

## GEOLOGIE UND PALÄONTOLOGIE

## The Late Cretaceous gastropod fauna from Ajka (Bakony Mountains, Hungary): a revision.

by KLAUS BANDEL & FRANK RIEDEL

(With 2 textfigures and 16 plates)

Manuscript submitted December 15<sup>th</sup> 1993,  
the revised manuscript on September 6<sup>th</sup> 1994

### Abstract

A revision of the gastropods from the Upper Cretaceous (Upper Santonian / ? Lower Campanian) coal deposits of Ajka is presented. While teleoconchs of most taxa have been described in the literature, the morphology of the protoconchs provides many new and striking results. Six new genera are thus introduced: *Schwardtina* (Neritidae), *Czabalaya* (Viviparidae), *Szaboella* (Potamididae), *Ariomphalus* (Valvatidae), *Leopoldium* (Ellobiidae) and *Ancylina* (Ancylidae). Five new species are coined: *Deianira ferdinandi*, *Deianira leopoldi*, *Czabalaya kordosi*, *Szaboella barthai* and *Melanopsis pauli*.

From the variable and extremely abundant genus *Pyrgulifera* species cannot be differentiated, however, a new genus *Szaboella* can be separated from it. The characters of protoconch and juvenile whorls clearly separate *Lavigeria* or *Paramelania* of Lake Tanganyika from the Cretaceous *Pyrgulifera*. The environment of the Ajka coal swamp is well characterized by its gastropod fauna indicating freshwater and more-or-less brackish influence. The paleoenvironment is compared with similar Late Cretaceous deposits and to the Late Jurassic Wealden facies.

**Keywords:** Upper Cretaceous, Ajka Coal Formation, gastropods, new genera and species, paleoecology.

### Zusammenfassung

Die Systematik der Gastropoden der oberkretazischen (oberes Santonium / ? unteres Campanium) Kohlelagerstätten von Ajka wird revidiert. Die Adultgehäuse der meisten Taxa sind in der Literatur schon gut beschrieben. Die systematisch wertvollen frühontogenetischen Gehäuseabschnitte werden hier jedoch erstmals dokumentiert und erfordern eine teilweise radikale Neugliederung bestimmter Taxa. Mit *Schwardtina* (Neritidae), *Czabalaya* (Viviparidae), *Szaboella* (Potamididae), *Ariomphalus* (Valvatidae), *Leopoldium* (Ellobiidae) und *Ancylina* (Ancylidae) werden sechs neue Gattungen eingeführt. *Deianira ferdinandi*, *Deianira leopoldi*, *Czabalaya kordosi*, *Szaboella barthai* und *Melanopsis pauli* werden als neue Arten vorgeschlagen.

Prof. Dr. Klaus BANDEL, Geol.-Paläont. Inst. Univ. Hamburg, Bundesstraße 55, D-20146 Hamburg. – Bundesrepublik Deutschland.

Dr. Frank RIEDEL, Institut für Paläontologie, Freie Universität Berlin, Malteserstraße 74-100, Haus D, D-12249 Berlin. – Bundesrepublik Deutschland.

Die sehr häufig auftretende und morphologisch variable Gattung *Pyrgulifera* kann bisher nicht in Arten untergliedert, die neue Gattung *Szaboella* jedoch von ihr abgetrennt werden. Die frühontogenetischen Gehäusewindungen zeigen deutlich eine systematische Abgrenzung zwischen der kretazischen *Pyrgulifera* und den im Tanganyika-See lebenden *Lavigeria* und *Paramelania*. Das limnische bis brackische Milieu des Ajka-Kohlensumpfes läßt sich mit Hilfe der Gastropoden gut charakterisieren und wird hier im Kontext faziell ähnlicher Ablagerungen der Oberkreide sowie der späturnjurassischen Wealden-Fazies diskutiert.

**Schlüsselwörter:** Ober-Kreide, Ajka-Kohlen-Formation, Gastropoda, neue Gattungen und Arten, Palökologie.

## Introduction

The coal bearing sediments of Ajka were deposited mainly during the Upper Santonian (pers. commun. Géza CSASZAR (Budapest) 1993; compare BARTHA 1962; GÓCZAN et al. 1986). The depositional environment was part of the coastal region of the Tethys. The land, perhaps consisting of islands, was covered by a tropical forest. Dead plants were transported by rivers or coastal currents and were accumulated in the estuaries or coves (see also STOLICZKA 1866) forming part of a large swamp separated from the open sea by sandbanks, islands and peninsulars. This coastal environment was not stable and changed its composition due to the effectiveness of the barriers and the shifting of freshwater inflow from land. Barriers became flooded when the sea level slightly rose or when storm tides damaged them. On the other hand new barriers developed seawards and run-off from land resulted in extensive flooding and freshwater influence. Monsoon rains may have caused rivers to rise and to flood the area periodically. Consequently the salinity of the water in this environment permanently changed. According to CZABALAY (1988) the maximum salinity was about mesohalin. During low salinity phases coal layers formed and allochthonous shells of terrestrial gastropods joined a typical freshwater molluscan fauna containing fully grown unionid shells. High salinity phases are characterized by members of the Potamididae dominating other mollusc taxa.

Leopold TAUSCH (1886) provided a comprehensive study of the gastropods of the "Ajka Coal Formation" (see GÓCZAN et al., 1986). OPPENHEIM (1892) was the first and last to revise the fauna (aside from the genus *Pyrgulifera* MEEK, 1872 by YEN 1958, 1965). In our revision new data regarding the protoconch morphology are included that resulted from the application of modern technology and changed the outlook of systematics quite a bit.

We recognize four subclasses (compare TAYLOR & SOHL 1962; GOLIKOV & STAROBOGATOV 1975; PONDER & WARÉN 1988; BANDEL 1992) constituting the class Gastropoda: Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostropha. Only representatives of the Archaeogastropoda are absent from the "Ajka Coal Formation".

## Materials and Methods

All the material described and illustrated in this paper was collected by the authors and companions from Hamburg from slag heaps of the Ajka coal-mines of the Csingertal and surroundings (for the location see e.g. HAAS et al. 1992). Additional material was used for comparison only and came from the Hungarian Geological Institute (Budapest), the National History Museum of Hungary (Budapest) and the Museum of Natural History, Vienna. The original material of F. BARTHA (1962) could be used to check the stratigraphy of our own samples. A section of the Ajka coal-mines could be visited (see Textfig. 1). The type mate-

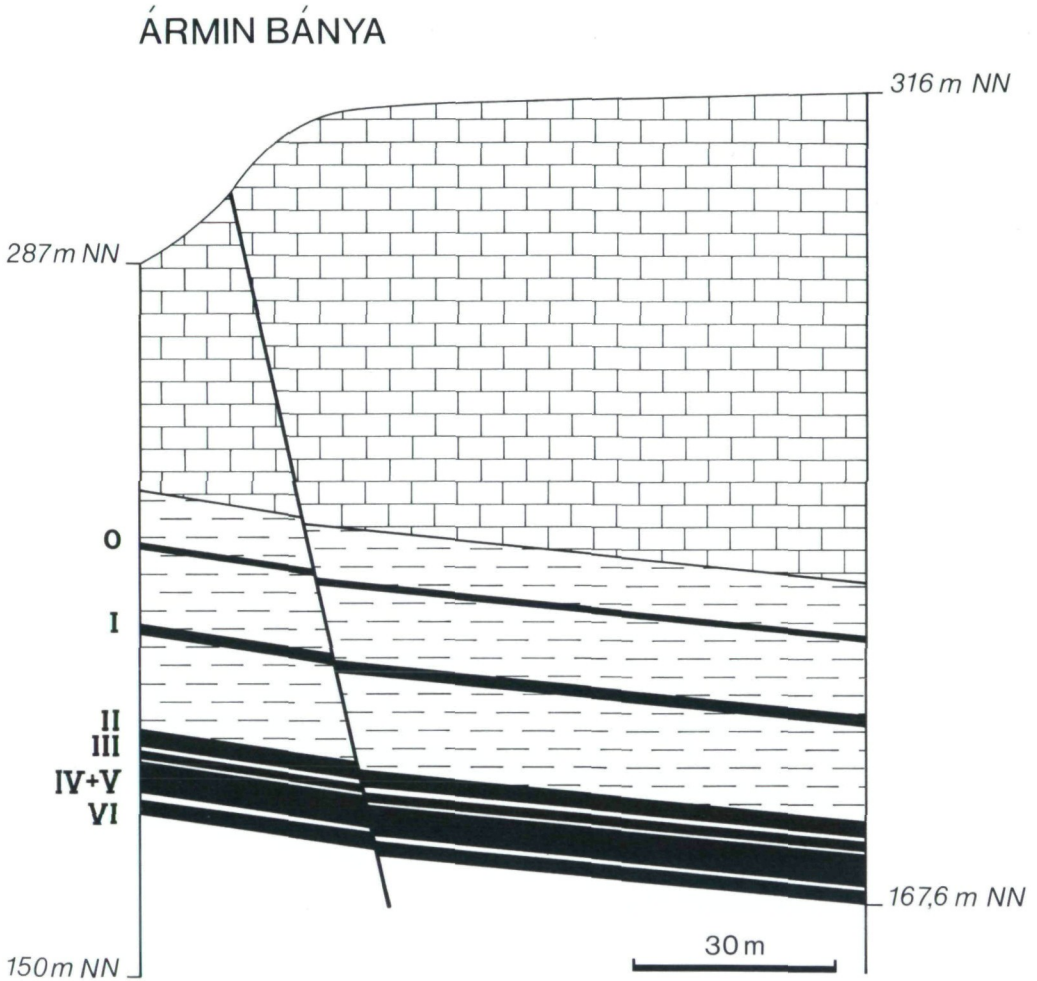


Fig.1: Section of the Ajka Coal Formation (Armin Banya) by courtesy of Karoly Koszma (Ajka coal-mines). Seven main coal layers (0–VI) are recognized. Arabic numbers indicate height above sea level.

rial of L. TAUSCH (1885, 1886) was neither found in Vienna nor in Budapest, however, one of the reviewers (Noel MORRIS) noted that some of the material can be found in the British Museum. Our material described here is deposited at the Museum of Natural History, Vienna (NHMWien). Usually numerous shells of a taxon could be examined except for *Szaboella barthai*, "*Rissoa*" sp., *Leopoldium balatonicum*, *Auriculinella whitei* and *Ancylina cretacea* where only few specimens were available.

The samples were processed using  $H_2O_2$ . Additional material from rocky deposits was exposed by mechanical preparation. Shells of small size were mounted on stubs, coated with gold and examined using a scanning electron microscope (CamScan). Larger specimens were photographed (Wild) with the aid of a light microscope (Leitz). The strontium content was measured using X-ray spectrometry (Phillips PW 1410). The method of counting whorls and measuring the diameter of protoconchs is demonstrated in Textfig. 2. In the generic

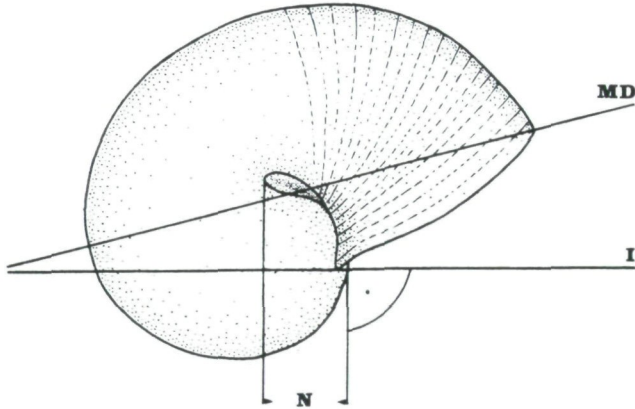


Fig.2: Apical view of an embryonic shell with explanation of measurements. **I** = initial point (axis) of counting whorls; **MD** = max. (horizontal) diameter; **N** = nonspiral (initial cap).

descriptions the term size means the largest dimension of a shell. Generic description is not synonymous with diagnosis. This term is used to provide an emended description of a genus, i.e., to include the protoconch characters. These are usually not known from members of the type-series.

### Systematic descriptions

#### SUBCLASS NERITIMORPHA

Superfamily Neritoidea, family Neritidae ?

#### *Schwardtina* gen. nov.

Type species: *Helix cretacea* TAUSCH, 1886

Derivatio nominis: in honour to our colleague Anette SCHWARDT (Hamburg) who is working on the systematics of fossil neritimorph gastropods.

Diagnosis: size around 2 mm; globular teleoconch, resembling *Hydrocena*, of about 3 whorls; spire angle about 50°, columella resorbed; aperture without septum, inner lip thickened and covering the umbilical region; protoconch egg-shaped, inflated, about 0.35 mm across.

Differences: *Fluvinerita* PILSBRY, 1932 is larger and has no callus on the inner lip. The aperture of *Neritilia* MARTENS, 1879 is much wider and a septum is well pronounced, while the spire is less developed. Shape and sculpture of the protoconch is different. *Hydrocena* PFEIFFER, 1847 has a protoconch which differs in ornamentation. The columella is not resorbed.

Attributed species: *Helix cretacea* TAUSCH, 1886



***Schwardtina cretacea* (TAUSCH, 1886)**

(Pl. 1, figs. 1–6)

1886 *Helix cretacea* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 14–15, Pl. 2, Fig. 13.

**Description:** the protoconch is egg-shaped and inflated (Pl. 1, figs. 3–4). Its length ranges from 320 to 400  $\mu\text{m}$  with a width from 230 to 280  $\mu\text{m}$ . The periostracum shows irregular punctation. The initial shell cap is demarcated by a circular groove and has a diameter of 120  $\mu\text{m}$  (Pl. 1, fig. 5). In the centre of the initial cap a circular region can be distinguished, which measures about 30  $\mu\text{m}$  and is characterized by minute pits. The teleoconch consists of about 3 whorls, which are smooth (aside from growth lines), except for the first 1/3 whorl where diagonal (nearly spiral) striae can be recognized. The shell has a maximum diameter of about 2 mm and a height of little more than 2 mm. The last whorl occupies 3/4 of the total height. The aperture has a sharp outer lip and a broad inner lip that is thickened to form a callus at the umbilical region (Pl. 1, fig. 1). The columella of protoconch and teleoconch whorls is totally resorbed (Pl. 1, fig. 6).

**Remarks:** The protoconch is typical for non-planktotrophic species, which may consume large amounts of food (e.g. nurse eggs or albumen held in the egg capsule) during their embryogeny. Therefore the embryonic shell is inflated and succeeded by the teleoconch and not by a larval shell. The protoconch type, in combination with the resorption of the columella, is diagnostic for aquatic Neritoidea (BANDEL 1982). However, a similar teleoconch among the neritimorphan gastropods is only known from the terrestrial genus *Hydrocena*, which is still unknown from Mesozoic deposits.

***Deianira* STOLICZKA, 1859**

(Pl. 2, figs. 1–6; Pl. 3, figs. 1–8)

**Type species:** *Rotella bicarinata* ZEKELI, 1852

**Generic description:** size around 1 cm; teleoconch rotelliform, broader than high, with 3–4 dextral whorls, bordered by a carina; inner walls of whorls not resorbed; spire depressed or dome-shaped; base convex, no umbilicus; aperture about semi-egg-shaped, oblique, notched at carina, with one or more columellar plaits; protoconch (not known from type) typically neritidid, sculptured by axial ridges, inner walls of whorls resorbed.

ZEKELI (1852) described *Rotella bicarinata* from the “Edelbachgraben” near Gosau (Austria). His description was later emended by REUSS (1854). STOLICZKA (1859) found two similar species at the “Neualpe im Russbachthale” near Abtenau (Austria) for which he introduced the genus *Deianira* (wife of the Greek God Herakles). STOLICZKA (1859) did not name a type species, but he supposed and later (1865) was sure that one of his species was identical with *Rotella bicarinata*.

TAUSCH (1886) described *Deianira bicarinata* from Ajka. However, he did not recognize that there are two species of *Deianira* in that fauna and that the one he described is not identical with ZEKELI’s (1852) or with STOLICZKA’s (1859) species. Therefore there are two new species to be introduced here. Both show a protoconch that has not been described in literature and is considered to be diagnostic for the genus.

**Description of protoconch:** the maximum diameter of the protoconch ranges from 300 to 350  $\mu\text{m}$ . In general outline it resembles that of Recent *Smaragdia* ISSEL, 1869.

There are one embryonic and two larval whorls, the younger whorls always covering much of the preceding ones (Pl. 2, figs. 1–2). The inner walls of the whorls are resorbed. The early larval shell is more-or-less corroded in all specimens. However, remains of axial ridges can be recognized as sculptural elements. The axial ridges usually are well preserved on the second larval whorl (Pl. 2, fig. 3) where they number about 50. The last quarter whorl is characterized by a broad longitudinal indentation, which demarcates the width of the protoconch aperture.

