulder is flattened, the side is somewhat flattened and the base has a wide conical umbilicus. Ornament consists of strong spiral ribs which also enter the umbilicus. The aperture is round and a weakly oblique.

<u>Holotype</u>, origin of the name and type locality: The individual in fig. 126 represents the holotype. It was collected by MÜLLER-PAL in Dombovar, and is named accordingly *Jekeliella dombovarensis*. The stratigraphical position is the higher Pontian of the Balaton area south of Lake Balaton. The holotype is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4707.

<u>Description</u>: The shell consists of almost 5 whorls of which the first three have rounded outline, while the last ones are more angular. The shell is about 4 mm wide and high. The protoconch measures about 0.4 mm and is nearly planispiral with rounded whorls, but not well preserved. Ornament of the teleoconch consists of about 7 strong spiral ribs which may have finer spiral ribs between them. The two peripheral ribs form the corners to the flattened apical side and to the weakly convex side. Another strong spiral rib represents the edge to the conical umbilicus that is also spirally ornamented on its sides. The individuals were collected at Dombovar a village south of Lake Balaton, Hungary.

Genus *Kerchia* n. gen. (Pl. 11/135–139.)

<u>Diagnosis</u>: The shell with evenly rounded whorls is widely coiled when juvenile and more closely when fully grown. The umbilicus is relatively large in the juvenile shell and narrower with fully grown shell. The protoconch is rounded with granular ornament and no growth lines on the first whorl and growth lines to the margin of the older embryonic shell. The aperture is round and oriented almost vertical to the coiling axis. The type is *Kerchia yurkynensis* from the bryozoan reefs in Cape Chrony.

<u>Origin of the name</u>: The type species lived at the Sarmatian–Maeotian transition near to the locality which now is Kerch, Crimea, and is called according to this city.

Kerchia yurkynensis n. sp. (Pl. 11/135–139)

Diagnosis: As genus.

<u>Origin of the name, holotype and locus typicus</u>: The *Kerchia* that occurs on Cape Chrony just to the east of the fishing village Yurkyne on the shore of the Sea of Asov. *Kerchia yurkynensis* lived in the cavities of the bryozoan algal reefs which are exposed in the slopes of Cape Chrony below the village Osovyny and in stratigraphical position just below the bivalve limestone of the base of the Maeotian deposits. The illustrated specimen in fig. 135 represents the holotype which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4708.

<u>Characteristic occurrence</u>: In cavities of the bryozoan-stromatolite reef that formed during the time of the Sarmatian– Maeotian transition in the somewhat brackish sea.

<u>Description</u>: The shell when fully grown consists of a little more than three whorls and is about 1.5 mm wide and high. The protoconch is 0.3 to 0.4 mm in size with fine granular ornament which may join to form thin spiral ribs. The first whorl without growth increments is succeeded by embryonic shell with growth lines. The time of hatching to bottom life is indicated by strong growth increments. The two, evenly rounded teleoconch whorls increase in diameter rapidly. The ornament consists only of growth lines. The margin of the aperture is relatively thin and touches the inner whorls without being interrupted.

Difference: Kerchia yurkynensis resembles Hauffenia, Horatia, Islamia and similar hydrobiid genera which have many species living in springs and fresh water lakes in Europe (BODON et al., 2001). It differs regarding the more rapid increase in the diameter of the whorls in the juvenile shell. When fully grown the shell of Kerchia is similar and also the embryonic shell resembles that of some species of these modern genera. I contrast to the modern valvatiform Hydrobioidea Kerchia has lived in brackish water, while living counterparts occur in fresh water of caves and springs. Kerchia yurkynensis lived within the cavities of bryozoan reefs during a time when their top was covered by stromatolites, and when water was not of normally marine salinity, but brackish.

6 Transition from shells of the shape as in *Jekeliella* to such of *Pyrgula*, connected to a short summary on the deposits of ancient Lake Brasov extracted from JEKELIUS (1932)

In his well illustrated study on the gastropods from the deposits of the Lake Brasov in Transylvania (Kronstadt, Siebenbürgen) of Romania, JEKELIUS (1932) documented clearly the transition from planispiral and valvatiform species and from species with their shell about as high as wide to such with higher than wide and or pyrguliform shape. JEKELIUS (1932) noticed that in near shore deposits of that Pliocene Lake Brasov the species he had determined as *Pyrgula eugeniae*, *Valvata eugeniae* and *Gyraulus quadrangulus* had extremely variable shell shapes. When the many good illustrations of JEKELIUS (1932) are consulted it becomes quite evident that the documented varieties connect not only different morphs within a species and subspecies but also connect species to each other that had been regarded by him to represent different genera.

Lake Brasov existed at Dacian time which should have been close to or somewhat after the Messinian salinity crisis in the Mediterranean Basin. This lake may have been up to 100 km long bordered by the Muntii Harghita (part of the Carpathians) which consist of volcanic rock which, in part, are intercalated with the lake deposits. Lake Brasov existed in a new basin that formed where land had been from which Pannonian deposits of former Lake Pannon had been eroded. Deposition began in swamps, which became successively flooded by Lake Brasov when is grew in size. Later on this Lake Brasov decreased in size, swamps formed, and finally rivers filled the remaining basin with gravel. The sedimentary column of the lake basin consists of more than 300 m in thickness.

The lake deposits in the northern part of the lake were chalky limestone, in the southern part less calcareous. Since there are still springs of mineral water in that northern region and lake deposits intercalate in part with deposits of such springs the mineral water was made responsible for speciation that was observed by JEKELIUS (1932). The bivalve *Limnocardium* lived, at least periodically, in the lake, so it probably contained not pure fresh water but was somewhat brackish in composition. Near the shore swamp deposits have fresh water gastropods such as *Viviparus, Ancylus, Radix, Bithynia, Pseudamnicola* and some *Hydrobia*. At the shore of the lake and near the shore in the lake a rich fauna of gastropods was living with rather unique character of their shell.

JEKELIUS (1932) placed species with a flat shell into the genus Gyraulus. This determination can be accepted even without knowing the protoconch since growth lines are inclined and the aperture is strongly oblique. Species with a higher shell as in Valvata piscinalis were determined as Valvata, those with a the shell a little higher than wide as *Pseudamnicola*, and those with shell higher than wide and resembling modern *Pyrgula* were included in that genus. JEKELIUS (1932) documented that all such species which are characterized by spiral keels as part of their ornament are actually connected to each other by individuals with transitional morphology. A transition can be noted that ranges from the lowly trochispiral specie placed with Valvata to elongate spiral species which resemble Pyrgula. The common Gyraulus quadrangulus (NEUMAYR, 1875) was found to be variable in shape (JEKELIUS 1932: pl. 19, figs. 1-24) ranging from about 6 mm in width and only 0.5 mm high to such with up to 1 mm in height, at other localities even up to 3 mm height. Ornament consists of keel bearing corners forming a flat to a stair-like shell and the base is deeply concave. Even though Gyraulus quadrangulus resembles some low varieties of Valvata eugeniae NEUMAYR, 1875 the growth lines and the aperture distinguish both from each other. The latter according to JEKELIUS (1932: pl. 6, figs. 1-41) varies strongly in shell height, while the base has a deep umbilicus, the corners of the whorls have a keel and the side between keels is more or less flattened. Also keels vary from weak to very sharp and shells may be as wide as high (6–7 mm) to a little higher than wide. Based on ornament species with well developed keels around the umbilicus and on the two corners JEKELIUS (1932) distinguished Valvata eugeniae eugeniae with all keels well developed, Valvata eugeniae sibinensis with the keel to the base indistinct, Valvata eugeniae bifrons with the keel to the shoulder less developed, and *Valvata eugeniae gibbulaeformis* with additional spiral ribs either on the shoulder or on the base. Transitions also connect to *Pseudamnicola* (JEKELIUS, 1932: pl. 9, figs. 1–38, pl. 10: figs. 1–39) with the shell about 3–7 mm high and 2.5 to 3 mm wide and narrow umbilicus. *Pseudamnicola bithynioides* JEKELIUS, 1932 has two additional spiral ribs, *Pseudamnicola margarita* (NEUMAYR, 1975) has two keels separated from each other by a channel-like suture, and *Pseudamnicola pagoda* (NEUMAYR, 1875) has a more slender shell. The later has been placed with *Pyrgula* by WENZ (1926), while JEKELIUS (1932) distinguished it from *Pyrgula* by its well developed umbilicus. Similar shells as in *Pseudamnicola pagoda* of JEKELIUS (1932) were also encountered from the Pliocene of Kerch (own data) and also the transition to *Pseudamnicola trochiformis* JEKELIUS, 1932 as documented by JEKELIUS (1932: pl. 11, figs. 1–13) and the similar *Pseudamnicola trochisimilis* JEKELIUS, 1932 and *Pseudamnicola carinata* JEKELIUS, 1932 can be noted in the layer studied near Kerch, as in Lake Brasov. Finally *Pyrgula eugeniae* NEUMAYR and several similar species were distinguished by JEKELIUS (1932), all of them may be connected by transitional species.

