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# Late Miocene (Pannonian) Gastropods of Lake Pannon with Special Emphasis on Early Ontogenetic Development

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(With 5 text-figures and 13 plates)

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## Summary

An extraordinarily well-preserved brackish to freshwater gastropod fauna of the Early Pannonian (Late Miocene) is described. The assemblage derives from the Austrian part of the Eisenstadt-Sopron Basin (sand pit "Zollhaus" close to St. Margarethen in Burgenland, Austria) and represents a typical assemblage of the Pannonian Zone C/D. Green to greyish fine sand, deposited below wavebase off the coast of Lake Pannon, yields high numbers of synchronous, allochthonous shells of melanopsids and scattered autochthonous congerias and cardiids (Lymnocardiinae). Along with inhabitants of the adjacent rivers, such as *Tinnyea escheri vasarhelyii* and *Unio atavus*, the melanopsids were shed from coastal biotas of Lake Pannon into the somewhat deeper environment. Most of the shells acted as shuttle for micro-gastropods and thus allowed a sediment-microfauna bypass from the now eroded coastal habitat to the preserved basinal environments. A total of 34 gastropod taxa are described; among these, *Boistelia soceni* is introduced as new species or new hybrid.

For the first time, attention is directed especially to the protoconchs and early ontogeny of several characteristic Lake Pannon gastropods. These studies also shed light on the until now rather dubious systematic treatment of the characteristic Pannonian genus *Orygoceras* BRUSINA, 1882, which is demonstrated to be of planorbid origin. This also results in the clear separation of the European, Late Miocene, endemic genus *Orygoceras* from the North American hydrobiids erroneously affiliated with this genus. Rarely reported and until now insufficiently documented representatives of the genera *Theodoxus, Neritina, Goniochilus,* and *Gyraulus* are described. Additionally, the systematic status of the oversplit *Melanopsis fossilis*-group is discussed.

**Keywords:** Lake Pannon, Eisenstadt-Sopron Basin, Late Miocene, Pannonian, Gastropoda, early ontogeny, species concepts

## Zusammenfassung

Eine ungewöhnlich gut erhaltene Gastropodenfauna aus dem frühen Pannonium (Pannonium Zone C/D, Oberes Miozän) wird beschrieben. Die Fauna stammt aus dem österreichischen Anteil des Eisenstadt-Sopron Beckens aus der Sandgrube "Zollhaus" nahe der ungarisch/österreichischen Grenze bei St. Margarethen im Burgenland. Die aufgeschlossenen grün-grauen Feinsande enthalten zahlreiche Gehäuse dickschaliger Melanopsiden, die ebenso wie vereinzelte Fluß-Elemente wie *Unio atavus* und *Tinnyea escheri vasarhelyii,* aus dem Küstenbereich in das etwas tiefere Seebecken transportiert wurden. Sedimentologie sowie die autochthonen Lymnocardiinae und Congerien deuten auf Ablagerung unterhalb der Wel-

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lenbasis hin. In den Sedimentfüllungen der Melanopsiden wurde so eine reiche Mikrogastropodenfauna aus den inzwischen erodierten Uferbiotopen des Pannonischen Sees in etwas uferfernere Bereiche eingetragen.

Insgesamt konnten 34 Taxa nachgewiesen werden, darunter wird *Boistelia soceni* als neue Art (oder als neuer Hybrid) eingeführt.

Erstmals wird bei der Beschreibung von Gastropden des Pannonischen Sees speziell auf frühontogenetische Schalenmerkmale eingegangen. Dadurch konnte die systematische Stellung der kontroversiell diskutierten Gattung *Orygoceras* BRUSINA, 1882 geklärt werden, die als Planorbide interpretiert wird. Daraus ergibt sich die klare Trennung dieser endemischen Gattung von den nordamerikanischen Hydrobiiden, die fälschlich zu *Orygoceras* gestellt wurden.

Neben der Beschreibung von seltenen und bisher ungenügend dokumentierten Arten der Gattungen *Theodoxus, Neritina*, *Goniochilus,* and *Gyraulus* wird die systematische Stellung der *Melanopsis fossilis*-Gruppe diskutiert.

**Schlüsselwörter:** Pannonischer See, Eisenstadt-Sopron Becken, Spätes Miozän, Pannonium, Gastropoden, frühe Ontogenie, Artkonzepte

## Introduction

The mollusc fauna of the slightly brackish Lake Pannon has been extensively studied for more than 160 years (e.g. PARTSCH 1835; CZJZEK 1849). Most of the "Grand Masters" of European Neogene molluscan studies dealt with the fascinating fauna of this ancient lake, whose biota is in fact the heritage of the marine Paratethys Sea. The isolated position of this vast lake granted a laboratory situation for Darwinists but also served as an ideal frame for biostratigraphers, who usually based their conclusions on the rapidly evolving molluscan fauna. During the 20$^{th}$ century the knowledge on the faunistic inventory of the ancient lake was steadily improved by rather modern-style monographs of LŐRENTHEY (1902), JEKELIUS (1944), and PAPP (1953), which are still the foundation for most subsequent studies. Finally, since the 1980s many papers have focused on systematic problems of Pannonian gastropod faunas (e.g. GEARY 1988, 1990; GEARY et al. 1989; FORDINAL 1991, 1993; BANDEL 2000). Modern REM-techniques, however, were rarely applied in identifying and describing the diverse lake fauna. Several species are still only published as drawings such as shown in PAPP (1953; 1985), not to mention the poor quality photographs in many papers of the 1970s and 1980s. These insufficiencies supported our decision to publish this late Early Pannonian gastropod fauna of the Eisenstadt-Sopron Basin, which may well serve as a reference fauna of this interval. The studied material derives from the Pannonian Zone C/D of St. Margarethen, and represents a gastropod assemblage from the western part of Lake Pannon during the older part of the Carpathian-Pannonian Cycle CPC 7 sensu BARÁTH & KOVÁČ 2000. The figured specimens are deposited in the collection of the Natural History Museum, Vienna.

## Geological Setting

The site St. Margarethen is situated in the Austrian/Hungarian Eisenstadt-Sopron Basin, which is bordered by the Leithagebirge in the N, the Fertörákos-Ruster Hügelland in the E, the Sopron Hills in the S and the Rosaliengebirge in the W. It is interpreted as a small satellite basin of the Vienna Basin (STEININGER 1991). St. Margarethen in Burgenland is one of the most important localities for Neogene studies in Austria. Near the village several fossiliferous outcrops encompass a succession from the Badenian (Middle Miocene) to the Sarmatian (Late Middle Miocene) and to the Pannonian (Late Miocene).

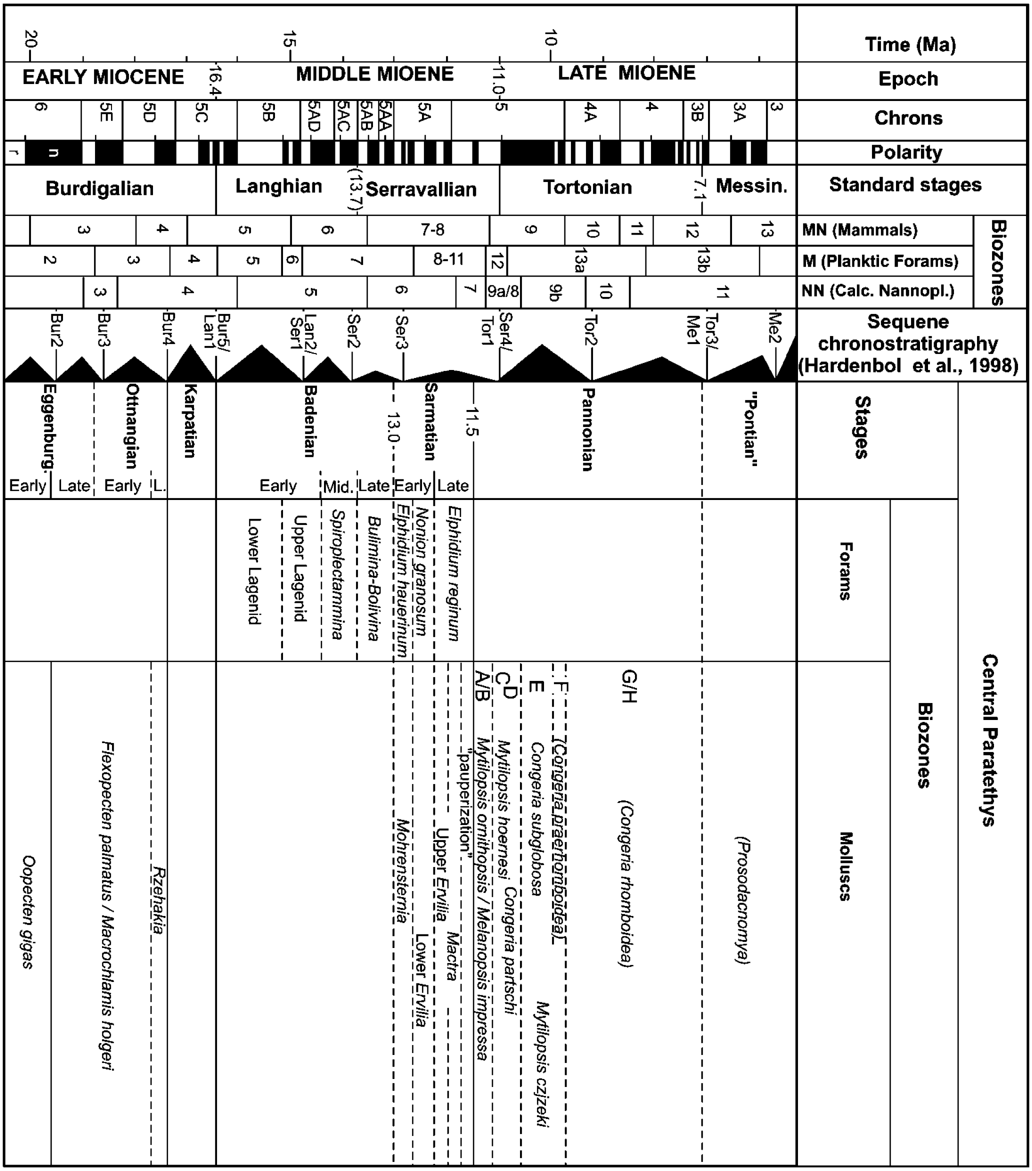


Fig. 1: Stratigraphic correlation chart of the standard scale with the Central Paratethys regional stage system and the foraminifera and mollusc biozones.

The Badenian sections are famous for the yellowish-white Leitha Limestone, which was already exploited during Roman times. An extensive introduction into the sedimentology, regional geology, and paleoecology of these deposits was given by SCHMID et al. (2001). Slightly younger sediments of the late Middle Miocene Sarmatian stage and the Late Miocene Pannonian stage crop out at the sand pit "Zollhaus". This pit is situated in the communal forest close to the Austrian/Hungarian border (geological map ÖK

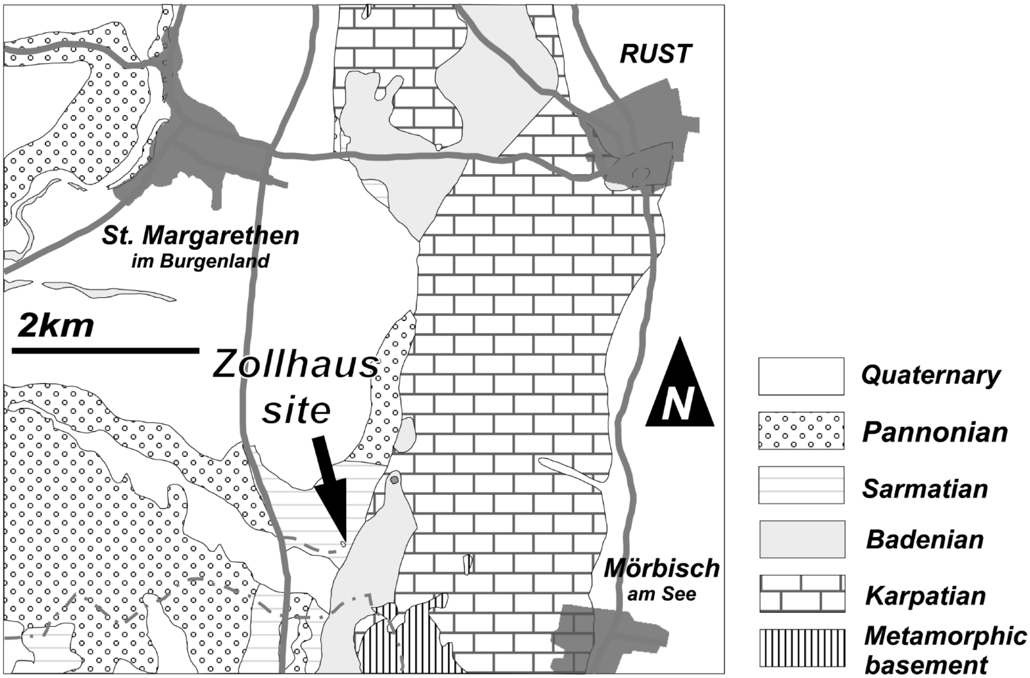



Fig. 2: Location of the section St. Margarethen "Altes Zollhaus".

1:50,000, sheet 78 Rust) and represents the largest Sarmatian/Pannonian outcrop within the Neogene Eisenstadt-Sopron Basin. The section St. Margarethen "Zollhaus" was intensively studied during the last years by PILLER & VAVRA (1991), ROSTA (1993), DECKER & PERESSON (1996), HARZHAUSER & MANDIC (1997), HARZHAUSER et al. (2000), WAGREICH et al. (2000), and HARZHAUSER & KOWALKE (in prep.). All these studies focused mainly on the Sarmatian part. This part is represented by an about 30-m-thick succession of gravel, marly sand, and scattered detritic limestones. Its rich molluscan fauna allows a dating into the Late Sarmatian *Mactra* Zone; a detailed paleoecological description of this part is given by HARZHAUSER & KOWALKE (in prep.). Upsection follows a second cycle comprising sand and silt of the Pannonian (Zone B and Zone C/D sensu PAPP 1951, 1953). The Sarmatian part of the succession ends with a characteristic 30-cm-thick top bed of calcareous marls bearing a diverse molluscan fauna with in-situ *Cerastoderma latisulcum*. The unusual lithology of this limy bed may point to a subaerial phase of erosion. The chronostratigraphic gap from the Sarmatian *Mactra* Zone to the Pannonian Zone B, which spans the entire Sarmatian "pauperisation Zone" and the Pannonian Zone A, coinciding with the generally accepted lowstand at the Sarmatian/Pannonian boundary (KOVÁČ et al. 1998; BARÁTH & KOVÁČ 2000), would support this conclusion. The occurrence of extraordinary numbers of *Melanopsis impressa* accompanied by *Mytilopsis ornithopsis* in the base of the overlying gravel indicate the deposition of the gravel during the Pannonian Zone B. This about 2-4-m-thick layer is concordantly overlain be greenish grey, fine- to middle sand of the Pannonian Zone C/D sensu PAPP (1951; 1953) with frequent shells of *Melanopsis fossilis*.

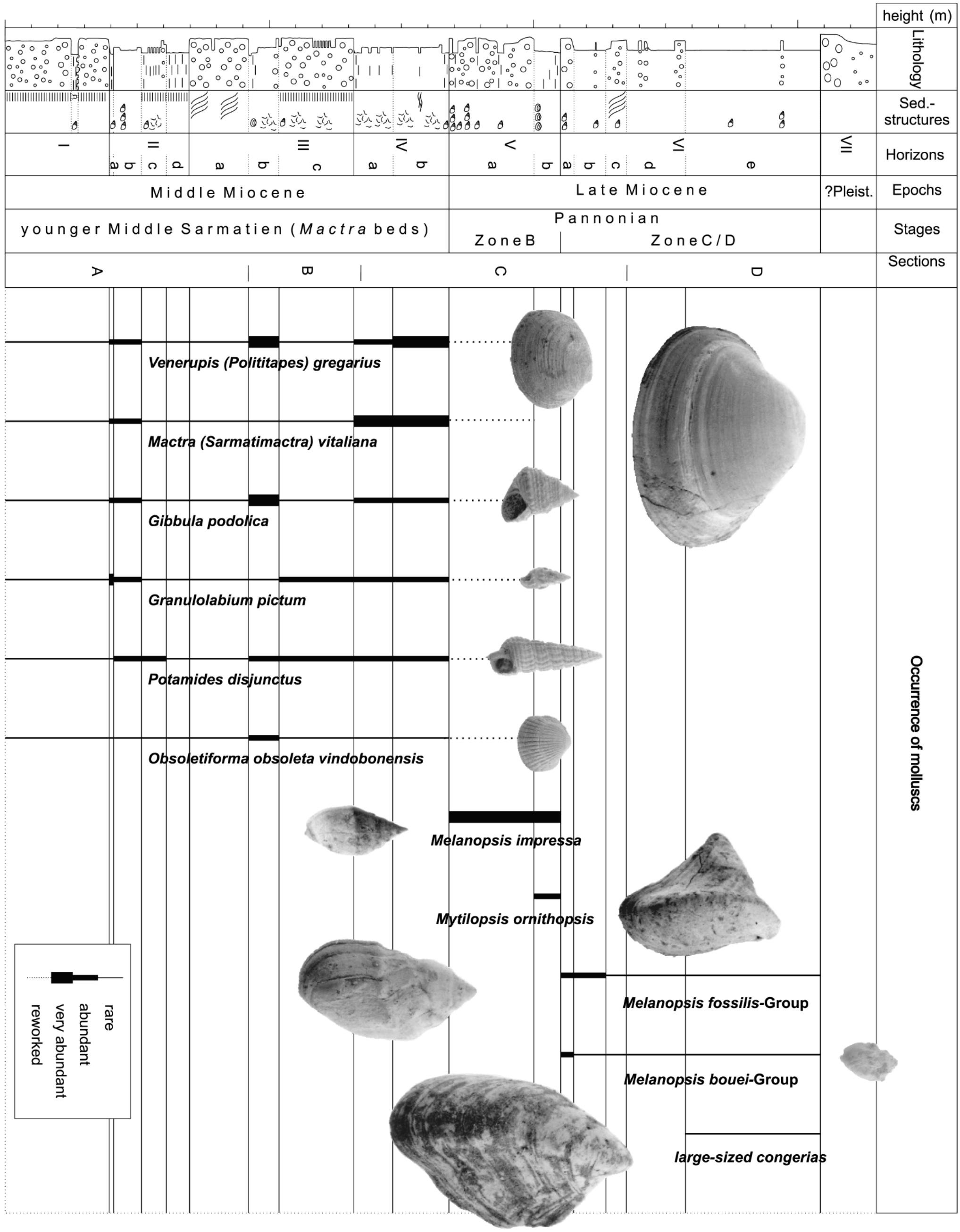



Fig. 3: Idealised log of the section with correlation of biozones.

Towards the top of the succession, only scattered layers (1-4 cm thickness) of fine gravel can be detected which are enriched in shells of various melanopsid species. Rare lithoclasts of Late Sarmatian marl are bound either to the high energetic, basal marls of

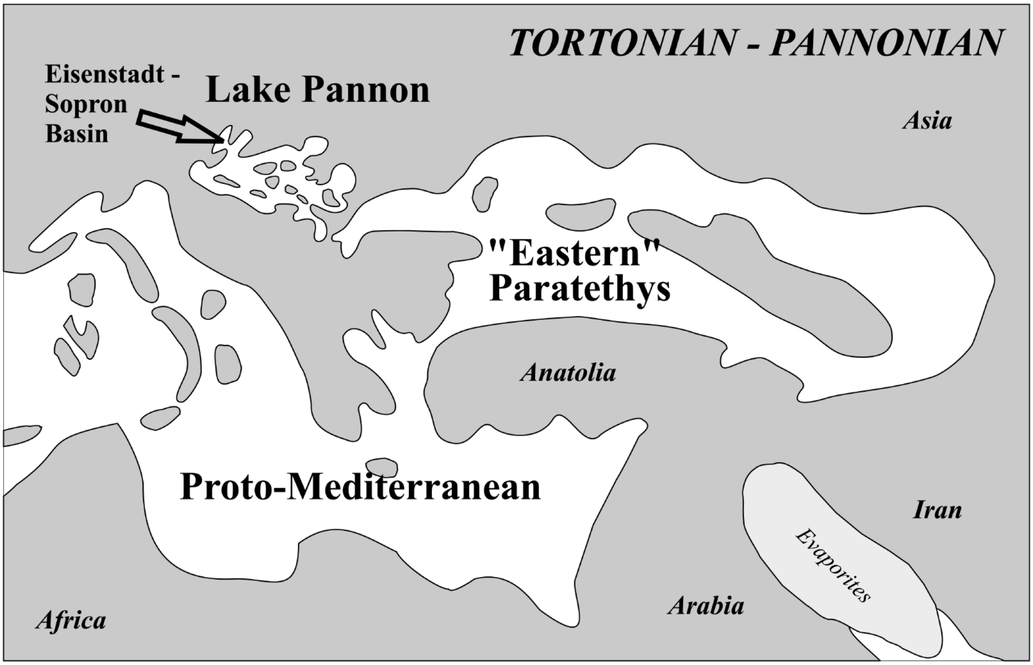



Fig. 4: Paleogeography of Lake Pannon, the Eastern Paratethys, and the Proto-Mediterranean during the Pannonian (after RÖGL, 1999)

the Pannonian zone B or to the gravel layers at the top. Whilst *Melanopsis fossilis* may also be found in the fine to medium sand, especially *Melanopsis inermis* and the theodoxids are bound to the coarse layers, indicating an allochthonous occurrence. The same holds true for all specimens of *Unio atavus* and for most *Tinnyea escheri vasarhelyii,* which are also more common in layers with *Melanopsis inermis* and theodoxids.

The scattered, large-sized and partly articulated congerias and Lymnocardiinae document a paleoenvironment off the coast of Lake Pannon and may even indicate water depths below wave base. Neither the congerias nor the lymnocardiine bivalves are enriched in coquinas or recognisable layers. Especially in the lower units, even the melanopsids appear only as scattered shells. Towards the top, which is definitely part of the Pannonian Zone D, thin gravel layers with frequent gastropod shells increase in number, pointing to stronger fluvial influx. Hence, the increase of coarse sand and fine gravel, coinciding with increasing numbers of unionids, theodoxids, and melanopisds, can be interpreted as a minor shallowing and coarsening upward cycle. Such a development correlates well with a minor sea level fall in the late Pannonian Zone D (PAPP 1951), which is considered to represent 4th order lowstand systems tracts by KOVÁČ et al. (1998).