**Remarks:** TAUSCH (1886), OPPENHEIM (1892) and later WENZ (1938) use *Dejanira* instead of *Deianira*. OPPENHEIM (1892) was the first to propose that *Deianira* should constitute an own family but did not provide a name. WENZ (1938) therefore coined the family Dejaniridae, which later was corrected (in spelling) by KNIGHT et al. (1960) to Deianiridae. OPPENHEIM (1892) suggested a systematical placement of this taxon intermediating between Neritoidea and Helicinoidea.

***Deianira ferdinandi* sp. nov.**

(Pl. 3, figs. 5–8)

1886 *Dejanira bicarinata* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 10, Pl. 1, Figs. 39a–b?

1892 *Dejanira bicarinata* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 771–774.

**Holotype:** NHMWien 1994/227.

**Paratype:** NHMWien 1994/133.

**Derivatio nominis:** after Ferdinand STOLICZKA who coined the genus *Deianira*.

**Locus typicus:** Csingertal, near Ajka (Bakony Mountains), Hungary.

**Stratum typicum:** Ajka Coal Formation

**Diagnosis:** as for the genus; spire depressed, with prominent carina and spiral keel; aperture with two columellar plaits.

**Description:** for protoconch see under the genus. The teleoconch of adult specimens has about 3 whorls that account to a diameter of about 8 mm and a height of 4 mm (Pl. 3, figs. 5, 7, 8). The spire is more-or-less depressed, the base convex. There is no umbilicus. The inner walls of the whorls are not resorbed. The first half teleoconch whorl is sculptured with spiral striae that are joined by distinct growth increments, forming a cancellated pattern. After that a peripheral carina, which demarcates a sutural ramp, and a spiral keel develop. The keel is comparatively broad. It forms at the suture, with one side connected to the preceding whorl and the other side increasingly falling away during ontogeny. The keel on the last whorl loses its character and finally forms the slope of the sutural ramp. The peripheral carina and the sutural “keel” both are accompanied by distinct grooves bordering the middle part of the sutural ramp. The grooves deepen increasingly during ontogeny, while the shell between them bows up and finally forms a prominent keel. The aperture of the specimens is 2 to 2.5 mm wide and of semi-circular (angulated) shape. The lateral view reveals a significant angle to the apical axis (the apertural whorl shorter at the base). The shape of the aperture at the outer lip is effected (notched) by the keels and the carina (Pl. 3, fig. 6). The columellar side shows a callus plate, which spreads widely over the base. The apertural columella shows on its upper part a sharp fold and on its lower part a broad, low, callus-like plait. A septum is not present. The operculum is unknown.

**Differences:** *Deianira bicarinata* (ZEKELI, 1852) is larger, has three columellar plaits and the peripheral carina is less prominent. The conch of *Deianira hörnesi* STOLICZKA, 1859 is nearly globular, the aperture comparatively larger and more rounded at its base. Keels and carina are less prominent. *Deianira leopoldi* sp. nov. is larger, the spire less depressed.

***Deianira leopoldi* sp. nov.**

(Pl. 3, figs. 1–4)

1886 *Dejanira bicarinata* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 10, Pl. 1, Figs. 36–38.

1892 *Dejanira bicarinata* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 771–774, Pl. 33, Figs. 15, 15a–b.

**Holotype:** NHMWien 1994/228.

**Paratype:** NHMWien 1994/229.

**Derivatio nominis:** after Leopold TAUSCH who described the species.

**Locus typicus:** Csingertal, near Ajka (Bakony Mountains), Hungary.

**Stratum typicum:** Ajka Coal Formation

**Diagnosis:** as for the genus; comparatively large, spire dome-shaped, but outline not globular.

**Description:** for protoconch see under the genus. The teleoconch has 3 to 3.5 whorls, which amount to a height of about 8 mm. The maximum diameter is 12 to 13 mm. The spire is more-or-less pagodiform, dome-shaped; the base is convex (Pl. 3, figs. 1–2). The increase in diameter per whorl is comparatively large. The last whorl occupies about 3/4 to 4/5 of the total height. The aperture is about as high as wide, with a straight columellar side, a convex base with a distinct siphonal canal and a concave outer lip, which is characterized by the two keels terminating at its margin. The columellar side shows a callus plate that spreads widely over the base. At 4/5 of the height of the aperture, a prominent, sharp columellar plait is formed, which is not present in juvenile specimens.

The development of the keels during ontogeny is very similar to that of *Deianira ferdinandi* sp. nov. However, the development of a sutural slope occurs earlier, resulting in a less depressed spire.

**Differences:** *Deianira bicarinata* (ZEKELI, 1852) has three columellar plaits and the peripheral carina is less prominent. *Deianira hoernesii* STOLICZKA, 1859 is smaller and nearly globular. *Deianira ferdinandi* sp. nov. is smaller and the spire is more depressed.

**Remarks:** the family attribution of *Deianira* remains unclear as two many gaps of knowledge of neritimorphan paleontology have to be bridged. KNIGHT et al. (1960) list the family *Deianiridae* WENZ, 1938, which, however, was questioned by WENZ (1938) himself. Neither WENZ (1938) nor KNIGHT et al. (1960) had the knowledge of the protoconch, which fits very well to those of several Recent Neritidae, known to have planktotrophic development (see BANDEL 1982, 1991). It is confusing that *Deianira* does not resorb the inner walls of the teleoconch whorls, which is usually the case in the Neritidae. The resorption of the inner walls of the larval shell of *Deianira*, however, is characteristic for Neritidae. The inner walls of protoconch and teleoconch whorls are not resorbed in Neritopsidae, which also differ from *Deianira* in protoconch characteristics. *Deianira* fills much of its apical shell with calcareous material, so that its visceral mass must have been much smaller as is the case

in comparable modern neritids (e.g. *Neritina*) that live in the same environment. The systematic value of resorbing walls has not been sufficiently checked for Neritimorpha.

## SUBCLASS CAENOGASTROPODA

### Superfamily Cyclophoroidea ?

TAUSCH (1886) described five new species of *Megalomastoma* SWAINSON, 1840, two species of *Palaina* SEMPER, 1865, two species of *Strophostoma* DESHAYES, 1828 (= *Ferrussina* GRATELOUP, 1827) (see below), one species of *Cyclophorus* MONTFORT, 1810 and he coined the megalomastomid genus *Ajkaia* with three species attributed to.

We follow OPPENHEIM (1892) in synonymizing *Megalomastoma supracretaceum* TAUSCH, 1886 with *Cyclophorus eburneus* TAUSCH, 1886. However, OPPENHEIM (1892) attributed this species to the pupinid genus *Schistoloma* KOBELT, 1902 (= *Coptochilus* = *Coptocheilus* GOULD, 1862), which is as arbitrary as the placement among the Megalomastomidae or Cyclophoridae. The aperture of the species is quite similar to that of Recent *Pollicaria* GOULD, 1856, which is a diplommatinid genus. However, we leave the family attribution open, since there exists convergence among shells of numerous species of land snails.

The genus *Ajkaia* TAUSCH, 1886 is very dubious. *Ajkaia gregaria* TAUSCH, 1886 cannot be distinguished from what TAUSCH (1886) called *Megalomastoma*. *Ajkaia gracilis* TAUSCH, 1886 cannot be safely differentiated from several Recent diplommatinid genera and *Ajkaia* sp. nov. TAUSCH, 1886 (indet.) appears to be a cerithioidean species.

TAUSCH's descriptions and figures (pl. 3, figs. 21 and 22) indicate that *Palaina antiqua* TAUSCH, 1886 is a younger ontogenetic stage of *Palaina europaea* TAUSCH, 1886 and therefore represents a synonym. The attribution of this species to Recent *Palaina* must be doubted, however, "*Palaina*" *europaea* possibly is a diplommatinid gastropod (Pl. 4, figs. 1-4).

### Family Strophostomatidae

#### ***Strophostomella* FISCHER, 1883**

Type species: *Boysia reussi* STOLICZKA, 1859

Generic description: size around 1 cm; teleoconch more-or-less flattened, with about 5 dextral whorls set with numerous axial ribs; initial whorls dome-shaped, late whorls with carina; umbilicus pronounced; aperture holostome, thick-lipped, projecting on sutural ramp of preceding whorl; protoconch (not known from type) simple, more-or-less smooth, around half a millimeter across.

#### ***Strophostomella cretacea* (TAUSCH, 1886)**

(Pl. 4, figs. 5-8)

1886 *Strophostoma cretaceum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 21, Pl.3, Figs. 23-26.

1892 *Strophostomella cretacea* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 791-792.

Description: nearly 5.5 whorls reach a diameter of 11 mm. The height amounts to 3-4 mm. The first whorl measures 0.6 mm across and shows an indifferent sculpture, which

appears somewhat like hammered (Pl. 4, fig. 7). Distinct growth lines appear after 0.9 whorls and transform into weak axial ribs during the following half whorl. Later the axial ribs do not increase in size and thus become very numerous on late ontogenetic whorls. The first 4 whorls are more-or-less dome-shaped (Pl.4, fig. 8), whereas the last 1.5 whorls coil nearly planispiral. After 4 whorls a carina develops, which increases in strength and finally forms the outer top of the nearly triangular aperture. The terminal part of the last whorl coils upwards and inwards at the same time. The inner lip (and part) of the aperture then occupies about 2/3 of the width (sutural ramp) of the preceding whorl (Pl. 4, fig. 5-6). The peristome is continuous and thick. The umbilicus is pronounced.

**R e m a r k s :** *Strophostomella* was coined by FISCHER (1883) as a subgenus to Recent *Boysia* PFEIFFER, 1849. The type species of *Strophostomella* is *Boysia reussi* STOLICZKA, 1859 from the Late Cretaceous of Austria. We treat *Strophostomella* as independent genus from *Boysia*, which belongs to the Pupilloidea (Stylommatophora). It cannot be excluded that *Strophostomella* belongs to the Stylommatophora, but a placement among the Cyclophoroidea is possible as well. Similar teleoconchs can be recognized in both taxa and the protoconch of *Strophostomella* is also not diagnostic. It reflects a lecithotrophic development with much liquid yolk uptake, as would be the case in both taxa of land snails.

OPPENHEIM (1892), judging from figures only, attributed another species to *Strophostomella*: *Strophostoma* (= *Ferrussina*) *fragile* TAUSCH, 1886. The figures by TAUSCH (1886) cannot justify this generic attribution as they demonstrate characters, which fit in the diagnosis of *Ferrussina* GRATELOUP, 1827 (= *Strophostoma* DESHAYES, 1828). However, fig. 27a (pl. 3) in TAUSCH (1886) could be identified with specimens from our material. The umbilical view (fig. 27b, pl. 3 (TAUSCH, 1886)) of the same specimen (as in fig. 27a) demonstrates *Ferrussina* characters. The specimens of our material (Pl. 5, figs. 1-2) do not show these characters (which would be a widened terminal whorl with thick continuous peristome that bends and covers the umbilicus). It can be assumed that TAUSCH (1886) had confused two different taxa, which is also indicated by his figures. Neither OPPENHEIM (1892) nor we could recognize *Ferrussina*. The existence of this genus in Ajka remains unclear.

#### Superfamily Ampullarioidea, family Viviparidae

##### *Czabalaya* gen. nov.

**Type species:** *Czabalaya kordosi* sp. nov.

**Derivatio nominis:** named after our Hungarian colleague Lenke CZABALAY (Hungarian Geological Institute, Budapest) who contributed much to the knowledge of the Ajka Coal Formation.

**Diagnosis:** size around 1 cm; teleoconch with about 4 whorls and a similar outline as *Viviparus*; smooth except for growth increments; aperture egg-shaped and oblique with continuous peristome; with umbilicus; protoconch about one whorl, not pointed, more-or-less wrinkled, around 0.5 mm across

**Differences:** *Viviparus* MONTFORT, 1810 is usually larger, the early protoconch shows axial grooves and wrinkles (RIEDEL 1993), the early teleoconch is set with spiral striae.

**Attributed species:** *Czabalaya kordosi* sp. nov.



*Czabalaya kordosi* gen. et sp. nov.

(Pl. 5, figs. 3–6)

1886 *Paludina prisca* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 11, Pl. 1., Fig. 41.1892 *Paludina prisca* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 775.

Holotype: NHMWien 1994/116.

Paratype: NHMWien 1994/115 and 1994/117.

Derivatio nominis: in honour to our Hungarian colleague Laszlo KORDOS (Hungarian Geological Institute, Budapest).

Locus typicus: Csingertal, near Ajka (Bakony Mountains), Hungary.

Stratum typicum: Ajka Coal Formation

Diagnosis: as for the genus, with about 10 mm high conch

Description: adult specimens usually reach 5 whorls which amount to a height of 10 mm and a maximum diameter of 7 to 7.5 mm (Pl. 5, figs. 3–4). The first whorl has a diameter within a range of 500 to 550  $\mu\text{m}$ , the initial cap (nonspiral) measures 180–200  $\mu\text{m}$  in width. The shell of the first 1/2 to 3/4 whorls is irregularly folded, due to a retarded calcification during the embryogeny (Pl. 5, figs. 3, 6). The teleoconch whorls are smooth (aside from growth lines). The last whorl occupies half of the total height of a specimen. The aperture is egg-shaped and more-or-less oblique. The peristome is continuous but appears to be interrupted where the body whorl is slightly constricting the width of the aperture. The inner lip is more thickened (but not thick) than the outer lip.

Remarks: TAUSCH (1886) coined a new species *Paludina prisca* and provided three figures (pl. 1, figs. 40, 41a, 41b). The scale in the text (p. 11) refers to figure 40. It must be assumed that the description also refers to this figure, in which no diagnostic characters can be recognized. A safe correlation with the description is therefore impossible. Figs. 41a and 41b show one or two specimens with diagnostic characters, which cannot, however, be discovered in the description of *Paludina prisca*. Our material contains several specimens, which could be identified with figs. 41a, 41b and are described here as a new genus and new species. A lectotype for *Paludina prisca* is fixed here (figure 40 of TAUSCH) to avoid nomenclatural complications. However, it should be pointed out that the original material, which was described by TAUSCH (1886) could not be examined by us.

The systematic position of *Czabalaya* gen. nov. is more-or-less vague because there are few diagnostic characters. Recent species of *Viviparus* have a similar teleoconch, but the protoconch is sculptured differently, although showing also a retarded calcification (see BANDEL 1982; RIEDEL 1993). The Recent cerithioid *Tanganyicia rufofilosa* (SMITH, 1880) from Lake Tanganyika has a protoconch, which is nearly identical to that of *Czabalaya kordosi* gen. et sp. nov. (RIEDEL, 1993). The teleoconch, however, shows a similar outline but is not typically viviparid (BROWN 1980; pers. observation). The differences in protoconch sculpture between viviparids where this character has been examined and the new genus *Czabalaya* (in our opinion) is smaller than the difference among teleoconch characters noted between *Czabalaya* gen. nov. and *Tanganyicia* CROSSE, 1881. A placement of *Czabalaya* among the Viviparidae is here preferred.

## Superfamily Rissooidea (= Truncatelloidea), family Rissoidae

*“Rissoa”* sp.

(Pl. 5, figs. 7, 8)

**Description:** the conch consists of 4.5 to 5 whorls, which regularly increase to a maximum diameter of about 1.25 mm and a height of 1.65 mm. The spire angle is 30°. The first 3.5 whorls are smooth except for growth lines. The first whorl measures 160 to 170 µm in diameter, the initial cap (nonspiral) is 50 µm wide. The last 1.2 to 1.5 whorls of the conch are set with about 14 to 16 axial ribs, which increase in size during ontogeny. The whorls are more-or-less angulated, separating a sculptured (ribbed) ramp from a smooth (aside from growth lines) base. The aperture reaches half of the total height of a specimen and is more-or-less angulated four times (slightly constricted by the body whorl). A juvenile specimen has sharp outer and inner lips and an umbilicus can be recognized, whereas in adult conchs the inner lip forms a callus covering the umbilicus.

**Remarks:** This gastropod has not been recognized by TAUSCH (1886) or OPPENHEIM (1892). However, the species of the *Rissoa* group are difficult to be separated by conchological characters only as these usually are not diagnostic. In correspondence with Winston PONDER (pers. comm., 1993) we refrain from coining a new taxon.