7 New genera of ?Basommatophora, Planorbidae

Fuchsogyra n. gen. may belong to the Planorboidea RAFINESQUE, 1815 but it differs from the usual representatives of the Planorbidae RAFINESQUE, 1815 by the shape and ornament of its embryonic shell. The shells of the different species here recognized are quite variable in ornament, which was also noted by STRAUSZ (1942). He suggested the inclusion of a number of other species mentioned by WENZ (1928) into the species that he called *Planorbis (Gyraulus) radmanesti* FUCHS, 1870. Most of the listed species here placed in *Fuchsogyra* have been described by BRUSINA (1902).

Genus Fuchsogyra n. gen.

<u>Diagnosis</u>: The shell is planispiral, discus-like with a corner or keel at the edge to the flattened base. The apical side is rounded or flat with well developed suture. The basal side has flattened whorls and a wide shallow umbilicus with all whorls visible. Ornament is collabral or spiral (FUCHS, 1870a: figs. 13, 16). The protoconch consists of two parts. The initial about one whorl is smooth and planispiral with rounded sides. The final part consists of about half a whorl and may be ornamented with rounded radial ribs. The embryonic shell ends with onset of strong growth lines. The change from protoconch to teleoconch may be connected to a change in ornament.

<u>Remarks</u>: The genus is based on *Planorbis radmanesti* FUCHS, 1870 that had been described from the Pontian of Radmanesti in Romania. This species has been again described by GILLET & MARINESCU (1971: pl. 25, figs. 10–11) and determined as *Gyraulus varians* (FUCHS, 1870) and subgenus *Gyraulus varians radmanesti*. This latter determination cannot be supported, since *Planorbis varians* FUCHS, 1870 can be recognized quite well and clearly represents a different species from *Planorbis radmanesti*, as is shown below.

The material was in part collected by MÜLLER-PAL, who showed to us the outcrops near the Balaton Lake where we could collect additional material from the Pontian beds of the deposits of the Pannonian Lake. GILLET & MARINESCU (1971) documented the material from Radmanesti mostly based on shells that had been collected by JEKELIUS. Their illustrations add information to the drawings of FUCHS (1870a) and aided the recognition of those individuals which are not from the type locality.

<u>Origin of the name</u>: Free combination of the name of the author Fuchs with the name of the common genus *Gyraulus* of the Basommatophora.

Fuchsogyra radmanesti (FUCHS, 1870) (Pl. 12/140–145)

The protoconch consists of one whorl with smooth surface and half a whorl that has ribs on its apical side and is smooth on its basal side. Protoconch diameter amounts to about 0.5 to 0.6 mm. The begin of the teleoconch is indicated by axial ribs which run across the apical surface in an even curving way, a little more straight towards the suture. The ribs seen on the whorls of the spire of which a part is covered by the succeeding whorl thus appear relatively straight. Next to the outer margin their curving shape is more evident, and the end in the sharp corner to the base. There are up to 30 ribs on a whorl of the teleoconch. On the flattened base these ribs are much

weaker and almost straight. Growth lines may as strong as the ribs. The fully grown shell has about 3.5 whorls and is about 3 mm in diameter but only about 0.8 mm high.

<u>Remarks</u>: The apical side of the shell of *Fuchsogyra radmanesti* differs strongly from its lower side (arranged as dextral coiled shell). The species was found in the sample washed from the Pontian deposits of Kötese south of Lake Balaton (locality was called Köttse by STRAUSZ, 1942).

HARZHAUSER et al. (2002) distinguishes six species of *Gyraulus* from the Pannonian of the Vienna Basin, based on a study of SAUERZOPF (1953), who recognized 37 species and subspecies of Planorbidae. But *Gyraulus turrislavicus* JEKELIUS, 1944 is described and illustrated by HARZHAUSER et al. (2002: pl. 13, figs. 1–4) and was interpreted to resemble the stratigraphically younger *Gyraulus radmanesti* (FUCHS, 1870). The protoconch was not well preserved, but they suggested the presence of spiral threads. The characteristic axial ribs of the last portion in the embryonic shell are well visible, while of the spiral lines nothing is seen in their illustration. They suggested that *Gyraulus turrislavicus* may have developed into *Gyraulus radmanesti* and is related to *Gyraulus rhytidophorus* (BRUSINA, 1902).

Gyraulus turrislavicus as illustrated by HARZHAUSER et al. (2002) is not a member of *Gyraulus* but has the protoconch and shell shape of *Fuchsogyra*. Also MÜLLER (1989: pl. 8, fig. 10) illustrated the flatly coiled shell with rounded apical side and flat umbilical side described by JEKELIUS (1944: pl. 58, figs. 19–21) as *Gyraulus turrislavicus*.

Fuchsogyra balatonica n. sp. (Pl. 12/146–150; Pl. 13/151–152)

<u>Diagnostic characters</u>: The protoconch has half a whorl without ornament succeeded by more than half a whorl with strong axial ribs found on both sides of the shell. The apical side of the teleoconch is rounded. Its ornament consists of strong, curving growth lines. Its outer margin of the shell is represented by a corner to the flat side. The base has a wide and shallow umbilicus. Here ornament consists of fine and almost straight growth lines.

<u>Difference</u>: *Fuchsogyra balatonica* differs from *Fuchsogyra radmanesti* by ornament and shape of the protoconch as well as ornament of the apical side of the teleoconch. The protoconch of *Fuchsogyra balatonica* has strong and continuous axial ribs on both sides of the shell and the initial smooth part is relatively short. In case of *Fuchsogyra radmanesti* the protoconch has almost one smooth whorl on the apical side and is totally smooth on the basal side, and teleoconch has curving axial ribs on the upper side.

<u>Origin of the name, holotype and typical locality</u>: The type of *Fuchsogyra balatonica* comes from Tihany, and the species was also found among the shells washed from the Pontian sands at Varpalota and Tab. The locality at Tihany lies on the slope to the Lake Balaton near the ancient monastery and in the slope exposing the Pontian lake deposits. The illustrated specimen in fig. 150 represents the holotype which is housed in the collection of the Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, no. 4709.

<u>Description</u>: The protoconch consists of two parts, of which the early half whorl is smooth and the second three quarters whorl is ornamented by straight and rounded axial ribs. The end of the embryonic shell is well indicated by change in ornament to the teleoconch as well as change in shape of the shell from rounded to angular (fig. 147). On the apical side the smooth part of the protoconch consists of almost one whorl and the ribbed part of less than half a whorl (fig. 148). The axial ribs on the later whorl of the protoconch are inclined sinuous on the side (fig. 151). The teleoconch has growth lines as ornament and a corner to the base. The apical side is well rounded and the basal side flattened with the umbilical wide and shallow. With more than three whorls the shell may reach a diameter of almost 4 mm and a height of 0.5 mm.

Genus Marinescugyra n. gen.

<u>Diagnosis</u>: The planispiral shell has a flattened base and a rounded apical side with median depression and strong spiral keel. The protoconch is smooth and coiled in a plane.

<u>Difference</u>: In general shell shape this genus resembles *Fuchsogyra*, with its main difference in the ornament and size of the protoconch. *Marinescugyra* has a smooth protoconch of 1.5 whorls. The genus is based on *Planorbis varians* FUCHS, 1870 from Radmanesti, also documented by GILLET & MARINESCU (1971: pl. 25, fig. 24–29) in part as *Gyraulus* (*Gyraulus*) varians varians (FUCHS, 1870).

<u>Origin of the name</u>: The genus name is to honor father and son Marinesecu, the older (Florian) who published on the mollusks of the Paratethys in Romania, and the younger (Bogdan) having transferred some of his knowledge to the author.

Marinescugyra varians (FUCHS, 1870) (Pl. 13/153–158)

The shell is discus-like in shape and consists of four whorls which increase in size slowly and regularly. Ornament is by two keels, one on the upper side and one forming the corner to the base. The apex lies in a conical pit with rim formed by the apical keel. Between keels the side has a differing number of fine spiral lines, which may also be absent. The base is flattened and whorls form a stair-case to the umbilicus. Here surface of the whorls is smooth. The aperture is oblique and with rounded outer lip. The diameter of the shell may be up 8 mm and it is up to 2 mm high.

Regarding the protoconch FUCHS (1870a) provided no information. It consists of about 1.5 smooth whorls in plane coiling mode. Diameter is about 0.5 mm with the initial part about 0.2 mm wide. Hatching occurred with the smooth embryonic whorl completed and that rim can be fractured and repaired as is seen in fig. 155.

The variability of this species is also documented in differences in height of the shell. But differences of the embryonic shell to those of *Fuchsogyra radmanesti* clearly document, that that species is not closely related to *Marinescugyra varians*. The species was found in fine Pontian sands of Balatonkenese and from Kötese at Lake Balaton. *Planorbis varians* FUCHS, 1870 was described from Radmanesti and FUCHS (1870b) recognized it also from Tihany. Possibly *Gyraulus protectus* JEKELIUS, 1944 is this species as well (JEKELIUS, 1944: pl. 58, fig. 23). JEKELIUS noted a difference to *Gyraulus kochi* PAVLOVIC, 1928 which has a concave base with a keel around the wide umbilicus, as is the case in *M. varians*.