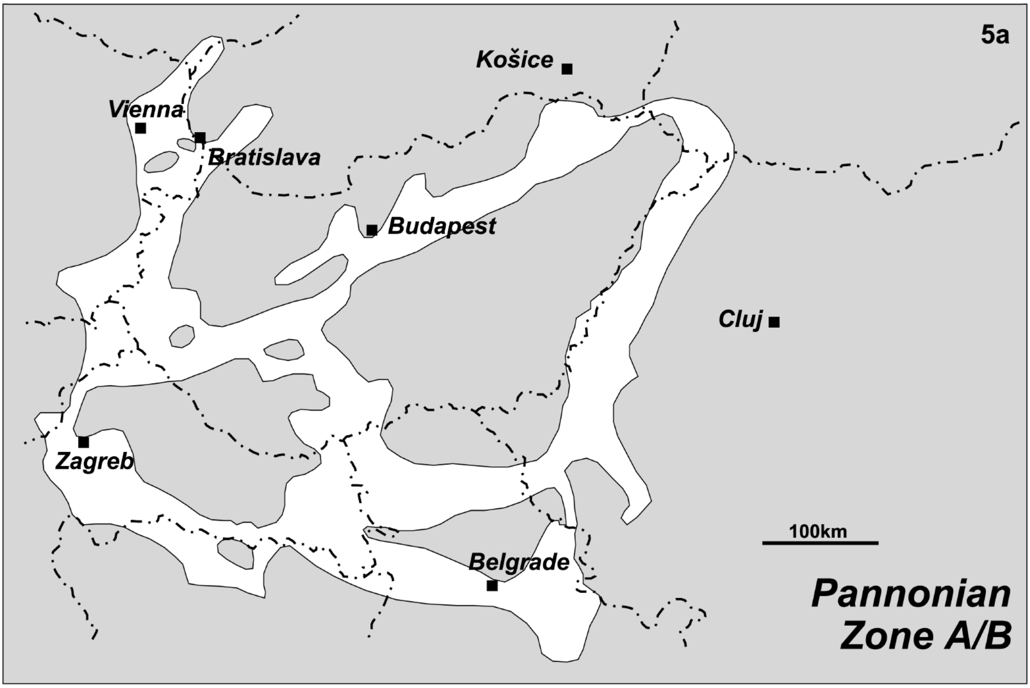
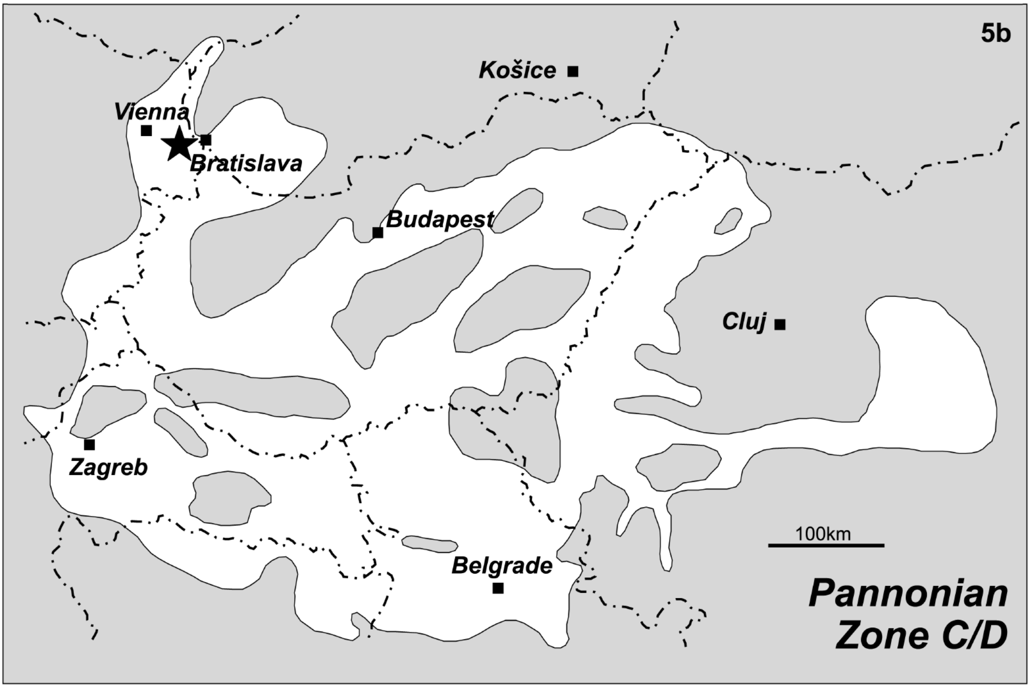



Fig. 5a: Paleogeography of Lake Pannon in 3 timeslices (after MAGYAR, GEARY & MÜLLER, 1999)

5a: Lowstand of the Pannonian Zones A and B. In the Northern Vienna Basin the sedimentation of coarse gravel of the Hollabrunn-Mistelbach Formation prevails. Correspondingly, fluvial gravel with *Melanopsis impressa* and *Mytilopsis ornthopsis* - shed by drainage systems from the south or south east - crop out in the Eisenstadt-Sopron Basin.

5b: Paleogeography during the Pannonian Zones C/D. This timeslice represents the interval when the investigated fauna flourished. The Leitha Mountains and the Ferörákos-Rust Mountains were largely flooded by Lake Pannon. Offshore conditions below wave base were esteblished in the study area. Emerged parts of the nearby Ferörákos-Rust Mountains, however, acted as highs, from where reworked Badenian Limestone, Sarmatian marl and sandstone, and rare crystalline lithoclasts were shed into the basin during the HST of the late Pannonian Zone D.

5c: The situation during Pannonian Zones E/F. After a minor lowstand during the latest Pannonian Zone D, which is also expressed in the upper part of the section "Altes Zollhaus", Lake Pannon experienced its maximum flooding stage in the early Pannonian Zone E. A rather drastic change in the composition of the gastropod fauna occurred around this flooding event, probably triggered by a marked change of water chemistry.



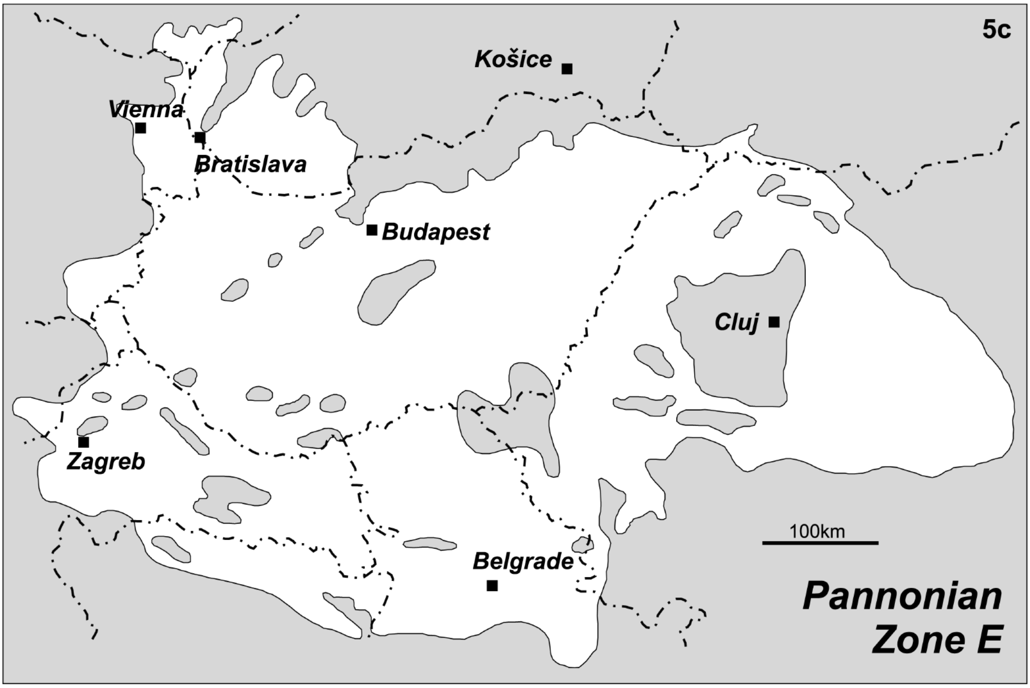




Fig. 5b-c (continued): Paleogeography of Lake Pannon in 3 timeslices (after MAGYAR, GEARY & MÜLLER, 1999)

## Systematic Paleontology

Subclass Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily Neritoidea RAFINESQUE, 1815

Family Neritidae RAFINESQUE, 1815

Subfamily Neritinae RAFINESQUE, 1815

Genus: *Theodoxus* MONTFORT, 1810

### *Theodoxus cunici* (BRUSINA, 1892)

(Plate 1, Figs. 1-2, 4)

1892 *Neritodonta Cunici* BRUSINA n. sp. – BRUSINA, p. 65
1902 *Neritina (Neritodonta) Cunici* BRUSINA in litteris – LŐRENTHEY, p. 245, pl. 18, fig. 29
1902 *Neritodonta Cunici* BRUSINA – BRUSINA, pl. 15, fig. 1-3
1979 *Theodoxus (Theodoxus) cunici* (BRUSINA) – JURIŠIĆ-POLŠAK, p. 24, pl. 7, fig. 1-2.

**Description:** Very small shell of approximately 3 mm maximum diameter with very low spire. A few specimens are nearly fully involute, whereas most display a slightly emerged spire. The convex whorls are somewhat flattened in the posterior part, sometimes forming a sutural ramp. Its strongly inflated last whorl terminates in a broad, obliquely elongated aperture. The flat, sunken septum is limited by a slightly concave edge. No dentition is developed in the Austrian specimens; only the anterior part sometimes diplays a weak convexity. The shell bears a very dense and distinct pattern of growth lines, yielding a characteristic, strongly sculptured surface. Colour ornament consists of three thin rows of small speckles which run along the flanks. Two specimens document a tendency to develop somewhat detached body whorls.

The protoconch consists of 1.2 rounded whorls measuring 0.08-0.1 mm in the width of the initial cap and 0.35 mm in maximum diameter. Sculpture is not evident. The protoconch is terminated by a slightly thickened rim on the shell and the transition to the teleoconch is indicated by the onset of the dense regular growth lines.

**Remarks:** The species is well characterised by its conspicuous ornament of growth lines and the slightly detached body whorl. Some variability is documented only in the columellar plate, which may rarely bear indistinct folds or may develop a weak dentition (cf. LŐRENTHEY 1902). The protoconch is indicative of a direct development without a free larval stage.

The depressed elongated shape is highly reminiscent of *Theodoxus perlongus* JEKELIUS, 1944, which can be distinguished by its distinct dentitions of the columellar plate. Further, the shell surface of *Theodoxus perlongus* is smooth. SAUERZOPF (1950) described a similarly small *Theodoxus* with distinctly detached body whorl from the Pannonian Zone E of the Styrian Basin. His *Theodoxus pappi* (nomen nudum) differs also by its smooth shell surface. The much younger *Theodoxus pilidei* (TOURNOUER, 1879) as described by WENZ (1942) from Romania is one of the few species which develops a comparable axial ornamentation. In contrast to *Theodoxus cunici*, the growth lines of *Theodoxus pilidei* are enlarged into lamellae.

**Distribution:** The rarely reported species occurs in Hungary and Romania during the Pannonian Zones C and D. In Austria it is mentioned for the first time and it is a frequent species at St. Margarethen during the Pannonian Zone C/D.

### *Theodoxus soceni* Jekelius, 1944
(Plate 1, Figs. 3, 5, 13)

1944 *Theodoxus soceni* n. sp. - Jekelius, p. 51, pl. 5, fig. 7-26, p. 113, pl. 41, fig. 25-46
1953 *Theodoxus (Theodoxus) soceni* Jekelius – Papp, p. 96, pl. 2, fig. 12-15
1959 *Theodoxus (Theodoxus) soceni* Jekelius – Boda, p. 727, pl. 33, fig. 1-4
1979 *Theodoxus (Theodoxus) pilari soceni* (Jekelius) – Jurišić-Polšak, p. 42, pl. 4, fig. 3-6
1997 *Theodoxus (Theodoxus) soceni* Jekelius – Fordinál, p. 267, pl. 1, fig. 5

**Description:** The subspherical shells of rapidly increasing whorls and hardly emerging spire measure up to 5 mm in height and width. Solid, flat septum with slightly concave and distinctly serrated columellar edge. Colour ornament consists of black or dark brown elongated triangles with their apex directed towards the aperture.

The protoconch consists of slightly more than one shiny whorl measuring 0.48 mm in maximum diameter.

**Remarks:** The large size, the dentate columellar edge, and the characteristic colour ornament allow a distinct separation from all other theodoxids at the section St. Margarethen. *Theodoxus millepunctata* (Brusina, 1902) is slightly reminiscent but bears broad dots and no triangles; furthermore, its columellar edge is less dentate or smooth. Jurišić-Polšak (1979) treats the taxon as a subspecies of *Theodoxus pilari* (Brusina, 1884). This relation is doubted herein, based on the less spherical shell and the expanding body whorl of *Theodoxus pilari*. The protoconch of *Theodoxus soceni* differs from that of *Theodoxus cunici* by its distinctly larger size.

**Distribution:** A Sarmatian relic, which is frequent in the Pannonian of Romania. In Austria it is only known from the Pannonian Zones D and E of the Vienna Basin and from the Pannonian Zone C/D of the Eisenstadt-Sopron Basin.

### *Theodoxus intracarpatica* Jekelius, 1944
(Plate 1, Figs. 6-8)

1944 *Theodoxus intracarpaticus* n. sp. - Jekelius , p. 112, pl. 41, fig. 1-24
1950 *Theodoxus intracarpaticus* Jekelius – Sauerzopf, p. 110, textfig.
1953 *Theodoxus (Theodoxus) intracarpaticus* Jekelius – Papp, p. 97, pl. 2, fig. 4-11
1980 *Theodoxus intracarpaticus* Jekelius – Lueger, p. 116
1997 *Theodoxus (Theodoxus) intracarpaticus* Jekelius – Fordinál, p. 268, pl. 1, fig. 3

**Description:** Large-sized shell with expanding body whorl and slightly emerging spire measures up to 7 mm in height. The septum is flat and smooth, the columellar edge is concave and bears no dentition. In its posterior part a weak swelling may rarely cause an indistinct convexity. Colour ornament of irregular dark brown speckles or triangles arranged in broad spiral lines which are separated by less coloured intervals of different width.

**Remarks:** The more elongated outline and the smooth columellar edge allow a separation from the co-occurring, spherical *Theodoxus soceni*.

**Distribution:** The species is frequent in the Vienna Basin, the Eisenstadt-Sopron Basin, and the Styrian Basin in the Pannonian Zones C, D, and E.

## Genus: *Neritina* LAMARCK, 1816

### *Neritina vetranici* (BRUSINA, 1902)

(Plate 1, Figs. 9-10, 12)

1902 *Neritodonta Vetranici* – BRUSINA, pl. 15, fig. 17-18
1944 *Theodoxus vetranici* BRUSINA – JEKELIUS, p. 113, pl. 42, fig. 1-3
1979 *Theodoxus (Theodoxus) vetranici* (BRUSINA) – JURIŠIĆ-POLŠAK, p. 43, pl. 6, fig. 1-3
1980 *Theodoxus vetranici* (BRUSINA) – LUEGER, p. 103, fig. 5/8

**Description:** A single, very small, spherical shell with equally rounded whorls and low spire measures slightly more than 2 mm in height. The cream-white protoconch consists of about two slightly convolute whorls measuring 0.3 mm in maximum diameter. The first half whorl is partly covered by the succeeding one. It is clearly demarcated from the teleoconch by its termination in a thickened rim and by the abrupt onset of the colour ornament. Colour ornament of the teleoconch consists of more than 25 narrow brown lines which are separated by slightly broader white interspaces. A large, flat callus partly covers the base; the columellar edge is concave and lacks folds or dentitions. The aperture is semicircular, the outer lip thin.

**Remarks:** The specimen differs from typical "*Theodoxus*" *vetranici* from Croatia as illustrated by BRUSINA (1902) mainly by its colour ornament. *Neritina vetranici* usually displays fewer black lines and the interspaces are about twice as broad. Nevertheless, specimens with delicate ornamentation, such as BRUSINA's fig. 18 or JEKELIUS's fig. 3 are very similar, whereas the younger shells illustrated in BARTHA (1959) differ considerably by their elongate shell and the blunt spiral colouring. Hence, the insufficient material available allows no definitive identification of the probably juvenile specimen from St. Margarethen.

The size and dimensions of the protoconch indicate an indirect development including a planktonic veliger stage, enabling a separation from juvenile specimens of *Theodoxus soceni*.

**Distribution:** In the Eisenstadt-Sopron Basin the species was already described by LUEGER (1980) from the Pannonian Zone E. It is a common species, which is documented from the Pannonian of Romania and Croatia.

### *Neritina mariae* HANDMANN, 1887

(Plate 1, Figs. 11, 14)

1887 *Neritina Mariae* – HANDMANN, p. 9
1907 *Neritina Mariae* HANDMANN – TROLL, p. 46, pl. 2, fig. 1
1944 *Theodoxus mariae* (HANDMANN) – JEKELIUS, p. 115, pl. 42, fig. 22-24
1950 *Theodoxus mariae* (HANDMANN) – SAUERZOPF, p. 112
1953 *Theodoxus (Theodoxus) mariae* (HANDMANN) – PAPP, p. 101, pl. 3, fig. 9-12
1979 *Theodoxus (Theodoxus) mariae* (HANDMANN) – JURIŠIĆ-POLŠAK, p. 25, pl. 7, fig. 6-7

**Description:** Small, elongated shell with flat spire but incised sutures. Septum sunken with slight concavity; columellar edge concave with weak dentition. Shell surface smooth except for growth lines. The protoconch with about two smooth and shiny, partly convolute whorls measuring 0.23 mm in maximum diameter. A thickened rim indicates the termination of the protoconch.

A distinct colour pattern of brownish small dots appears with the very beginning of the teleoconch. These dots are arranged in spirals; on the body whorl the dots form axial zigzag lines.

**Remarks:** "*Theodoxus*" *tortuosus* JEKELIUS from the Sarmatian and earliest Pannonian is very closely related. It differs slightly in the strict zigzag arrangement of the dots but develops an equal columellar structure. Although the zigzag pattern is less common in *Neritina mariae*, it is mentioned by JEKELIUS (1944) and PAPP (1953) to occur within all populations. Yet, *Neritina mariae* might only represent a late morph of *Neritina tortuosa,* which then would be a younger synonym of HANDMANN's *Neritina mariae.*

The protoconch indicates an indirect development. It differs from that of *N. vetranici* by its smaller size and by the stronger convolute arrangement of the initial whorls. *N. mariae* and *N. vetranici* closely resemble modern *Neritina glabrata* SOWERBY, 1849 from the West African Coast (BROWN 1980, BANDEL & KOWALKE 1999). *Neritina glabrata* differs by its slightly larger size and by the straight columella.

**Distribution:** *Neritina mariae* is restricted to the Pannonian Zones C and D in the Vienna Basin, the Styrian Basin, and the Eisenstadt-Sopron Basin. The reminiscent or conspecific "*Theodoxus*" *tortuosus* appears during the Sarmatian and is reported in Romania and Austria up to the Pannonian Zone B.

Subclass: Caenogastropoda COX, 1959

Order: Littorinimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily: Rissooidea GRAY, 1847

Family: Hydrobiidae TROSCHEL, 1847

Genus: *Hydrobia* HARTMANN, 1821

(Subgenus: *Baglivia*, BRUSINA 1892)

### *Hydrobia ambigua* (BRUSINA, 1892)

(Plate 3, Figs. 1-10)

1892 *Caspia ambigua* – BRUSINA, p. 148
1897 *Hydrobia (Liobaikalia?) sopronensis* – HOERNES, p. 71, pl. 2, fig. 13
1902 *Baglivia ambigua* BRUSINA – BRUSINA, pl. 10, fig. 30-37
1902 *Baglivia sopronensis* HOERNES sp. – LŐRENTHEY, p. 233, pl. 17, fig. 37-39
1939 *Caspia (Baglivia) ambigua* (BRUSINA) – WENZ, p. 605, fig. 1674
1944 *Caspia ambigua* BRUSINA – JEKELIUS, p. 65, pl. 13, fig. 10-18, non. 9
1950 *Baglivia ambigua* BRUSINA – SAUERZOPF, p. 117, pl. 3, fig. 9, 10
1952 *Hydrobia (Baglivia) ambigua* (BRUSINA) – PAPP, p. 28
1953 *Hydrobia (Baglivia) ambigua* (BRUSINA) – PAPP, p. 114, pl. 8, fig. 19-23
1985 *Hydrobia (Baglivia) ambigua* (BRUSINA) – PAPP, p. 280, pl. 31, fig. 10-13

**Description:** Small turreted shells of up to 5 whorls measuring up to 3 mm in height; the protoconch is strongly convex, whilst the early teleoconch usually detaches from the spire and later whorls are loosely coiled, are less convex and develop slightly flattened flanks. The species is characterised by its tendency to uncoil, and may produce slightly loose shells or even screwdriver like shells. Only the protoconch is never uncoiled and usually the first teleoconch whorl is also attached. In this case, the sutures are always strongly incised. Apertures are egg-shaped with slightly acute parietal portion and may terminate in an indistinct thickening; they never form lips. Shell surface smooth except for growth lines, which are strongest in the umbilical side of the whorls.

The low conical protoconch comprises 2-2.2 slightly rounded whorls measuring 0.35-0.36 mm in maximum diameter. The first whorl measures 0.13-0.14 mm in maximum diameter and 0.03 mm in the width of the initial cap. The embryonic shell comprises slightly more than one whorl. It is terminated by an indistinct rim. The following larval shell is smooth except for fine growth lines. It rapidly increases in diameter. The protoconch is terminated by a straight, slightly thickened rim. The onset of the teleoconch is indicated by the formation of dense, regular growth lines accompanied by regularly arranged, slight varices.

**Remarks:** The protoconch points to an indirect development with a small embryonic shell and a subsequent larval shell comprising about one whorl, which reflects a brief veliger phase. Embryonic and larval shell can be differentiated and the dimensions indicate that the larva was free swimming and fed on phytoplankton. The protoconch of the recent *Hydrobia ulvae* (PENNANT, 1777) from the North Sea has been described by KOWALKE (1998: 72, pl. 10, fig.1). The shape and dimensions of the protoconch are very similar to those of *Hydrobia ambigua*. The larval shell of *Hydrobia ulvae* differs by bearing very fine spiral threads.