## Family Hydrobiidae (?)

TAUSCH (1886) coined five new species, which he attributed to *Hydrobia* HARTMANN, 1821. Probably none of these actually belongs to this genus. “*Hydrobia*” *bodeica* is the juvenile of *Esperia* (= *Fagotia*) *obeloides* (TAUSCH, 1886) (see Melanopsidae) and “*Hydrobia*” *baconica* probably is identical with the apical whorls of *Campylostylus heberti* HANTKEN, 1878 (see Melanopsidae). “*Hydrobia*” *mana* could not be distinguished from “*Hydrobia*” *balatonica* and may represent the same species. OPPENHEIM (1892) coined the new (hydrobiid) genus *Parateinostoma* and includes all species TAUSCH (1886) attributed to *Hydrobia*. However, the character he suggested to be diagnostic (the outer apertural lip) for his genus can be found only in “*Hydrobia*” *mana* (= “*H.*” *balatonica*). It remains doubtful if “*Hydrobia*” *mana* represents a new genus, however, we use the name *Parateinostoma* OPPENHEIM, 1892 as we do not have a better proposal.

Shape and size of protoconch and teleoconch of “*Hydrobia*” *veszprimica* TAUSCH, 1886, as well as the paleoenvironment, indicate that this species possibly belongs to the Hydrobiidae.

*Parateinostoma* OPPENHEIM, 1892

**Type species:** *Hydrobia mana* TAUSCH, 1886

**Generic description:** size around 3–4 mm; teleoconch slender, of 6–7 dextral, rounded, more-or-less smooth whorls; aperture with characteristically waved outer lip, inner lip twisted, peristome not continuous; protoconch about one whorl, slightly hammered, around 0.3 mm across.

***Parateinostoma mana* (TAUSCH, 1886)**

(Pl. 6, figs. 1–2)

1886 *Hydrobia mana* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 11, Pl. 1, Fig. 44.1886 *Hydrobia balatonica* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 11, Pl. 1, Fig. 43.1892 *Parateinostoma mana* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 777–778, Pl. 34, Fig. 9.

**Description:** about 6 rounded whorls amount to a height of 3 mm and a diameter of about 1 mm. The last whorl reaches 1/3 of the total height. The first whorl has a width of 220  $\mu\text{m}$ . The protoconch is composed of about 1.4 whorls, the surface of which has a hammered ornament. The transition to the teleoconch is demarcated by comparatively strong growth increments. Aside from growth lines the conch is characterized by faint spiral striae, which begin their appearance on the protoconch. The aperture is more-or-less egg-shaped, the upper part channelled. The peristome is not continuous. The inner lip is twisted (in axial direction) at the transition to the columella and partly covers the umbilicus, which is hardly visible. The outer lip is waved, which is proposed by OPPENHEIM (1892) to be diagnostic for the genus.

**“*Hydrobia*” *veszprimica* TAUSCH, 1886**

(Pl. 6, figs. 3–4)

1886 *Hydrobia veszprimica* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 12, Pl. 1, Fig. 45.1892 *Parateinostoma veszprimica* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 777–778.

**Description:** about 4–4.5 whorls amount to a height of 2 to 2.2 mm and a maximum diameter of 1.2 to 1.3 mm. The last whorl reaches about 2/5 of the total height, terminating in a holostome, perfectly egg-shaped aperture. The peristome is more-or-less thickened. The umbilicus can be clearly recognized. The first whorl of the conch measures about 280  $\mu\text{m}$ , the nonspiral (initial cap) is 90  $\mu\text{m}$  wide. Weak growth lines set in after one whorl. They become distinct at 1.5 whorls, indicating the transition from the protoconch to the teleoconch. Aside from the growth increments the shell is smooth. Close to the aperture the growth increments increase in strength.

TAUSCH (1886) recognized the bithyniid (?) (sub-) genus *Stalioa* BRUSINA, 1870, with the species *S. nitida* TAUSCH, 1886. Neither OPPENHEIM (1892) nor we could find this gastropod in Ajka material. This applies also to the baicalioid (?) genus *Gypsobia* TAUSCH, 1886, with the single species *G. cretacea* TAUSCH, 1886.

**Superfamily Cerithioidea, family Potamididae**

The attribution of the following species to the Potamididae is more-or-less provisional. Much of the phylogeny of the Cerithioidea has been elucidated and published by HOUBRICK (see 1988). However, cerithioideans living in brackish and freshwater habitats, have not been sufficiently examined, neither conchologically nor anatomically. Moreover, several families (e.g. the Thiaridae) have been defined in a different way by different authors (see e.g., PILSBRY & BEQUAERT 1927; THIELE 1929; MANDAH-L-BARTH 1954; MORRISON 1954; BRANDT 1974; STARMÜHLNER 1976; BROWN 1980; HOUBRICK 1984, 1988, 1991). It is thus not possible to include e.g., *Pyrgulifera* MEEK, 1872 or *Szaboella* gen. nov., safely in any known family (see discussion).

***Hadraxon* OPPENHEIM, 1892**

Type species: *Hemisinus csingervallensis* TAUSCH, 1886 by designation.

Generic description: size around 10–15 mm; teleoconch turriculate, thin-shelled, dextrally coiled, of about 20 whorls; sutural keel, spiral lirae and axial ribs pronounced; columella comparatively strong; aperture with columellar callus, anteriorly channelled; no umbilicus; protoconch of two whorls with wrinkled shell, around 0.3 mm across.

***Hadraxon csingervallense* (TAUSCH, 1886)**

(Pl. 6, figs. 5–7; Pl. 7, figs. 1–3)

1886 *Hemisinus csingervallensis* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 8, Pl. 1, Figs. 28, 30, 32.

1892 *Hadraxon csingervallensis* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 797, Pl. 35, Figs. 17, 20, Pl. 36, Fig. 1.

Description: the conchs have a shape similar to that of *Turritella* LAMARCK, 1799. They are always damaged, due to their thin shell. A complete specimen would probably have about 19–20 whorls, but usually at least 2–3 apical whorls are missing. Comparatively well preserved adult shells reach a height of 12–15 mm, with a maximum diameter of 2–3 mm (Pl. 6, figs. 5–6). The first whorl measures 160–230  $\mu\text{m}$  across, the nonspiral (initial cap) is 50–90  $\mu\text{m}$  wide. The shell of the initial whorls 1 and 2 is wrinkled (Pl. 7, fig. 2). The strength of the wrinkles decreases on the second whorl, the third whorl is free from wrinkles.

The transition from the second whorl to the third whorl is characterized by the onset of distinct growth lines, faint spiral striae, which later become more distinct, and the formation of a spiral keel on the apical part of the whorl. The apical sutural keel vanishes on the fourth to fifth whorl, while at the basal suture of the fourth whorl another spiral keel forms, which is more-or-less prominent on all following whorls. Axial ribs usually appear first on the middle of third whorl (Pl. 7, fig. 1). The following 2–4 whorls show 14–18 prominent curved axial ribs, which dominate distinct spiral lirae. The number of ribs in later ontogeny varies greatly, e.g., it may decrease to about 10 for the rest of the whorls or in other specimens later increases again to about 15 for only one or two whorls and then decreases again. The body whorl reveals that the spiral keel separates a non-ribbed base, which is set with one or sometimes two keels, from the rib-bearing sutural ramp. The aperture is comparatively small and occupies only 1/7 to 1/8 of the total height (of fully grown conchs). The columellar side is broadly covered by a regular callus – there is no umbilicus. The outer apertural lip is regularly rounded, while the basal part of the aperture is more-or-less channelled.

Remarks: OPPENHEIM (1892) coined the species *Hadraxon baconicus*. His description and figure do not indicate close relationship to *H. csingervallense*, however, to the species, which are described here under *Pirenella*. The gender of the genus is neuter.

***Pirenella* GRAY, 1847**

(Pl. 7, figs. 4–7; Pl. 8, figs. 1–6)

Type species: *Cerithium conicum* BLAINVILLE, 1825

Generic description: size around 2 cm; high-spired teleoconch of more than 10 slightly rounded, dextral whorls; with sutural keel, axial ribs and rows of nodules on sutural ramp; aperture with rounded outer lip, short anterior siphonal canal and broad callus on

columellar side; no umbilicus; protoconch (not known from type) about one and a half whorls, simple but with sinus-like hook, around 0.3 mm across.

### *Pirenella balatonica* (TAUSCH, 1886)

1886 *Cerithium balatonicum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 22–23, Pl. 3, Figs. 29–31.

1892 *Bittium balatonicum* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 793–795.

**Description:** fully grown specimens probably would have about 15 whorls, however, at least two apical whorls are corroded. Therefore most specimens consist of 10–12 whorls, which reach a height of 18–19 mm (Pl. 8, figs. 5–6). The maximum diameter is about 4.5–5 mm. The increase in diameter is regular in early ontogenetic whorls, but (the increase) decreases on late ontogenetic whorls. Consequently the spire angle changes, from about 15° to 5°. The first whorl measures 220–260 µm in diameter, the initial cap is 90–120 µm wide. The end of the protoconch is clearly demarcated by a sinus-like hook at about 1.5 whorls (Pl. 7, fig. 5). The shell of the protoconch is slightly wrinkled (Pl. 7, fig. 7), growth lines can be recognized at the beginning of the second whorl. As characteristic feature the first half whorl is comparatively inflated (Pl. 7, fig. 6). The early postnuclear whorls show faint spiral rows of tubercles, which later fuse to distinct lirae. The basal part of the whorls shows an angulation, which during later ontogeny transforms to a smooth spiral keel (carina). The postnuclear whorls 1 and 2 are usually free from axial ribs, however, the onset of such ornamentation varies. The number of ribs (or axial rows of nodules) increases from about 10 on juvenile whorls to about 15 on the body whorl. The onset of the nodule formation may occur between fifth and tenth whorl. The axial ribs are constricted by the spiral lirae to three nodules each. The nodules are completely smooth and about as large as the interspaces between them. On the body whorl the spiral keel separates the sutural ramp from the base, which is ornamented by two more spiral keels. The more basal of these is regular, while the other forms a spiral row of nodules. A comparatively broad callus spreads over the whole columellar side of the aperture and partly covers the keels. There is no umbilicus. The outer lip of the aperture is regularly rounded, whereas the basal part of the peristome extends into a short and weakly developed siphonal canal. The aperture occupies 1/5 to 1/6 of the total height of a specimen (Pl. 8, fig. 5).

**Remarks:** this species and *P. supracretacea* are assigned to the Recent genus *Pirenella*, which lives in a similar habitat and has a comparable teleoconch. There are several species among the Potamididae, which also show affinities, like Recent *Cerithidea* SWAINSON, 1840 (see HOUBRICK 1984). Fossil genera of the “*Potamides*”-group (see e.g. COSSMANN 1906 or WENZ 1938) partly show very similar teleoconchs, however, the early ontogenetic whorls of these are not described and their living environment is often not well defined. The two species of *Pirenella* had been attributed to *Cerithium* BRUGUIÈRE, 1789 (in TAUSCH, 1886) or *Bittium* LEACH, 1847 (in OPPENHEIM, 1892). Modern *Cerithium* and *Bittium* represent marine genera and thus have most probably not lived in the fresh water or weakly brackish surrounding of the Ajka fauna.

The clear demarcation of the *Pirenella* protoconch indicates that the embryos had hatched out as free-swimming larvae. Probably the veligers were non-planktotrophic, because no larval shell can be differentiated from the embryonic part, which is usually the case in fully lecithotrophic development. Moreover, planktotrophic Cerithioidea usually hatch out with about an one-whorl-conch, which measures only circa 100 µm across (see BANDEL 1975).



***Pirenella supracretacea* (TAUSCH, 1886)**

1886 *Cerithium supracretaceum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 23, Pl. 3, Figs. 32–33.

1886 *Cerithium epagogum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 24, Pl. 3, Figs. 35–36.

1886 *Cerithium hemilissum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 23, Pl. 3, Fig. 34.

1892 *Bittium supracretaceum* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 793–795.

**Description:** protoconch and teleoconch are very similar to those of *Pirenella balatonica*. Fully grown specimens in all cases have broken apicis, reducing the number of whorls from hypothetical 16–17 to actual 11–12 (if well-preserved), which amount to a height of about 20 mm (Pl. 8, figs. 3–4). The maximum diameter is 5 mm. The increase in diameter resembles that of *P. balatonica*. The protoconch as well as early juvenile whorls show the same characters as described for *Pirenella balatonica* (Pl. 8, fig. 2). The axial ribs transform to rows of nodules within the same ontogenetic range as in the other species. However, four nodules per row are formed. The axial ribs (or rows of nodules) on early whorls number about ten. The increase of this number during later ontogeny is correlated to the strength of the nodules. The increase of the axial rows is moderate (from 10 to 12–13) if strong nodules are developed, and considerable (from 10 to about 20) with weak nodules pronounced. The apertural characters of this species cannot be differentiated from those of *P. balatonica* (see there). The base of the body whorl also bears two spiral keels, which usually are more prominent than in the other species.

**Remarks:** TAUSCH (1886) described and figured two more species: *Cerithium hemilissum* and *Cerithium epagogum*. We follow OPPENHEIM (1892) who proposed that they cannot be differentiated from *Cerithium* (= *Pirenella*) *supracretaceum* TAUSCH, 1886.

OPPENHEIM (1892) discussed intermediate forms (number of nodules) that question the possibility to differentiate *Pirenella balatonica* from *P. supracretacea*. However, in about 120 specimens, less than 3% show a different number of nodules (3) on juvenile whorls than on late ontogenetic whorls (4 per row). No specimens had the number of nodules (per row) reduced from 4 to 3. Thus *Pirenella balatonica* is always three-noduled, whereas *P. supracretacea* rarely begins with 3 nodules and always bears 4 nodules on the following whorls. The two species can therefore be differentiated very well.

***Pyrgulifera* MEEK, 1872**

(Pl. 8, figs. 7–9; Pl. 9, figs. 1–16; Pl. 10, figs. 1–8)

**Type species:** *Melania humerosa* MEEK, 1860

**Generic description:** size from about 1–4 cm; teleoconch subovate, thick-shelled; turreted spire with two primary spiral keels; whorls dextral and shouldered, more-or-less set with axial ribs, nodules and spiral ornamentation; aperture egg-shaped, holostome, anterior notch more-or-less channelled; protoconch (not known from type) about one and a half whorl, simple but clearly demarcated by a postembryonic hook, around 0.3–0.4 mm across.

“Nur schwer findet man sich in dem chaotischen Wirrwarr wunderbarer Formen, wie sie diese Gattung in Ajka darbietet, zurecht; wollte man consequent sein, müsste man hier fast jedes Individuum mit einem Namen belegen” (OPPENHEIM 1892).

(It is difficult to find one's way in the chaotic confusion of wonderful forms this genus performs in Ajka; to be consequent, almost every individual should be provided with an own name.)

OPPENHEIM's statement indicates that definition of species in *Pyrgulifera* is not possible, but it was neither followed by himself nor by other authors. The type of *Pyrgulifera* originates from the Bear River Formation (Wyoming, USA). YEN (1958, 1965) reviewed the literature and provided a comprehensive study on *Pyrgulifera*, recognizing 21 species and subspecies world-wide, from which eight are attributed to the Ajka fauna. The authors of this paper examined several hundred specimens of *Pyrgulifera* collected near Ajka and also the material described by BARTHA (1962). We follow OPPENHEIM (1892) regarding teleoconch characters that are too variable to define species. All of the so-called "species" are associated with intermediate forms, which interconnect to numerous kinds of morphological types. We provide a description of the protoconch and the juvenile whorls of the teleoconch of *Pyrgulifera*, which both have not been described.

**Description:** the protoconch usually consists of about 1.5 whorls with a shell surface that is more-or-less wrinkled. It clearly differs from the juvenile teleoconch, which is characterized by two spiral keels and minor tubercles (Pl. 8, figs. 7–9). The diameter of the first whorl varies between 250 to 300  $\mu\text{m}$ . The nonspiral has a width ranging from 100 to 140  $\mu\text{m}$ . The diameter of the first two whorls amounts to between 310 to 390  $\mu\text{m}$ . The number of axial ribs on a complete juvenile whorl varies between 8 and 9.

Two further varieties are present: in one protoconch type the first whorl measures only 230  $\mu\text{m}$  and the initial cap is only 90  $\mu\text{m}$  wide. This protoconch is much more wrinkled and early juvenile whorls each bear 10 axial ribs. In the other protoconch (and juvenile conch) the first whorl measures about 430  $\mu\text{m}$  across and early juvenile whorls each bear 12–13 axial ribs.

**Remarks:** the measurements of the early ontogenetic shell give evidence that there are actually different species of *Pyrgulifera* in Ajka as three types of juveniles could be found. However, the apical whorls of all known adult teleoconchs are broken off, usually at a diameter of about 2 mm. There are few juveniles, which could intermediate between the very early and the late ontogenetic shell. However, several reasons prevent a successful assignment. The nuclear whorls in most cases are corroded (during life time) beginning at a specimen size of 6–7 whorls (less than 2 mm diameter). The axial ribs in later ontogeny are very variable in appearance as well as in their number. They may vanish for some whorls and later reappear in equal or unequal numbers. Secondary spiral keels may be intercalated during a certain ontogenetic phase and later vanish.