Marinescugyra kochi (PAVLOVIC, 1928) has a flat shell that consists of up to 4.5 whorls, is about 1 mm high and 3.5 mm wide. The last whorl has an apical keel that comes to lie in the suture in earlier whorls. The shell is widest at the corner to the base. The base is flattened with wide shallow umbilicus. The teleoconch is ornamented by fine spiral lines. The aperture is rhombic in shape (PAVLOVIC, 1928: pl. 6, figs. 11–12). He compared it with *Planorbis tenuis* from Kup described by FUCHS (1870b) and noted that the aperture in his species is more angular, and strong growth increments in the first whorl of the shell. *Marinescugyra kochi* thus differs from *Marinescugyra tenuis* by the ornament of spiral lines, possibly also by having a protoconch that is closer to that of *Fuchsogyra* with axial ornament in the later portion of the embryonic shell.

Marinescugyra tenuis (FUCHS, 1870) (Pl. 13/159–162; Pl. 14/163–165)

<u>Diagnostic characters</u>: The planispiral shell has a concave base with flattened whorl sides and a convex apical side with rounded whorl sides and two keels. The protoconch consists of about 1.3 smooth rounded whorls of about 0.5 mm in diameter. Its margin in thickened and well distinguished from onset of the teleoconch. The first whorl of the teleoconch has rounded shape on its apical side with dense pattern of evenly curving growth lines. A corner is present to a flattened base. Within this first whorl the corner and the middle of the apical whorl develop a keel, and later a further corner may appear between keel and corner. The base is concave with the marginal keel above surface. The aperture is angular and inclined towards the base.

<u>Remarks</u>: *Planorbis tenuis* FUCHS, 1870 was characterized as having a very shallow shell (FUCHS, 1870b: pl. 20, figs. 15–18). GILLET & MARINESCU (1971: pl. 25, figs. 20–29) also described this species as *Gyraulus varians varians* (FUCHS, 1870) from Radmanesti. According to their interpretation ornament of this species is variable and with or without apical carina and additional spiral lines. *Marinescugyra tenuis* was noted in the fauna extracted from Pontian deposits of Lake Pannon at Tihany, Varpalota, and Kötese.

Fuchsogyra and *Marinescugyra* differ from convergent valvatiform rissooidean gastropods in regard to the size and ornament of the protoconch. In *Fuchsogyra* it is larger, plane in coiling and its ornament is smooth in begin and has radial ribs in the end. The Hydrobioidea such as *Muellerpalia* have a dextral trochispiral embryonic whorl of about 0.3 mm in diameter or less that has groove and ridge pattern or is more or less smooth. The embryonic shell of Planorbidae such as *Gyraulus* CHARPENTIER, 1837, *Planorbis* MÜLLER, 1774 *Planorbarius* FRORIEP, 1806, *Anisus* STUDER, 1820 and *Segmentina* FLEMING, 1817 differ by ornament of regular or irregular spiral ribs of the protoconch and its gradual transition into the teleoconch. The *Valvata* relation usually has a

smaller protoconch consisting of only one whorl and a more uniform spiral ornament of the embryonic shell that does not include axial ribs.

Carinifex quadrangulus NEUMAYR, 1875 and a similar shell documented by JEKELIUS (1932) as *Gyraulus quadrangulus* from the Lake Brasov resemble *Marinescugyra*. *Carinifex* BINNEY, 1865 is based on a living species of the Planorbinae from North America (WENZ & ZILCH, 1960: fig. 405) with relatively high shell. *Gyraulus quadrangulus* was found to be very variable in shape (JEKELIUS, 1932, pl. 19, figs. 1–24). Individuals with about 6 mm in width may be only 0.5 mm high and they range to forms up to 1 mm high. In other localities they may even be up to 3 mm high. Ornament consists of keel bearing corners forming a flat to a stair-like shell and the base is deeply concave. Even though *Gyraulus quadrangulus* resembles some low varieties of *Valvata eugeniae* NEUMAYR, 1875 the growth lines and the aperture distinguish both from each other. The corners are with keels, the protoconch has the ornament as in *Gyraulus*, and the growth line pattern reflects a quite strongly inclined outer lip, as is the case in *Gyraulus quadrangulus* from the Brasov Lake. This species was relatively variable in shape as documented by JEKELIUS (1932). The shell from the older Pontian deposits of Tihany is from a very similar species.

8 Notes on some Planorbidae

Family Planorbidae RAFINESQUE, 1815

The shell is mostly coiled in planispiral mode. Development of the eggs continues in the spawn until crawling young hatch with a shell of a little more than one whorls. Usually the protoconch is coiled in a plane, but sometimes a slight twist to the left is preserved. Ornament of the embryonic shell usually consists of spiral striation. RIEDEL (1993) documented its presence in species of the genus *Gyraulus* CHARPENTIER, 1837, *Anisus* STUDER, 1820, *Planorbis* MÜLLER, 1774, *Armiger* HARTMANN, 1840, *Hippeutis* CHARPENTIER, 1837, *Segmentia* FLEMING, 1817, and *Planorbarius* FRORIEP, 1806. *Planorbarius* is the largest when fully grown (more than 20 mm) and it also has the largest protoconch with 1.6 whorls and 1.2 mm in diameter. *Planorbis* grows to about 10 mm in size of the shell that bears a keel or edge. *Anisus* has many whorls which are rounded in *Anisus (Anisus)* and have an edge or keel in *Anisus (Disculifer)* BOETTGER, 1944. *Bathyomphalus* CHARPENTIER, 1837 has up to 6 mm large shell with high rounded whorls and tight aperture. Shells are smaller than 3 mm in case of *Armiger* with ornament and have a flattened side in *Menetus* H. & A. ADAMS, 1855 in *Hippeutis* the keel lies in the middle, and in *Segmentina* whorls overlap strongly (GLÖER & MEIER-BROOK, 1998).

MEIER-BROOK (1983) suggested that all Planorbidae are morphologically sinistral since the genital openings and the anus are on the left. Consequently all *Gyraulus* snails were considered to have a left-coiled shell. But most Planorbidae carry their shell when in locomotion as do dextrally coiled species and their aperture is inclined accordingly. The species of the Planorbidae have been recognized to belong into one phylogenetically related group (ALBRECHT et al., 2007) that has been documented in its existence from the paleontological record since the Jurassic (more than 170 million years) (BANDEL, 1991: here references).

The shape and size of the initial (embryonic) whorls can distinguish some genera of Planorbinae quite well. Low whorls characterize *Gyraulus*, rounded and higher whorls are found in *Planorbis*, and a rather large protoconch is present in *Planorbarius*.

Genus *Planorbis* MÜLLER, 1774 (Pl. 14/168–171)

The size of the shell is about 10 to 20 mm and the outer corner of the whorl has a keel. The type is *Helix planorbis* LINNAEUS, 1758 from Europe and lives in fresh water ponds and lakes.

Planorbis planorbis has its whorls plane on the apical side, convex at the wide umbilicus, with keel near to the lower side. The shell consists of up to 6 whorls and is up to 18 mm wide. The suture is deeper on the lower side than on the upper side. Collabral growth lines form a regular pattern. RIEDEL (1993) described the development of the embryo. Its shell when hatching after about 9 days of development is 0.6 mm in diameter and consists of 1.3 whorls. The rounded initial part of the embryonic shell is about 0.1 mm wide and commonly covered by irregular folds. In most cases transition from the protoconch to the teleoconch gradational because protoconch ornament ceases earlier or continues onto the teleoconch.

Early teleoconch whorls may be rounded and the keel develops later. *P. planorbis* occurs all over Europe and it also lived in the Pliocene of Romania (WENZ, 1942: pl. 26, figs. 403–406). The very similar *Planorbis romani* JODOT, 1958 from the late Miocene of Spain in the Granada Basin (Arenas des Rey) resembles modern *Planorbis planorbis* (LINNAEUS, 1758) but has more rounded whorls. The protoconch is like that of the living species and also resembles that of *Gyraulus* but is larger (BANDEL et al., 2000). A *Planorbis* from the Apolakkia

Formation of Rhodes (Pliocene) is quite similar also with rounded whorls of the juvenile teleoconch and the protoconch with very indistinct transition into the teleoconch and diameter of about 0.8 mm (figs. 168–169). The juvenile shell of a *Planorbis* extracted from the lacustrine sand of the Pontian deposits near Balatonaligna on Lake Balaton has the protoconch with about 0.5 mm wide first whorl and a fine ornament of spiral lines on it, disappearing with begin of the teleoconch (figs. 170–171).

In case of *Planorbis carinatus* MÜLLER, 1774 it was noted by GLÖER & MEIER-BROOK (1998) and GLÖER (2002) that apical and umbilical side have the same concavity and the fully grown shell consists of five whorls, one whorl less as is the case in *Planorbis planorbis*. The whorls are rounded above and below and the side carries a median keel and the shell measures about 12 mm in diameter. The species is common in Europe in standing water and slow rivers and creeks.