The generic and subgeneric affiliation of this frequent species was rather unclear since BRUSINA described the species in 1892. JEKELIUS (1944) already doubted the validity of the subgenus *Baglivia* BRUSINA, 1892. In respect to the transition from "normal", coiled specimens to "screwdrivers" within each population, he supposed the separation of *Baglivia* to be unjustified.

The fewer whorls and the rather stout shell outline allows a clear separation of *Hydrobia ambigua* from other Sarmatian and Pannonian hydrobiids. Other Pannonian to Pontian hydrobiids which develop *Bagilivia*-morphs can be distinguished easily by their very slender shape (cf. *Baglivia gonyogyra, B. strongylogyra, B. streptogyra* in BRUSINA 1902) or by their sculptured shell (*Baglivia rugosula* in BRUSINA 1902).

**Distribution:** The species is first recorded from the Sarmatian of Austria and Romania. It is a frequent element in drillings in the latest Sarmatian "pauperisation" Zone and appears also in the Early Pannonian Zone B (Zemendorf in the Eisenstadt-Sopron Basin, Hartberg in the Styrian Basin). At least in the Austrian basins the occurrence in the Pannonian Zone D at St. Margarethen is the latest occurrence of this species. The continuous fossil record of *Hydrobia (Baglivia) ambigua* proves the Sarmatian specimens to be conspecific with those from the Pannonian rather than to represent two convergent uncoiling events in hydrobiid phylogeny.

### *Hydrobia* sp.
(Plate 2, Figs. 7-8)

**Description:** The slender shell comprises up to six slightly rounded whorls with deep sutures measuring up to 3 mm in height. Ornament consists of dense orthocline to slightly opisthocyrte growth lines. The aperture has an elongate egg shape with a pointed parietal portion. The columellar lip is bent.

The protoconch comprises 1.3 smooth whorls measuring 0.06 mm in the width of the initial cap and 0.24 mm in maximum diameter. The protoconch is terminated by a thickened rim. The onset of the teleoconch is indicated by the formation of dense, regular growth lines.

**Remarks:** *Hydrobia* sp. differs from *H. ambigua* by its direct development, and by its closely coiled shell with elongate, egg-shaped aperture. *Nematurella* SANDBERGER, 1874 with the type-species *N. flexilabris* SANDBERGER, 1874 is very similar (WENZ 1938-1944: 557, fig. 1493). It differs by more flattened whorls and by the detached, broader aperture with strongly acute parietal portion.

Family: Stenothyridae FISCHER, 1885

Genus: *Pseudamnicola* PAULUCCI, 1878

Subgenus: *Staja* BRUSINA, 1897

### *Pseudamnicola (Staja) turislavica* (JEKELIUS, 1944)
(Plate 2, Fig. 4)

1944 *Staja turislavica* n. sp. – JEKELIUS, p. 121, pl. 44, fig. 30-37
1950 *Staja turislavica* JEKELIUS – SAUERZOPF, p. 118, pl. 3, fig. 5-6
1953 *Pseudamnicola (Staja) turislavica* (JEKELIUS) – PAPP, p. 118, pl. 7, fig. 12

**Description:** A single, slightly corroded shell of 4 whorls measuring up to 2 mm in height, with hardly emerging but partly destroyed protoconch. The convexity of the whorls is weak, the sutures are shallow. Only the large body whorl develops a faint angulation between flank and base. Aperture egg-shaped with an angulation in the posterior part and a well-rounded anterior margin. Inner lip well developed and slightly bent, thus producing a thin, slit-like furrow.

**Remarks:** The described shell differs from the specimens of PAPP (1953) from the Vienna Basin by its more depressed outline and the convexity of the whorls. These features have already been recognised by JEKELIUS (1944) to be highly variable. An identification of the specimen from St. Margarethen with the Romanian species seems to be acceptable.

**Distribution:** *Pseudamnicola (Staja) turislavica* appears during the Pannonian Zones C and D in the Vienna Basin, the Styrian Basin, and the Eisenstadt-Sopron Basin. In Romania the species is also recorded from this interval.

## Family: Pyrgulidae WENZ, 1923
## Genus: *Micromelania* BRUSINA, 1874

### *Micromelania sulcata* BRUSINA, 1892
(Plate 2, Figs. 2-3)

1892 *Micromelania sulcata* BRUSINA n. sp. – BRUSINA, p. 49
1902 *Micromelania sulcata* BRUSINA – BRUSINA, pl. 7, fig. 52-55
1953 *Micromelania (Micromelania) sulcata* BRUSINA - PAPP, p. 120, pl. 5, fig. 6

**Description:** Small-sized, turreted shell of 5 teleoconch whorls measuring about 3 mm in height. Moderately convex whorls with the maximum convexity in the abapical part, separated by distinct sutures. Body whorl high, evenly rounded, measuring more than ? of the total height. Aperture ovoidal with posterior angulation. Outer lip thin; columellar lip broad, well defined and attached to the base without any umbilicus. In its middle an indistinct swelling is developed. Delicate, very thin spiral keels cover the otherwise smooth shell surface of the spire whorls but vanish on the body whorl.

The protoconch comprises one flat smooth whorl measuring 0.24 mm in maximum diameter and 0.06-0.07 mm in the width of the initial cap. The protoconch is terminated by a thickened rim. The onset of the teleoconch is indicated by the formation of dense, regular growth lines.

**Remarks:** The specimen corresponds to the specimens from the Vienna Basin described by PAPP (1953) fully in its outline as well as in its protoconch features. The comparison with the original material shows that the convexities of the whorls are underrated in the illustration given in PAPP (1953). A slight difference of all Austrian specimens to those from Croatia, described by BRUSINA (1892), is the higher body whorl and the more elongated aperture.

*Micromelania sulcata* differs from the type species *Micromelania cerithioides* BRUSINA, 1874 by the lack of axial ribs (WENZ 1938-1944: 594, fig. 1629). *Pyrgula* CHRISTOFORI & JAN, 1832 with the recent type species *Pyrgula annulata* JAN, 1830 (WENZ 1938-1944: 583, fig. 1591) from the Lake Garda (N. Italy) with a similar, slightly larger protoconch differs by the formation of two prominent spiral keels.

**Distribution:** The species occurs in the Pannonian Zones C and D in the Vienna Basin, the Eisenstadt-Sopron Basin, and Croatia.

## Genus: *Socenia* JEKELIUS, 1944

### *Socenia moesia* JEKELIUS, 1944
(Plate 4, Figs. 6-9)

1902 *Caspia* sp. – BRUSINA, pl. 11, fig. 14, fig. 15?
1944 *Socenia moesia* n. sp. – JEKELIUS, p. 125, pl. 46, fig. 14-18
1950 *Caspia (Socenia) moesia* JEKELIUS – SAUERZOPF, p. 124, pl. 2, fig. 1

**Description:** A slender, turreted shell of at least 7 whorls measuring about 2 mm in height. Whorl convexity varies considerably and depends on the ornamentation. Sutures are narrow. Its sculpture consists of 5-8 spiral ribs, separated by interspaces of different width. The spiral ribs may further separate into two thin spiral threads. The number and strength of all spiral ornaments is variable. Especially the ribs in the posterior half of the whorls may become relatively strong and then may form a weak angulation.

The protoconch comprises slightly more than one inflated whorl measuring about 0.27-0.3 mm in maximum diameter and 0.09-0.1 mm in the width of the initial cap. The protoconch is smooth aside from indistinct spiral folds of the initial quarter whorl. The protoconch is terminated by a thickened rim and the onset of the teleoconch is indicated by the formation of the prominent adult sculpture.

**Remarks:** *Socenia incerta* BRUSINA differs clearly in its strong angulations, which separates the whorls into a nearly straight posterior shelf and a hardly convex anterior part. *Socenia soceni* JEKELIUS, 1944 can be distinguished by its high and slightly inflated body whorl. A very closely related species was described by JEKELIUS (1944) as *Socenia tenella*. It differs only by minor features, such as its even more slender shape and the delicate ornamentation; the separation of this rather similar form might therefore be superfluous. In any case, the shells from the Pannonian Zone C of the Vienna Basin described by PAPP (1953; 1985) as *Caspia (Socenia) tenella* should probably also be treated as the less delicate and less gracile *Socenia moesia*.

**Distribution:** The species appears in the Pannonian Zone C of Croatia and Romania and is known in the Austrian Eisenstadt-Sopron Basin from the Pannonian Zone C/D up to Zone E (SAUERZOPF 1950).

## *Socenia soceni* JEKELIUS, 1944
(Plate 2, Figs. 5-6)

1944 *Socenia soceni* n. sp. – JEKELIUS, p. 67, pl. 13, fig. 23-32
1944 *Socenia soceni turislavica* n. var. – JEKELIUS, p. 124, pl. 46, fig. 4-13
1944 *Caspia (Socenia) soceni turislavica* (JEKELIUS) - PAPP, p. 126, pl. 8, fig. 3-4

**Description:** Small-sized, slender, turreted shell of 5 whorls measuring up to 2 mm in height. The high, spire whorls have low convex flanks and are separated by weakly impressed sutures; the outline of these spire whorls is more or less parallel-sided. The body whorl, measuring about one half of the total height, is characterised by a slightly allometric growth, which is expressed by a sudden increase in convexity. Its inner lip is bent and forms a narrow, slit-like umbilicus.

The protoconch comprises nearly two flat whorls which rapidly increase in diameter. The maximum diameter of the protoconch amounts to 0.3 mm. The first whorl measures 0.11 mm in maximum diameter and 0.03 mm in the width of the initial cap. The protoconch is terminated by an indistinct rim. The onset of the teleoconch is indicated by the formation of growth lines.

**Remarks:** JEKELIUS (1944) separated a Pannonian chronosubspecies because of the higher percentage of smooth specimens within the Pannonian populations and because of the usually more evenly rounded whorls. The *turislavica*-morph, however, can also be observed within the Sarmatian populations, whilst several Pannonian shells do not differ at all from their Sarmatian ancestors. A separation of a subspecies is therefore probably superfluous.

The specimen from the Eisenstadt-Sopron Basin represents a somewhat atypical morphology regarding the markedly inflated body whorl. A tendency of *Socenia soceni* to allometric growth of the last whorl is also indicated by some shells from Romania (cf. JEKELIUS, 1944, pl. 13, fig. 32, pl. 46, fig. 10). The described specimen is completely smooth; nevertheless, as discussed by PAPP (1953), *Socenia soceni* may develop smooth and sculptured shells. The sunken protoconch is the most characteristic feature in this species.

The protoconch points to a short planktonic veliger stage, indicated by a very small initial whorl and a rapid increase of whorl diameter in the course of the second whorl. The veliger was free swimming, feeding on phytoplankton during a short larval stage. With regard to the planktotrophic early ontogeny, *Socenia soceni* differs from *Socenia moesia,* which underwent direct development.

**Distribution:** A common species in the Early Pannonian; it can be traced back to the Sarmatian.

### *Socenia* cf. *politioanei* JEKELIUS, 1944
(Plate 2, Fig. 1)

1944 *Socenia politioanei* nov. sp. – JEKELIUS, p. 67, pl. 13, fig. 34
1953 *Caspia (Socenia) politioanei* (JEKELIUS) – PAPP, p. 126, pl. 8, fig. 13

**Description:** Very slender shell of more than 6 whorls measuring up to 2 mm in height. Moderately convex whorls with shallow sutures; shell surface smooth except for weak growth lines. The aperture is destroyed.

**Remarks:** The species was first described by JEKELIUS (1944) from the Sarmatian of Romania. Later, PAPP (1953) reported *Socenia politioanei* also from the Early Pannonian of the Vienna Basin. In both populations, the shell surface of *Socenia politioanei* bears weak spiral grooves. In contrast, the shell from St. Margrethen is completely smooth. It is therefore questionable if the specimen is conspecific with the sculptured species. At any rate, the sculpture seems to be a very variable feature in several representatives of *Socenia*. As discussed above, *Socenia soceni* is known to lose its spiral sculpture gradually from the Sarmatian into the Pannonian. Hence, the described specimen might be the result of a similar development within *Socenia politioanei*.

The specimen's protoconch is highly reminiscent of *Socenia moesia* JEKELIUS, which has identical dimensions. The extremely slender teleoconch and the higher whorls of *Socenia politioanei* allow a clear separation from *Socenia moesia*.

**Distribution:** The shell derives from the Pannonian Zone C/D of the Eisenstadt-Sopron Basin. *Socenia politioanei* arises during the Sarmatian and is known until the Early Pannonian of Austria.

## Genus: *Goniochilus* SANDBERGER, 1875

### ***Goniochilus glandulinus haidingeri* (STOLICZKA, 1862)**
(Plate 4, Figs. 3-4)

1862 *Tricula haidingeri* STOLICZKA, p.536, pl. 17, fig. 7
1950 *Goniochilus glandulinus haidingeri* STOLICZKA - SAUERZOPF, p. 121, pl. 4, fig. 3
1953 *Micromelania (Goniochilus) glandulina haidingeri* STOLICZKA - PAPP, p. 121, pl. 6, fig. 1-4

**Description:** The small-sized, about 2-mm-high shell comprises about four slightly rounded whorls. Teleoconch sculpture consists of 15-20 wavy spiral keels, crossed by 20 straight axial ribs; the latter are thickened in the median portion of the whorls and may be elongated into short spines. The body whorl amounts about 60 % of total shell height. The base is sculptured by 10-12 spirals, of which the uppermost (adapical) three are most strongly developed. The large aperture is subangular.

The protoconch comprises 1.25 very smooth and shiny whorls. It measures 0.4 mm in maximum diameter. The first whorl measures 0.31 mm in maximum diameter and 0.09-0.1 mm in the width of the initial cap. The first half whorl is somewhat loosely coiled. Indistinct growth lines are visible on the last quarter whorl of the protoconch. It is terminated by an indistinct rim. The onset of the teleoconch is indicated by the formation of the distinct and regular adult sculpture.

**Remarks:** PAPP (1953) treats the shell as a subspecies of *Goniochilus glandulinus* (STOLICZKA). It differs from *Goniochilus glandulinus glandulinus* only by the prominent ornamentation. Additionally, SAUERZOPF (1950) emphasises the much higher body whorl of *Goniochilus glandulinus glandulinus*. This feature cannot be confirmed if the illustrations of STOLICZKA (1862) are taken in consideration. Hence, the specimens of SAUERZOPF (1950) seem to represent rather a *Goniochilus banaticus fuchsi* (PAPP). Thus, based on minor differences in ornamentation, the separation of *G. g. haidingeri* as a natural subspecies is questionable. Further material will probably result in a uniting of *Goniochiuls glandulinus haidingeri* (STOLICZKA) and *Goniochilus glandulinus formosa* (TROLL) into *Goniochilus glandulinus* (STOLICZKA). Typical shells of *Goniochilus variabilis* are usually more elongate and tend to lose the sculpture towards the aperture.

The type species of *Goniochilus* - *Pleurocera costulata* FUCHS, 1870 (WENZ 1938-1944: 595, fig. 1634) - differs by its more slender shell, the higher number of whorls and by its stronger axial sculpture.

**Distribution:** *Goniochilus glandulinus haidingeri* is known from the Pannonian Zones C and of the Vienna Basin and the Eisenstadt-Sopron Basin. In the Styrian Basin it is documented from the Pannonian Zone E.

### ***Goniochilus breviformis* (PAPP, 1953)**
(Plate 4, Fig. 5)

1950 *Goniochilus* aff. *schwabenaui* FUCHS – SAUERZOPF, p. 120, pl. 4, fig. 1
1953 *Micromelania (Goniochilus) breviformis* n. sp. – PAPP, p. 123, pl. 6, fig. 8

**Description:** A stout shell of 4-5 angulated whorls. The angulation coincides with a row of nodes which fade into axially elongated swellings towards the abapical suture. A hardly convex sutural shelf is developed posterior to this row, whilst the anterior part is nearly straight-sided. Only the body whorl is well rounded, but still bearing traces of an angulation. The entire teleoconch is covered by slightly wavy spiral threads which cross even the axial swellings.

**Remarks:** "*Pleuroploca Schwabenaui"* of FUCHS (1870, p. 539, pl. 20, fig. 10-12) differs distinctly in its much more elongated shell and the prominent axial ribs. It therefore displays hardly any similarities that would allow to place the shell from St. Margarethen in close relation to FUCHS' species as suggested by SAUERZOPF (1950). Similarly, *Goniochilus breviformis* differs from all other species attributed to *Goniochilus* by its stout shell and by its prominent spiral ornamentation. The species, however, is obviously closely related to the *Goniochilus variabilis*-group and *Goniochilus glandulinus*, which develop a very similar sculpture and can only be distinguished by the less stout shell (cf. *Goniochilus variabilis* in FORDINÁL, 1997). *Goniochilus glandulinus* is also very similar in protoconch morphology, with identical dimensions, and thus *Goniochilus breviformis* may represent a subspecies of *Goniochilus glandulinus*.

**Distribution:** *Goniochilus breviformis* is only known from the Pannonian Zones C and D of the Vienna Basin, the Eisenstadt-Sopron Basin, and the Styrian Basin.

Genus: *Caspia* DYBOWSKI, 1888

### *Caspia vujici* BRUSINA, 1892
(Plate 2, Figs. 9-10)

1892 *Caspia vujici* BRUSINA – BRUSINA, pl. 45
1902 *Caspia (Caspia) vujici* BRUSINA – BRUSINA, pl. 10, fig. 57-63
1950 *Caspia (Caspia) vujici* BRUSINA – SAUERZOPF, p. 123, pl. 2, fig. 8-9
1953 *Caspia (Caspia) vujici* BRUSINA – PAPP, p. 125, pl. 8, fig. 11-12

**Description:** The small-sized, subcylindrical shell comprises four rather flat-sided whorls measuring up to 2 mm in height. The width of the whorls increases very slowly, whereas the height increases rapidly. Its apex is very flat due to the flat protoconch. The convexity of teleoconch whorls decreases distinctly towards the body whorl. Aperture ovoidal with weak posterior angulation. Inner lip rather broad, forming a slit-like umbilicus.

The protoconch comprises 1.25 flat, smooth whorls measuring 0.24 mm in maximum diameter. The first whorl measures 0.18-0.19 mm in maximum diameter and 0.06 mm in the width of the initial cap. The initial half whorl is characterised by a slight depression of the apical portion of the shell. The transition to the teleoconch is indistinct, indicated by the successive onset of the adult ornament of thickened, slightly sinuous growth lines.

**Remarks:** Differs from the Sarmatian *Stenothyrella schwartzi* (HÖRNES, 1856) by its elongated aperture and by the less thick-shelled conch. The protoconch of *Stenothyrella schwartzi* is higher and its protoconch whorls are strongly convex. *Stenothyrella ovoidea* (PAVLOVIC) from the Pannonian of Serbia, Austria, Romania, and Slovakia forms a similar aperture but develops a less cylindical outline. The outer lip of *Caspia vujici* is thinner compared to that of both mentioned species of *Stenothyrella*.

The type species of *Caspia*, the recent species *Caspia baerii* DYBOWSKI, 1888 from the Caspian Sea, is very similar and differs only by its slightly less cylindrical shell (WENZ 1938-1944: 605, fig. 1669).

**Distribution:** The species was first recorded from the Pannonian of Croatia. In Austria it is known from the Pannonian Zone C/D of the Eisenstadt-Sopron Basin and from the Pannonian Zone E of the Styrian Basin.

### *Caspia compacta* JEKELIUS, 1944
(Plate 4, Figs. 1-2, 10-12)

1944 *Caspia compacta* n. sp. – JEKELIUS, p. 124, pl. 45, fig. 30-34
1950 *Caspia dybowskii* BRUSINA - SAUERZOPF, p. 122, pl. 2, fig. 2-3
1952 *Caspia (Caspia) dybowskii* BRUSINA - SAUERZOPF, p. 5
1953 *C. (C.) dybowskii* BRUSINA – PAPP, p. 126

**Description:** Stout shell of 4 slowly growing teleoconch whorls, measuring about 2 mm in height; convexity low; sutures very shallow. Maximum whorl diameter is developed in their anterior third. Body whorl large, measures more than one half of total height. A dense pattern of spiral threads of different strength covers the teleoconch whorls. These spirals are usually interrupted by axial growth lines which disintegrate the spiral threads into spirally connected, elongated beads. Aperture moderately elongated, egg-shaped with posterior angulation; outer lip slightly flaring and thin. Inner lip thin, bent, and forms a slit-like umbilicus.

The protoconch comprises 1.5 slightly rounded whorls measuring 0.3 mm in maximum diameter. The first whorl measures 0.21 mm in maximum diameter and 0.04-0.05 mm in the width of the initial cap. The protoconch is smooth aside from indistinct growth lines on the last 0.3 whorls.

**Remarks:** In Austria this species was mentioned by SAUERZOPF (1950; 1952) and PAPP (1953) as *Caspia dybowskii* BRUSINA. A comparison of the material studied by these authors with that from the Eisenstadt-Sopron Basin proved the specimens to be conspecific. The apical angle, ranging from 35-40°, allows a clear separation from the more cylindrical *Caspia dybowskii* (as emphasised by JEKELIUS 1944, only fig. 17, 19 and 20 of the illustrated specimens of BRUSINA 1902 can be referred to as *Caspia dybowskii*).

**Distribution:** The species is known from the Pannonian Zone C/D of the Eisenstadt-Sopron Basin and the Styrian Basin in Austria and from Turislav in Rumania.

Order: Cerithiimorpha GOLIKOV & STAROBOGATOV, 1975

Superfamily: Cerithioidea FÉRUSSAC, 1819

Family: Melanopsidae H. & A. ADAMS, 1854

Genus: *Melanopsis* FÉRUSSAC, 1807

**Remarks to the species concepts**: For a long time, paleontologists almost universally used the morphological species concept when describing molluscs from Lake Pannon. This phenetic approach yielded a vast number of nominal taxa in the literature. Among the gastropods, the melanopsids are the most outstanding example for this situation of taxonomic overcompleteness. Especially the manifold *Melanopsis impressa-fossilis-vindobonensis* group of the Pannonian Zones C, D and E offers a broad field for the identification of morphospecies. About 15 of these taxa are well established in the literature (cf. PAPP, 1953). It is hardly acceptable to interpret all these taxa of Pannonian melanopsids, which are often linked by several transitional morphs, as having developed as reproductively isolated populations in geographically separated areas of the early lake. Hence, the status of most of these taxa as separate biological species seems to be unacceptable (see also GEARY, 1990). Even the status of chronosubspecies sensu WILLMANN (1987) cannot be applied for most melanopsid lineages because several potential candidates such as *Melanopsis fossilis coaequata, M. f. rugosa,* or *Melanopsis f. handmanniana* form synchronous populations during the Pannonian Zone D. By no means can they be treated as biological subspecies because they represent sympatric populations. In contrast they clearly interbred and developed a variety of transitional morphs.