BARTHA (1962) concluded that in the succession from freshwater to a brackish or nearly marine habitat, the teleoconch of *Pyrgulifera* changed to a larger size, to a thicker shell and from a smooth to a strongly ribbed shell. This statement cannot be disproved. However, comparison with Recent habitats similar to that of Ajka, suggest that there may have been (short term) environmental changes (e.g. storm tides, floods or pouring rain; see introduction), on which a species cannot react if not already adapted. The strontium content (as a possible indicator for the environment) in 35 different teleoconchs varies from 559 (freshwater) to 1471 ppm (brackish/marine). There is no correlation between the strontium content and shape, size or sculpture of the teleoconch. Probably each individual of *Pyrgulifera* tolerated freshwater as well as brackish water.

NEUBRANDT (1949) described the new species *Pyrgulifera pannonica* from the youngest layers of the Ajka Coal Formation. This species is very rare and cannot be documented very

well as the early ontogenetic whorls are not preserved. We provide here the first apertural view of an adult specimen (Pl. 10, fig. 8). *P. pannonica* would be the largest known variation of *Pyrgulifera*, however the attribution to that genus is doubtful. The characteristic two primary keels of *Pyrgulifera* cannot be recognized, the protoconch is not known and the suture is deepened, which is not the case in "true" *Pyrgulifera*. There are no forms intermediating between *P. pannonica* and variations of *Pyrgulifera*.

*Cosinia* STACHE, 1880 from the Kozina beds (Liburnian Formation) of the northwest Dinarids (Slovenia) was interpreted by STACHE (1889) to represent a subgenus of *Pyrgulifera*. The Kozina beds are thought to be of Paleocene age (e.g. PAVLOVEC & PLENICAR 1983). *Cosinia* STACHE, 1880 is very variable in shape and size. There are several forms of *Pyrgulifera* from Ajka that cannot be distinguished from *Cosinia* (Pl. 9, figs. 3–4). We refrain from arbitrarily defining species or subgenera of *Pyrgulifera* and recognize *Cosinia* STACHE, 1880 as a synonym to *Pyrgulifera* MEEK, 1872 (see also discussion).

In this case with fossil shells the taxonomy on species or genus level cannot be resolved. However, the knowledge of the early ontogenetic shell of *Pyrgulifera* can be used to end the speculations (e.g. WHITE 1883, 1885; TAUSCH 1885, 1886; OPPENHEIM 1892; YEN 1958) whether *Paramelania* SMITH, 1881 and *Lavigeria* BOURGUIGNAT, 1888 (both Thiaridae) from Lake Tanganyika are living representatives of *Pyrgulifera* MEEK, 1872. The protoconch of *Lavigeria* has been figured (RIEDEL 1993) and can be clearly distinguished from that one of *Pyrgulifera*. *Lavigeria* and possibly all Thiaridae (if defined by the following character) have a brood pouch, which in several cases has influence on the formation of the early ontogenetic shell (see RIEDEL 1993). The transition between protoconch and teleoconch, in such species having developed in a brood pouch, is blurred and hatching can often not be connected to a marker on the shell. These features cannot be found in *Pyrgulifera*. Here the protoconch is clearly demarcated by a hook (which is not known from thiarids). This indicates that the embryos may even have hatched out as (lecithotrophic) veligers (see *Pirenella bala-tonica*).

### *Szaboella* gen. nov.

(Pl. 11, figs. 1–8)

**Type species:** *Pyrgulifera ajkaensis* TAUSCH, 1885

**Derivatio nominis:** named after our Hungarian colleague Janos SZABÓ (Natural History Museum, Budapest).

**Diagnosis:** size from about 2–3 cm; early teleoconch: spire angle of about 20°, one prominent primary keel, minor tubercles; late teleoconch: of viviparid shape, spire depressed with apical angle of about 50°, one primary keel on most whorls, which is more sutural than on early teleoconch, aperture more or less egg-shaped with distinct inner lip and minor anterior siphonal canal, umbilicus pronounced; faint spiral striation on most teleoconch whorls; protoconch: about one and a half whorls, clearly demarcated, with wrinkled shell, around 0.25 mm across.

**Differences:** *Pyrgulifera* MEEK, 1872 has two primary keels, the apical whorls of the late teleoconch are not depressed, the protoconch is lower. *Bohaispira* YOU LUO, 1978 is smaller, but with similar teleoconch. The juvenile teleoconch in contrast is not turreted, the protoconch is nearly planispiral.

**Attributed species:** *Pyrgulifera ajkaensis* TAUSCH, 1885; *Pyrgulifera riethmuelleri* OPPENHEIM, 1892; *Szaboella barthai* sp. nov.

**Remarks:** the protoconch and the juvenile teleoconch in all known specimens of the genus are broken off. Only a single type of embryonic and juvenile shell could be found (Pl. 11, figs. 1–2). The about 1.3 protoconch whorls are comparatively loosely coiled. The mean diameter is 260  $\mu\text{m}$ , the nonspiral is 110  $\mu\text{m}$  wide in average. First growth lines can be recognized at about 0.8 whorls. The juvenile shell is not wrinkled and a prominent spiral keel develops immediately. Both characters clearly demarcate the end of the protoconch. It is proposed that the embryos, like in *Pirenella* or *Pyrgulifera*, hatched out as lecithotrophic larvae (pediveligers). The first postnuclear whorl is set with minor tubercles, which on the following whorls increasingly form faint spiral striae. Usually four whorls (including the protoconch) are missing on the spire of the adult specimen. A hypothetical, totally preserved specimen, would have about nine whorls. Beginning with the fourth whorl the diameter of the teleoconch increases rapidly.

YEN (1958, 1965) already doubted that the species of *Szaboella* gen. nov. belong to *Pyrgulifera*. However, he did not coin a new genus as his arguments were not sufficient. YEN (1958, 1965) did not examine the protoconchs.

### *Szaboella barthai* sp. nov.

(Pl. 11, figs. 7–8)

**Holotype:** NHMWien 1994/146.

**Derivatio nominis:** after the Hungarian geologist F. BARTHA who contributed much to the knowledge of the biostratigraphy of the Ajka Coal Formation.

**Locus typicus:** Csingertal, near Ajka (Bakony Mountains), Hungary.

**Stratum typicum:** Ajka Coal Formation, "Bernsteinflöz"

**Diagnosis:** as for the genus, but last teleoconch whorl with several prominent keels

**Description:** the single complete, fully grown specimen, has five teleoconch whorls, which amount to a height of 2.4 cm and a width of 1.6 cm. The aperture is more-or-less egg-shaped and has a minor anterior siphonal canal. The inner lip is well developed, the outer lip is broken. The umbilicus is pronounced. The apical teleoconch on three whorls shows one prominent spiral keel forming a carina. At the transition to the fourth whorl two additional secondary keels appear on the sutural ramp. A third spiral keel is developed near the suture, shortly before the fifth and final whorl forms. This last whorl then shows eight secondary keels and the primary keel, which has lost its dominance.

**Differences:** *Szaboella ajkaensis* (Pl. 11, figs. 3–4) has a smooth last teleoconch whorl (except for growth lines and faint spiral striation). The preceding whorls bear a single prominent spiral keel. *Szaboella riethmuelleri* (Pl. 11, figs. 5–6) bears one primary prominent keel (aside from growth lines and faint spiral striation) on all whorls, forming a sutural ramp also on the last whorl. The last whorl shows a distinct secondary keel, which appears where the suture ends. The secondary keel is less prominent than the primary one.

## Family Melanopsidae

*Melanopsis* FÉRUSAC, 1807

Type species: *Buccinum praemorsum* LINNÉ, 1758

Generic description: size from about 0.5–4.0 cm; teleoconch with cyrtocoenoid outline, body whorl more-or-less inflated; whorls dextral, hardly rounded, smooth or sculptured; spire usually comparatively short; aperture depressed egg-shaped with regularly rounded outer lip, anterior channel, smooth columellar side often thickened by callus; no umbilicus; protoconch simple, not clearly demarcated, about 0.2–0.4 mm across.

*Melanopsis ajkaensis* TAUSCH, 1886

(Pl. 11, figs. 9–10; Pl. 12, fig. 1)

1886 *Melanopsis ajkaensis* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 9, Pl. 1, Fig. 35.

1892 *Melanopsis ajkaensis* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 769–770, Pl. 34, Fig. 11.

1892 *Melanopsis baconica* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 770, Pl. 34, Fig. 10.

Description: the conch consists of about nine whorls, which amount to a height of nearly 5 mm and measure 1.7–1.8 mm in diameter. The spire angle is 18–20°, the increase in diameter is regular. The first whorl has a width of 230–270 µm, the initial cap (nonspiral) measures 90–120 µm across. The nuclear whorl is somewhat wrinkled. This sculptural element divides the protoconch from the teleoconch, which is not wrinkled, but set with faint spiral striae (and growth lines). The aperture, which is the main diagnostic conchological character in *Melanopsis* FÉRUSAC, 1807, is typically pronounced (Pl. 11, fig. 9). The columellar side is covered by a callus, which is thick in the upper part (slightly constricted in the middle) and less prominent in the lower part. The shape of the aperture is similar to a bird's head. The neck would be the broadly channelled base and the posterior part of the aperture is beak-like. The aperture occupies nearly half of a specimen's height. There is no umbilicus, however, sometimes a pseudumbilicus is more-or-less pronounced.

Remarks: *Melanopsis baconica* OPPENHEIM, 1892 is recognized as a synonym of *Melanopsis ajkaensis*. OPPENHEIM (1892) proposed that a weakly developed callus and the lack of an (pseudo-) umbilicus in certain *Melanopsis* specimens are diagnostic for a new species to be separated from *Melanopsis ajkaensis*. However, the pseudumbilicus is usually also very weakly or even not developed in *M. ajkaensis*. Moreover, the strength of the columellar callus of *M. ajkaensis* also varies. The callus often is missing in juvenile specimens, but usually well pronounced in fully grown conchs. OPPENHEIM's figures (1892: pl. 34, figs. 10, 11) indicate that he compared different ontogenetic stages of a single species.

*Melanopsis pauli* sp. nov.

(Pl. 12, figs. 2–6)

1886 *Melanopsis laevis* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 9, Pl. 1, Fig. 34.

1892 *Melanopsis laevis* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 769–770.

Holotype: NHMWien 1994/148.

Paratype: NHMWien 1994/149.

Derivatio nominis: after Paul OPPENHEIM (Berlin) who worked on the Ajka fauna.



**Locus typicus:** Csingertal, near Ajka (Bakony Mountains), Hungary.

**Stratum typicum:** Ajka Coal Formation

**Diagnosis:** typical *Melanopsis* outline, size about 6–7 mm, indistinct sculpture, outer apertural lip projecting on preceding whorl

**Description:** adult conchs usually show about 7 whorls, which amount to a height of 6–6.5 mm and have a diameter of about 3 mm (Pl. 12, figs. 2–3). A complete specimen probably has nearly 10 whorls, however, about 3 apical whorls are usually corroded. The spire angle varies around 25°. The first whorl has a width in a range of 250–290 µm, the initial cap measures 80–120 µm across. The shell of the nuclear whorl is slightly wrinkled, first growth lines can be recognized at about 0.5 whorls. The transition to the teleoconch is characterized by the onset of very faint spiral striae while the wrinkles disappear (Pl. 12, fig. 6). The aperture occupies half of the total height of a specimen. The outer lip is regularly rounded, the upper part projects on the preceding whorl in some distance to the actual aperture of the shell. The columellar side at its upper portion is covered by a broad callus. The peristome in this part is nearly straight (Pl. 12, fig. 4). The callus is constricted at the median and basal portion of the aperture. The basal part of the aperture is channelled.

**Differences:** *Melanopsis laevis* STOLICZKA, 1859 is much larger, the spire is relatively shorter and the aperture occupies about 2/3 of the total height. *Melanopsis ajkaensis* TAUSCH, 1886 is more slender, the upper part of the columellar side of the aperture is rounded and the outer lip does not project on the preceding whorl as far as in *M. pauli* sp. nov.

**Remarks:** the protoconchs and juvenile whorls of *M. ajkaensis* and *M. pauli* sp. nov. can hardly be differentiated in morphology and size. The characters of the teleoconch are diagnostic, however, they possibly can be also interpreted in the context of sexual dimorphism (not described for *Melanopsis*) of a single species.

Recent *Melanopsis* species from the Mediterranean are usually larger and the protoconch is more-or-less smooth. Therefore it is possible that the two species described belong to a new subgenus (also seen in the context of the geological age).

### ***Esperiana* BOURGUIGNAT, 1877**

**Type species:** *Melanopsis esperi* FÉRUSAC, 1823

**Generic description:** size from about 1–2 cm; teleoconch cyrtoconoid with well pronounced spire; about 10 dextrally coiling whorls, usually smooth and slightly rounded; aperture egg-shaped with regularly rounded outer lip, basal part scarcely channelled, columellar side smooth with regular callus; no umbilicus; protoconch (not known from type) about one and a quarter whorls, with faint axial grooves, around 0.25 mm across.

### ***Esperiana obeloides* (TAUSCH, 1886)**

(Pl. 12, figs. 7–8; Pl. 13, figs. 1–2)

1886 *Melania obeloides* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 7, Pl. 1, Figs. 16–18.

1886 *Hemisinus lignitarius* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 8, Pl. 1, Figs. 25–27.

1886 *Hydrobia bodeica* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 12, Pl. 1, Fig. 47.

1892 *Parateinostoma bodeica* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 777–778.

1892 *Melania (Campylostylus) obeloides* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 757–758.

**Description:** the conch of a complete adult specimen would consist of about 12 whorls. However, usually the apical 4–5 whorls are broken off. The remaining 7–8 whorls account to a height of 15–18 mm, the maximum diameter is 6–7 mm (Pl. 12, figs. 7–8). The first whorl measures 200  $\mu\text{m}$  across, the initial cap (nonspiral) is 60–70  $\mu\text{m}$  wide. The first half whorl shows faint spiral rows of axial grooves (Pl. 13, fig. 2). Growth lines and weak spiral striae can be recognized after about 1 whorl. At 1.3 whorls a low varix is formed, determining the end of the protoconch. The spiral striae continue to the teleoconch but do not increase in strength and therefore can be hardly recognized on late ontogenetic whorls. The teleoconch whorls are usually well rounded to weakly angulated. The aperture is egg-shaped with a comparatively slightly channelled basal part and occupies about 2/5 of the total height of the conch. The peristome is interrupted by the preceding whorl, which slightly constricts the width of the aperture. The inner lip is turned up to the umbilicus, which can be clearly recognized in juvenile specimens (Pl. 13, fig. 1). In adult specimens the inner lip forms a callus, which covers the umbilical region and spreads over the columellar side of the aperture.

**Remarks:** we follow OPPENHEIM (1892) in synonymizing *Hemisinus lignitarius* TAUSCH, 1886 with *Esperiana obeloides*. Neither TAUSCH (1886) nor OPPENHEIM (1892) recognized that *Hydrobia bodeica* TAUSCH, 1886 represents a juvenile stage of *Esperiana obeloides* (see under Hydrobiidae). OPPENHEIM (1892) attributed *Esperiana obeloides* (= *Melania obeloides* TAUSCH, 1886) to the genus *Melania* LAMARCK, 1799, subgenus *Campylostylus* SANDBERGER, 1870. *Melania* is a younger synonym of *Thiara* RÖDING, 1798 and later evolved to a composite taxon comprising several genera, e.g., *Melanopsis* FÉRUSSAC, 1807, to which TAUSCH (1886) and OPPENHEIM (1892) obviously compared their specimens.

*Esperiana obeloides* does not belong to *Campylostylus* as was proposed by OPPENHEIM (1892) because that (sub-) genus can be clearly differentiated by several characters (see *Campylostylus heberti*). *Esperiana* BOURGUIGNAT, 1877 (= *Fagotia* BOURGUIGNAT, 1884) has a Recent type. However, our Campanian species cannot be differentiated on generic level and we therefore (as in *Melanopsis*) prefer to use a name of a living representative. *Esperiana obeloides* represents the oldest known species of the genus.

### ***Campylostylus* SANDBERGER, 1870**

**Type species:** *Melanopsis galloprovincialis* MATHERON, 1843

**Generic description:** size from about 4–5 cm; teleoconch subovate, thick-shelled with cyrtoconoid spire; dextral whorls scarcely convex with deepened suture and numerous spiral striae; aperture more-or-less egg-shaped but with short anterior siphonal canal, peristome not continuous, outer lip regularly rounded, inner lip with prominent regular callus; no umbilicus; protoconch about one whorl, with flat nonspiral, around 0.4 mm across.