Genus *Planorbarius* FRORIEP, 1806 (Pl. 14/166–167)

The shell is coiled in a plane with about five evenly convex whorls and about 30 mm in diameter quite large and up to 12 mm high. The apical side is less concave than the umbilical side. The type species is *Helix cornea* LINNAEUS, 1758 from Europe. *Planorbarius corneus* occurs all over Europe, and it lived in the Pliocene of Romania (WENZ, 1942: pl. 26, figs. 397–401).

The embryonic shell of *P. corneus* is ornamented by spiral rows of pits and the juvenile shell has spiral ridges with periostracal spines. When these disappear due to the disintegration of the organic periostracum, rows of pits accompanied by ridges remain on the surface of the mineral shell (BANDEL, 1991). The embryo hatches from its egg after nine days of development with about 1.2 mm wide shell that has almost to whorls. The shell begins to appear on the third day of development and is continuously formed during the next three days and is plan spiral with 1.3 whorls. Ornament consists of growth increments and 10–15 faint spiral lines (RIEDEL, 1993: pl. 5, figs. 4–5).

From the Pliocene of the Granada Basin *Planorbarius thiollierei* (MICHAUD, 1855) with up to 22 mm large shell with 9 mm height consists of up 5 whorls (ROYO-GOMEZ, 1922: fig. 37). Its protoconch with about 2 mm in width consists of almost 2 whorls (BANDEL et al., 2000. This species was also documented from the Pliocene (Maeotian) of Romania (WENZ, 1942: pl. 26, figs. 392–393).

Planorbarius mantelli (DUNKER, 1848) was recorded by STOJASPAL (1989: pl. 2, fig. 1) from the Egerian to the Pontian of the Vienna Basin. It represents a *Planorbarius* which appears to be the same as the modern species or have very similar shell shape. The protoconch of *Planorbarius* from the Pontian sands of Papkesi near Balatonkenese on the Lake Balaton is well preserved and measures about 1.5 mm in width (figs. 166–167). The first whorl is ornamented by spiral rows of shallow round pits, on the second whorl the ornament is if spiral ridges crossed by growth lines. Near hatching the growth lines are more prominent and after hatching the teleoconch is smooth with only growth lines.

Genus *Gyraulus* CHARPENTIER, 1837 (Pl. 14/172–173; Pl. 15/174–183; Pl. 16/184–189)

The small planispiral shell has a flattened apical side and the umbilical side is concave with rounded whorls. The type species is *Gyraulus albus* (O.F. MÜLLER, 1776) from Europe with the shell of 4–7 mm maximum diameter and 1.2 to 1.8 mm height with 4 to 4.5 whorls, which rapidly increase in width. Whorls are equally rounded, scarcely embrace one another and there is rarely a trace of an angle. The protoconch of *Gyraulus* resembles that of *Valvata* in shape and ornament. In contrast to *Valvata* its margin is not straight but inclined, and increase in shell diameter is more rapid (figs. 177, 179, 187).

Gyraulus albus has the same shell shape as in *Gyraulus* from Soceni (figs. 172–173), from the Pontian of Balatonaligna (figs. 170–171) and of Papkesi (figs. 184–185).

Gyraulus usually has a more rapid increase in shell width than found in *Planorbis*. Species are found worldwide and occur in any kind of fresh water environment with normal chemistry. Fossil species resembling *Gyraulus* are present from Lower Jurassic onward with very similar shell shape, size and ornament (BANDEL, 1991; BANDEL & RIEDEL, 1994). *Gyraulus loryi* (COQUAND, 1855) from the Weald (Jurassic–Cretaceous transition) has the same shape of its shell and micro-sculpture of its protoconch as present in living species. Older species than those of the Late Jurassic are not known (WENZ & ZILCH, 1960).

Living species of *Gyraulus* in Europe are difficult to distinguish by shell shape (MEIER-BROOK, 1983). He noted that *Gyraulus albus* and *Gyraulus laevis* (ALDER, 1838) never produce an angle on their shell whorls. The upper side is slightly concave and deeply concave of the lower side. Curving growth lines are crossed by spiral lines forming a reticulate ornament. This is weaker in case of *Gyraulus laevis* that may have only of curving growth

lines on its teleoconch. *Gyraulus rossmaessleri* (AUERSWALD, 1851) is smaller than 4 mm and closely resembles *Gyraulus laevis*. Its umbilicus is shallower and the aperture less oblique and with a thickened ridge. *Gyraulus acronicus* (FERUSSAC, 1807) is larger with up to 7 mm wide shell with relatively flat whorls, with the last whorl deflected and weak sculpture (MEIER-BROOK, 1983; GLÖER & MEIER-BROOK, 1998). *Gyraulus arconicus* may coexist with *Gyraulus albus* and *Gyraulus riparius* (WESTERLUND, 1865) in the same pond. The discus-like shell of the later is never larger than 2.3 mm and 0.6 mm in height with marginal angle and fringe. *Gyraulus parvus* (SAY, 1817) has no keel and 4.5 rounded whorls. This species originally from North America, and is now common in Europe (GLÖER & MEIER-BROOK, 1998). From Asia *Gyraulus chinensis* (DUNKER, 1848) was introduced with up to 4 whorls and up to 5 mm wide shell with rounded upper and lower side and some collabral ornament. It closely resembles *Armiger crista* and *Gyraulus riparius*. While the shell may be quite similar among species, they all have a distinctive male reproductive organ.

The sediments of Lake Pannon that have been deposited quite far from its shore contain a *Gyraulus* together with limnocardiid bivalves. It is commonly found on bedding planes in the large quarry of the Frusca Gora in Serbia. It lived in the brackish of Lake Pannon during Pannonian time. Only *Gyraulus laevis* among the living species in Europe also tolerates slightly brackish water, while the species of *Gyraulus* usually live only in fresh water. *Gyraulus kleini* GOTTSCHICK & WENZ, 1916 entered the lake produced by the impact of a meteor about at 15 ma and had a most amazing evolution during which teleoconch shape changed strongly, while the protoconch retained shape and ornament (NÜTZEL & BANDEL, 1993, here also references). This evolution occurred within a relatively small lake of Steinheim in southern Germany and lasted several 100000 years until the basin was filled up with sediment.

From the Pannonian of the Vienna Basin HARZHAUSER et al. (2002) determined six different species of *Gyraulus* which obviously are all very similar to each other. They distinguished species by slight differences of protoconch size and teleoconch width and coiling mode. JEKELIUS (1944) had also distinguished six species from the Pannonian of Soceni, but they apparently differ from those mentioned by HARZHAUSER et al. (2002) who discussed one of the species described by Jekelius. Actually the distinction of different species from Pannonian to Pontian deposits is problematic and species limits are difficult to draw. This may also explain the difference of species determination of the *Gyraulus* as discussed by JEKELIUS (1944) and those described by HARZHAUSER et al. (2002) since all these species lived near the shore of the same Lake Pannon.

Gyraulus turrislavicus JEKELIUS, 1944 has a marginal keel, on the apex rounded whorls, is flattened and has a depressed umbilicus (JEKELIUS, 1944: pl. 58, figs. 19–21) while *Gyraulus sabljari* (BRUSINA, 1892) has rounded lower and upper sides of its whorls, concave apex and rounded outer sides (JEKELIUS, 1944: pl. 58, figs. 15–18). *Gyraulus protectus* JEKELIUS, 1944 is a 2 mm large species with the shape of *Gyraulus turrislavicus* but the upper side of whorls is flattened and there is an edge in its middle (JEKELIUS, 1944: pl. 58, fig. 23). This species resembles *Gyraulus jukici* (BRUSINA, 1902) but in contrast to it has a flattened lower side, and *Gyraulus kochi* PAVLOVIC that has a wide conical umbilicus. *Gyraulus ptychophorus* (BRUSINA, 1892) has axial folds and thus a little angular shape (JEKELIUS, 1944: pl. 58, fig. 24). From the eastern shore of Lake Pannon *Gyaulus solenoeides* (LÖRENTHEY, 1902) has a strongly evolute shell with rounded whorls and 1.2 mm in diameter (JEKELIUS, 1944: pl. 26, figs. 17–18). *Gyraulus soceni* JEKELIUS, 1944 from the Pannonian of Soceni has a concave apical side and flat umbilical side with corner on the outside and it resembles *Gyraulus turrislavicus and Gyraulus sabljari* from younger beds (JEKELIUS, 1944: pl. 26, figs. 19–20).