The discussion has now been enriched by the observation of HELLER (1999) that the genus *Melanopsis* is susceptible to hybridisation. According to BANDEL (2000) interbreeding is not only restricted to different species within the genus *Melanopsis,* but may also occur between *Melanopsis* and species that are usually considered to be separate genera, such as representatives of *Melanoptychia*. Nonetheless, the definition of Pannonian melanopsids as biological species or "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (cf. MAYER, 1942) became extremely difficult to apply.

We decided to treat the *Melanopsis fossilis* types of the section St. Margarethen as extreme morphologies of a single species, but do not renounce describing the characteristic phenotypes. Although we are aware that these taxa might not fit accurately to the biological species concept, the biostratigraphic value of certain taxa would be lost in a binominal superspecies.

### ***Melanopsis fossilis* (GMELIN, 1790)**
(Plate 6, Figs. 5-10, Plate 7, Figs. 4-5, 10-12)

**Description of the protoconch:** The protoconch comprises one inflated whorl. It measures 0.14-0.15 mm in the width of the initial cap and nearly 0.4 mm in maximum diameter. Ornamentation and transition to the teleoconch are not preserved.

### ***Melanopsis fossilis* phenotype *handmanniana* FISCHER, 1996**
(Plate 7, Figs. 11-12)

1996a *Melanopsis handmanniana* nov. nomen pro *constricta* HANDMANN – FISCHER, p. 27, fig. 3-11 (cum syn.)

**Description:** Very large-sized form reaching more than 50 mm in height; develops a more or less prominent spiral keel close to the adapical suture. The area between this keel and the angulated shoulder is concave. Height/diameter ratio extremely variable.

**Remarks:** This type was traditionally reported as *Melanopsis fossilis constricta* HANDMANN or *Melanopsis constricta* HANDMANN. As demonstrated by FISCHER (1996a), *constricta* is already preoccupied by *Melanopsis constricta* BRUSINA, 1878. Consequently he introduced *Melanopsis handmanniana* as a new name for HANDMANN's "species".

**Distribution:** Appears in the Pannonian Zone C and is a common phenotype in the Zone D. According to PAPP (1953), small sized specimens are also represented even in the Zone E.

### *Melanopsis fossilis* phenotype *coaequata* HANDMANN, 1887
(Plate 6, Figs. 5-6, 8-10)

1996b *Melanopsis coaequatata* HANDMANN – FISCHER, p. 19, fig. 1-5 (cum syn.)

**Description:** The shell measures up to 55 mm in height. Spire short due to a rapid increase in width of the early teleoconch whorls. The concavity of the sutural ramp is weaker than in *Melanopsis fossilis* phenotype *handmanniana* and the sutural rim is less distinct or even missing.

**Distribution:** Typical during the Pannonian Zones C and D. LUEGER (1980) mentions the species also from the Pannonian E of the Eisenstadt-Sopron Basin.

### *Melanopsis vindobonensis* FUCHS, 1870
(Plate 7, Figs. 1-3)

1953 *Melanopsis vindobonensis vindobonensis* FUCHS – PAPP, p. 137, pl. 11, fig. 13-16 (cum syn.)

**Description:** Medium-sized to large, almost spherical shells reaching up to 40 mm in height, with projecting spire and huge, inflated body whorl. A prominent angulation separates a narrow, concave sutural ramp from the conical base.

**Remarks:** Whatever theory may apply best *Melanopsis vindobonensis* as a descendant of *Melanopsis fossilis* as suggested by GEARY (1990) or as a descendant of *Melanopsis impressa* as discussed by PAPP (1953) it is probably not a result of speciation in a cladistic sense. Even the obvious predominance of *Melanopsis vindobonensis* in the Pannonian Zone E, when most other morphospecies of the *Melanopsis fossilis* lineage have disappeared, is caused only by a bottleneck-effect (STANLEY, 1978) at the boundary of Pannonian Zone D to Zone E, but not by any kind of speciation. This viewpoint is supported by the occurrence of *Melanopsis vindobonensis* already in the Pannonian Zones C and D together with several representatives of the *Melanopsis fossilis* lineage.

**Distribution:** The stout form already appears in the Pannonian Zone C and reaches up to the Pannonian Zone E. According to PAPP (1985) it becomes gradually more frequent within the melanopsid populations from Pannonian Zone C to D and finally is the predominating form in the Pannonian Zone E.

### *Melanopsis bouei* FÉRUSSAC, 1823
(Plate 5, Figs. 6-8)

2000 *Melanopsis bouei* FERUSSAC – BANDEL, p. 159, fig. 37-42, 45

**Description:** Stubby to moderately elongated shells of 5-7 whorls measuring up to 20 mm in height. Early whorls display a slow but regular increase in width, whereas the body whorl and the penultimate whorl reflect an allometric growth. The whorls are usually angulated and bear one or two rows of spines or nodes. These nodes are sometimes axially elongated. The inner lip develops a strong callus.

**Remarks:** *Melanopsis bouei* was described by JEKELIUS (1944) and PAPP (1953) by several subspecies such as *Melanopsis bouei rarispina* LŐRENTHEY, 1902, *Melanopsis bouei affinis* HANDMANN, 1887 and *Melanopsis bouei multicostata* HANDMANN, 1887. Both authors recognised the variability of *Melanopsis bouei* and mention the transitions between all morphologies. Recently, BANDEL (2000), too, concluded that there is no difference between the various subspecies if the identification is based on the classical monographs of LŐRENTHEY (1902), JEKELIUS (1944), and PAPP (1953).

At St. Margarethen all the "subspecies" are represented, although the typical *Melanospsis bouei bouei* predominates. In our opinion the species is another good example for the morphological plasticity of melanopsid species during the Late Early Pannonian, and the various "subspecies" should best be regarded as phenotypes. In the Austrian basins this morphological plasticity is severely narrowed after the Pannonian Zone E, when the slender *Melanopsis bouei sturi* phenotype is the predominating morph.

**Distribution:** The *Melanopsis bouei* group can be traced back into the Sarmatian. During the Pannonian it displays an extraordinary peak coinciding with the development of a high number of morphologies. In Austria, the lineage disappears in the Pannonian Zone H.

### *Melanopsis inermis* HANDMANN, 1882
(Plate 5, Figs. 4-5, Plate 6, Figs. 1-4)

1944 *Melanopsis inermis* HANDMANN – JEKELIUS, p. 135, pl. 54, fig. 1-20
1953 *Melanopsis inermis* HANDMANN – PAPP, p. 138, pl. 9, fig. 24-27
1980 *Melanopsis inermis* HANDMANN – LUEGER, p. 131, pl. 1, fig. 20
2000 *Melanopsis inermis* HANDMANN – BANDEL, p. 164

**Description:** Stubby, subspherical shell with huge body whorl and short, slender spire. It measures up to 15 mm in height. The flanks of the body whorl vary from convex to subparallel and may sometimes even develop a shallow concavity. Shell surface smooth without any traces of sculpturing. Some shells still display the colour ornament consisting of a characteristic pattern of irregular, axial zigzag lines. Inner lip strongly callous; in the posterior part of the aperture it forms a prominent swelling, which usually reaches to the very end of the angulation without forming a distinct tooth.

The protoconch comprises one slightly rounded whorl measuring 0.32 mm in height and in maximum diameter. The width of the initial cap is 0.1 mm. Ornamentation and transition to the teleoconch are not preserved.

**Remarks:** The variability of the species is perfectly documented by the specimens illustrated in JEKELIUS (1944). Within the Austrian material, the variability is mainly expressed in the height and apical angle of the spire and the more or less distinct concavity of the body whorl.

According to PAPP (1953), *Melanopsis textilis* BRUSINA and *Melanopsis avellana* LŐRENTHEY are synonymous with *Melanopsis inermis*.

Regarding the shape and dimensions the protoconch and the early teleoconch closely resemble those of modern *Esperiana acicularis audebartii* (PREVOST, 1823) as described by KOWALKE (1998: 42-43, pl. 4 figs. 13, 17). However, *Esperiana* differs by its slender shell and the lack of a columellar callus.

**Distribution:** *Melanopsis inermis* appears in the Pannonian Zone B and is a frequent species in all Austrian basins of Lake Pannon until the Pannonian Zone D.

### *Melanopsis pygmaea* HÖRNES, 1856
(Plate 5, Fig. 9, Plate 6, Figs. 11-13)

1856 *Melanopsis pygmaea* PARTSCH – HÖRNES, p. 599, pl. 49, fig. 13
1870 *Melanopsis pygmaea* PARTSCH – FUCHS, p. 545, pl. 22, fig. 9-10
1953 *Melanopsis pygmaea pygmaea* HOERNES – PAPP, p. 149, pl. 12, fig. 28-30, 33-34
1980 *Melanopsis pygmaea pymaea* M. HOERNES – LUEGER, p. 131, pl. 1, fig. 6
1985 *Melanopsis pygmaea pymaea* HOERNES – PAPP, pl. 34, fig. 27-29
1989 *Melanopsis pygmaea* – GEARY et al., p. 981, fig. 2
1993 *Melanopsis pygmaea pymaea* M. HOERNES – FORDINÁL, p. 64, pl. 13, fig. 5
1997 *Melanopsis pygmaea pymaea* M. HOERNES – FORDINÁL, p. 271, pl. 3, fig. 12
2000 *Melanopsis pygmaea* HOERNES – BANDEL, p. 163

**Description:** Slender shell of 6-7 weakly convex whorls measuring about 12 mm in height. Early whorls display a rather obtuse apical angle of approximately 45°, whilst later teleoconch whorls are more or less straight-sided and sub-parallel. Aperture elongated ovoidal, with distinct swelling on the columellar lip close to its posterior angulation. Inner lip strongly callous. No ornamentation was observed; shell surface smooth.

The protoconch comprises one slightly rounded whorl. It measures 0.06 mm in the width of the initial cap and 0.15-0.16 mm in maximum diameter. Ornamentation is not preserved. The protoconch is terminated by a thickened, slightly sinuous rim. The onset of the protoconch is indicated by the formation of dense growth lines.

**Remarks:** The species is a rare element at the investigated section. Its slender outline is strongly reminiscent of shells from the Pannonian Zone D of the Vienna Basin, which have been traditionally named *Melanopsis pygmaea mucronata*. The systematic separation of these taxa, which are well connected by intermediate shells, is doubted herein.

*Melanopsis doriae* ISSEL and *Melanopsis buccinoidea* FÉRUSSAC, as described by HELLER (1999) and BANDEL (2000) from Jordan, are morphologically similar but differ by their higher body whorl and the much weaker callus.

**Distribution:** An ubiquitous species in the entire Lake Pannon area. It appears in the Vienna Basin, the Eisenstadt-Sopron Basin, and the Styrian Basin in the Pannonian Zone C and reaches up to the Pannonian Zone F. The slender type, which was described as *Melanopsis pygmaea mucronata* HANDMANN, develops its acme during the Pannonian Zone D.

### *Melanopsis banatica* JEKELIUS, 1944
(Plate 7, Figs. 7-8)

1944 *Melanopsis banatica* n. sp. – JEKELIUS, p. 132, pl. 50, fig. 3-8, 12-14

**Description:** Early whorls bear a sharp keel which soon disintegrates into spiny nodes. On the last whorl these nodes are axially elongated. The entire shell carries weak spiral threads, which are best developed on the base of the last whorl. The columella is smooth without any fold or plication.

The protoconch comprises 1.3 bulbous, rounded whorls. It measures 0.3 mm in maximum diameter. The first whorl measures 0.27 mm in maximum diameter and 0.1 mm in the width of the initial cap. The protoconch is terminated by a slight rim. The onset of the teleoconch is indicated by the formation of the prominent spiral and axial adult sculpture.

**Remarks:** The shell is very similar to the specimen of St. Margarethen, which is described herein as *Melanoptychia brusinai*. Besides the columellar fold, which seems to be a rather dubious feature (cf. PAPP, 1953, BANDEL, 2000), *Melanopsis banatica* differs in its slender shell, the keeled whorls, the straight and more numerous axial swellings, and the strong adsutural concavity. Nevertheless, the separation of these taxa, based on the features of two specimens only, is not convincing.

**Distribution:** The species occurs in the Pannonian C of Romania and the Pannonian Zone C/D of the Eisenstadt-Sopron Basin.

Genus: *Melanoptychia* NEUMAYR, 1880

### *Melanoptychia brusinai* JEKELIUS, 1944
(Plate 7, Fig. 9)

1944 *Melanoptychia brusinai* n. sp. - JEKELIUS, p. 137, pl. 56, fig. 1-23.
1953 *Melanoptychia brusinai* JEKELIUS – PAPP p. 129
1980 *Melanoptychia brusinai* JEKELIUS – LUEGER, p. 103, fig.5/9

**Description:** Biconical, turreted, moderately slender shell of about 5 whorls. The protoconch is missing. A considerable angulation in the middle of the whorls coincides with a row of rounded nodes, which pass into strongly oblique axial swellings towards the anterior suture. Adapically to the angulation the whorls are flat or may even develop a shallow concavity. Indistinct spiral threads cover the base of the body whorl. The columella bears a distinct fold.

**Remarks:** see *Melanopsis banatica* JEKELIUS.

**Distribution:** In Austria the species is recorded from the Pannonian Zone C of the Vienna Basin, and from the Pannonian Zone C/D and E of the Eisenstadt-Sopron Basin.

Genus: *Boistelia* COSSMANN, 1909

### *Boistelia soceni* nov. sp.
(Plate 7, Fig. 6)

**Holotype:** NHMW 2001z0126/0049

**Locus typicus et stratum typicum:** St. Margarethen (Burgenland, Austria); sand of the Pannonian Zone C/D.

**Derivatio nominis:** The species name is derived from *Melanopsis soceni* JEKELIUS, which is the morphological counterpart with smooth columella.

**Description:** An extremely slender shell of 7 whorls. The protoconch is strongly convex. This convexity fades out within the first teleoconch whorl; later whorls are nearly flat, separated by very shallow sutures. A prominent columellar fold is developed; aperture elongated ovoidal. Outer lip is broken.

The protoconch comprises one rounded whorl. It measures 0.15 mm in the width of the initial cap and 0.3 mm in maximum diameter. Ornament and transition to the teleoconch are not preserved. With start of the second whorl, however, the shell outline becomes flat.

**Remarks:** The shell closely resembles *Melanopsis soceni* JEKELIUS. This slender form was interpreted by JEKELIUS (1944) to stand close to the *Melanopsis impressa*-group but is morphologically characterised by its smaller size, the consequently much more elongated outline, and the very short body whorl. Nonetheless, the prominent columellar fold of the shell from St. Margarethen is a feature, that was never observed within *Melanopsis soceni*. On the other hand, the spire of the plicate *Melanoptychia moesiensis* JEKELIUS is strongly reminiscent of the newly described shell. It differs, however, in the allometric growth of the body whorl, which furthermore develops nodes. Therefore, the combination of a smooth shell and a columellar fold prevents an identification as a *Melanopsis* or as a *Melanoptychia* but calls for a placement within *Boistelia*. In respect to the presumed hybridisation within these three genera (see BANDEL, 2000), such morphologies as presented by "*Boistelia soceni*" should not be overemphasised. It remains impossible to identify the interbreeding parent-species of the potential hybrids and a taxonomic solution as practised by botanists when describing hybrids is unrealisable.

**Distribution:** Only known from the Pannonian Zone C/D of the Eisenstadt-Sopron Basin. The resembling *Melanopsis soceni* was described from synchronous deposits of Romania (JEKELIUS, 1944) and from the Pannonian Zone B of Austria (PAPP, 1953).

Family: Pachychilidae TROSCHEL, 1857,

Subfamily: Melanatriinae THIELE, 1929,

Genus: *Tinnyea* HANTKEN, 1887

### *Tinnyea escheri* phenotype *vasarhelyii* HANTKEN, 1887

(Plate 5, Fig. 1)

1887 *Tinnyea Vásárhelyii* n. sp. – HANTKEN, p. 347, pl. 4
1902 *Melania (Melanoides) Vásárhelyii* HANTKEN – LŐRENTHEY, p. 203, pl. 14, fig. 1-2, pl. 15, fig. 1, textfig. 1
1939 *Brotia (Tinnyea) vásárhelyii* (HANTKEN) – WENZ, p. 687, fig. 1974
1944 *Brotia (Tinnyea) vásárhelyii* HANTKEN – JEKELIUS, p. 127, pl. 47, fig. 1-2
1994 *Brotia vasarhelyii* (HANTKEN) – FISCHER, p. 16, fig. 2

**Description:** Large-sized shell of up to 75 mm height and 35-40 mm maximum diameter, it is the largest *Tinnyea* found in the Miocene of Europe. Shell solid, turreted, with oblique axial ribs on early whorls which pass into wide-spaced, strongly oblique, axial swellings which terminate in apically bent spines.

The spines are situated along a sharp angulation in the posterior third of the whorls. A concave or flat sutural shelf may be developed. Spiral threads cover the shelf; number and strength of these spiral ornaments are highly variable; in most shells the spiral threads are formed by discontinuous, spirally elongated beads. Similarly, the strength and the number of the spiral ornaments running anterior to the spines are very variable. Apertures and apex are broken in all available specimens from Austria. A satisfactory description of the ovate aperture is given by LŐRENTHEY (1902).

The protoconch of a specimen from Leobersdorf (Plate 5, Figs. 2-3) comprises about two whorls measuring 0.5 mm in height. The first whorl measures 0.3 mm in maximum diameter and 0.1 mm in the width of the initial cap. The first whorl is characterised by a slightly folded surface. In the course of the second whorl about 10 spiral folds develop. The transition to the teleoconch is indistinct, indicated by a successive onset of the spiral and axial adult sculpture.

**Remarks:** The morphological plasticity of *Tinnyea escheri* led to the separation of several superfluous taxa which describe only phenotypes of a single species. Among these all Central Paratethyan specimens described as *Melania auingeri* HANDMANN, *Melania dactylodes* SANDBERGER, *Melanatria flumineiformis* TROLL, and *Brotia inornata* WENZ are considered by the present authors to represent solely *Tinnyea escheri* (BRONGNIART). The modern *Brotia costula* (RAFINESQUE) displays a similar range in morphology. The wide geographic distribution and the different habitats settled by this giant Indo-Pacific *Brotia* "caused an extremely large variety of forms which gave reason for the establishment of numerous taxa many of which can not even be considered as races or local forms" (BRANDT, 1974, p. 180).

*Tinnyea vasarhelyii* sensu HANTKEN (1887) differs from *Tinnyea escheri* mainly by its larger size, whilst the aperture features mentioned by HANTKEN (1887) were shown by LŐRENTHEY (1902) to occur within the entire *Tinnyea escheri*-group. Apart from their size, the shells could be characterised by the very strong sculpture consisting of prominent, axially fading spines and a coarse spiral ornament. At least the latter two features are already developed in the Pannonian Zone C and can be observed at scattered specimens within a large population of *Tinnyea escheri* from Leobersdorf in the Vienna Basin. There, a sandy layer yielded an extraordinary number of *Tinnyea escheri* shells. Among these the slender type with small or even absent spines predominates, but some shells develop prominent spines and a considerable sutural shelf and are therefore highly reminiscent of a small-sized *vasarhelyii*. This type is also present in the Pannonian Zone D of the Eisenstadt-Sopron Basin and was described as *Brotia escheri auingeri* (HANDMANN) by LUEGER (1980). Further, it is known from the Pannonian Zone E of the Styrian Basin, where it was identified as *Brotia escheri pilari* (NEUMAYER) by SAUERZOPF (1950). None of these shells, however, reached the size of *Tinnyea escheri* phenotype *vasarhelyii*. Probably *Tinnyea escheri vasarhelyii* represents an offspring of this *Tinnyea escheri* type, forming a short-lived giant race during the late Early Pannonian. Be that as it may, we are inclined to reject a species-level separation of this taxon based solely on the large size.

The shell illustrated by STEVANOVIĆ (1990b, pl. 14, fig. 8) as *Melania (Brotia) vasarhelyii* HANTKEN from the Portaferrian (Pontian) of Serbia is a small, slender, and little ornamented *Tinnyea* and probably represents another species or race.

*Melanatria* BOWDICH, 1822 with the recent type species *Melania fluminea* GMELIN, 1767 from Madagascar is very similar. It differs by the more slender, less solid shell and by the formation of straight axial ribs (WENZ 1938-1944: 689, fig. 1979; BROWN 1980: 99, figs. 56a, b). Recent *Brotia* H. ADAMS, 1866, with the type-species *Melania pagodula* GOULD, 1862 from Southeast Asia, differs by its more stout conical shell with a subangular aperture (WENZ 1938-1944: 686-687, fig. 1973). Recent *Potadoma* SWAINSON, 1840, with the type-species *Melania freethi* GRAY, 1831 from West- and Central Africa, differs by the lack of axial sculpture WENZ 1938-1944: 689, fig. 1980; BROWN 1980: 101, figs. 56c, d). The early ontogenetic shell of *Potadoma zenkeri* (MARTENS, 1901) from Cameroon is very similar to that of *Tinnyea escheri*. The large embryonic shell with similar dimensions bears slight spiral folds (KOWALKE, in press.). *Tinnyea* probably derives from the Tethyan coastal swamp inhabitant *Nodifaunus* OLSSON, 1944, which shares the angulated shell and the subordinated spiral sculpture with *Tinnyea* and which only differs by the lack of axial ribs and spines (KOWALKE, in press). A relation of *Tinnyea* within the Melanatriidae is feasible. The Paratethyan lineage could represent a relic of the brackish marginal Tethys fauna, which disappeared after the Pliocene due to a temperature drop, whereas the remainder settled fuviatile habitats of subsaharian Africa.

The early ontogenetic development of *Brotia* aff. *costula* (RAFINESQUE, 1833) from Cebu (Philippines) has been investigated by BANDEL & RIEDEL (1998). The protoconch is indicative of a development within a brood pouch. The initial 1.5 whorls are wrinkled, spiral folds are absent (BANDEL & RIEDEL 1998: 175, fig. 3K) and thus differ from the protoconch of *Tinnyea escheri*, whose early development did not take place within a brood pouch.