### ***Campylostylus heberti* (HANTKEN, 1878)**

(Pl. 13, figs. 3–8)

1878 *Melania Heberti* HANTKEN, Die Kohlenflöze und der Kohlenbergbau etc.: 179, 180 Fig. 23.

1886 *Melania Héberti* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 7, Pl. 1, Figs. 13–15.

1892 *Melania (Campylostylus) Héberti* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 756–757, Pl. 34, Figs. 4–6.

**Description:** adult specimens are usually comparatively thick-shelled and consist of about 8 whorls (Pl. 13, fig. 3). A hypothetical complete specimen would have 11 whorls, however, usually at least two whorls (mean 3 whorls) are broken off (apically). The spire angle is about 20°. Eight-whorled specimens reach a height of 4–4.5 cm and a diameter of 1.8–2.0 cm. The first whorl measures 350 µm across, the nonspiral (initial cap) is about 100 µm wide and comparatively flat (Pl. 13, figs. 7–8). First growth lines can already be recognized at the end of the nonspiral (initial shell cap). The nuclear whorl is somewhat slightly wrinkled. Very faint spiral striation sets in on the second whorl (Pl. 13, fig. 8). The striae increase in strength on the last five whorls. On the base of the body whorl the striae number about ten and are more distinct than on the sutural ramp. The growth increments develop a waveform during ontogeny. The aperture is dominated by a regular callus covering the columellar side and the umbilical region. In all specimens the outer lip of the aperture is broken, however, it can be recognized that the peristome is not continuous. The basal part of the aperture is slightly channelled in juveniles (Pl. 13, fig. 6) and formed to a short siphonal canal in fully grown conchs. The aperture occupies about 2/5 of the total height of a specimen.

**Remarks:** *Campylostylus* is treated by us as a genus. It is doubtful if this genus actually belongs to the Melanopsidae, because certain taxa of the Pachychilidae (i.e. *Potadoma* SWAINSON, 1840 or *Brotia* ADAMS, 1866) may be closely related. HOUBRICK (1988) suggests that the family Melanopsidae is the adelphotaxon to the Pachychilidae (= Pleuroceridae). Possibly the two families became distinct from each other during the Late Cretaceous and therefore are difficult to be differentiated in the Ajka fauna.

#### Family Pachychilidae (= Pleuroceridae)

TAUSCH (1886) introduced the new species *Goniobasis hungarica* (pl. 1, figs. 20–23). We follow OPPENHEIM (1892) who proposed that TAUSCH's fig. 20 might show a juvenile *Pyrgulifera*. Specimens, which could be identified with figs. 21, 22 and 23 were not found in our material. OPPENHEIM (1892; pl. 35, figs. 14–15a) figures a specimen, which he thought that TAUSCH (1886) would have placed it with *Goniobasis*. OPPENHEIM (1892) assumed that this species could be attributed to *Cosinia* STACHE, 1880, which, however, is a synonym of *Pyrgulifera*. Finally, it has to be mentioned that *Goniobasis* LEA, 1862 is a genus, which is only known from North-America (see e.g. HANNIBAL 1912; WENZ 1938).

### SUBCLASS HETEROSTROPHA

#### Order Allogastropoda, family Valvatidae

#### *Ariomphalus* gen. nov.

**Type species:** *Pachystoma varicatum* TAUSCH, 1886

**Derivatio nominis:** named after our Dutch colleague Arie JANSSEN (National Museum of Natural History, Leiden).

**Diagnosis:** size from about 2–3 mm; planorbid, dextral conch with 3 to 4 whorls; teleoconch with 7 to 8 varices regularly arranged, whorls angulated or not, with distinct growth lines only or cancellated; protoconch about one whorl, sculpture very similar to that of Recent *Valvata*, diameter about 0.3 mm.

**Differences:** *Stiphrostoma* OPPENHEIM, 1892 is a Pliocene genus (see remarks), which is larger, shows only a single varix, bears longitudinal ribs on the last whorl and has a circular aperture not connected to the preceding whorl. Recent *Valvata* MÜLLER, 1774 has no varices, the protoconch is usually larger.

**Attributed species:** *Pachystoma varicatum* TAUSCH, 1886 and *Pachystoma involutum* TAUSCH, 1886.

**Remarks:** *Pachystoma* SANDBERGER, 1875 from the Pliocene is preoccupied by *Pachystoma* GUILDING, 1828. OPPENHEIM (1892) proposed *Stiphrostoma* as a replacement name and the type species remained the same ("*Valvata*" *marginata* MICHAUD). *Pachystoma* SANDBERGER, 1875 and *Stiphrostoma* OPPENHEIM, 1892 resp. can not be used for the new genus (see differences).

The similarities of *Ariomphalus* gen. nov. to taxa in other families are sometimes striking, however are due to superficial convergences. The species of the Planorbidae are planispiral and all known protoconchs are larger, their longitudinal striae are not connected by bows (BANDEL 1991; NÜTZEL & BANDEL 1993; RIEDEL 1993). Recent *Phreatodrobia* HERSHLER & LONGLEY, 1986 (Hydrobiidae) has no spiral striation on the embryonic shell. Recent *Balconorbis* HERSHLER & LONGLEY, 1986 (Littorinidae) has no varices, the protoconch is smaller and its spiral striation is somewhat confuse.

### *Ariomphalus varicatus* (TAUSCH, 1886)

(Pl. 14, figs. 1–3)

1886 *Pachystoma varicatum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 13, Pl. 2, Figs. 6–7.

1892 *Valvata* (*Pachystoma*) *varicatum* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 775–776.

**Description:** the conch is more-or-less planispiral. An apical and an umbilical side can be clearly distinguished, determining the coiling as dextral. Adult specimens usually reach 3 whorls with a maximum diameter of 2.5 mm and a height of about 1 mm. All of the whorls can be also observed from the umbilical side. There are seven distinct varices (which vary in strength) on the teleoconch that are arranged regularly and increase in size during ontogeny. The aperture is thick-lipped and nearly circular in cross section, partly deformed by the preceding whorl. The first whorl has a diameter of 300–320  $\mu$ m. Growth increments can be recognized after 0.7 whorls. At 1.1 whorls the growth lines become prominent, probably indicating hatching size. The protoconch can be also distinguished from the teleoconch by other sculptural elements. The first 1.1 whorls are set by about 20 longitudinal striae (apically visible) that are interconnected by little bows, the convex side pointing to the aperture. On all teleoconch whorls a cancellation can be found, which develops from strong growth increments crossing spiral striae (or weak ribs).

**Remarks:** see *Ariomphalus involutus*

***Ariomphalus involutus* (TAUSCH, 1886)**

(Pl. 14, figs. 4–7)

1886 *Pachystoma involutum* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 14, Pl. 2, Fig. 9.1892 *Valvata involuta* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 775–776.

**Description:** the more-or-less planorbid conch is coiled dextrally. Adult specimens have about 3.5 to 4 whorls, from which the last one is dominating all the preceding whorls, giving the conch an involut character. The maximum diameter of specimens is about 2 mm. The maximum height of 1.2 mm can be measured along the aperture, which on its inner part is fully connected to the preceding whorl. There are 7 to 8 varices on the teleoconch, which are comparatively weakly developed and sometimes hard to recognize. The initial whorl measures 260–280  $\mu\text{m}$  across. The protoconch probably ends at about 1.1 whorls, where strong growth increments appear. From the apical side there are about 15 spiral striae visible (Pl. 14, fig. 6), which are interconnected by tiny bows in the same way as in *A. varicatus*. The teleoconch may be more-or-less cancellated (like in *A. varicatus*). There are several specimens where the cancellation is missing and the whole teleoconch is smooth (aside from growth lines). The teleoconch whorls are more-or-less angular (*Heliosoma*-like). The angularity is more pronounced on the apical side (Pl. 14, fig. 5).

**Remarks:** the differences between the two species, in diameter and visible number of striae of the nuclear whorl, are caused by the different mode of coiling. The second whorl of *A. involutum* covers more of the embryonic shell than is the case in *A. varicatus*. Therefore the diameter of the first whorls appears to be smaller and the number of striae to be lower. Very young specimens of the different species cannot be differentiated by size or sculpture of the protoconch, but by the shape of the aperture, which is already diagnostic shortly after hatching size. Both species (i.e. *A. involutus*) in their sculptural elements vary comparatively strong. Some specimens are close to *Valvata* (i.e. to *Valvata cristata* MÜLLER, 1774) in their appearance, so that *Ariomphalus* gen. nov. could be considered a closely related genus to that taxon.

## Order Archaeopulmonata, family Ellobiidae

***Leopoldium* gen. nov.****Type species:** *Auricula balatonica* TAUSCH, 1886**Derivatio nominis:** after Leopold TAUSCH who described the type species.

**Diagnosis:** size around 2.5 mm; teleoconch nearly globular with about 4 whorls, spire angle about 55°, last whorl about 3/4 of total height; whorls with spiral striae and distinct growth increments, inner walls resorbed; aperture semi-egg-shaped, outer lip more-or-less sharp, inner lip broader with two columellar plaits at basal half; no umbilicus; protoconch about one whorl, heterostrophic, slightly wrinkled shell, clearly demarcated, around 0.3 mm across.

**Differences:** *Ellobium* RÖDING, 1798 (= *Auricula* LAMARCK, 1799) is much larger, more slender, has more whorls, inner and outer lip of the aperture are thickened. *Auriculinnella* TAUSCH, 1886 is larger, less globular, has prominent axial ribs on the teleoconch, the protoconch is larger and demarcated differently from the teleoconch.



Attributed species: *Auricula balatonica* TAUSCH, 1886 and *Auricula hungarica* TAUSCH, 1886.

***Leopoldium balatonicum* (TAUSCH, 1886)**

(Pl. 15, figs. 1–4)

1886 *Auricula balatonica* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 16, Pl. 2 Fig. 24.

1892 *Auricula balatonica* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 782–783.

**Description:** the largest conchs that could be found consist of 5 whorls with a height of about 2.6 mm and a width of about 2 mm (compare TAUSCH 1886). A juvenile specimen of 3.5 whorls with a height of 1.3 mm and a width of 1 mm has exactly the same proportions (Pl. 15, figs. 1–2).

The protoconch is similar to that of Recent *Ovatella* BIVONA, 1832. It consists of about one whorl, which has a different coiling axis than the teleoconch whorls, indicating heterostrophy. The maximum diameter of the protoconch ranges from 310 to 330  $\mu\text{m}$ . The initial part of it is somewhat inflated (Pl. 15, fig. 4). The periostracum of the protoconch is slightly wrinkled, first growth lines can be recognized after 0.6 whorls. The teleoconch whorls are set with numerous spiral striae, which do not increase in size during ontogeny. The growth increments vary in strength. The columella is resorbed.

The aperture reaches  $\frac{3}{5}$  of the total height and has a sharp outer lip in juvenile specimens and a more-or-less thickened outer lip in adult specimens. The columellar side on its more basal part is characterized by a callus forming two plaits. The upper columellar plait is situated just below half of the height of the aperture and is more prominent than the lower plait. The callus covers the umbilical region.

**Remarks:** TAUSCH (1886: *Auricula hungarica*) described a second species of *Leopoldium* gen. nov. The conch of *L. hungaricum* is more slender, the whorls are less involut and the columellar plaits are situated less basal. However, it cannot be decided if these characters are diagnostic to distinguish *L. hungaricum* from *L. balatonicum*. It seems possible that *L. hungaricum* represents a variation of *L. balatonicum*.

***Auriculinella* TAUSCH, 1886**

**Type species:** *Auriculinella whitei* TAUSCH, 1886

**Generic description:** size around 5 mm; teleoconch egg-shaped with about six whorls, set with prominent axial ribs and spiral lirae; whorls more-or-less shouldered with deepened suture; no umbilicus; aperture semi-egg-shaped with two columellar plaits; protoconch of about 1 whorl, heterostrophic, clearly demarcated, with faint wrinkles, about 0.4 mm across.

***Auriculinella whitei* TAUSCH, 1886**

(Pl. 15, figs. 5–7)

1886 *Auriculinella whitei* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 17, Pl. 1, Figs. 26–27.

1892 *Auriculinella whitei* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 782–783.

**Description:** adult specimens reach 5 to 6 whorls. A specimen of 5 whorls has a height of 3 mm and a width of 1.7 mm. TAUSCH (1886) figured a six-whorled specimen with a height of about 5 mm and a width of about 3 mm. The increase in diameter is very regular. The spire angle is about 50°.

The protoconch consists of about one whorl that coils in a different axis than the teleoconch whorls, indicating heterostrophy. The diameter of the protoconch ranges from 360 to 400  $\mu\text{m}$ . The surface is smooth except for faint periostracal wrinkles and growth lines, which can be recognized after 0.6 whorls. The protoconch is clearly demarcated from the teleoconch by the onset of a thicker, sculptured shell. The "demarcation-line" (outer lip of protoconch aperture) is oblique to the apical axis of the conch (the basal part shorter).

The teleoconch is characterized by about 20 spiral lirae and prominent growth increments on its very early part. The growth increments transform to axial ribs in the second half of the first teleoconch whorl (Pl. 15, fig. 7). The second teleoconch whorl is set with about 30 prominent axial ribs, dominating the spiral striation. The ribs are less developed on the lower part of a whorl. The last teleoconch whorl shows that the ribs axially transform from well pronounced to scarcely distinct (at the base). The aperture occupies half of the total height of the conch and is semi-egg-shaped. The outer lip is more-or-less thickened, the columellar side is characterized by a callus forming two plaits. The upper columellar plait is located at about 3/5 of the aperture height. It is more prominent (sharper) than the lower plait, which forms at about 1/3 of the aperture height. The umbilical region is covered by the callus.

#### Order Basommatophora, family Ancyliidae

##### *Ancylina* gen. nov.

**Type species:** *Ancylus cretaceus* TAUSCH, 1886

**Derivatio nominis:** from *Ancylus*

**Diagnosis:** size around 4 mm; limpet, comparatively flat, width about 3/4 of length; apex ancyliid, hooked, situated left from the length axis, on the posterior half of the conch; early ontogenetic conch with radial rows of pits, late ontogenetic conch with coarse radial ridges.

**Differences:** *Ancylus* MÜLLER, 1774 has a conch, which is usually higher, the apex lies more posterior, without radial rows of pits. The apex of *Burnupia* WALKER, 1912 is always situated right from the length axis (PILSBRY & BEQUAERT 1927; BROWN 1980). The apex of *Ferrissia* WALKER, 1903 is obtuse (never hooked) and does not show radial rows of pits (BROWN 1980).

**Attributed species:** *Ancylus cretaceus* TAUSCH, 1886

##### *Ancylina cretacea* (TAUSCH, 1886)

(Pl. 16, figs. 1–4)

1886 *Ancylus cretaceus* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 17, Pl. 2, Fig. 29.

1892 *Ancylus (Velletia) cretaceus* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 783.

**Description:** The adult specimens in average measure 4 mm in length, 3 mm in width and about 1 mm in height. The apex is situated at about 2/3 of the total length, measured

from the anterior end of the shell. The apex is hooked and indented at the same time. An initial circular shell cap with a diameter of 60  $\mu\text{m}$  can be recognized that is smooth except for a central hollow. The following early ontogenetic shell is characterized by radial rows of pits (which form axial rows at the same time) up to a diameter of about 350  $\mu\text{m}$ . At this diameter coarsely set radial ridges and distinct growth increments appear, forming a cancellated pattern for the rest of the conch.

**R e m a r k s :** TAUSCH (1886) coined a second ancyloid species: *Ancylus vetustus*. From his description, which does not coincide with his figures, it cannot be safely differentiated from *Ancylina cretacea*. Our material does not reveal a second species. From the knowledge of Recent *Ancylus* it seems possible that *Ancylus vetustus* is a variation of *Ancylina cretacea* and therefore a synonym.

OPPENHEIM (1892) attributed *Ancylus cretaceus* TAUSCH, 1886 and *Ancylus vetustus* TAUSCH, 1886 to the (sub-)genus *Velletia* GRAY, 1840, which, however, is a synonym of *Acroloxus* BECK, 1837 (Acroloxidae). The protoconch of *Acroloxus* is not indented (see RIEDEL 1993) but otherwise is similar to that of ancyloid species. Teleoconchs of modern *Acroloxus* species usually do not have the prominent ribbing of ancyloid species.

#### Order Stylommatophora

TAUSCH (1886) described several terrestrial gastropods from which only few could be recognized in our material. One of his new species of *Helix* LINNÉ, 1758 could be identified as a neritoidean gastropod (see *Schwardtina* gen. nov.), other species appear to be juveniles (compare OPPENHEIM 1892). However, figures and description given by TAUSCH (1886) are not sufficient to correlate his (probably) juvenile specimens to other taxa.