Gyraulus verticillus (BRUSINA, 1892) according to HARZHAUSER et al. (2002) who relied on the study of SAUERZOPF (1953) has characteristic subsutural swellings on both sides of the shell. Its angular whorl sides are actually quite like those of *Muellerpalia carinata*. *Gyraulus marinkovici* (BRUSINA, 1892) also based on the determination by SAUERZOPF (1953) has an up to 3 mm wide and narrow shell with flat apical side and a concave umbilical side with ornament of growth lines and sometimes spiral lines. The protoconch is described as smooth. HARZHAUSER et al. (2002) distinguished it from *Gyraulus fuchsi* (LÖRENTHEY, 1902) by larger size and larger body whorl. The protoconch of this species that is the most common one in St. Margarethen with 0.3 mm in size is larger and considered as species specific. *Gyraulus haueri* (STOLICZKA) has more elongate shell diameter and *Gyraulus sabljari* has narrower umbilicus. *Gyraulus micromphalus* (FUCHS, 1870) according to HARZBURGER et al. (2002) has the umbilicus narrow, sides rounded and the apex concave. They consider it to represent the same species as *Gyraulus popovici*. It occurs frequently in the Pannonian of the Vienna Basin. A species with wider umbilicus was described by them as *Gyraulus primiformis* (SAUERZOPF, 1953) originally suggested to be a *Planorbis*.

A *Gyraulus subptychophorus* (HALAVATS, 1911) is illustrated by STOJASPAL (1989: pl. 1, fig. 9) from the Pontian of the Vienna Basin. From the Pliocene of Romania only *Gyraulus rumanus* WENZ, 1931 was determined (WENZ, 1942: pl. 27, figs. 411–413). It consists of 4 rapidly increasing whorls which are flat on the apical side and concave on the umbilical side with body whorl with rounded keel.

Genus Armiger HARTMANN, 1843 (Pl. 16/186–187)

Only *Armiger crista* (LINNÉ, 1758) occurs in Europe and North Africa and represents the type to the subgenus, other species live in North America, western Asia. *Armiger crista* has up to 2.7 rapidly increasing whorls with flattened top and rounded base. The periphery is angled, the angle being to the upper side. The last whorl does not embrace the penultimate whorl but is loosely attached to its upper side. The shell is almost flat on the upper side and deeply concave on the lower side. The whorls are traversed by ridges. The shell is 2.2 to 3 mm wide and up to 0.9 mm high (WENZ & ZILCH, 1960: fig. 362). *A. crista* lives in small pools and among rocks in rapid streams. GLÖER & MEIER-BROOK (1998) considered *Armiger crista* as a member of the genus *Gyraulus*. From lake deposits of the Granada Basin in Spain *Armiger* has a flat shell on the apical side and is slightly concave on the umbilical side with ornament of fine collabral ribs. The shell measures about 2.5 mm in diameter and 0.5 mm in height. The aperture is rounded and oblique (BANDEL et al., 2000). It closely resembles *A. crista* as described by GORTHNER (1992) and is also reported from the late Neogene of Greece by RUST (1997: pl. 10, figs. 6–8). Individuals resembling *A. crista* are among the documented fossil species those from the Plocene of Al Qarn Formation of Jordan, and these are just like the individuals that have been studied from the modern Lake Razim in eastern Romania.

Genus Anisus STUDER, 1820 (Pl. 17/195–199, 200–203)

The type is *Anisus spirorbis* (LINNAEUS, 1758) with the shell very low and at its lower side almost plane with 5–8 whorls, reaching a size of up to 10 mm. Whorls do not overlap much which differs from *Bathyomphalus*. Five species live in Europe, and outside of that region it is found in the Palaearctis (Sibiria) and North Africa (Algeria). It is quite problematic to distinguish species by characters of their shell, while it is not problematic to distinguish the genus from the other genera of the Planorbidae. The protoconch measures about 0.3 mm and has the characteristic ornament of the Planorbidae with fine spiral rows of tubercles crossed by regular fine axial lines (fig. 199). This ornament ends in the transition to the teleoconch and in the margin of the shell that is carried by the hatching young. Its aperture is inclined indicating a dextral mode of the hatching individuals. The umbilical view of the shell indicates the sinistral coiling mode of the protoconch (fig. 196).

Anisus krambergeri (HALAVATS, 1911) (Pl. 17/195–199)

The fossil species closely resembles *Anisus leucostoma* (MILLET, 1813) as was recorded by STOJASPAL (1989: pl. 1, fig. 8) from the Pontian of the Vienna Basin. SCHLICKUM (1978: pl. 18, fig. 8) illustrated this species that has the flat shell about 7 mm wide and consists of more than 5 whorls. It closely resembles the individuals from the Pontian of Papkesi (figs. 195–198) and Varpalota (figs. 198–199).

Anisus was also described by BARTHA (1955: pl. 1, fig. 5) and WENZ & ZILCH (1960: fig. 353). The latter placed it in the subgenus *Odontogyrorbis* LÖRENTHEY, 1906 with shell as in *Anisus* but the outer lip of the body whorl thickened.

Remarks: In case of the living *Anisus vortex* (LINNAEUS, 1758) the upper shell side is cup-like, 9–10 mm wide with basal keel. 6.5 to 7 whorls have indistinct sutures on the flat side and deep sutures on the umbilical side (figs. 200–203). The protoconch has a distinct left-sided coiling mode (figs. 201, 203) and is ornamented by fine spiral lines. The keel may lie more to the middle as is the case in *Anisus vorticulus* (TROSCHEL, 1834), but in the later the keel is more rounded (GLÖER & MEIER-BROOK, 1998). This later species has been recognized from the Pliocene of Romania (WENZ, 1942: pl. 27, figs. 407–410). It lives in slow moving and standing water all over Europe. *Anisus vorticulus* has concave base and top and whorls are separated by deep sutures. The 5 to 5.5 whorls have a dull median keel. The shell measures up to 4.5 mm in diameter, but is usually smaller. *Anisus spirorbis* (LINNÉ, 1758) has 4.5 whorls in a 4 to 5.5 mm wide shell. The upper side is flat, the lower concave and there is a dull edge to the base. The species prefers temporary shallow pools (GLÖER & MEIER-BROOK, 1998). *Anisus leucostoma* (MILLET, 1813) has 6 to 6.5 whorls which increase in diameter more regularly than is the case in *Anisus spirorbis*. The upper side is plane and the lower side concave and the shell is up to 7 mm in diameter. It occurs in temporary shallow ponds and can survive periods of dried conditions (GLÖER & MEIER-BROOK, 1998). This species was recognized from late Neogene lake deposits in Greece by RUST (1997: pl. 10, figs. 4–5). *Anisus septemgyratus* (ROSSMAESSLER, 1835) represents a variety of *Anisus leucostoma* according to GLÖER &

MEIER-BROOK (1998) but has 7.5 to 8 whorls. It lives to the east of the main race and is characteristic to temporary pools and flood plains.

The fossil *Anisus mariae* (MICHAUD, 1862) lived in a Late Miocene to Pliocene lake in the Granada Basin in Spain. Here six whorls are very regular with rounded aperture (ROYO-GOMEZ, 1922: fig. 32) and the shell has 5.5 mm in diameter is 0.7 mm high (BANDEL et al., 2000).

Bathyomphalus CHARPENTIER, 1837 with the type species *Bathyomphalus contortus* (LINNÉ, 1758) differs from *Anisus* by having the whorls of its plane shell more strongly overlapping onto each other. Its shell is 5–6 mm wide shell and consists of 7–8 tightly coiled whorls with deep, wide umbilicus, flattened apical side and aperture higher than wide (GLÖER & MEIER-BROOK, 1998). With its many whorls it resembles *Anisus* but whorls are coiled more tightly, and there are more whorls than in *Gyraulus*. The genus occurs from the Mediterranean region to Mongolia, in Europe all over in ponds and rivers.

Genus Segmentina FLEMING, 1817 (Pl. 16/190–194)

The shell is coiled in a plane with whorls overlapping and a rounded apical side and a flattened base. The type species is *Segmentina nitida* (O.F. MULLER, 1774) with whorls covering each other partly. The umbilicus is narrow and the apical whorls are largely hidden under the body whorl. Ornament consists of fine growth lines and the shell is shiny. Its aperture is inclined and the shell measures about 4–6 mm in diameter. *Segmentina nitida* was noted in the Pliocene lake of Arenas del Rey and Fuensanta in the Granda Basin in southern Spain. It closely resemble that described by RUST (1997: pl. 10, figs. 11–13) from the late Neogene of Greece. According to RUST (1997) this species has not changed in regard to shell shape since the Pannonian and occurs in Greece and Hungary. *Segmentina filocincta* (SANDBERGER, 1875) from the Levantin of Romania has the disc-like shell consisting of five somewhat angular whorls (WENZ, 1942. pl. 27, figs. 416–419). *Segmentina* closely resembles *Hippeutis* CHARPENTIER, 1837 with the shell of about four whorls coiled in a plane. The sides form a rounded keel, the top is rounded and the base is flattened with a wide umbilicus. The whorls of the teleoconch overlap onto each other. The type is *Hippeutis complanatus* (LINNAEUS, 1758) living in central Europe (WENZ & ZILCH, 1960: fig. 367).