Recent representatives of the genera *Melanatria*, *Brotia,* and *Potadoma* are exclusively freshwater dwellers who favour riverine environments; *Brotia* is seldomly found in still water (BRANDT, 1974). A similar habitat preference is likely for the Oligocene to Pontian *Tinnyea* inhabiting the Central Paratethys and Lake Pannon. Consequently, the shells of *Tinnyea escheri vasarhelyii* are always damaged at the section St. Margarethen and partly even display traces of abrasion. The shells are therefore good indicators for the repeated influx of fluvial elements into the otherwise calm lake environment.

**Distribution:** In the Central Paratethys the history of this species can be traced back to the Oligocene of Hungary, Bavaria, and Slovenia, where its ancestor *Brotia escheri* is documented. The Paleogene representatives are rather small and slender but display a variability similar to their Miocene relatives. Spines may or may not be developed and the sutural shelf of fully grown shells may bear continuous spiral threads or discontinuous, beaded spirals (cf. BALDI, 1973; MIKUZ & PAVŠIC, 2000). After its first acme during the Late Oligocene, the *Tinnyea escheri*-group becomes a rarely reported element in Early and Middle Miocene faunas (e.g. STRAUSZ, 1966). It experienced its second and maximum bloom during the Pannonian and again declines distinctly in the Pontian and finally becomes extinct in Europe during the Pliocene cooling.

Subclass: Heterostropha FISCHER, 1885

Order: Allogastropoda HASZPRUNAR, 1985

Superfamily: Valvatoidea GRAY, 1840

Family: Valvatidae GRAY, 1840

Genus: *Valvata* MÜLLER, 1774

Subgenus: *Cincinna* FERUSSAC, 1821

### *Valvata (Cincinna) gradata globulosa* JEKELIUS, 1944
(Plate 8, Figs. 3-8)

1944 *Valvata (Cincinna) gradata globulosa* n. var. - JEKELIUS, p. 117, pl. 43, fig. 18-20
1997 *Valvata (Cincinna) gradata globulosa* JEKLIUS - FORDINÁL, p. 268, pl. 1, fig. 6

**Description:** Small-sized, depressed trochiform shell measuring up to 3 mm in maximum diameter, with strongly increasing body whorl. The last whorl usually develops a moderately convex ramp delimited by a spiral thread. 7-10 spiral threads of different strength cover the flanks and the base; along the flanks two or three of these spirals are usually more prominent. The ramp bears only very weak spirals. A dense pattern of weaker axial growth lines crosses the spiral ornamentation. The umbilicus is wide, the circular aperture terminates in an indistinct swelling.

The protoconch comprises 1.5 slightly rounded, low whorls. It measures 0.25-0.28 mm in maximum diameter. The first whorl measures 0.17-0.18 mm in maximum diameter and 0.17 mm in height (in the visible part). The width of the initial cap is 0.05-0.06 mm. The surface of the embryonic shell appears to be smooth. The protoconch is terminated by a thickened. The onset of the teleoconch is indicated by the formation of dense orthocline growth lines.

**Remarks:** *Valvata gradata globosa* differs from *Valvata gradata gradata* as described by JEKELIUS (1944) by its distinctly less gradate spire and the more convex ramp. This feature, however, is less obvious within the Austrian material, and even the shells described by FUCHS (1870) as *Valvata gradata* are rather intermediate. It is therefore questionable whether these sympatric and synchronous taxa represent natural subspecies.

The younger *Valvata subgradata* LŐRENTHEY is well distinguished by its much larger and very solid shell. *Valvata gradata* differs from the type species of the subgenus *Cincinna, Nerita piscinalis* O. F. MÜLLER, 1774 (WENZ 1938-1944: 506, fig. 1323), by its depressed shell, and by prominent spiral keels sculpturing the teleoconch.

**Distribution:** The subspecies is known from the Pannonian Zones C/D of the Eisenstadt-Sopron Basin, from Romania, and from the Pannonian Zone E of Slovakia.

### *Valvata* (*Cincinna*) *soceni* JEKELIUS, 1944
(Plate 8, Figs. 1-2)

1944 *Valvata soceni* n. sp. – JEKELIUS, p. 117, pl. 43, fig. 11-13

**Description:** Small-sized, conical shell of 3 teleoconch whorls measuring about 2 mm in height, with moderately high spire. The strongly convex body whorl is slightly inflated, measuring nearly one half of the total height. Aperture semicircular with very weak adapical angulation. Umbilicus deep, circular, rather narrow for a valvatid. Shell surface bears distinct growth lines.

The protoconch comprises about 1.5 slightly rounded low whorls measuring about 0.33 mm in maximum diameter and 0.06 mm in the width of the initial cap. The apparently smooth protoconch is terminated by a thickened. The onset of the teleoconch is indicated by the formation of dense, slightly prosocline growth lines.

**Remarks:** Corresponding to the Romanian shells illustrated by JEKELIUS (1944) the spire height displays a remarkable variability within the populations from the Eisenstadt-Sopron Basin. The shells are reminiscent of *Valvata obtusaeformis* LŐRENTHEY, 1902 in shape but differ considerably by their smaller size and by the convex whorls. *Valvata minima* FUCHS, 1877 and *Valvata kupensis* FUCHS, 1870 differ by their depressed shell. *Valvata banatica* (BRUSINA, 1902), which was mentioned by LUEGER (1980) from the Eisenstadt-Sopron Basin, can also be distinguished by its low spire. *Valvata varians* LŐRENTHEY, 1902 may develop shells of similar outline but differs by a keel at the umbilicus. *Valvata* (*Cincinna) soceni* differs from *V*. (*C*.) *gradata* by the lack of spiral keels, by the formation of prosocline growth lines, and by its slightly larger protoconch dimensions. *Valvata (Cincinna*) *piscinalis* is very similar. It differs by its larger shell and by its more rounded aperture, wider umbilicus and more strongly developed growth lines.

**Distribution:** The species is reported for the first time from the Eisenstadt-Sopron Basin and was originally described from synchronous deposits in Romania (JEKELIUS 1944).

Order Pulmonata CUVIER, 1817

Family Planorbidae RAFINESQUE, 1815

Genus: Gyraulus CHARPENTIER, 1837

### *Gyraulus verticillus* (BRUSINA, 1892)

(Plate 9, Figs. 6-8, Plate 10, Figs. 1-4)

1902 *Planorbis verticillus* BRUSINA – BRUSINA, pl. 4, fig. 36-39
1902 *Planorbis verticillus* BRUSINA – LŐRENTHEY, p. 187 in parte, pl. 13, fig. 12
1950 *Anisus (Gyraulus) verticillus* BRUSINA – SAUERZOPF, p. 138, pl. 7, fig. 3
1953 *Planorbis (Gyraulus) verticillus verticillus* BRUSINA – SAUERZOPF, p. 54, pl. 6, fig. 1

**Description:** The shell measures about 1.3 mm in maximum diameter. The planispirally coiled protoconch consists of 1.25 whorls measuring 0.26-0.27 mm in maximum diameter. The first whorl measures 0.18 mm in maximum diameter and 0.04 mm in the width of the initial cap. The first 0.25 whorls are slightly folded. The sculpture consists of 8-10 distinct, wide-spaced spiral lirae. The onset of strong growth lines indicates the beginning of the teleoconch, which is characterised by strong adsutural swellings on both sides of the shell. Towards the periphery a shallow concavity is developed adjacent to both swellings. The carina separates the planispiral shell into a more convex apical side (measuring approximately 3/5 of total height) and a less convex umbilical side. Sculpture of strong, collabral growth lines usually more strongly developed on apical side.

**Distribution:** *Gyraulus verticillus* is restricted in the Vienna Basin, the Eisenstadt-Sopron Basin, and the Styrian Basin to the Pannonian Zone D (SAUERZOPF, 1953) and seems to be an excellent biostratigraphic marker.

### *Gyraulus turislavicus* JEKELIUS, 1944
(Plate 13, Figs. 1-4)

1944 *Gyraulus turislavicus* JEKELIUS, p. 140, pl. 58, fig. 19-21
1953 *Planorbis (Gyraulus) turislavicus turislavicus* (JEKELIUS) – SAUERZOPF, p. 58, pl. 9, fig. 3
1953 *Planorbis (Gyraulus) turislavicus posterior* n. ssp. – SAUERZOPF, p. 58, pl. 9, fig. 2

**Description:** Very asymmetrical shell measuring about 2.2 mm in maximum diameter, with flat lower side and deeply sunken spire. Profile moderately high, flanks rounded with the maximum diameter close to the lower side of the shell. A characteristic spiral groove on the lower side of the shell separates a keel-like swelling close to the periphery. Growth lines become more prominent towards the aperture; generally the lower side is stronger sculptured, whereas the upper side is nearly smooth and glossy.

The protoconch is not well preserved. The first whorl measures 0.17-0.18 mm in maximum diameter and 0.04 mm in the width of the initial cap. It bears remains of spiral threads.

**Remarks:** SAUERZOPF (1953) defined the subspecies *Gyraulus turislavicus posterior* based on the slightly higher shell. He concluded that the older *Gyraulus turislavicus turislavicus* from the Pannonian Zones B and C is the ancestor of the younger and less flat *Gyraulus turislavicus posterior* of the Pannonian Zone D. This concept distinguishes two chronosubspecies. At the investigated section both morphologies can be collected even in the Pannonian Zone D. The chronosubspecies are rejected herein, and *Gyraulus turislavicus* is interpreted as a species that shows a slight shift in the height/diameter ratio during the Pannonian.

The flat shell and the distinct growth lines of the stratigraphically younger *Gyraulus radmanesti* (FUCHS) allow a separation from *Gyraulus turislavicus*. Specimens from the Pannonian Zones D and E from Austria which were described as *Gyraulus radmanesti* by LUEGER (1980) are therefore considered to represent rather *Gyraulus turislavicus*. The same problem arises when the relation of *Gyraulus turislavicus* with *Gyraulus rhytidophorus* (BRUSINA) is considered. This species, as indicated by SAUERZOPF (1953), seems to represent the direct descendant of *Gyraulus turislavicus* during the Pannonian Zone E. A strict use of the biological species concept would thus require a treatment of the whole lineage as *Gyraulus rhytidophorus* (BRUSINA, 1902)

**Distribution:** *Gyraulus turislavicus* appears in the Early Pannonian of Austria and Romania and has its acme during the Pannonian Zones C and D.

### *Gyraulus marinkovici* (BRUSINA, 1892)
(Plate 11, Figs. 1-9)

1892 *Planorbis Marinkovici* – BRUSINA, p. 129
1902 *Planorbis marinkovici* BRUSINA – BRUSINA, pl. 3, fig. 43-45
1953 *Planorbis (Gyraulus) marinkovici* BRUSINA – SAUERZOPF, p. 59, pl. 5, fig. 1-2

**Description:** Flat, medium-sized *Gyraulus* with 2 teleoconch whorls measures up to 3 mm in maximum diameter. Lower side concave with broad body whorl. The flanks are very low, passing in a weak convexity into the nearly flat upper side. Shell surface covered by dense, delicate growth lines. Rarely a spiral groove is developed close to the periphery of the lower side. This groove is usually shallow, developed only over a short distance, and appears in different positions.

The protoconch comprises 1.2-1.5 whorls measuring 0.33 mm in maximum diameter. The first whorl measures 0.21 mm in maximum diameter and 0.03 mm in the width of the initial cap. The surface of the protoconch seems to be smooth. The onset of the teleoconch is indicated by the formation of dense, regular growth lines.

**Remarks:** Differs from *Gyraulus fuchsi* by its larger size, the flatter shell, and the rather sharp angulation of the flanks, and by the larger initial whorl of the protoconch. The body whorl of *Gyraulus marinkovici* covers the preceding whorl to a larger degree.

*Gyraulus haueri* (Stoliczka) from the Pannonian of the Vienna Basin cannot be treated as conspecific as proposed by Sauerzopf (1953). The lentil-like outline in cross-section and the less expanding body whorl of *Gyrauls haueri* illustrated in Stoliczka (1862) allow a clear separation. *Gyraulus sabljari* (Brusina) differs by its narrow and deeper umbilicus.

**Distribution:** In Austria the species is known from the Pannonian Zones C, D, and E of the Eisenstadt-Sopron Basin and the Pannonian Zones E and F of the Styrian Basin.

### *Gyraulus micromphalus* (Fuchs, 1870)
(Plate 9, Figs. 1-5)

1870 *Planorbis micromphalus* Fuchs – Fuchs, p. 346 (non pl. 14, fig. 24-27)
1902 *Planorbis micromphalus* Fuchs – Brusina, pl. 4, fig. 50-52
?1953 *Planorbis* (*Gyraulus) popovici complanatus* n. ssp. - Sauerzopf, p. 59, pl. 3, fig. 4.
?1953 *Planorbis* (*Gyraulus) popovici popovici* Pavlovic – Sauerzopf, p. 59, pl. 3, fig. 3.
1971 *Gyraulus (Gyraulus) micromphalus* (Fuchs) – Gillet & Marinescu, p. 60, pl. 25, fig. 12-19
1980 *Gyraulus (Gyraulus) micromphalus* (Fuchs) – Lueger, p. 108, fig. 4/2

**Description:** Small-sized, moderately flat shell measuring up to 1.4 mm in maximum diameter, of hardly two teleoconch whorls. Flanks and lower side are well rounded; the upper side is less convex. Umbilicus extremely narrow.

The protoconch comprises 1.25 whorls measuring 0.27-0.28 mm in maximum diameter. The first whorl measures 0.22 mm in maximum diameter and 0.06-0.07 mm in the width of the initial cap. The embryonic shell seems to be smooth. The onset of the adult shell is indicated by the formation of dense regular growth lines.

**Remarks:** The specimens from the Pannonian Zones E and F of the Styrian Basin which are identified as *Gyraulus popovici* by Sauerzopf (1953) are reminiscent of *Gyraulus micromphalus* and are probably conspecific with the specimens from St. Margarethen. Unfortunately, it was not possible to compare the specimens with the original description or illustration of *Gyraulus popovici*, and therefore the relation between these species remains unclear.

**Distribution:** *Gyraulus micromphalus* is a frequent species in the Eisenstadt-Sopron Basin from the Pannonian Zones C through E. In Romania it occurs in the Late

Pannonian and Pontian. The probably conspecific *Gyraulus popovici* of SAUERZOPF (1953) is recorded in the Pannonian Zones D, E, and F of the Styrian Basin.

### *Gyraulus primiformis* (SAUERZOPF, 1953)
(Plate 12, Figs. 1-8)

1953 *Planorbis (Gyraulus) primiformis* n. sp. – SAUERZOPF, p. 60, pl. 10, fig. 1

**Description:** Small-sized shells hardly attaining 2 mm in diameter, with deep, moderately narrow umbilicus on lower side. Preceding whorls and protoconch reamin visible. Upper side planispiral. Periphery rounded with slightly flattened upper part and a weak angulation closer to the lower side. On both sides, the onset of the teleoconch is indicated by marked growth lines. On later whorls these colabral growth lines are stronger on the lower side, whereas they become weaker towards the suture on the upper side.

The protoconch comprises about 1.2 whorls measuring 0.35 mm in maximum diameter. The first whorl measures 0.31 mm in maximum diameter and 0.06 mm in the width of the initial cap. Sculpture consists of 15-20 distinct spiral threads, which seem partly to continue on the early teleoconch.

**Remarks:** Differs from *Gyraulus micromphalus* distinctly by the wider umbilicus, the larger size, the asymmetric convexity of the periphery, and by the distinctly sculptured embryonic shell. *Gyraulus globosus* (SAUERZOPF) also develops a wide umbilicus but its whorls are more convex and the shell is higher.

**Distribution:** A rarely reported species, which is known from the Pannonian Zone B of the Styrian Basin and from the Pannonian Zones C/D of the Eisenstadt-Sopron Basin.

### *Gyraulus fuchsi* (LŐRENTHEY, 1902)
(Plate 10, Figs. 5-8)

1870 *Planorbis micromphalus* FUCHS – FUCHS, pl. 14, fig. 24-27, (non p. 346)
1902 *Planorbis (Giraulus) fuchsi* nov. sp. – LŐRENTHEY, p. 189, pl. 12, fig. 14.
1953 *Planorbis (Gyraulus) fuchsi fuchsi* LŐRENTHEY – SAUERZOPF, p. 60, pl. 8, fig. 3
1980 *Gyraulus (Gyraulus) fuchsi* (LŐRENTHEY) – LUEGER, p. 108, fig. 4/1

**Description:** Small-sized, planispiral shell measuring about 1.4 mm in maximum diameter, with slightly sunken spire and wide, shallow umbilicus. Periphery convex with rounded angulation slightly closer to the lower side. Aperture parallel to the plane of coiling. Most characteristic is the large-sized, somewhat projecting protoconch. It comprises 1.25 whorls and measures 0.33 mm in maximum diameter. The first whorl measures 0.31 mm in maximum diameter and 0.06 mm in the width of the initial cap. The surface of the embryonic shell seems to be smooth. The onset of the teleoconch is indicated by the formation of dense regular growth lines.

**Remarks:** The most frequent *Gyraulus* at the section St. Margarethen. Originally this species was illustrated by FUCHS (1870). His description, however, was that of *Gyraulus micromphalus*. This mistake was already recognised by LŐRENTHEY (1902), who introduced *Gyraulus fuchsi*.

**Distribution:** Appears in the Pannonian Zones C, D, and E in the Eisenstadt-Sopron Basin and in the Zones B and C of the Styrian Basin. In Romania it was also recorded from the Lower Pontian.

Genus: *Orygoceras* BRUSINA, 1882

***Orygoceras fuchsi* (KITTL, 1886)**
(Plate 13, Figs. 5-8)

1886 *Creseis Fuchsi* - KITTL, p. 50, pl. 2, fig. 1-3
1892 *Orygoceras corniculum* n. sp. - BRUSINA, p. 57
1902 *Orygoceras corniculum* - BRUSINA, pl. 2, fig. 34-37
1902 *Orygoceras corniculum* BRUSINA - LŐRENTHEY, p. 194, pl. 11, fig. 20-22, pl. 12, fig. 11
1903 *Orygoceras Fuchsi* KITTL - LŐRENTHEY, p. 2
1936 *Orygoceras Fuchsi* KITTL sp. - VITÁLIS, p. 631 (cum syn.)
1944 *Orygoceras Fuchsi* KITTL - JEKELIUS, p. 118, pl. 43, fig. 22-23
1950 *Orygoceras fuchsi fuchsi* KITTL - SAUERZOPF, p. 115
1953 *Orygoceras fuchsi fuchsi* (KITTL) - PAPP, p. 112, pl. 5, fig. 3
1962 *Orygoceras fuchsi fuchsi* (KITTL) - PAPP, p. 204, fig. 1-2
1980 *Orygoceras fuchsi* (KITTL) - LUEGER, p. 107
1985 *Orygoceras fuchsi* (KITTL) - PAPP, p. 288, fig. 38-40
1999 *Orygoceras fuchsi* (KITTL) – LENNERT et al., p. 75, pl. 5, fig. 10-11

**Description:** Small, asymmetrical, uncoiled shells of up to 3 mm length. Even the planispirally coiled protoconch indicates tendencies to uncoil after ? whorls. A dense pattern of 16-18 spiral lirae covers the protoconch. It comprises about one whorl and measures 0.26 mm in maximum diameter and 0.08-0.09 mm in the width of the initial cap. The onset of the teleoconch is marked by an abrupt change of sculpture; the striation vanishes and the later shell surface is smooth except for growth lines, which become more prominent towards the subcircular aperture.

**Remarks:** The genus *Orygoceras* experienced an astonishing odyssey through systematics and has been treated variously as a descendant of the valvatids (WENZ, 1939; SAUERZOPF, 1950; PAPP, 1953) or as an uncoiled planorbid (PAPP, 1962; 1985). Even a close relationship to the Caecidae was advocated (BOETTGER 1884; LŐRENTHEY 1902). Finally, to complete the confusion, TAYLOR (1974) gave an excellent description of the protoconch of a Recent shell from Texas, concluding that it is quite different from that of valvatids and therefore affiliates his shells within the hydrobiids. However, as can be confirmed by the herein described and illustrated protoconch of *Orygoceras fuchsi*, the protoconch of the American shells has little in common with the European *Orygoceras* sensu BRUSINA (1892). Therefore, the shells from Idaho and Texas, formerly identified as *Orygoceras* by TAYLOR (1974) and DAVIS (1983), are definitely not congeneric with the European, endemic *Orygoceras*. According to TAYLOR (1974) the protoconch of the American genus is characterised by irregular oval, elongate, raised elements that are seldom branched. The raised elements do not form spiral threads, but rather a spirally aligned, discontinuous, sometimes wavy sculpturing. Further differences can even be stated from the teleoconchs of both genera. *Orygoceras* is more slender, very elongated and its protoconch is much smaller in relation to the total shell length.

As discussed extensively by RIEDEL (1993), the difficulties in distinguishing planorbids from valvatids based on protoconch features is hampered by convergencies in shape and sculpture. Uncoiling is also a feature observable in both groups, e.g. within the valvatids a modern uncoiled species is recorded as *Valvata sincera ontariensis* KLOTZ by CLARKE (1973) from the Canadian Interior Basin. Among the planorbids, several uncoiled species are documented from the Miocene of the Steinheim Basin by NÜTZEL & BANDEL (1993). Generally, however, the protoconchs of valvatids as illustrated by BINDER (1967) and RIEDEL (1993) differ from that of the presented *Orygoceras* by more numerous finer spiral lirae and by the formation of connections between the spiral ornament. In contrast, the protoconchs of planorbids such as *Gyraulus crescens* (HILGENDORF), *Gyraulus triquetrus* (HILGENDORF), and *Gyraulus protocrescens* NÜTZEL & BANDEL illustrated in NÜTZEL & BANDEL (1993) correspond to a high degree to the protoconch of *Orygoceras fuchsi*, which is therefore considered to represent a planorbid. This observation confirms the systematic treatment already proposed by PAPP (1962), although his argumentation was based on weak ground.