We provide an emendation of the description of *Bulimus munieri* HANTKEN, 1878. *Bulimus* is an invalid name, therefore WENZ (1940) introduced the genus *Gastrobulimus*. The teleoconch is similar to Recent *Megalobulimus* MILLER, 1878, which, however, is much larger. The protoconch of *Gastrobulimus munieri* is typical for Stylommatophora. We leave the family attribution open. WENZ (1940) coined two more genera for gastropods described by TAUSCH (1886) under "*Bulimus*". WENZ (1940) introduced *Conobulimus* and *Juvavina* on the basis of TAUSCH's figures (ZILCH 1960). The figures by TAUSCH (1886) in our opinion are not diagnostic. Moreover, we could not recognize comparable shells in our material.

#### *Gastrobulimus* WENZ, 1940

**Type species:** *Bulimus munieri* HANTKEN, 1878

**Generic description:** size around 3 cm; teleoconch more-or-less egg-shaped with short spire, about 3 dextral whorls with distinct growth increments and numerous, waved, spiral lirae; aperture large, egg-shaped, posteriorly angled; peristome continuous, thick-lipped, with prominent regular columellar callus; no umbilicus; protoconch about one and a half smooth whorls, 2–2.5 mm across.

***Gastrobulimus munieri* (HANTKEN, 1878)**

(Pl. 16, figs. 5–8)

1878 *Bulimus Munieri* HANTKEN, Die Kohlenflöze und der Kohlenbergbau etc.: 180, Fig. 24.1886 *Bulimus Munieri* TAUSCH, Abh. k.k. Geol. Reichsanstalt, 12: 15, Pl. 2, Figs. 18, 19.1892 *Bulimus Munieri* OPPENHEIM, Z. Deutsch. Geol. Ges., 44: 780, Pl. 36, Figs. 8, 8a and 9.1940 *Gastrobulimus munieri* WENZ in ZILCH, Handbuch der Paläozoologie 6/2: 502, Fig. 1764.

**Description:** the adult conch consists of nearly four whorls, which amount to a height of 30 mm and reach a maximum diameter of 17 mm. The first whorl is smooth and measures about 1.5 mm across. After that distinct growth increments can be recognized. At the transition from the second to the third whorl numerous spiral striae appear and continue to the aperture. The axial growth increments and the spiral striae form a pattern that is somewhat cancellated. However, the striation is usually more prominent. The aperture is egg-shaped (the upper part channelled) and occupies about 4/5 of the total height of the conch. The peristome is continuous and thick-lipped. There is no umbilicus.

Terrestrial gastropods of comparable localities to Ajka, like the Gosau Beds, have been examined by several authors (e.g. HRUBESCH 1965). It is not possible to differentiate these gastropods from the Ajka specimens at species or even at genus level, because no protoconchs have been documented. However, it is evident that the same family taxa occur (see also discussion).

**Discussion**

The interpretation of a fossil fauna stands or falls by the correctness of assumptions. The attribution of species to certain taxa usually goes back to the morphology of the conch as well as to environmental conditions. These are of course trivial statements, however, it has to be emphasized that the morphology of the gastropods of Ajka actually has not been known until this revision provided the essential protoconch characters. Consequently systematics, environment and also paleogeography have been misinterpreted in several cases.

Due to the knowledge of the early ontogenetic whorls, a terrestrial stylommatophoran *Helix cretacea* has "transformed" to an aquatic neritimorph *Schwardtina cretacea*, which means that the ecology is totally different. A species of *Hemisinus* is recognized here to belong to *Esperiana*, which is important for paleogeographical considerations (*Hemisinus* is a North-American genus). It is shown that the neritimorph genus *Deianira* had a planktotrophic veliger, which easily explains its distribution and means that at least the larvae developed in a marine habitat.

The adults of *Deianira* were assumed to have lived in brackish water (e.g. HARBECK 1989; SCHENK 1972; TAUSCH 1886). This is quite possible, however, some facts have been overlooked. There are no early juvenile specimens of *Deianira* in the Ajka sediments, which is in contrast to the species of all other genera. The conchs of *Deianira* are the only ones that were drilled by a hunting gastropod. Potential predators like Naticoidea or Muricoidea are usually marine animals, however, in several cases may enter brackish water. There are no shells of such predators in the Ajka fauna. It can be considered that *Deianira* was a marine genus, which could tolerate brackish influence.

The environmental conditions of *Pyrgulifera* have been discussed several times (e.g. CZABALAY 1988; HARBECK 1989; MERTIN 1939; SCHENK 1972; STACHE 1889; YEN 1958). It

always has been concluded that *Pyrgulifera* is a freshwater genus, which may tolerate brackish influence and can be attributed to the Thiaridae (e.g. HARBECK 1989; YEN 1958). This reasoning partly may have also resulted from the discussion if *Pyrgulifera* could be identical with Recent *Paramelania/Lavigeria* (actual thiarids) from Lake Tanganyika (see remarks on *Pyrgulifera*). It has been shown here that these two genera are no synonyms. The protoconchs indicate that *Pyrgulifera* very probably had a similar early ontogenetic development to that of *Pirenella*, a genus, from which authors assume to demonstrate marine influence on a fauna. Some specimens of *Pyrgulifera* were corroded by clionid sponges, which are marine animals, sometimes can be recognized in brackish habitats (see e.g. LAWRENCE 1969), however, do not occur in freshwater. Finally the huge number of specimens is another hint on brackish environment, where densely populated areas (by a single species) are known (which is usually in contrast to freshwater faunas). For these reasons we interpret *Pyrgulifera* as a brackish water genus, which could tolerate freshwater inflow (as usual for animals of such a habitat) and not vice versa. *Pyrgulifera* (like *Pirenella*) at the moment is placed best in the Recent family Potamididae.

The following genera of the Ajka gastropods are supposed to indicate the brackish water habitat: *Auriculinella*, *Deianira*, *Hadraxon*, *Leopoldium* gen. nov., *Pirenella*, *Pyrgulifera*, "*Rissoa*" and *Szaboella* gen. nov.. *Deianira* may have lived in brackish water as well as in a marine environment. Modern *Neritina* like *Deianira* needs fully marine environment during the early ontogeny, but later tolerates also brackish water or even freshwater.

*Ancylina* gen. nov., *Ariomphalus* gen. nov., *Campylostylus*, *Czabalaya* gen. nov., *Esperiana* and *Melanopsis* are probably indicating freshwater, however, *Melanopsis* possibly also lived in the brackish influence, which is the case among modern species of New Zealand.

*Schwardtina* gen. nov. and *Parateinostoma* at the moment cannot be attributed to a certain habitat.

Many species of Ajka are endemic. Comparing this locality with similar Late Cretaceous or Early Paleocene fossil assemblages, e.g., of the southern Pyrenees (see HARBECK 1989), the Provence (see FABRE-TAXY 1948, 1951, 1958; OPPENHEIM 1895), Austria (see CZABALAY 1983; HERM 1977; SCHENK 1972; STOLICZKA 1860), Dalmatia (see STACHE 1889), Romania (see HANTKEN, 1878) or the northern Harz Mountains/Germany (see FRECH 1887; MERTIN 1939), it is evident that about the same family taxa occur. Several genera like *Pyrgulifera*, *Pirenella*, *Melanopsis* or *Viviparus* usually can be recognized. However, the taxonomy at species level can be clearly distinguished, giving the different localities their own faunistic character.

The characteristic connecting link of these similar faunas is the genus *Pyrgulifera*, which also occurs in the Bear River Formation of Wyoming (see e.g. WHITE 1895; YEN 1954). However, the Bear River Formation is the only known American stratum where *Pyrgulifera* can be found. In other Late Cretaceous faunas of Wyoming, Montana or Alberta, *Pyrgulifera* is missing (see TOZER 1956; YEN 1951). STEPHENSON (1952) described a very doubtful *Pyrgulifera* from the Cenomanian Woodbine Formation of Texas.

The distribution of *Pyrgulifera* on the Asian continent is unclear. MATUMOTO (1938) described a species from the Cretaceous of Japan, which very probably cannot be attributed to *Pyrgulifera* (see also YEN 1958). This accounts also for the figure by KASE (1984), which, however, possibly represents a member of the Potamididae and therefore might be closely

related to *Pyrgulifera*. *Pyrgulifera* has not been described from geographically intermediating faunas, e.g. of southern China (WEN 1977).

The family taxa composition of most Late Cretaceous non-marine gastropod faunas is similar to those of Recent faunas in comparable habitats (see e.g. PILSBRY & BEQUAERT 1927). Going back to the Jurassic-Cretaceous transition the Wealden facies yields well preserved non-marine gastropods (BANDEL 1991 and literature therein; HUCKRIEDE 1967). The taxa Potamididae, Archaeopulmonata, Viviparidae and Planorbidae are characteristic (see BANDEL 1991; YEN & REESIDE 1946), the Melanopsidae, however, are missing. This might indicate that the phylogeny of this family does not begin earlier than in the Cretaceous. The European Wealden shows a different character compared to the Ajka fauna. The taxa of the Planorbidae, Physidae, Valvatidae or Viviparidae clearly indicate a strong freshwater influence (BANDEL 1991), which is even stronger in the fauna of the comparable Upper Jurassic Morrison Formation (USA) (see YEN & REESIDE 1946). The amphibious Archaeopulmonata are represented by a larger number of species compared to the Ajka fauna (see BANDEL 1991). The brackish or marine influence is comparatively low. The Wealden swamps were probably extended much more over the inland, while the Ajka fauna was more-or-less restricted to a river mouth coastal swamp. The low generic correspondence between the Upper Cretaceous deposits and the Wealden facies is not only correlated to different environments, but probably has to do with about 50 million years evolution. Paleogeographic arrangements possibly played an important role, determining the possibilities of distribution. In especially, (aside from land snails) differences are multiplied in freshwater gastropods that have difficulties to cross oceans. Considerable changes of the plant world occurring at the end of the Lower Cretaceous surely had strong influence on the environments. Among other groups, the rapid change in marine gastropod faunas or the rise of the rudists in lagoonal environments, feature major evolutionary events in the Aptian and Albian.

Gastropods are a good tool to characterize coastal swamps. However, it must be emphasized that the knowledge of fossil as well as of Recent faunas is far from being complete.

#### Acknowledgements

We are very grateful to our Hungarian colleagues Janos SZABÓ (Natural History Museum, Budapest) and Laszlo KORDOS (Hungarian Geological Institute, Budapest) and to our Austrian colleagues Heinz KOLLMANN and Ortwin SCHULTZ (Natural History Museum, Vienna) for kindly cooperating in loaning material. Géza CSÁSZÁR (Hungarian Geological Institute) and Karoly KOSZMA gave us the opportunity to visit a section of the Ajka coal-mines. K. HARBECK, N. LEHMANN, A. NÜTZEL, B. PETERS and U. ZIELINSKI (all Hamburg) helped collecting much of the material. H.J. LIERL and C. TAEBEL (both Hamburg) processed the samples and C. TAEBEL also improved some of the photographs. B. STÜTZE (Hamburg) provided the strontium analysis. Thanks a lot to all these persons.

This study was supported financially by the Deutsche Forschungsgemeinschaft in the framework of the research project Ba 675/7-1 and 12-1.

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## Plate 1

*Schwardtina* gen. nov.

fig. 1: fully grown conch of *Schwardtina cretacea*, NHMWien 1994/106. – Scale bar = 1.5 mm.

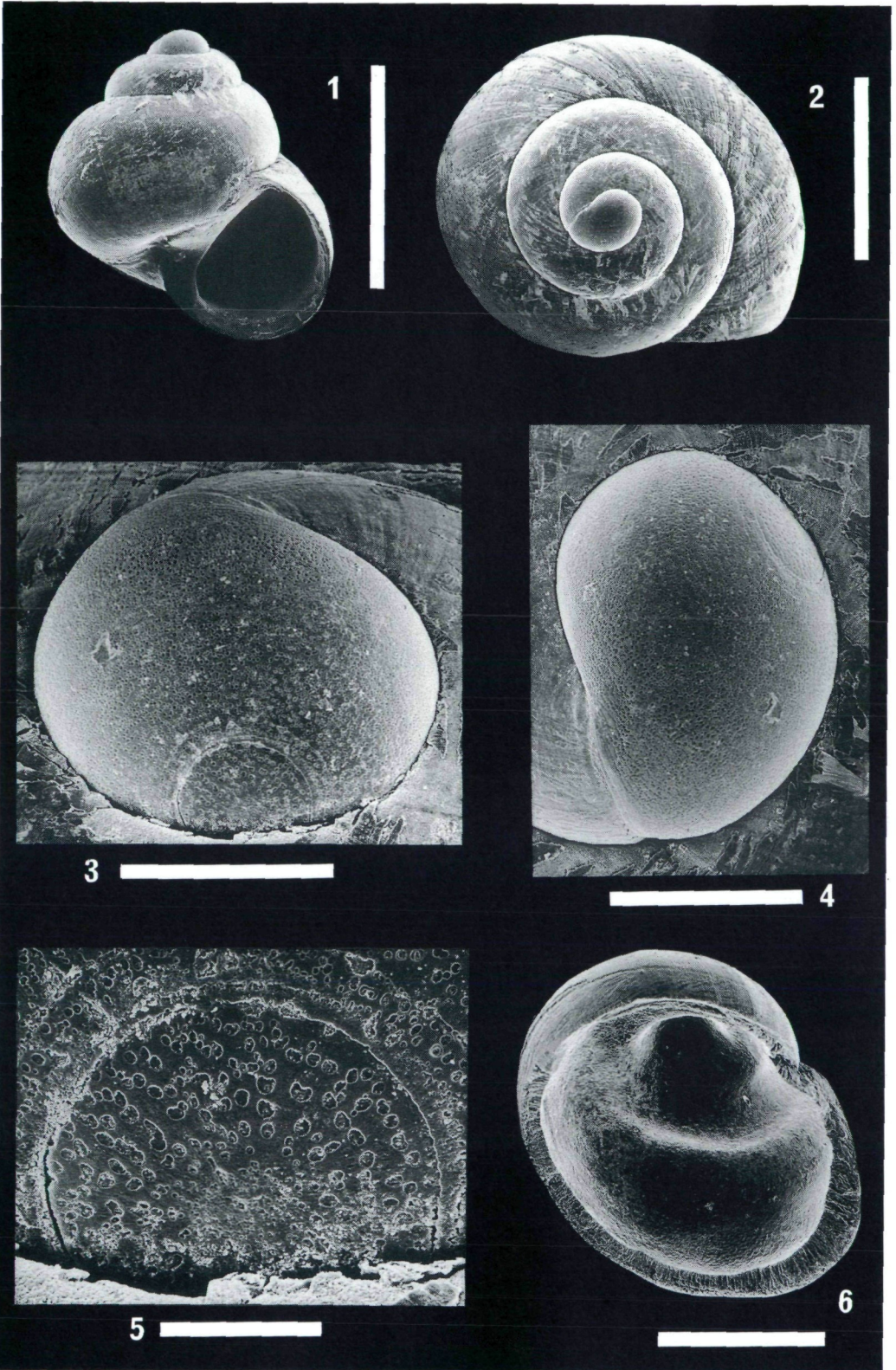
fig. 2: apical view of same specimen as in fig.1. – Scale bar = 1.0 mm.

fig. 3: lateral view of the protoconch of same specimen as in fig. 1. – Scale bar = 0.2 mm.

fig. 4: apical view of same protoconch as in fig. 3. – Scale bar = 0.2 mm.

fig. 5: magnification of fig. 3 showing the demarcation of the first shell secretion and the punctation of the periostracum. – Scale bar = 0.05 mm.

fig. 6: portion of *Schwardtina cretacea* demonstrating that the columella is resorbed, NHMWien 1994/224. – Scale bar = 0.5 mm.



## Plate 2

*Deianira* STOLICZKA, 1859

fig. 1: protoconch of *Deianira ferdinandi* sp. nov. or *Deianira leopoldi* sp. nov.; both species have the same protoconch type, NHMWien 1994/225. – Scale bar = 0.2 mm.

fig. 2: same photograph as in fig. 1 but with a marked suture.