Segmentina was noted from the Pontian of Papkesi and Varpalota at Lake Balaton. Here the shell is about 4 mm in diameter when fully grown and connected to a protoconch that is about 0.3 mm in diameter. The initial part of the embryonic shell is sinistral and dips below surface in the apical view of the shell (fig. 194). In juvenile shells the coiling appears to be with less overlapping whorls (figs. 190, 193) as in the later shell (fig. 191). While the teleoconch is basically smooth the protoconch has ornament of fine spiral ribs. This genus appears to have changed very little in its European occurrence since the late Miocene.

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- Fig. 1: Side view of *Cornirostra moesiensis* (JEKELIUS, 1944) from the Sarmatian of Soceni (Romania) with lowly coiled shell that measures 0.8 mm in width.
- Fig. 2: Cornirostra moesiensis from Soceni (Romania) with the shell 0.8 mm wide.
- Fig. 3: The same shell of *Cornirostra moesiensis* from Soceni as in fig. 1 in apical view.
- Fig. 4: The sinistral protoconch of *Cornirostra moesiensis* measures 0.15 mm and consists of 1.2 rounded whorls, detail to fig. 3.
- Fig. 5: Shell of *Cornirostra moesiensis* (JEKELIUS, 1944) from the Sarmatian near Yurkyne (Crimea) measures 0.9 mm in diameter.
- Fig. 6: Side view of *Cornirostra moesiensis* from the Badenian deposits of Bulganak, near Yurkyne (Crimea) with the shell about 0.7 mm high.
- Fig. 7: Transition from the smooth protoconch to the teleoconch of *Cornirostra moesiensis* from Yurkyne is quite indistinct. The shell is about 0.6 mm wide.
- Fig. 8: Detail to fig. 7 documents the protoconch of *Cornirostra moesiensis* from Yurkyne 0.15 mm and it consists of 1.2 rounded whorls.
- Fig. 9: Shell of *Vitrinella* C.B. ADAMS, 1850 from a subfossil reef near Cartagena Colombia is of a species still living in the Caribbean Sea at Santa Marta. This *Vitrinella* cf. *helicoidea* is about 1 mm wide. The protoconch is shown in fig. 10.
- Fig. 10: Protoconch of *Vitrinella* cf. *helicoidea* as in fig. 9 has a sinistral embryonic whorl half a larval whorl and diameter of about 0.15 mm.
- Fig. 11: Apical view of *Vitrinella urdunica* n. sp. from Aqaba (Gulf of Aqaba) (holotype) with the shell about 1.2 mm wide.
- Fig. 12: Protoconch of *Vitrinella urdunica* n. sp. from Aqaba with the end of the larval shell indicated by the thickened margin of the aperture (detail to fig. 11). The protoconch is 0.18 mm wide.



Plate 2 Fig. 13: Vitrinella jekelii n. sp. from the Sarmatian beds at Soceni in Romania with fig. 14 representing a detail and the shell about 1 mm wide. (Holotype) Fig. 14: Protoconch of Vitrinella jekelii n. sp. in the detail to fig. 13 with embryonic part sinistral and ending in a growth increment and larval part with thick margin of its aperture. Fig. 15: Shell of Tomura aqabaensis n. sp. from the Gulf of Aqaba is ornamented by growth lines and 0.8 mm in width. (Holotype) Fig. 16: Protoconch of Tomura aqabaensis n. sp. as detail to fig. 15 with the sinistral embryonic shell dipping below the surface of the plane larval shell and its end and onset of teleoconch. Fig. 17: View into the umbilicus of *Tomura agabaensis* n. sp. displays the sinistral protoconch with about 0.2 mm in width. Fig. 18: Shell of Tomura aqabaensis n. sp. seen from the side with wide umbilicus, view into it in fig. 17. Shell width 1.1 mm. Fig. 19: Shell of Sarmatorostra anistratenkoi n. sp. with rounded whorls and umbilicus is 1.3 mm high, from the Sarmatian of Cape Chrony at Yurkyne (Kerch Peninsula). (Holotype) Fig. 20: Juvenile shell of Sarmatorostra anistratenkoi n. sp. with the shell almost 1 mm high from Yurkyne. Fig. 21: Apical view of Sarmatorostra anistratekoi n. sp. of the shell in fig. 19. Fig. 22: Protoconch of Sarmatorostra anistratekoi with sinistral dip in the initial part of the embryonic shell. The protoconch measures 0.25 mm across. Protoconch Sarmatorostra anistratekoi in the detail to fig. 24 has a sinistral dip in the initial part Fig. 23: of the embryonic shell and is about 0.25 mm wide.

Fig. 24: Apical view of Sarmatorostra anistratenkoi n. sp. with the shell 1 mm wide.



- Fig. 25: Lateral view of *Spiricornirostra pantikapaionensis* n. sp. from Cape Takil at Zavitne, Kerch Peninsula shows a shell 1.3 mm wide with ornament of fine spiral ribs.
- Fig. 26: Spiricornirostra pantikapaionensis in apical view has the shell 1 mm wide. (Holotype)
- Fig. 27: Side view of *Spiricornirostra pantikapaionensis* of the holotype from the cliffs of Cape Takil south of Zavitne and shell 1.2 mm wide. Detail in fig. 28.
- Fig. 28: Protoconch of *Spiricornirostra pantikapaionensis* n. sp. has the initial part as sinistral and later as plane coil and is 0.25 mm wide. Detail to fig. 26.
- Fig. 29: Base of *Spiricornirostra pantikapaionensis* n. sp with wide umbilicus from Cape Takil near Zavitne.
- Fig. 30: Side view of *Spiricornirostra pantikapaionensis* n. sp. with 1.5 mm wide shell.
- Fig. 31: Protoconch of *Spiricornirostra pantikapaionensis* n. sp. with sinistral initial part and smooth larval portion ending in a ridge of the aperture, with 0.3 mm wide shell.
- Fig. 32: Side view of *Omalogyra helicinoides* (Stoliczka, 1862) from the Sarmatian of Cape Chrony at Yurkyne with shell 0.9 mm wide.
- Fig. 33: Shell of *Omalogyra helicinoides* with concave apical side and about 0.9 mm in diameter from the Sarmatian of Cape Takil near Zavitne, south of Kerch.
- Fig. 34: Omalogyra helicinoides from Yurkyne north of Kerch has the shell about 0.8 mm wide.
- Fig. 35: The embryonic whorl of *Omalogyra helicinoides* is planispiral and measures about 0.2 mm in diameter. Detail to fig. 34.
- Fig. 36: Shell of *Omalogyra helicinoides* from the Sarmatian near Zavitne with 0.5 mm in width.
- Fig. 37: Shell of *Omalogyra helicinoides* (STOLICZKA, 1862) from the Sarmatian of Soceni (Banat, Romania) with 0.7 mm wide shell.



- Fig. 38: Shell of *Omalogyra helicinoides* (STOLICZKA, 1862) from the Sarmatian of Cape Takil near Zavitne measures 0.8 mm in width.
- Fig. 39: Protoconch of *Omalogyra heliciinoides* in the detail to fig. 38 is seen in umbilical view with pit and ridge pattern and sinuous margin of the aperture, about 0.2 mm wide.
- Fig. 40: Valvata cristata from Lacul Razim lagoon of the Black Sea in Romania has a 1.8 mm wide shell.
- Fig. 41: Protoconch of *Valvata cristata* in fig. 40 has the end of the embryonic shell of about 0.22 mm in diameter and onset of the teleoconch well marked by strong growth increments.
- Fig. 42: Protoconch of *Valvata cristata* with the end of the embryonic shell not well indicated and growth increments present within the second embryonic whorl. The initial portion of the shell dips below surface due to sinistral coiling.
- Fig. 43: The shell of *Valvata cristata* from the Pliocene of Al Qarn Formation in the Jordan Valley has a shell of about 1.5 mm in diameter.
- Fig. 44: Umbilical view of *Valvata cristata* from the Pliocene Al Qarn Formation of the Jordan Valley has the embryonic whorl with sinistral initial coiling. The shell measures about 1.5 mm across.
- Fig. 45: *Valvata cristata* Müller, 1774 from the warm spring of Petea (Oradea, Romania) has a 3 mm wide shell.
- Fig. 46: Protoconch of *Valvata cristata* MÜLLER, 1774 from Petea has ornament of spiral ribs which become much weaker with begin of the teleoconch and is 0.4 mm wide.
- Fig. 47: Shell of just hatched *Valvata piscinalis* (MULLER, 1774) from a lake in North Germany with the first shell formed by a wrinkled cap and the further embryonic shell ornamented by spiral ribs and grooves, with 0.45 mm in width.
- Fig. 48: Embryonic shell of *Valvata piscinalis* (MULLER, 1774) demonstrating the same cap-like early shell distinct from the shell formed after detachment of the mantle from the shell by the embryo, with 0.45 mm in width.
- Fig. 49: *Valvata hellenica* TOURNOUER, 1877 from the Pliocene of Salakos Formation of Rhodes, width 1.3 mm.
- Fig. 50: Protoconch of *Valvata hellenica* TOURNOUER, 1877 from Salakos Formation, detail to fig. 51. The protoconch measures about 0.23 mm.
- Fig. 51: Apical view of Valvata hellenica TOURNOUER, 1877 from Salakos Formation, as in fig. 49.