**Distribution:** *Orygoceras fuchsi* is an ubiquitous element in the Early Pannonian (Zone B, C, D) and is endemic in Lake Pannon, where it is known from Hungary, Serbia, Romania, Croatia, and Austria. In Austria it is documented from the Vienna Basin (Leobersorf), the Eisenstadt-Sopron Basin (Siegendorf, Föllig, St. Margarethen, Wiesen) and from the Styrian Basin (Burgau, Oberschützen, Grafendorf, Buchberg). VITÁLIS (1936) describes different morphs of *Orygoceras* from the area around Sopron and Fertőrákos in Hungary, where he found his specimen - like in St. Margarethen - mainly in the apertures of *Melanopsis fossilis* and *Melanopsis vindobonensis*.

The genus is known to the present authors mainly from the Late Miocene Pannonian stage of Lake Pannon. An alleged record of *Orygoceras* from sediments older than Pannonian was described by JURIŠIĆ-POLŠAK et. al (1992) from the "Middle Miocene of Sinj, Novi bunar" in Croatia. However, the illustrations given by these authors clearly show a *Parastrophia* FOLIN, 1869, fully corresponding to the specimens described by BANDEL (1996, plates 9 and 10). The smooth protoconch of the Croatian species differs distinctly from those of Pannonian *Orygoceras* as well as from the North American shells erroneously ascribed to *Orygoceras* by TAYLOR (1974). Another non-Pannonian occurrence was mentioned by BITTNER (1888) from the slightly older Sarmatian (Late Middle Miocene) of Wiesen in Burgenland/Austria. This occurrence seems to be very doubtful, since BITTNER did not collect the shells personally but identified them from older collections. At Wiesen, fine sand of the Pannonian Zone C occurs directly above the Sarmatian sediments, which may thus explain the so-called Sarmatian *Orygoceras*. A Badenian occurrence at Forchtenau (Austria), as could be deduced from the description of *Creseis Fuchsi* by KITTL (1886), was earlier rejected by LŐRENTHEY (1903), who showed that KITTL's specimens were miss-labelled. One of the latest known occurrences of the genus is an unillustrated *Orygoceras* sp. from the Pontian of Serbia (STEVANOVIĆ, 1990a) and *Orygoceras fuchsi* from the same stratigraphic level of Hungary (LENNERT et al., 1999). Afterwards the genus apparently became extinct.

## Early Ontogenetic Development of Lake Pannon Gastropods

Most of the investigated gastropods were characterised by a direct development with hatching of crawling young after a more or less yolk-rich embryogenesis. However, the protoconch dimensions of several species reflect a free-swimming larval stage during which the larva fed on phytoplankton after hatching from the egg. The occurrence of planktotrophic species indicates the slightly brackish character of Lake Pannon during the investigated stratigraphic range. For example, *Neritina vetranici* and *Neritina mariae* (Neritidae) were characterised by small protoconchs, reflecting a planktonic larval stage. In this regard they could easily be distinguished from direct developers within the genus *Theodoxus*. *Hydrobia ambigua* (Hydrobiidae) was also characterised by a planktotrophic veliger. The protoconch is highly reminiscent of protoconchs of Recent hydrobiids (KOWALKE 1998). The larval shell comprises about one whorl, which indicates a shorter stay within the plankton. The protoconch morphology of *Socenia soceni* (Pyrgulidae?) is very similar; this enables a differentiation from syntopic, direct-developing species of the genus. The larval shell is indicative of a short-term veliger. The similarity of the protoconchs of Hydrobiidae and Pyrgulidae might indicate a very close relation of the families within the Rissooidea.

Among those gastropods that underwent direct development, the genera *Micromelania*, *Goniochilus,* and *Socenia* were characterised by very similar embryonic shells with a flat or slightly ermerging embryonic whorl. The shiny embryonic shells tend to uncoil in the first half whorl. The similarities regarding the protoconch morphologies confirm their systematic position within the Pyrgulidae.

Among the investigated Cerithioidea, planktotrophic development was absent. The cerithioidean fauna was dominated by melanopsids and the fluvial *Tinnyea*. The protoconchs of melanopsids allowed a clear differentiation of species based on different protoconch sizes. Two general types of melanopsid protoconchs occurred. 1. Protoconchs with a very large, bulbous initial whorl indicating a yolk-rich embryogenesis resembling the early ontogenetic shells of modern *Melanopsis* and *Esperiana* (KOWALKE 1998). 2. A protoconch with small initial cap and moderately small embryonic whorl. This indicates a different mode with small-sized eggs and a less yolk-rich embryogenesis. However, hatching of crawling young is indicated by the morphology of the terminus of the protoconch and by the subsequent early teleoconch.

*Tinnyea escheri* was characterised by a large, bulbous embryonic shell comprising almost two whorls; this reflects a similar development as in related modern *Potadoma* from West Africa with very similar protoconch dimensions and sculpture (KOWALKE, in press). The large freshwater gastropod develops from yolk-rich eggs that are arranged in strings embedded in a jelly mass. *T. escheri* most probably underwent a similar mode of development.

Within the genus *Gyraulus* (Planorbidae) two protoconch types occur: protoconchs with strong spiral sculpture and appearantly smooth ones. The lack of sculpture could also be due to corrosion of a formerly very weak ornamental feature. However, all *Gyraulus* spp. could clearly be differentiated by different protoconch sizes. The genus *Orygoceras* was characterised by a very similar protoconch morphology, and its systematic placement within the Planorbidae could be confirmed here.

## Conclusion

The composition of the fauna corresponds well to those from synchronous deposits of the Vienna Basin and those from the Styrian Basin. Together with the gastropod faunas from Romania and Croatia, these Austrian faunas document some uniformity during the late Early Pannonian in the entire area of Lake Pannon. Minor differences could only be distinguished within the planorbids, which are unknown so far from Romania. This, however, is probably rather a matter of investigation level than biogeography.

In the Eisenstadt-Sopron Basin and in all adjacent sedimentation areas the late Early Pannonian zones C/D bear witness to an extraordinary acme in speciation as well as in morphological plasticity within the molluscs. This might be interpreted as a reaction to the earliest Pannonian "shock", which was a result of the coincidence of a relative sea-level lowstand and the final turnover of water chemistry towards freshwater conditions. The recovery was initiated by the rising water level and the synchronously diversifying biotas. This bloom, however, was slightly interrupted in the Pannonian Zone E, which coincides with the maximum flooding surface from a sequence stratigraphic point of view (KOVÁČ et al., 1998). This minor trend is especially reflected in the melanopsids, which nearly lack the large-sized representatives of the *Melanopsis fossilis*-group with its manifold morphologies, whilst the relatively simple *Melanopsis vindobonensis* replaces *Melanopsis fossilis* in the Pannonian Zone E. In contrast, many bivalves experienced a major evolutionary bloom in the Pannonian Zone E. Thus, the presented fauna is a snapshot of the first phase of evolution and radiation of gastropods in the Late Miocene Lake Pannon.

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## Plate 1

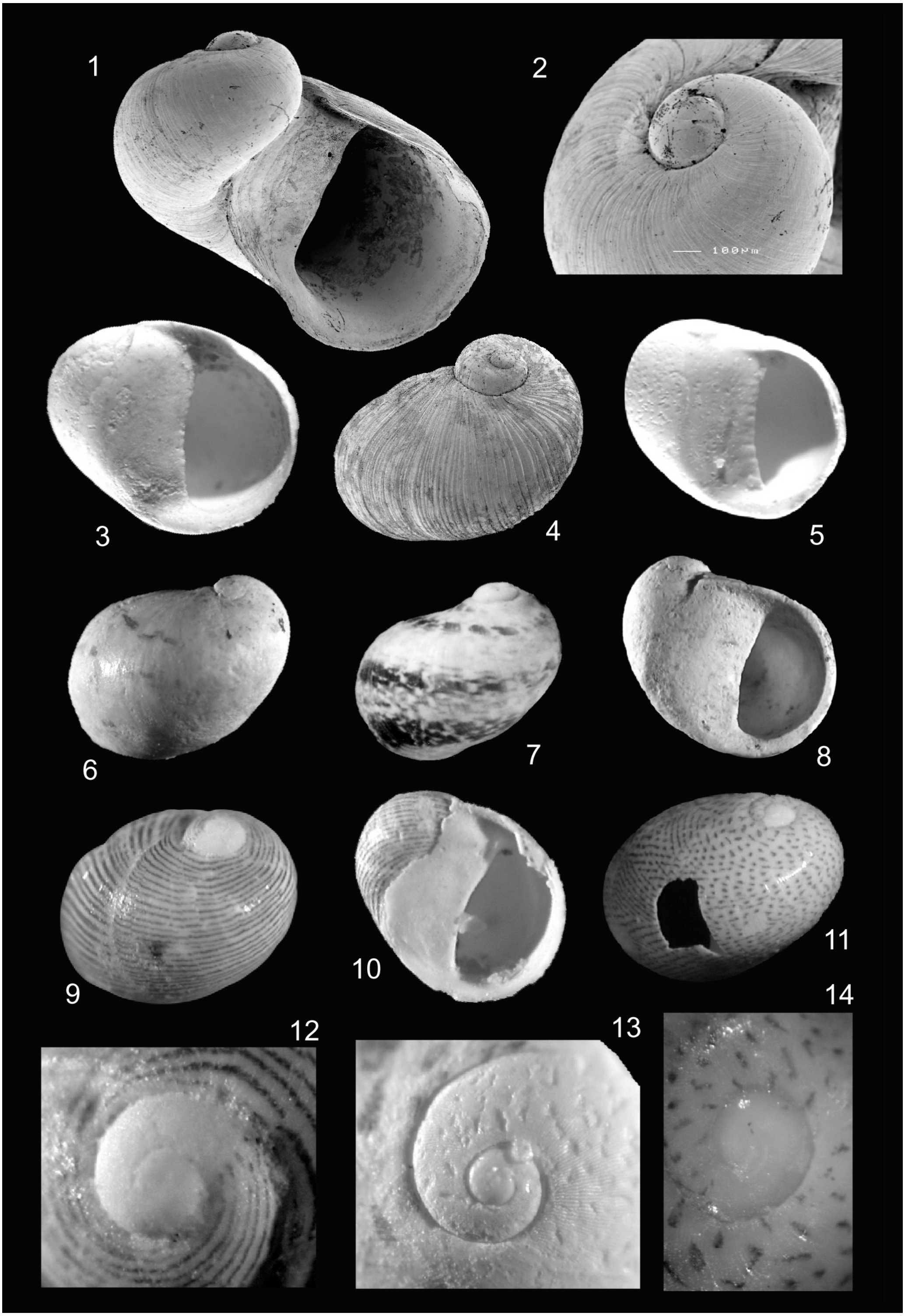
Fig. 1-2, 4: ***Theodoxus cunici* (BRUSINA, 1892)**
fig. 1 diameter: 2 mm (NHMW 2001z0126/0000)
fig. 4 diameter: 2.7 mm (NHMW 2001z0126/0001)

Fig. 3, 5, 13: ***Theodoxus soceni* JEKELIUS, 1944**
fig. 3 height: 3.3 mm (NHMW 2001z0126/0002)
fig. 5 height: 4 mm (NHMW 2001z0126/0003)
fig. 13 shows protoconch of fig. 3, maximum diameter: 0.48 mm

Fig. 6-8: ***Theodoxus intracarpaticus* JEKELIUS, 1944**
fig. 6 height: 7 mm (NHMW 2001z0126/0004)
fig. 7 height: 5.4 mm (NHMW 2001z0126/0005) – fig. 8 same specimen as fig. 6

Figs. 9-10, 12: ***Neritina vetranici* (BRUSINA, 1902)**
height: 2.2 mm (NHMW 2001z0126/0006)
fig. 12 shows protoconch of the specimen, maximum diameter: 0.3 mm

Figs. 11, 14: ***Neritina mariae* (HANDMANN, 1887)**
height: 1.9 mm (NHMW 2001z0126/0007)
fig. 14 shows protoconch of the specimen, maximum diameter: 0.23 mm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## Plate 2

Fig. 1: ***Socenia* cf. *politioanei* Jekelius, 1944**
height: 2.3 mm (NHMW 2001z0126/0008)

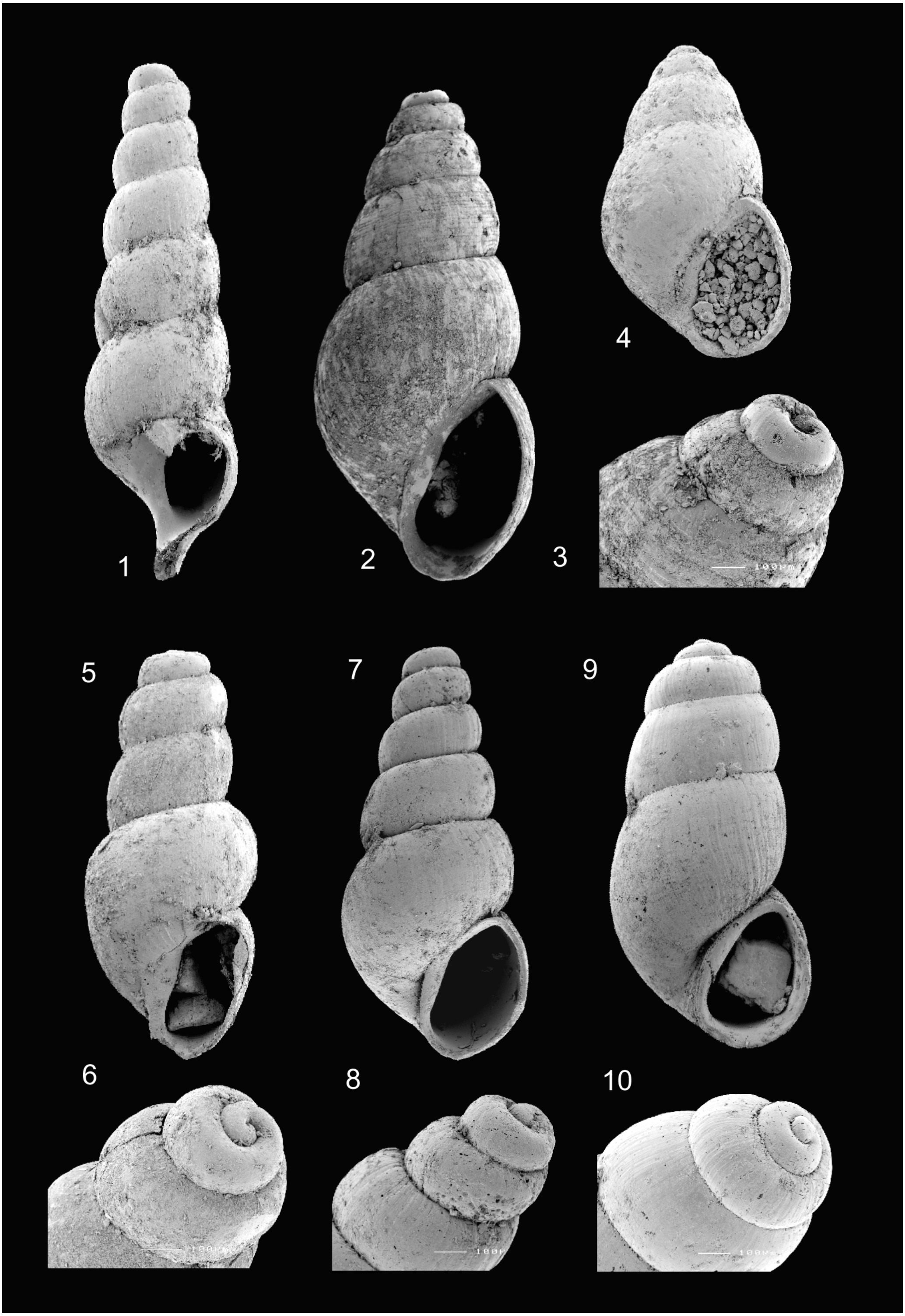
Figs. 2-3: ***Micromelania sulcata* (Brusina, 1892)**
height: 2.5 mm (NHMW 2001z0126/0009)
fig. 3 shows protoconch of fig. 2

Fig. 4: ***Pseudamnicola (Staja) turislavica* Jekelius, 1944**
height: 1.8 mm (NHMW 2001z0126/0010)

Figs. 5-6: ***Socenia soceni* Jekelius, 1944**
height: 1.9 mm (NHMW 2001z0126/0011)
fig. 6 shows protoconch of fig. 5

Figs. 7-8: ***Hydrobia* sp.**
height: 2.8 mm (NHMW 2001z0126/0012)
fig. 8 shows protoconch of fig. 7

Figs. 9-10: ***Caspia vujici* Brusina, 1902**
height: 1.9 mm (NHMW 2001z0126/0013)
fig. 10 shows protoconch of fig. 9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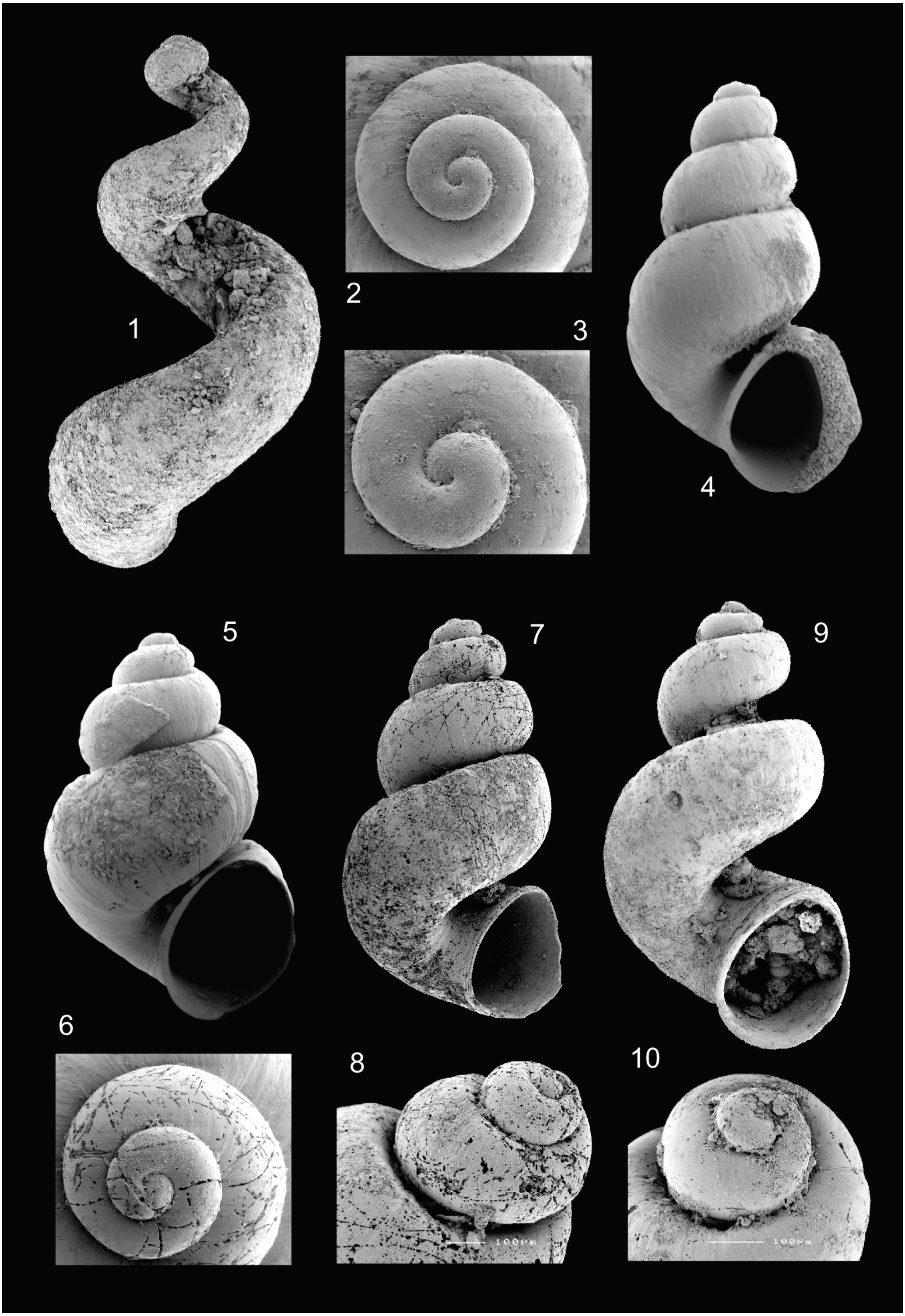
## Plate 3

Figs. 1-10: ***Hydrobia (Baglivia) ambigua*** **(BRUSINA, 1892)**

fig. 1 height: 2.0 mm (NHMW 2001z0126/0014)
fig. 4 height: 2.3 mm (NHMW 2001z0126/0015)
figs. 2-3 show protoconch of fig. 4
fig. 5 height: 1.97 mm (NHMW 2001z0126/0016)
fig. 6 shows protoconch of fig. 5
fig. 7 height: 2.1 mm (NHMW 2001z0126/0017)
fig. 8 shows protoconch of fig. 7
fig. 9 height: 1.9 mm (NHMW 2001z0126/0018)
fig. 10 shows protoconch of fig. 9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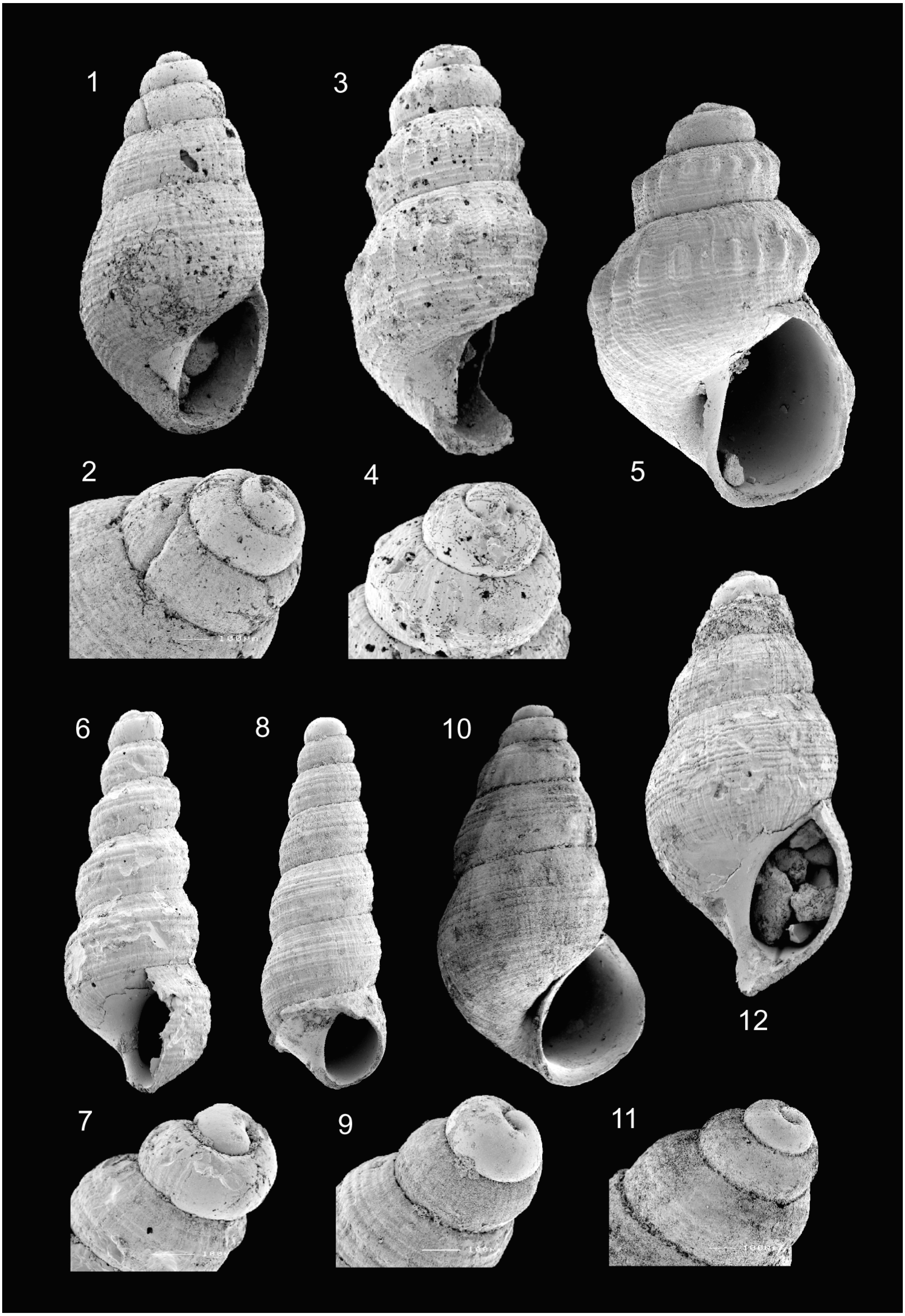
## Plate 4