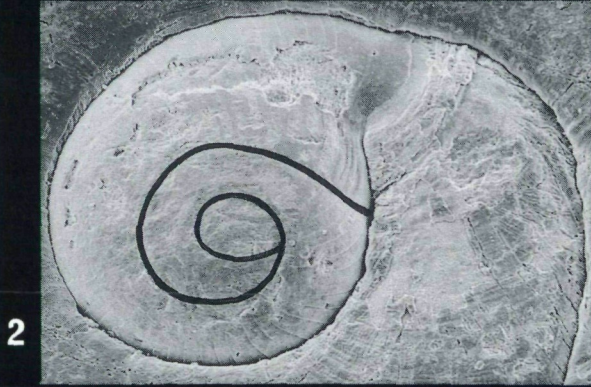
fig. 3: magnification of a larval whorl of same specimen as in fig. 1 showing the axial ridges. – Scale bar = 0.05 mm.

fig. 4: protoconch of *Deianira* sp. with the first juvenile whorl showing cancellation, same specimen as in fig. 1. – Scale bar = 0.3 mm.

fig. 5: protoconch in the spatial context of juvenile whorls showing the development of sculptural elements in *Deianira* sp., NHMWien 1994/226. – Scale bar = 1 mm.

fig. 6: typical borehole (drilled by a gastropod), which is present in several specimens of *Deianira* sp., same specimen as in fig. 5. – Scale bar = 0.2 mm.



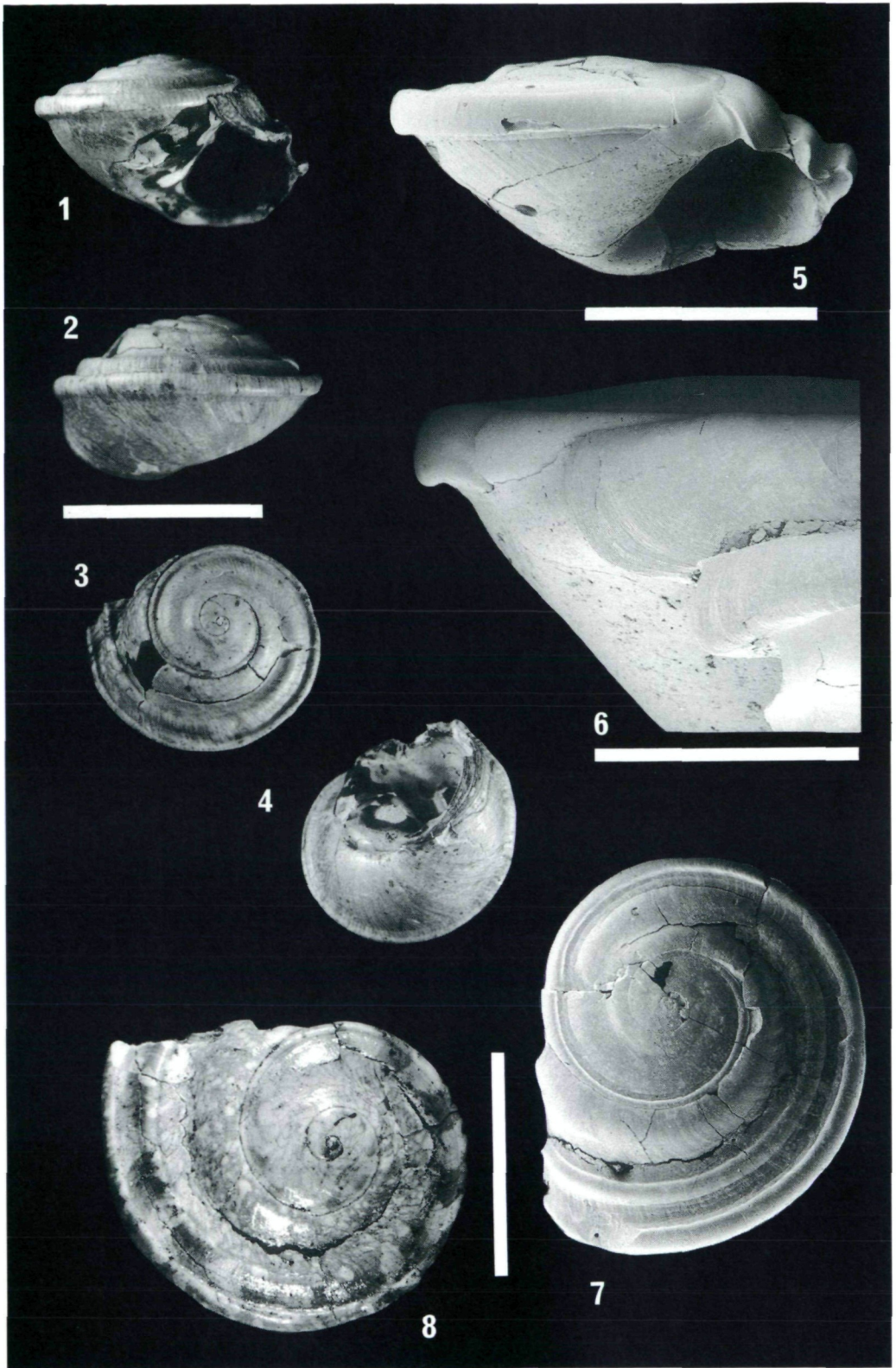


## Plate 3

***Deianira* STOLICZKA, 1859**

- figs. 1–4: several views of a fully grown shell of *Deianira leopoldi* sp. nov. – Scale bar = 1 cm.  
fig. 5: apertural view of holotype of *Deianira ferdinandi* sp. nov., NHMWien 1994/227. – Scale bar = 4 mm.  
fig. 6: lateral view of upper portion of the aperture; same specimen as in fig. 5. – Scale bar = 2 mm.  
fig. 7: apical view of holotype of *Deianira ferdinandi* sp. nov. – Scale bar = 4 mm.  
fig. 8: apical view of paratype of *Deianira ferdinandi* sp. nov. showing the colour pattern. – Scale bar as in fig. 7.





## Plate 4

**“Palaina” SEMPER, 1865 and Strophostomella FISCHER, 1883**

fig. 1: apical view of “*Palaina*” *europaea*, NHMWien 1994/107. – Scale bar = 0.5 mm.

fig. 2: same specimen as in fig. 1, apertural view. – Scale bar = 1 mm.

fig. 3: umbilical view of “*Palaina*” *europaea*, NHMWien 1994/108. – Scale bar = 0.5 mm.

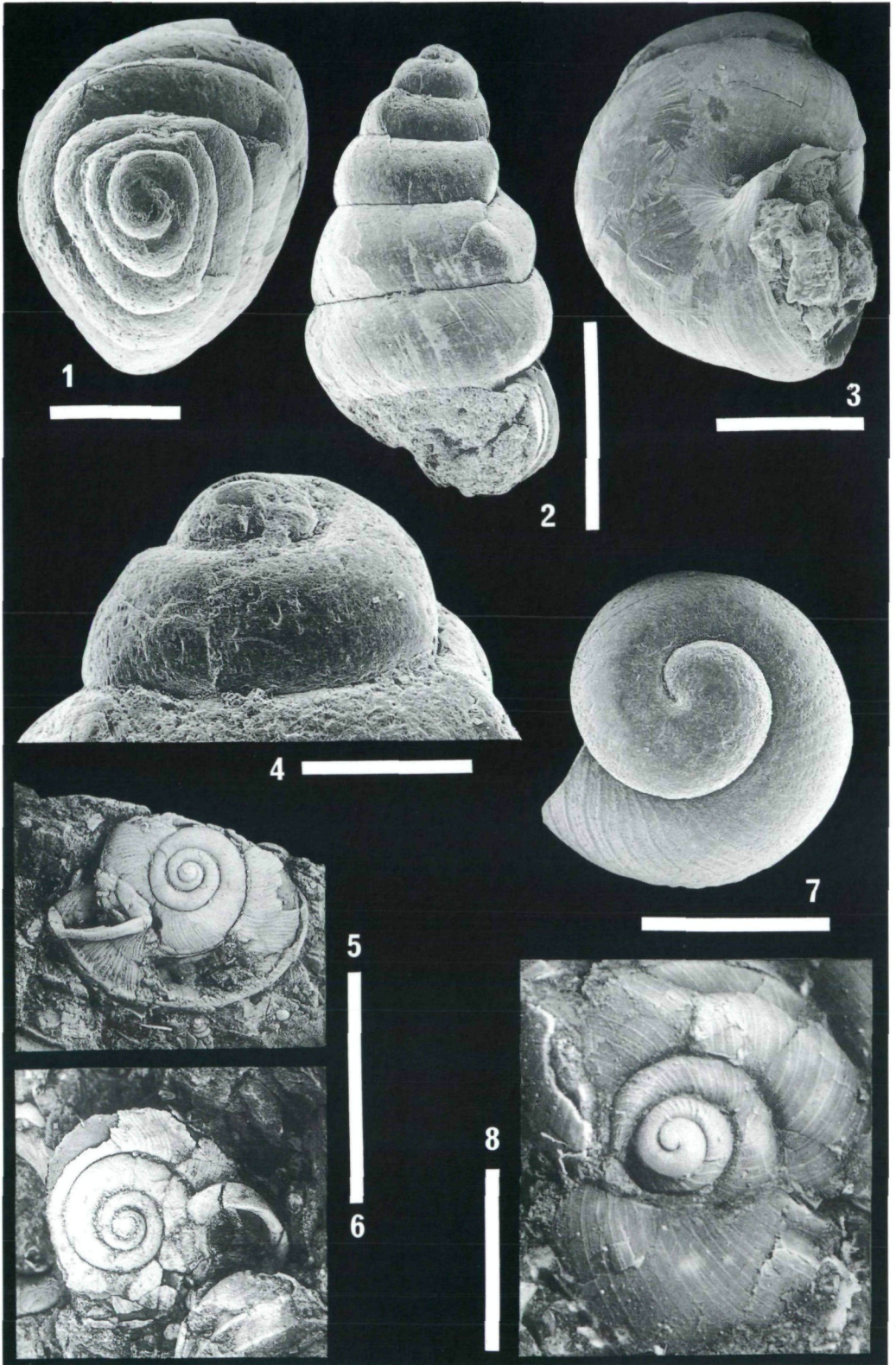
fig. 4: apical whorls of same specimen as in fig.1. – Scale bar = 0.2 mm.

figs. 5–6: apical views of two specimens of *Strophostomella cretacea*, NHMWien 1994/109 and NHMWien 1994/110. – Scale bar = 1 cm.

fig. 7: apex of *Strophostomella cretacea* showing the onset of axial ornamentation, NHMWien 1994/111. – Scale bar = 0.5 mm.

fig. 8: magnification of early ontogenetic whorls of *Strophostomella cretacea*. – Scale bar = 2 mm.





## Plate 5

***Czabalaya* gen. nov. and “*Rissoa*” FREMINVILLE, 1814**

figs. 1–2: cyclophoroid or stylommatophorid gastropod attributed by TAUSCH (1886) to *Strophostoma* DESHAYES, 1828 (= *Ferrussina* GRATELOUP, 1827), NHMWien 1994/114. – Scale bar = 1 mm.

figs. 3–4: holotype of *Czabalaya kordosi* gen. et sp. nov., NHMWien 1994/116. – Scale bar = 5 mm.

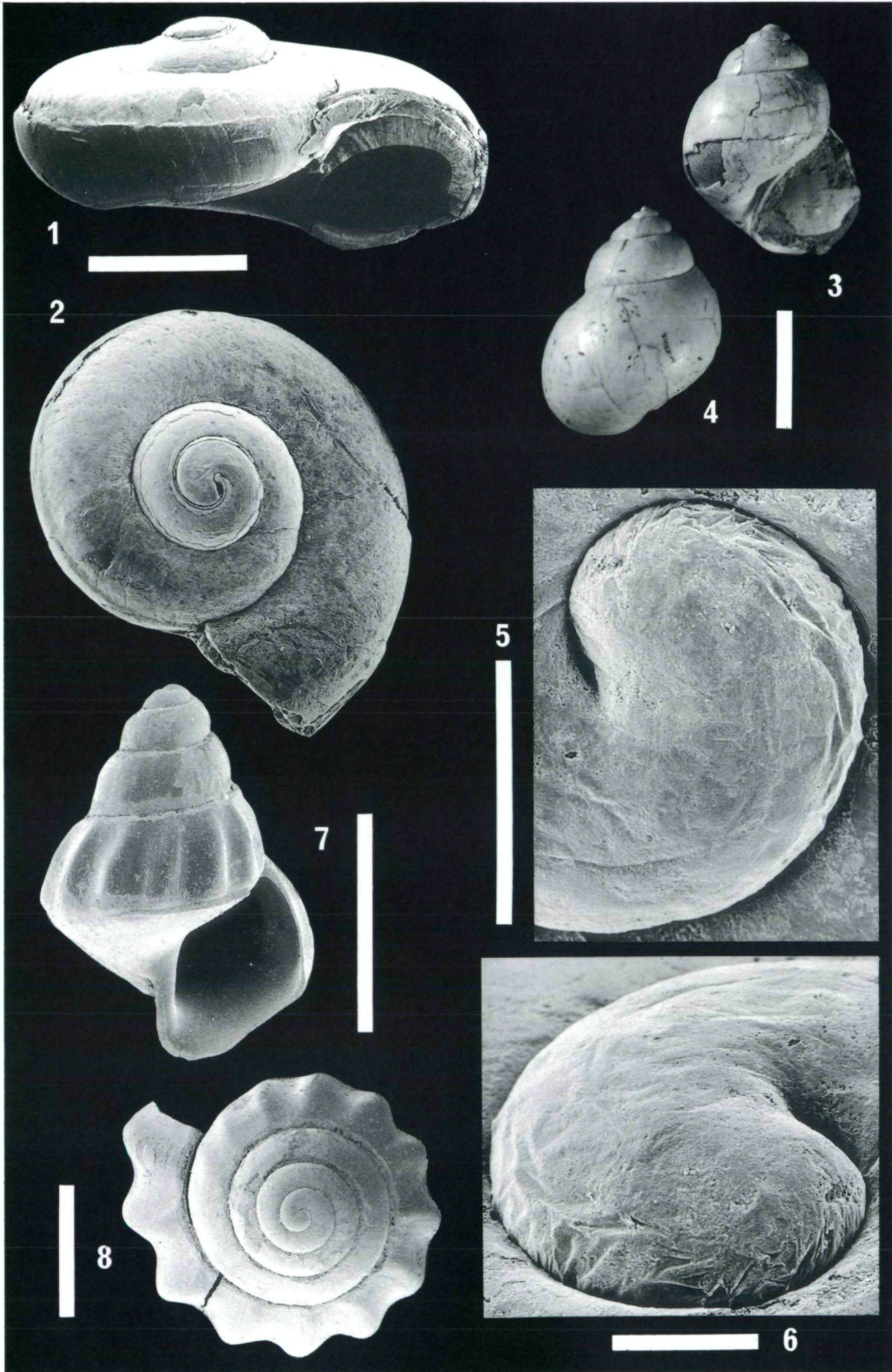
fig. 5: apical view of initial whorl of *Czabalaya kordosi*, NHMWien 1994/115. – Scale bar = 0.2 mm.

fig. 6: same apex as in fig. 5 in lateral view. – Scale bar = 0.1 mm.

fig. 7: fully grown shell of “*Rissoa*” sp. – Scale bar = 1 mm.

fig. 8: same specimen as in fig.7 in apical view. – Scale bar = 0.5 mm.





## Plate 6

***Parateinostoma* OPPENHEIM, 1892 and *Hadraxon* OPPENHEIM, 1892**

fig. 1: *Parateinostoma mana*, NHMWien 1994/118. – Scale bar = 1 mm.

fig. 2: apex of same specimen as in fig. 1. – Scale bar = 0.2 mm.