Plate 5 Fig. 52: Shell of Valvata cf. saulcyi from Al Qarn Formation in the northern Jordan valley of Jordan is 2.2 mm wide. Fig. 53: Protoconch of Valvata cf. saulcyi from Al Qarn Formation, detail to fig. 52. About 0.33 mm wide. Fig. 54: Protoconch of Valvata cf. saulcyi is about 0.33 mm wide and has a repaired fracture formed after hatching, detail to fig. 55. Fig. 55: Juvenile shell of Valvata naticina MENKE, 1845 is about 2 mm wide, from Lacul Razim in the Delta region of the Danube in Romania. Fig. 56: Protoconch of Valvata naticina MENKE, 1845 is about 0.3 mm wide with spiral ornament from Lacul Razim in eastern Romania. Fig. 57: Apical view of Valvata tricarinata SAY 1817 from Michigan, North America with the multispiral operculum and 2 mm wide shell. Fig. 58: Apical side of the shell with a keel in Valvata tricarinata as in fig. 57, about 2 mm in diameter. Fig. 59: Protoconch of Valvata tricarinata with characteristic spiral pattern as detail to fig. 58 has 0.4 mm wide first whorl. Fig. 60: Shell of Valvata heidemariae WILLMANN, 1981 from the Pontian of Varpalota is 2.2 mm wide. Fig. 61: Apertural view of the fully grown shell of Valvata heidemariae from Varpalota (Hungary) with two keels and diameter of 2.2 mm. Fig. 62: Valvata heidemariae WILLMANN, 1981 has a corner to the base with wide umbilicus and is the same as in fig. 61. Fig. 63: Protoconch of Valvata heidemariae WILLMANN, 1981 with 0.4 mm wide first whorl, detail to fig. 60.



Plate 6	
Fig. 64:	Valvata kamirensis WILLMANN, 1981 from Salakos Formation in Rhodos seen from the side with the three spiral keels is about 2.6 mm wide.
Fig. 65:	Protoconch of <i>Valvata kamirensis</i> (detail to fig. 66) from Salakos Formation in Rhodes with the first whorl about 0.3 mm wide and with fine spiral ornament.
Fig. 66:	<i>Valvata kamirensis</i> from Salakos Formation with peripheral keel and collabral ornament with shell about 2 mm wide.
Fig. 67:	Protoconch of <i>Valvata kamirensis</i> (detail to fig. 66) from Salakos Formation in Rhodes with fine dense spiral ornament, with about 0.4 mm.
Fig. 68:	Basal view of <i>Valvata kamirensis</i> from Salakos Formation with spiral rib around the conical umbilicus and shell about 2 mm wide.
Fig. 69:	Hauffenia POLLONERA, 1898 resembles Islamia and Horatia and also cf. Heraultia exilis from the Pannonian of Kötese at Lake Balaton, about 1 mm wide shell.
Fig. 70:	Protoconch of the <i>Heraultia</i> BODON, MANGANELLI & GUISTI, 2001; like specimen in fig. 69 from the Pannonian of Kötese at Lake Balaton, Hungary is 0.22 mm wide.
Fig. 71:	Shell of cf. <i>Heraultia</i> from the Pannonian of Soceni (Romania) has the protoconch in fig. 72 and is 0.9 mm wide.
Fig. 72:	Protoconch of cf. <i>Heraultia</i> from Soceni is about 0.2 mm wide and of the hydrobioid type with fine groove and ridge ornament and little more than one whorl.
Fig. 73:	Shell of cf. <i>Heraultia</i> from the Pannonian of Tihany that closely resembles <i>Müllerpalia simplex</i> (figs. 95–98) is 1.2 mm wide.
Fig. 74:	Protoconch of cf. <i>Islamia</i> RADOMAN, 1973 from the Pannonian of the cliff at Tihany, Lake Balaton is 0.22 mm wide with granular ornament, detail to fig. 73.
Fig. 75:	Fully grown shell of cf. <i>Islamia</i> from the Pontian of Balatonaligna near Lake Balaton, Hungary is 1 mm wide, detail in fig. 76.
Fig. 76:	Protoconch of cf. <i>Islamia</i> with granular ornament and distinct change in ornament at hatching is about 0.22 mm wide, detail to fig. 75.



Plate 7	
Fig. 77:	Cf. Horatia BOURGUIGNAT, 1887 from the Pliocene Al Qarn Formation of Jordan with shell 1 mm wide.
Fig. 78:	Protoconch of cf. Horatia from the Pontian of Papkesi is 0.22 mm wide, detail to fig. 79.
Fig. 79:	Fully grown shell of cf. <i>Horatia</i> from Papkesi near Balatonkenese on Lake Balaton is about 1.2 mm wide, with detail of the protoconch in fig. 78.
Fig. 80:	Final whorl of cf. <i>Horatia</i> detaches from adult shell from Pontian of Papkesi with detail in fig. 81.
Fig. 81:	Protoconch of fig. 80 with granular ornament, 0.22 mm in width and distinct change in ornament after hatching.
Fig. 82:	Shell of <i>Muellerpalia bicinata</i> (FUCHS, 1870) from the Pontian of Tihany seen with the base that has a wide umbilicus, shell about 1.2 mm wide.
Fig. 83:	Shell of <i>Muellerpalia bicinata</i> from Tihany at Lake Balaton, Hungary in apical view with the shell about 1.2 mm wide.
Fig. 84:	Shell of <i>Muellerpalia bicinata</i> from the Pontian Tihany with rounded aperture and 1.2 mm in width.
Fig. 85:	Protoconch of <i>Muellerpalia bicincta</i> with about 0.2 mm in width, dextral coiling mode, and ornament of fine granules, detail to fig. 82 from the Pontian of Tihany.
Fig. 86:	Apical view of <i>Muellerpalia carinata</i> (FUCHS 1870) from the Pontian of Kötese at the Balaton with shell about 1.2 mm wide.
Fig. 87:	Basal view of Muellerpalia carinata from Kötese with shell about 1.2 mm wide.
Fig. 88:	Protoconch of <i>Muellerpalia carinata</i> with 1.5 whorls and 0.27 mm in width. Detail to fig. 86.
Fig. 89:	Shell of Muellerpalia carinata from Kötese with 1.2 mm width.



Plate 8 Apical view of the shell of Muellerpalia varians (FUCHS 1870) from Kötese at Lake Balaton Fig. 90: Hungary, 1.2 mm wide. Fig. 91: Protoconch of Muellerpalia varians from Kötese with first whorl about 0.2 mm wide and granular ornament. Fig. 92: Juvenile shell of Muellerpalia varians from Tihany, 0.8 mm wide and transition from protoconch to teleoconch, detail in fig. 93. Fig. 93: Protoconch of the shell of Muellerpalia varians in fig. 92 is 0.25 mm with a groove and ridge pattern. Fig. 94: Shell of Muellerpalia varians from Köbanya Ujhegy, same as in fig. 91, with groove and ridge pattern while the teleoconch has ornament of growth lines. Fig. 95: Fully grown shell of Muellerpalia simplex (FUCHS, 1870) from the Pontian of Köbanya Ujhegy, Lake Balaton is 2 mm wide. Fig. 96: Shell of Muellerpalia simplex (FUCHS, 1870) from the Pontian of Tab, about 1 mm wide. Fig. 97: Shell of Muellerpalia simplex (FUCHS, 1870) from Tab, 1 mm wide with fine spiral ornament. Fig. 98: Detail to fig. 97 with the protoconch of *Muellerpalia simplex* from Tab, about 0.2 mm wide and ornament of groove and ridge pattern. Fig. 99: Shell of Muellerpalia tabensis n. sp, 1 mm wide from the Pontian of Tab. Fig. 100: Shell of *Muellerpalia tabensis* n. sp of the same as in fig. 99 with the ornament of spiral lines.

Fig. 101: Base of the shell of *Muellerpalia tabensis* n. sp. with wide umbilicus, 1.6 mm wide, from the Pontian of Tab.