Figs. 1-2, 10-12: ***Caspia compacta* JEKELIUS, 1944**
height: 2.3 mm
fig. 2 shows protoconch of fig. 1 (NHMW 2001z0126/0019)
fig. 10 height: 2.4 mm (NHMW 2001z0126/0020)
fig. 11 shows protoconch of fig. 10 - fig. 12 (NHMW 2001z0126/0021)
height: 2.7 mm

Figs. 3-4: ***Goniochilus glandulinus haidingeri* (STOLICZKA, 1862)**
height: 2.3 mm
fig. 4 shows protoconch of fig. 3 (NHMW 2001z0126/0022)

Fig. 5: ***Goniochilus breviformis* (PAPP, 1953)**
height: 2.1 mm (NHMW 2001z0126/0023)

Figs. 6-9: ***Socenia moesia* (JEKELIUS, 1944)**
fig. 6 height: 2.2 mm (NHMW 2001z0126/0024)
fig. 7 protoconch of fig. 6
fig. 8 height: 2.4 mm (NHMW 2001z0126/0025)
fig. 9 protoconch of fig. 8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## Plate 5

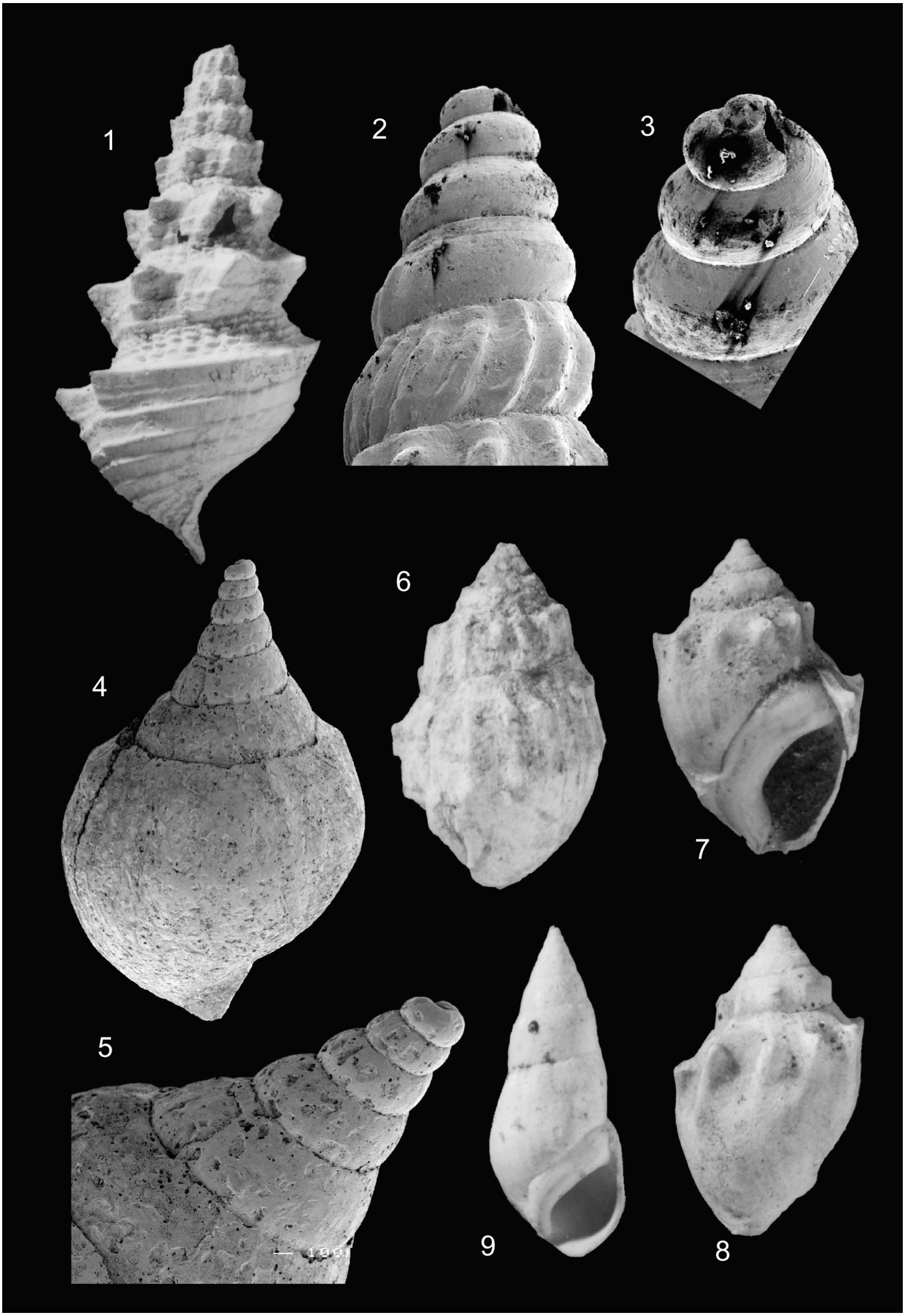
Fig. 1: ***Tinnyea escheri* phenotype *vasarhelyii* Hantken, 1887**
height: 68.2 mm (NHMW 2001z0126/0026)

Figs. 2-3: ***Tinnyea escheri* (Brongniart, 1822)**
specimen from Leobersdorf (Austria), Pannonian C (NHMW 2001z0126/0027)
height of fig. 2 corresponds to 1.8 mm

Fig. 4-5: ***Melanopsis inermis* Handmann, 1882**
(NHMW 2001z0126/0028)
fig. 4 height: 5.6 mm
fig. 5 shows protoconch of fig. 4

Figs. 6-8: ***Melanopsis bouei* Férussac, 1823**
fig. 6 height: 16 mm (NHMW 2001z0126/0029)
fig. 7 height: 15.3 mm (NHMW 2001z0126/0030)
fig. 9 height: 14.4 mm (NHMW 2001z0126/0031)

Fig. 9: ***Melanopsis pygmaea* Hörnes, 1856**
height: 11.4 mm (NHMW 2001z0126/0032)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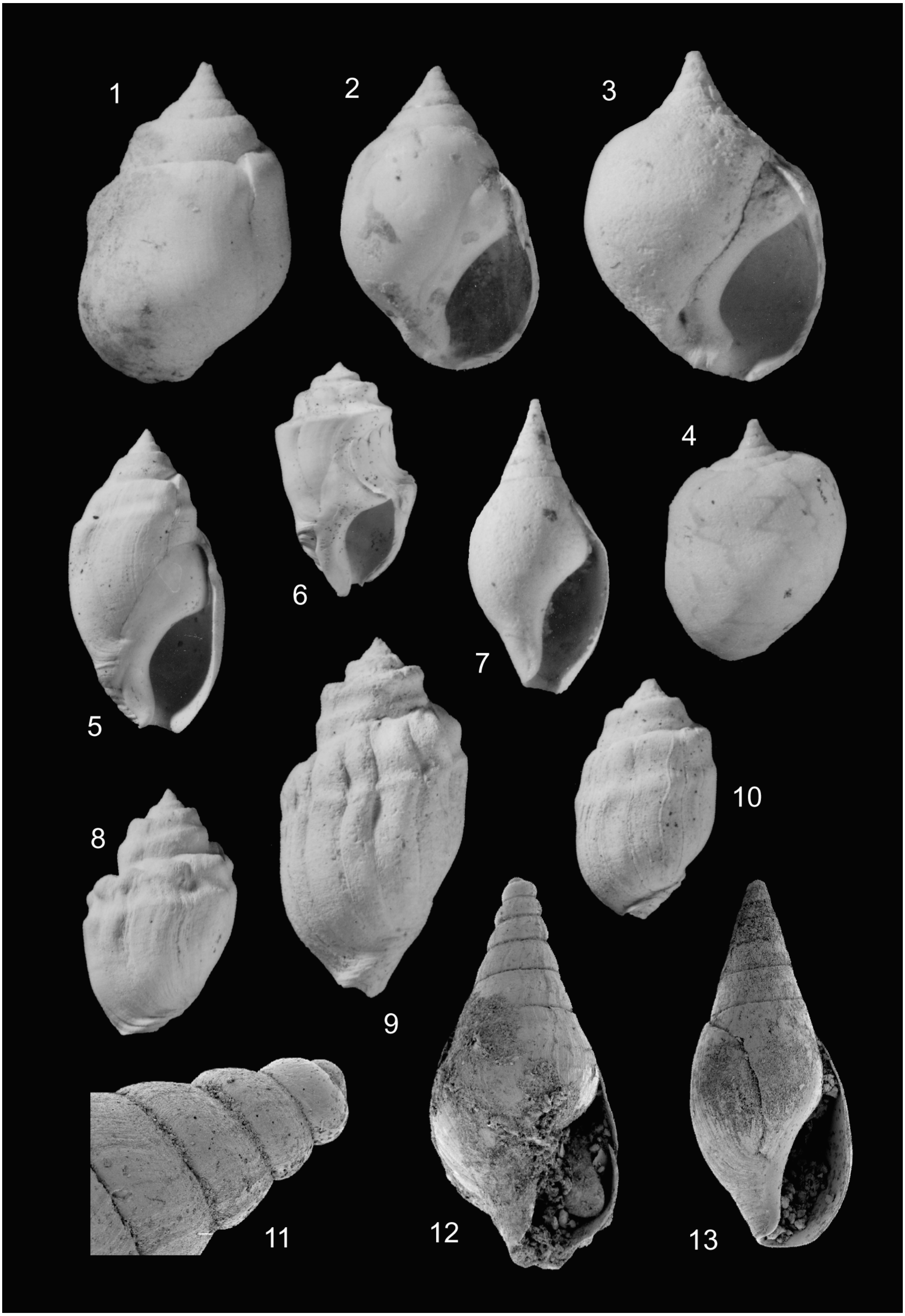
## Plate 6

Figs. 1-4: ***Melanopsis inermis*** **HANDMANN, 1882**
fig. 1 height: 14 mm (NHMW 2001z0126/0033)
fig. 2 height: 13.1 mm (NHMW 2001z0126/0034)
fig. 3 height: 12.2 mm (NHMW 2001z0126/0035)
fig. 4 height: 11.2 mm (NHMW 2001z0126/0036)

Figs. 5-10, 13 ***Melanopsis fossilis*** **(GMELIN, 1790**)
5-6, 8-10 - *Melanopsis fossilis* phenotype *coaequata* HANDMANN, 1887
fig. 5 height: 46.8 mm (NHMW 2001z0126/0037)
fig. 6 height: 36.4 mm (NHMW 2001z0126/0038)
fig. 7 height: 8.8 mm (NHMW 2001z0126/0039)
fig. 8 height: 38.5 mm (NHMW 2001z0126/0040)
fig. 9 height: 53.7 mm (NHMW 2001z0126/0041)
fig. 10 height: 37.3 mm (NHMW 2001z0126/0042)

Figs. 11-13: ***Melanopsis*** **pygmaea**
fig. 12 height: 2.1 mm (NHMW 2001z0126/0044)
fig. 11 shows protoconch of fig. 12
fig. 13 height: 4.8 mm (NHMW 2001z0126/0043)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## Plate 7

Figs. 1-3: ***Melanopsis vindobonensis* FUCHS, 1870**
fig. 1 height: 35.9 mm (NHMW 2001z0126/0045)
fig. 2 height: 24.5 mm (NHMW 2001z0126/0046)
fig. 3 height: 22.1 mm (NHMW 2001z0126/0047)

***Melanopsis fossilis* (GMELIN, 1790)**
fig. 4 height: 2.8 mm (NHMW 2001z0126/0048)
fig. 5 shows protoconch of fig. 4

Fig. 6: ***Boistelia soceni* nov. sp.** vel nov. hybrid
height: 3.8 mm (Holotype: NHMW 2001z0126/0049)

Figs. 7-8: ***Melanopsis banatica* JEKELIUS, 1944**
fig. 8 height: 2.4 mm (NHMW 2001z0126/0050)
fig. 7 shows protoconch of fig. 8

***Melanoptychia brusinai* JEKELIUS, 1944**
height: 2.6 mm (NHMW 2001z0126/0051)

Figs. 10-12: ***Melanopsis fossilis* (GMELIN, 1790)**
**phenotype *handmanniana* FISCHER, 1996**
fig. 10 height: 36.2 mm (NHMW 2001z0126/0052)
fig. 11 height: 50.1 mm (NHMW 2001z0126/0053)
fig. 12 height: 44.6 mm (NHMW 2001z0126/0054)

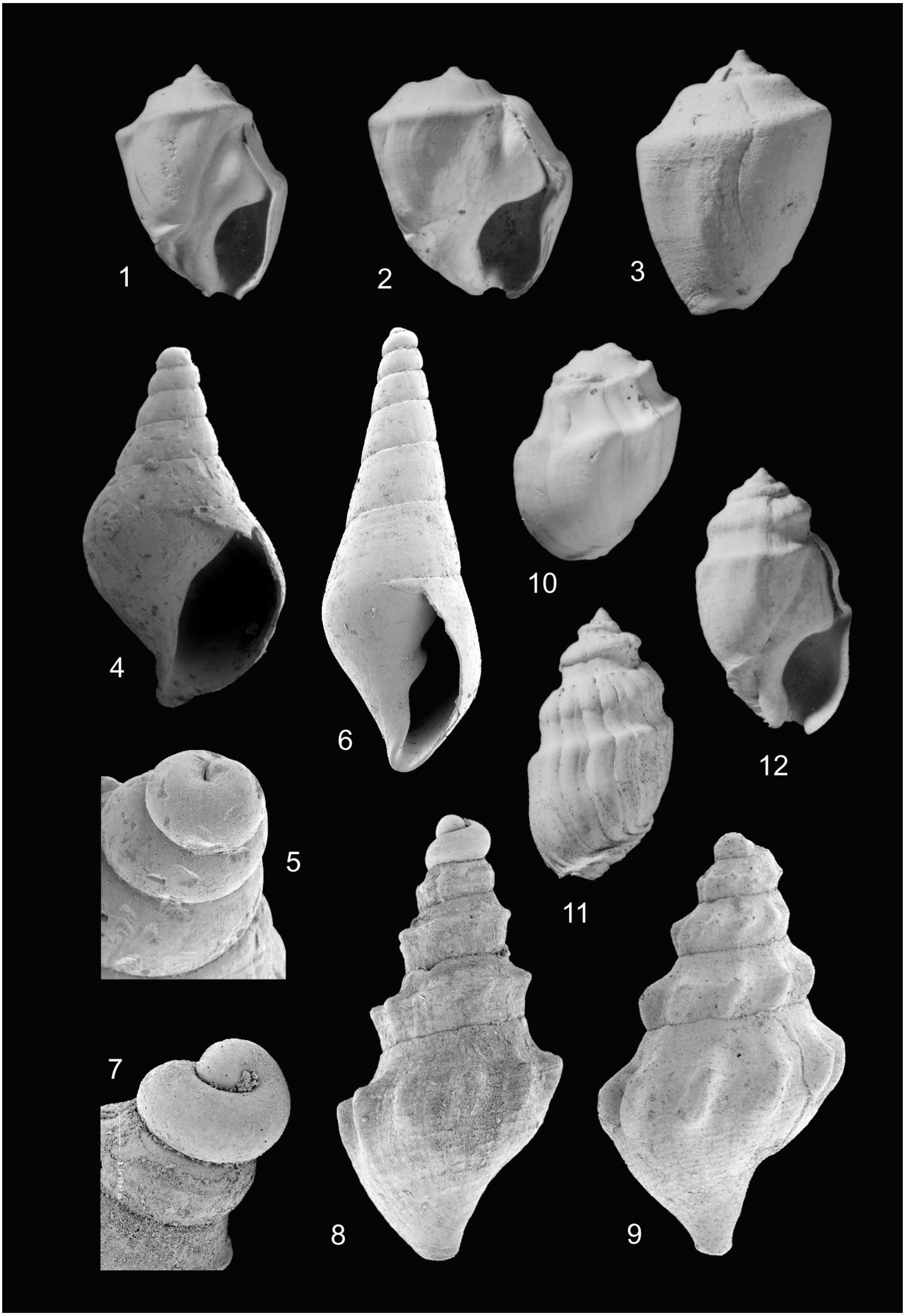
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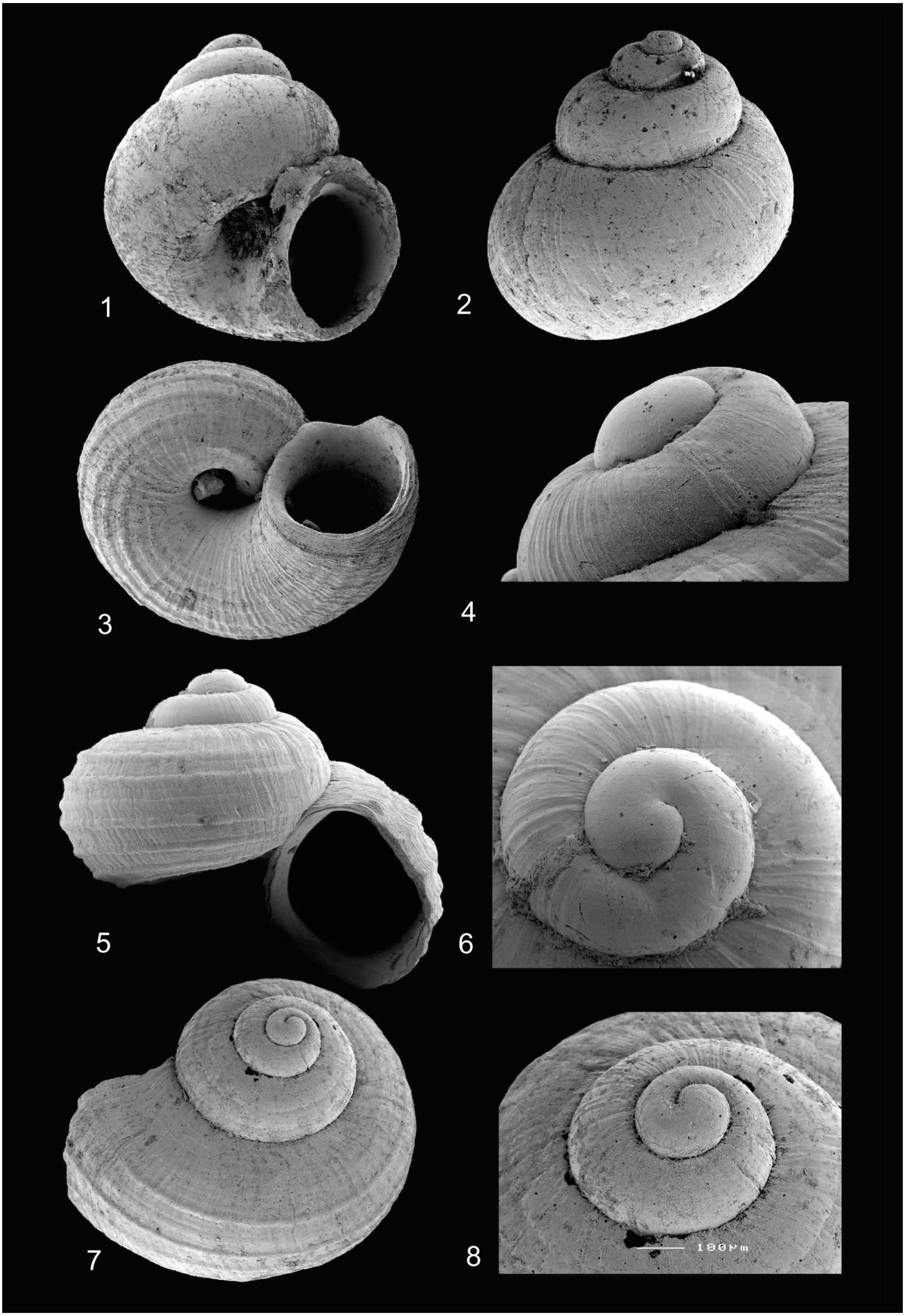
**Plate 8**

Figs. 1-2: ***Valvata (Cincinna) soceni*** **JEKELIUS, 1944**
fig. 1 height: 1.6 mm (NHMW 2001z0126/0055)
fig. 2 height: 1.2 mm (NHMW 2001z0126/0056)