Fig. 102: Shell of <i>Muellerpalia tabensis</i> n. sp. from the Pontian of Tab, 1	1.2 mm wide.
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- Fig. 103: Protoconch of *Muellerpalia tabensis* n. sp in detail to fig. 102 is about 0.2 mm wide.
- Fig. 104: Shell of *Muellerpalia striata* n. sp. from the Pontian of Balatonkenese Csittenyhegy is about 1.2 mm wide.
- Fig. 105: Shell of *Muellerpalia striata* n. sp. from the Pontian of Balatonkenese Csittenyhegy is 1.3 mm wide.
- Fig. 106: Base of *Muellerpalia striata* n. sp. from the Pontian of Csittenyhegy with wide umbilicus and shell width of 1.3 mm.
- Fig. 107: Apical side of *Muellerpalia striata* n. sp. is plane, from the Pontian of Balatonkenese Csittennyhegy level at the railway, Lake Balaton, Hungary, 1.5 mm wide.
- Fig. 108: Shell of *Graecamnicola* WILLMANN, 1981 from the Pontian of Köbanya Ujhegy is about 2 mm wide.
- Fig. 109: Fully grown shell of *Graecamnicola* from the Pontian of Köbanya Ujhegy is about 2 mm in size.
- Fig. 110: Apical view of *Graecamnicola* from the Pontian of Köbanya Ujhegy with the smooth protoconch about 0.4 mm wide.
- Fig. 111: Shell of *Jekeliella balatonica* (ROLLE, 1861) from the Pontian of west of Varpalota near Lake Balaton is 2 mm high.
- Fig. 112: Apical view of *Jekeliella balatonica* from the Pontian of Varpalota with the smooth protoconch that is in detail in fig. 114.
- Fig. 113: Fully grown shell of *Jekeliella balatonica* from the Pontian of Varpalota is 2 mm high with the aperture fractured.
- Fig. 114: Protoconch of *Jekeliella balatonica* as detail to fig. 112 from the Pontian of Varpalota is almost 0.5 mm wide and almost smooth.



- Fig. 115: The apical view of *Jekeliella gradata* (FUCHS, 1870) from the Pontian of Varpalota with about 1.5 mm wide shell.
- Fig. 116: Protoconch of *Jekeliellaa gradata* measures 0.3 mm in width with pitted ornament, detail to fig. 115 from Pontian of Varpalota just east of Lake Balaton, Hungary.
- Fig. 117: Shell of *Jekeliellaa gradata* from Varpalota is almost 2 mm wide.
- Fig. 118: Protoconch of *Jekeliella gradata* in fig. 119 with a bit more than 0.3 mm in diameter and pitted surface ornament.
- Fig. 119: Fully grown shell of *Jekeliellaa gradata* from Varpalota with about 1.8 mm wide shell.
- Fig. 120: Shell of *Jekeliellaa tenuistriata* (FUCHS, 1870) from the Pontian of Tab is more than 3 mm high.
- Fig. 121: Protoconch of *Jekeliellaa tenuistriata* from Tab is 0.3 mm wide with a wrinkles surface ornament. Detail to fig. 123.
- Fig. 122: Juvenile shell of *Jekeliellaa tenuistriata* from Tab is less than 1mm high and has the transition from rounded protoconch to rib bearing teleoconch.
- Fig. 123: Apical view of *Jekeliellaa tenuistriata* from Tab has the shell 0.8 mm wide.
- Fig. 124: Jekeliellaa tenuistriata from Tab has the ornament disappearing on the third whorl of the teleoconch.
- Fig. 125: Protoconch of *Jekeliella tenuistriata* detail to fig. 124 is 0.2 mm wide.



- Fig. 126: *Jekeliellaa dombovarensis* n. sp from Dombovar south of Lake Balaton, Hungary, holotype with 4 mm high shell.
- Fig. 127: Jekeliellaa dombovarensi n. sp. from Dombovar at the Lake Balaton is 4 mm wide.
- Fig. 128: Base of *Jekeliella dombovarensis* n. sp. with wide conical umbilicus from Dombovar.
- Fig. 129: Jekeliella dombovarensis n. sp. with about 4 mm high shell from Dombovar.
- Fig. 130: *Graecamnicola euomphala* (FUCHS, 1877) from Salakos Formation, Rhodes has the shell of almost 3 mm in width.
- Fig. 131: Juvenile shell of *Graecamnicola euomphala* from Salakos Formation from Rhodes is 1.2 mm wide.
- Fig. 132: Surface of the shell of *Graecamnicola euomphala* has frost-flower like calcite crystallites of about 2–5 micron in width which mineralized the periostracal layer.
- Fig. 133: Juvenile shell of *Graecamnicola euomphala* as in fig. 131 has the transition from the smooth protoconch to the ornamented teleoconch.
- Fig. 134: Detail of the protoconch of *Graecamnicola euomphala* as in fig. 133 with smooth surface and a diameter of almost 0.5 mm.
- Fig. 135: Protoconch of *Kerchia yurkynensis* n. sp. that is 0.4 mm wide, from Cape Chrony just east of Yurkyne, Kerch Peninsula.
- Fig. 136: Juvenile shell of *Kerchia yurkynensis* n. sp. with 1.8 mm high shell from Yurkyne.
- Fig. 137: Apical view of *Kerchia yurkynensis* n. sp. with shell 1.6 mm wide from Cape Chrony.
- Fig. 138: Protoconch of *Kerchia yurkynensis* n. sp. with fine groove and pit ornament an dextral coiling mode, about 0.3 mm wide up to the begin of growth lines.
- Fig. 139: Fully grown *Kerchia yurkynensis* n. sp. with 1.5 mm high shell, holotype from Cape Chrony, Yurkyne.



- Fig. 140: Apical side of the shell of *Fuchsogyra radmanesti* from Kötese at Lake Balaton, Hungary has a width of 4 mm.
- Fig. 141: Protoconch of *Fuchsogyra radmanesti* (FUCHS, 1870) from Kötese consists of the smooth primary shell and the axially ribbed secondary shell and is 0.6 mm wide.
- Fig. 142: Apical side of the shell of *Fuchsogyra radmanesti* from Kötese is 2 mm wide.
- Fig. 143: The smooth embryonic shell of the protoconch of *Fuchsogyra radmanesti* from Kötese is 0.3 mm wide and ends with strong growth increments.
- Fig. 144: Flat umbilical side of the shell of *Fuchsogyra radmanesti* from Kötese is 2.2 mm wide.
- Fig. 145: Umbilical side of the protoconch of *Fuchsogyra radmanesti* from Kötese, with first whorl about 0.55 mm wide.
- Fig. 146: Umbilical view of *Fuchsogyra balatonica* n. sp. from the Pontian of Tihany with 1.6 mm wide shell, detail in fig. 147. Holotype.
- Fig. 147: Protoconch of *Fuchsogyra balatonica* in detail to Fig. 146 with smooth first whorl succeeded by the late embryonic shell with strong axial ribs, protoconch measures 0.5 mm in width.
- Fig. 148: Apical side of *Fuchsogyra balatonica* from Tihany (detail in fig. 152) with the shell almost 1 mm wide.
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- Fig. 150: Fully grown shell of *Fuchsogyra balatonica* seen from the side is about 2 mm wide.



- Fig. 151: Side view of the shell of *Fuchsogyra balatonica* from Tihany with transition from the protoconch to the teleoconch is almost 1 mm wide.
- Fig. 152: Protoconch of *Fuchsogyra balatonica* in the detail to fig. 148 with transition of smooth initial part to ribbed second part.
- Fig. 153: Apical view of the shell of *Marinescugyra varians* (FUCHS, 1870) from the Pontian of Balatonkenese Csittenyhegy at the eastern side of Lake Balaton (Hungary) is almost 3 mm wide.
- Fig. 154: Protoconch of *Marinescugyra varians* as detail to fig. 153 with smooth surface, about 0.4 mm in width and change of ornament and shape to the teleoconch.
- Fig. 155: Juvenile shell of *Marinescugyra varians* from the Pontian of Balatonkenese with protoconch with repaired fracture right after hatching with about 1 mm wide shell.
- Fig. 156: Protoconch of *Marinescugyra varians* on the umbilical side with begin of the peripheral keel after hatching, detail to fig. 157.
- Fig. 157: Umbilical side of *Marinescugyra varians* from the Pontian of Balatonkenese with about 3 mm wide shell.
- Fig. 158: Side view of the shell of *Marinescugyra varians* from the Pontian of Balatonkenese is about 0.6 mm high.
- Fig. 159: Protoconch of *Marinescugyra tenuis* (FUCHS, 1870) from Kötese, detail to fig. 160. Embryonic shell ends with strong growth line and is 0.4 mm wide.
- Fig. 160: Apical view of the shell of *Marinescugyra tenuis*, with detail of its protoconch in fig. 159 from Kötese is about 1 mm wide.
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- Fig. 162: Shell of *Marinescugyra tenuis* from Varpalota is 2 mm wide.



- Fig. 163: Protoconch and early teleoconch of *Marinescugyra tenuis* from Varpolota with 1.2 mm wide shell.
- Fig. 164: Shell of *Marinescugyra tenuis* from Tihany is 1.5 mm wide.
- Fig. 165: Shell of *Marinescugyra tenuis* from Tihany is 1.5 mm wide.
- Fig. 166: Juvenile shell of 2.2 mm width of *Planorbarius* FRORIEP, 1806, cf. *Planorbarius corneus* (LINNEUS, 1758) from the Pannonian of Papkesi with the end of the embryonic shell in the transition from second to third whorl and is about 1.5 mm wide.
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- Fig. 171: Protoconch of *Planorbis* from Balatonaligna, detail to fig. 170, with fine spiral ornament on the first whorl and increase of growth lines in the transition to the teleoconch. The first whorl is about 0.5 mm wide.
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