Figs. 3-8: ***Valvata (Cincinna) gradata globulosa*** **JEKELIUS, 1944**
fig. 3 diameter: 1.7 mm (NHMW 2001z0126/0057)
fig. 4 length of picture: 0.4 mm (NHMW 2001z0126/0058)
fig. 5 diameter: 1.5 mm (NHMW 2001z0126/0059)
fig. 6 shows protoconch of fig. 5
fig. 7 diameter: 1.8 mm (NHMW 2001z0126/0060)
fig. 8 shows detail of fig. 7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## Plate 9

Figs. 1-5: ***Gyraulus micromphalus* (FUCHS, 1870)**
fig. 1 diameter: 1.3 mm (NHMW 2001z0126/0061)
fig. 2 diameter: 1.5 mm (NHMW 2001z0126/0062)
fig. 4 shows protoconch of fig. 2
fig. 5 diameter: 1.35 mm (NHMW 2001z0126/0063)
fig. 3 shows protoconch of fig. 5

Figs. 6-8: ***Gyraulus verticillus* BRUSINA, 1892**
fig. 6 diameter: 1.2 mm (NHMW 2001z0126/0064)
fig. 7 diameter: 1.3 mm (NHMW 2001z0126/0065)
fig. 8 shows protoconch of fig. 6

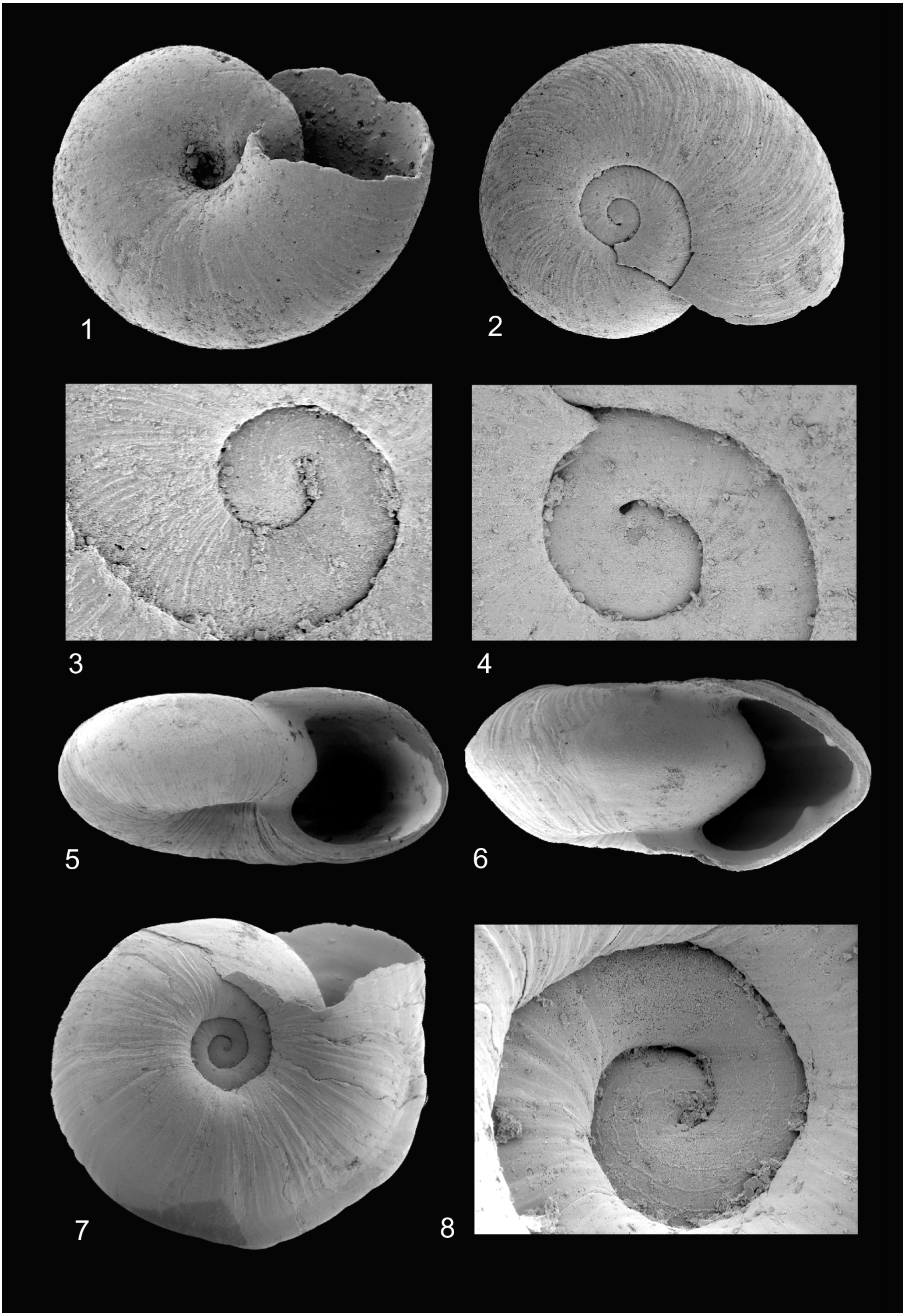
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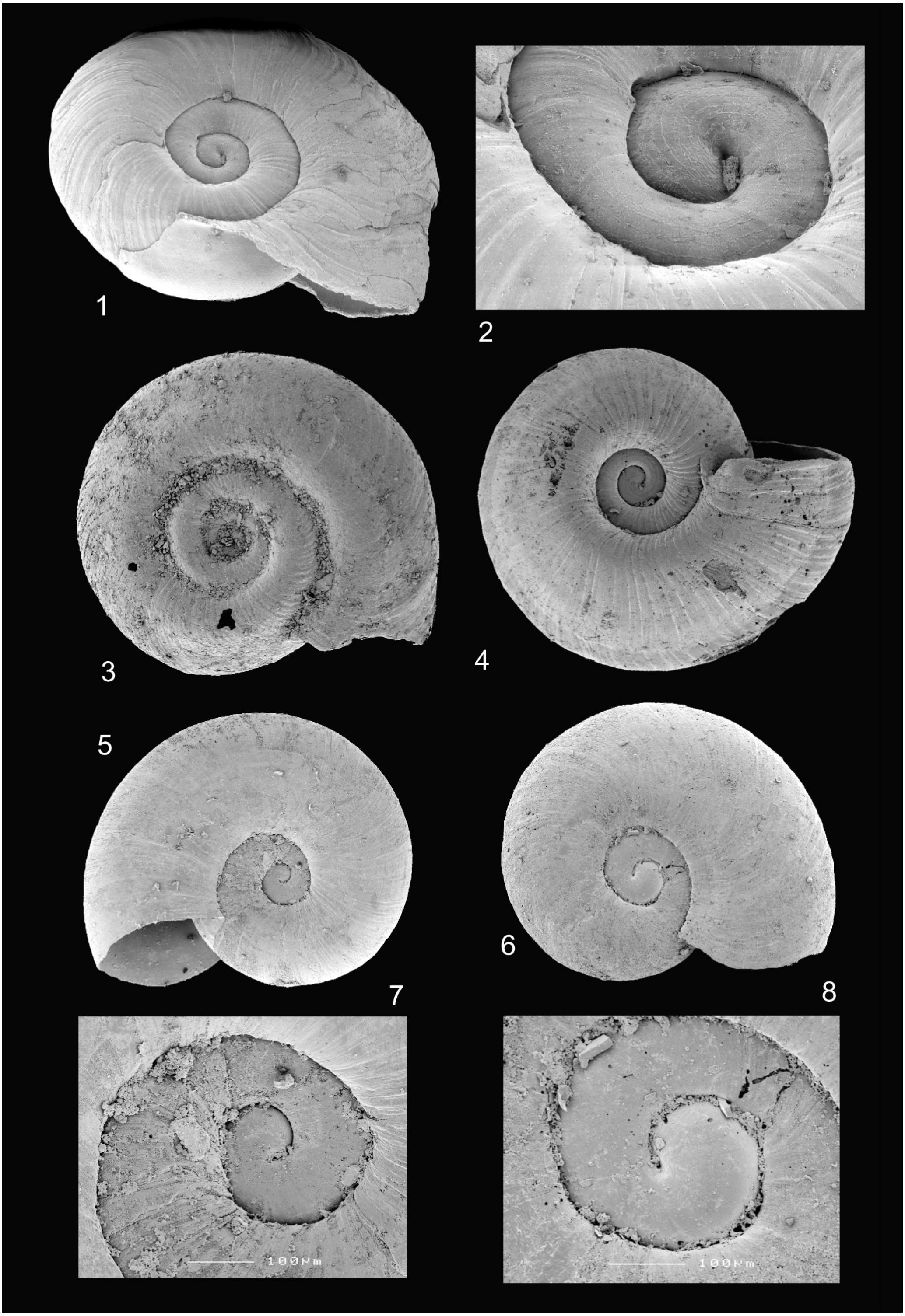
**Plate 10**

Figs. 1-4: ***Gyraulus verticillus* BRUSINA, 1892**
fig. 1: same specimen as plate 9 fig. 7 (NHMW 2001z0126/0065)
fig. 2 shows protoconch of fig. 1
fig. 3 diameter: 1.8 mm (NHMW 2001z0126/0066)
fig. 4 diameter: 0.9 mm (NHMW 2001z0126/0067)

Figs. 5-8: ***Gyraulus fuchsi* (LŐRENTHEY, 1902)**
fig. 5 diameter: 1.5 mm (NHMW 2001z0126/0068)
fig. 7 shows protoconch of fig. 5
fig. 6 diameter: 1.7 mm (NHMW 2001z0126/0069)
fig. 8 shows protoconch of fig. 6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## Plate 11

Figs. 1-9: ***Gyraulus marinkovici*** **(BRUSINA, 1892)**
fig. 1 diameter: 2 mm (NHMW 2001z0126/0070)
fig. 2 shows protoconch of fig. 1
fig. 3 & fig 9 diameter: 1.7 mm (NHMW 2001z0126/0071)
fig. 4 shows protoconch of figs. 3 & 9
fig. 5 & fig. 7 diameter: 2.5 mm (NHMW 2001z0126/0072)
fig. 8 shows protoconch of figs. 5 & 7

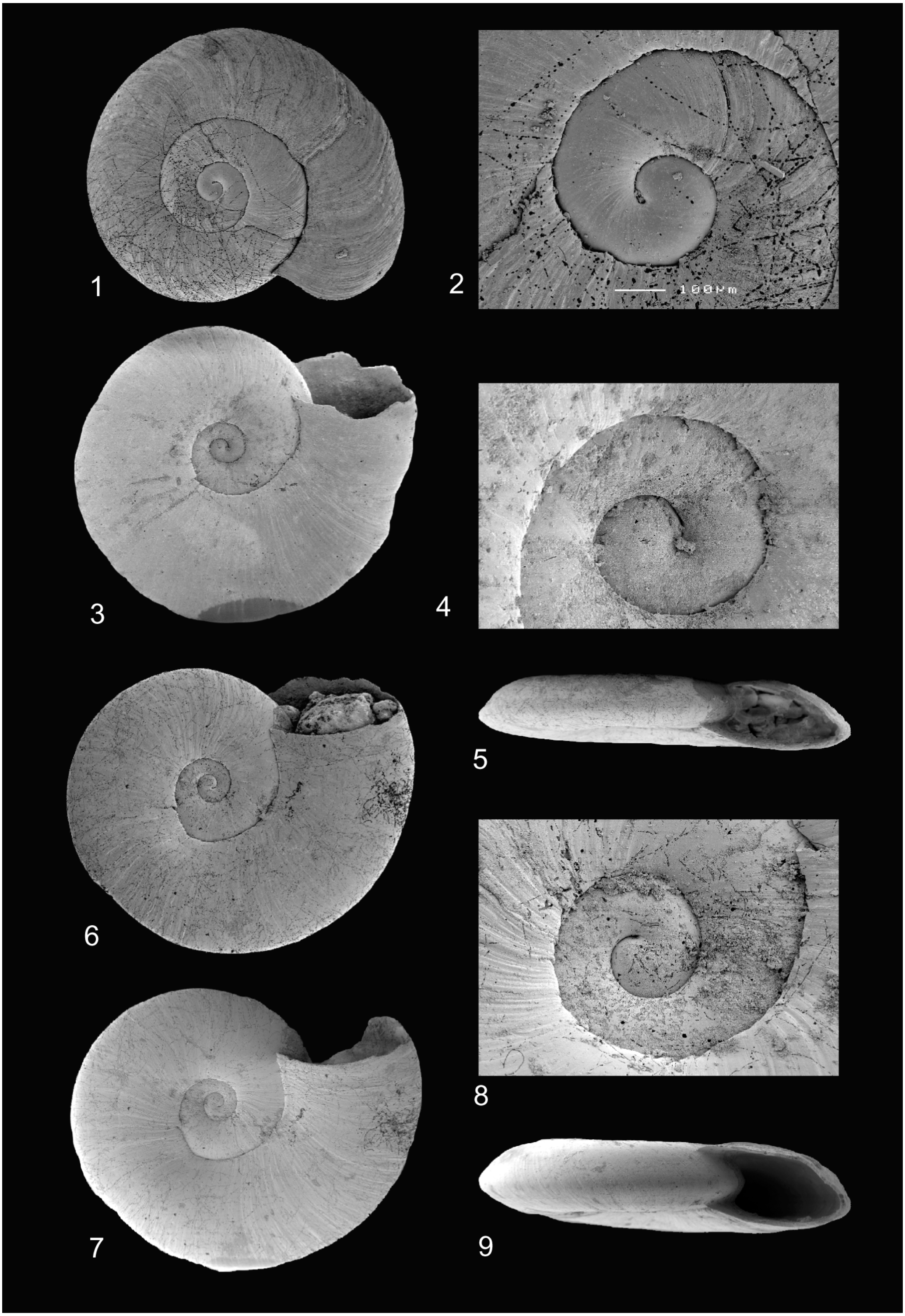
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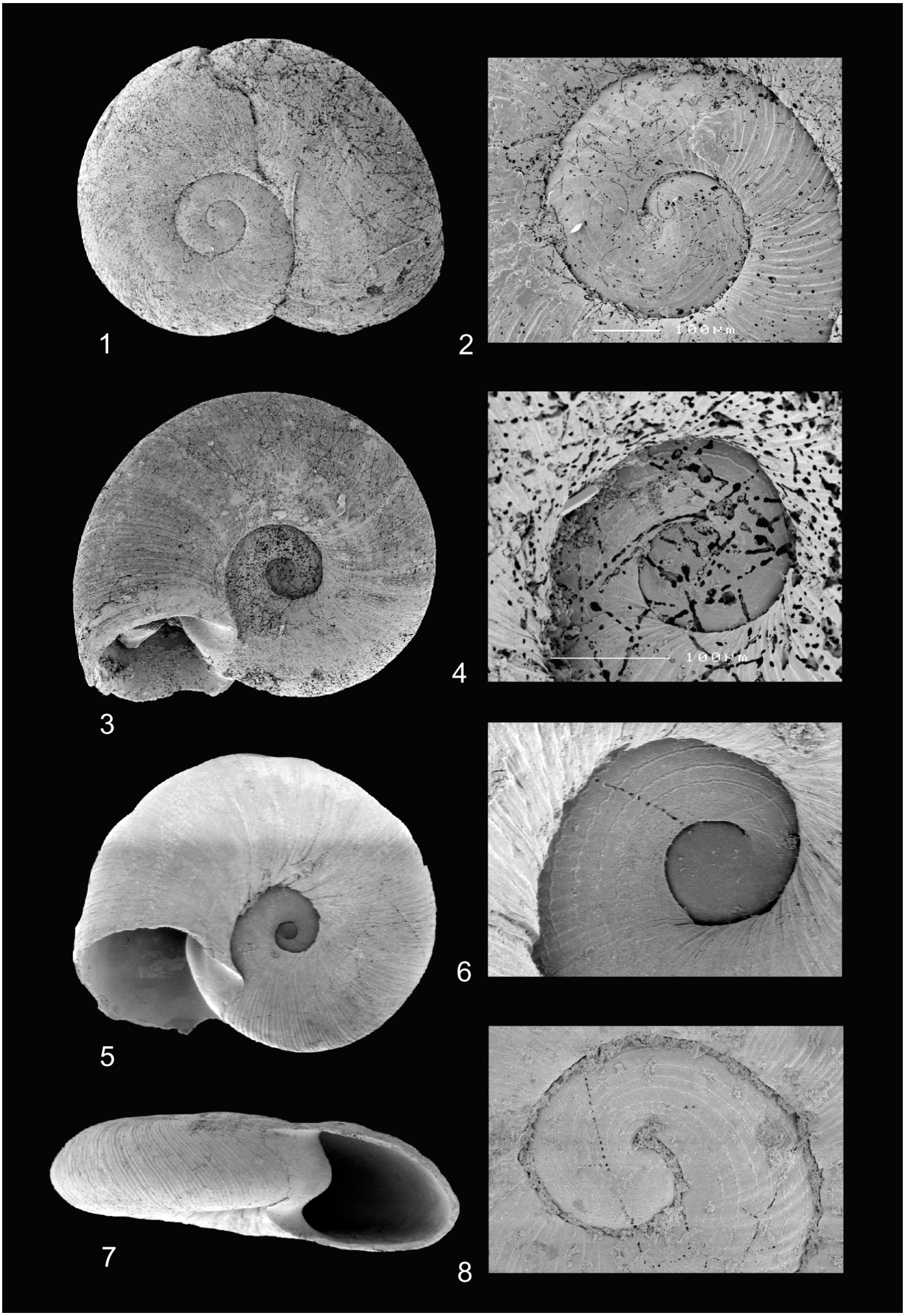
**Plate 12**

Figs. 1-8: ***Gyraulus primiformis* (SAUERZOPF, 1953)**
fig. 1 diameter: 1.8 mm (NHMW 2001z0126/0073)
fig. 2 shows protoconch of fig. 1
fig. 3 diameter: 2.2 mm (NHMW 2001z0126/0074)
fig. 4 shows protoconch of fig. 3
figs. 5 & 7 diameter: 1.6 mm (NHMW 2001z0126/0075)
figs 6 & 8 shows protoconch of figs. 5 & 7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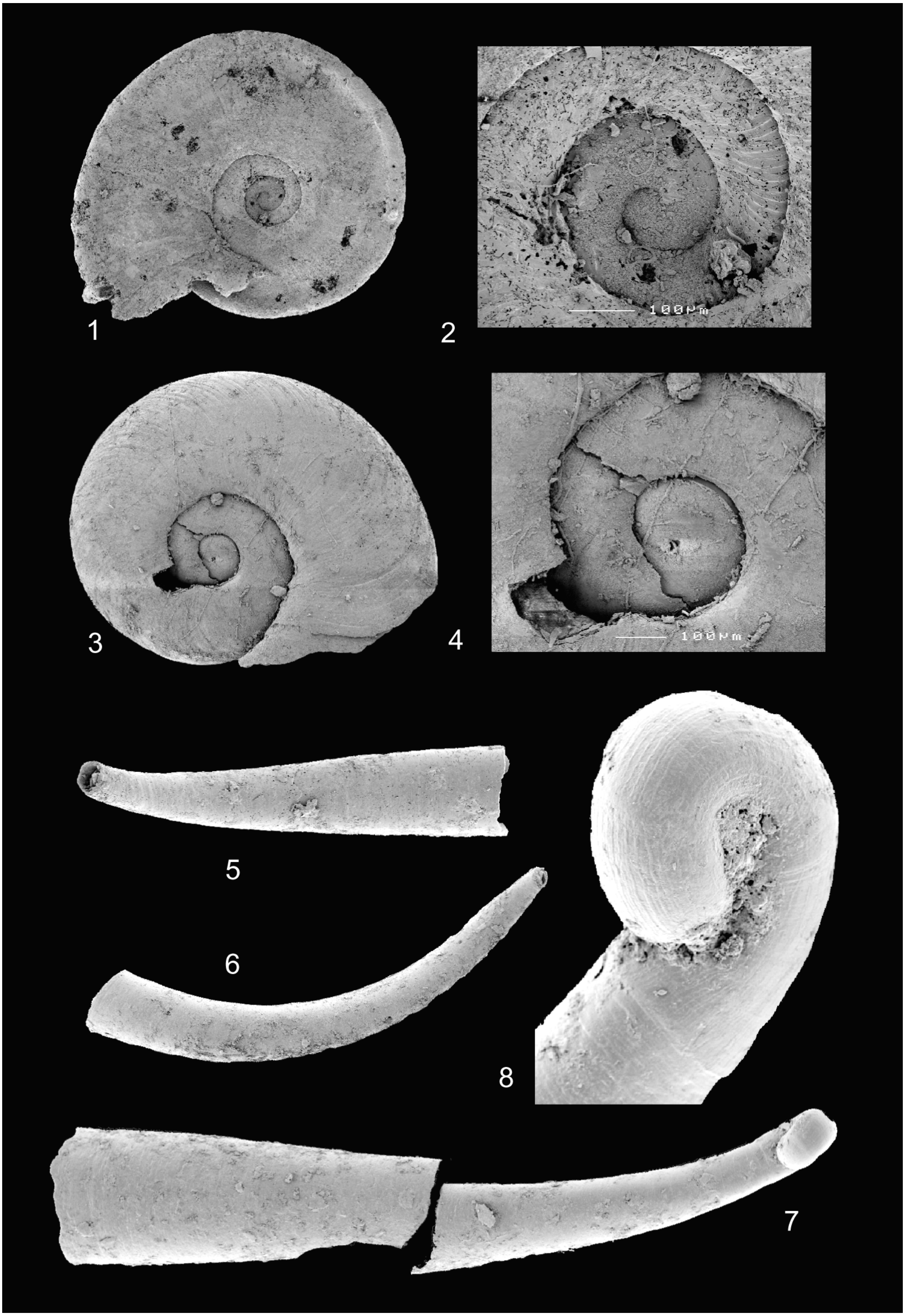
## Plate 13

Figs. 1-4: ***Gyraulus turislavicus* JEKELIUS, 1944**
fig. 1 diameter: 2.1 mm (NHMW 2001z0126/0076)
fig. 2 shows protoconch of fig. 1
fig. 3 diameter: 1.9 mm (NHMW 2001z0126/0077)
fig. 4 shows protoconch of fig. 3

Figs. 5-8: ***Orygoceras fuchsi* (KITTL, 1886)**
fig. 5 length: 2.5 mm (NHMW 2001z0126/0078)
fig. 6 length: 5.2 mm (NHMW 2001z0126/0079)
fig. 7 length: 3 mm (NHMW 2001z0126/0080)
fig. 8 shows protoconch of fig. 7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