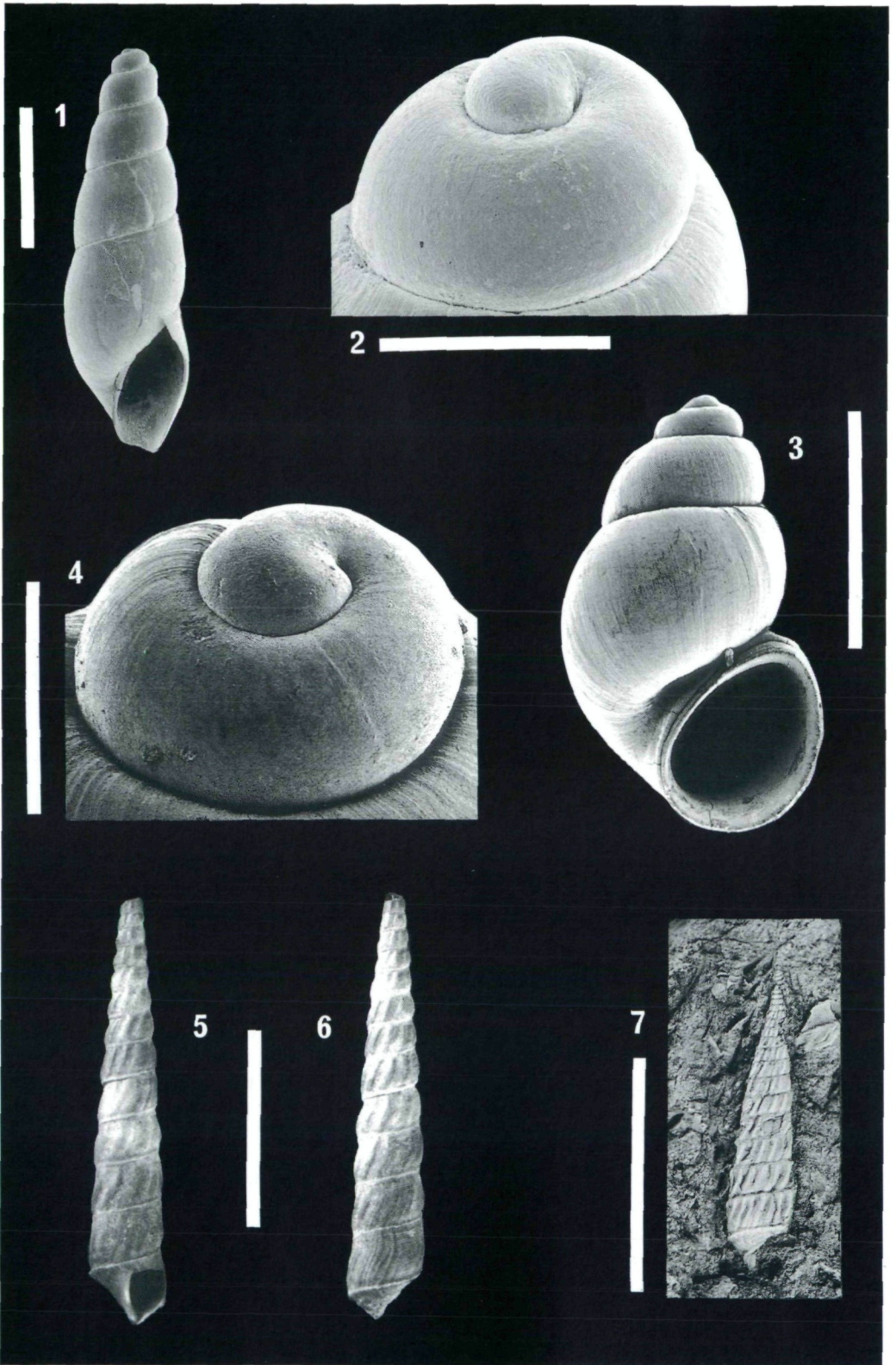
fig. 3: “*Hydrobia*” *veszprimica*, NHMWien 1994/119. – Scale bar = 1 mm.

fig. 4: apex of same specimen as in fig. 3. – Scale bar = 0.2 mm.

figs. 5–6: *Hadraxon csingervallense*, NHMWien 1994/120. – Scale bar = 5 mm.

fig. 7: typical preservation of *Hadraxon csingervallense*, NHMWien 1994/121. – Scale bar = 1 cm.



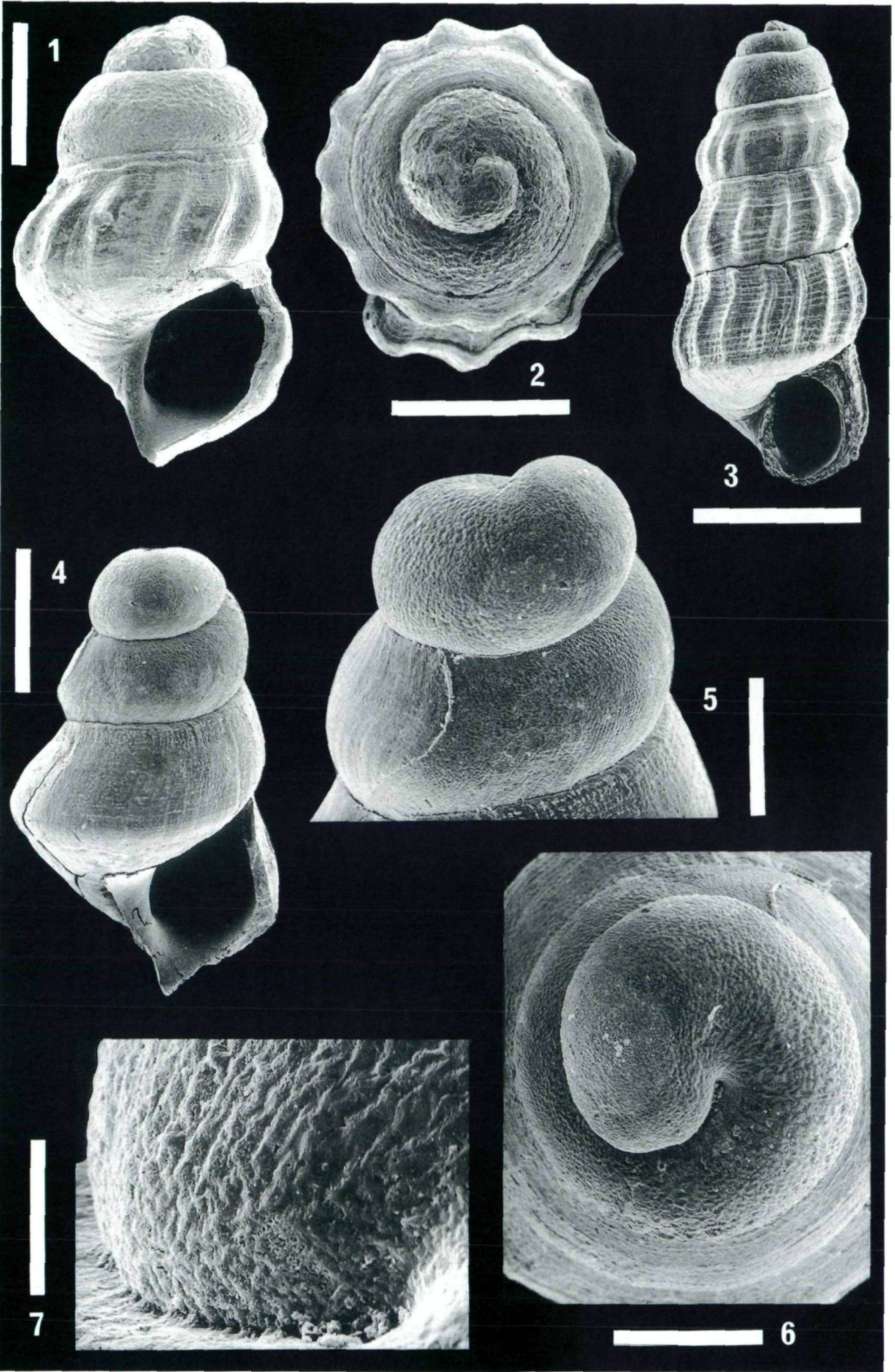


## Plate 7

***Hadraxon* OPPENHEIM, 1892 and *Pirenella* GRAY, 1847**

- fig. 1: early juvenile shell of *Hadraxon csingervallense*, NHMWien 1994/122. – Scale bar = 0.2 mm.  
fig. 2: same specimen as in fig. 1, apical view. – Scale bar = 0.2 mm.  
fig. 3: early ontogenetic whorls of *Hadraxon csingervallense* showing the development of the ornamentation, NHMWien 1994/112. – Scale bar = 0.5 mm.  
fig. 4: early juvenile shell of *Pirenella balatonica* and *P. supracretacea*. – Scale bar = 0.2 mm.  
fig. 5: magnification of protoconch of *Pirenella* showing the postembryonic hook. – Scale bar = 0.1 mm.  
fig. 6: same specimen as in fig. 5, apical view showing the voluminous initial whorl. – Scale bar = 0.1 mm.  
fig. 7: magnification of a *Pirenella* protoconch revealing wrinkles. – Scale bar = 0.02 mm.





## Plate 8

*Pirenella* GRAY, 1847 and *Pyrgulifera* MEEK, 1872

fig. 1: juvenile conch of *Pirenella supracretacea* demonstrating the possibility of an ontogenetically late onset of nodules, NHMWien 1994/123. – Scale bar = 3 mm.

fig. 2: the apical whorls of *Pirenella supracretacea* and *P. balatonica* are the same in both species, NHMWien 1994/124. – Scale bar = 0.3 mm.

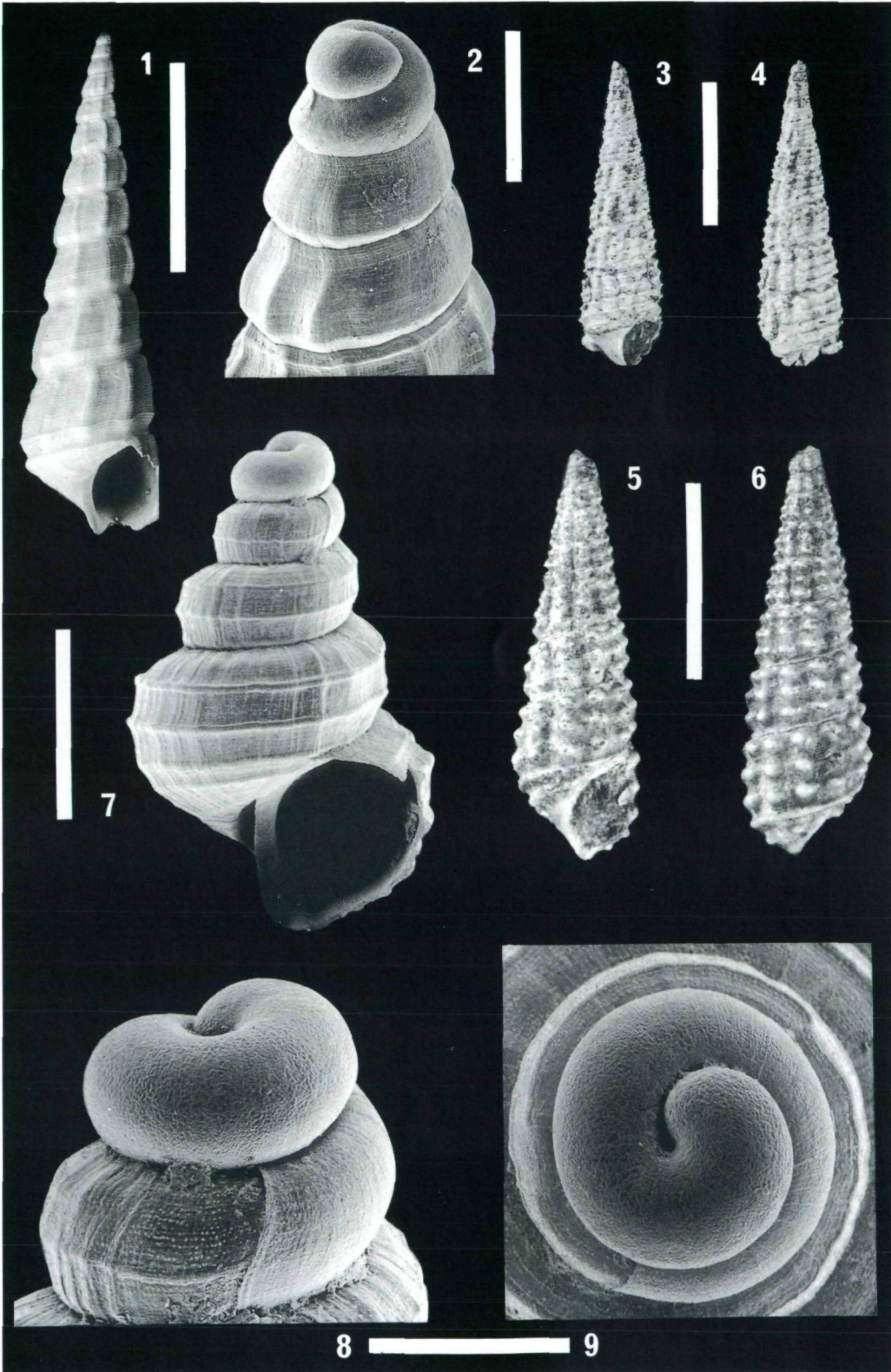
figs. 3–4: fully grown *Pirenella supracretacea*, NHMWien 1994/125. – Scale bar = 1 cm.

figs. 5–6: fully grown *Pirenella balatonica*, NHMWien 1994/127. – Scale bar = 5 mm.

fig. 7: juvenile conch of *Pyrgulifera*, NHMWien 1994/129. – Scale bar = 0.5 mm.

figs. 8–9: lateral and apical view of same specimen as in fig.7. – Scale bar = 0.2 mm.





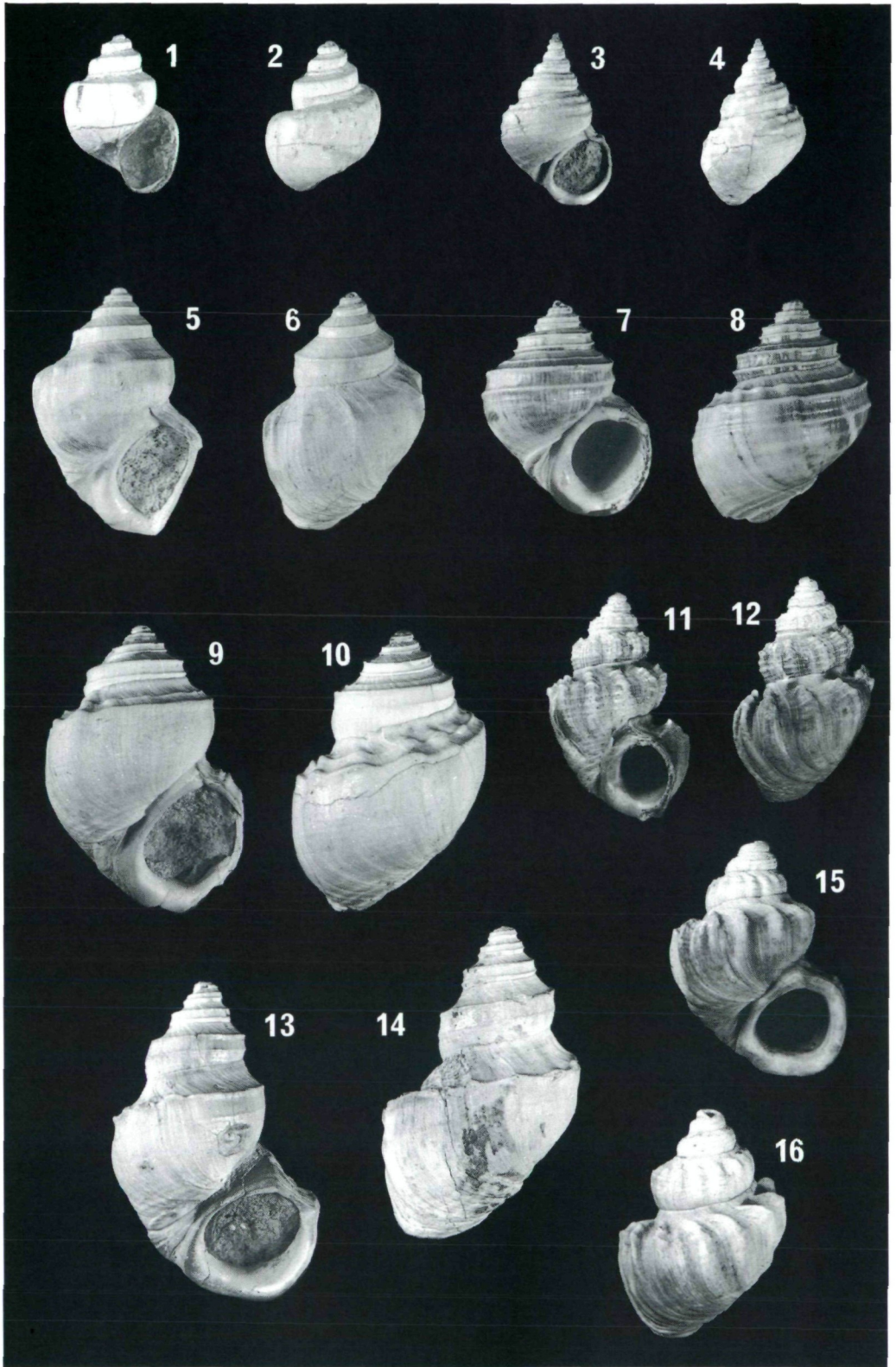
## Plate 9

***Pyrgulifera* MEEK, 1872**

figs. 1–16: some variations of *Pyrgulifera*, NHMWien 1994/130–132 and NHMWien 1994/134–138. – Scale bar = 2 cm.

figs. 3–4: typical "*Cosinia*", NHMWien 1994/131.





## Plate 10

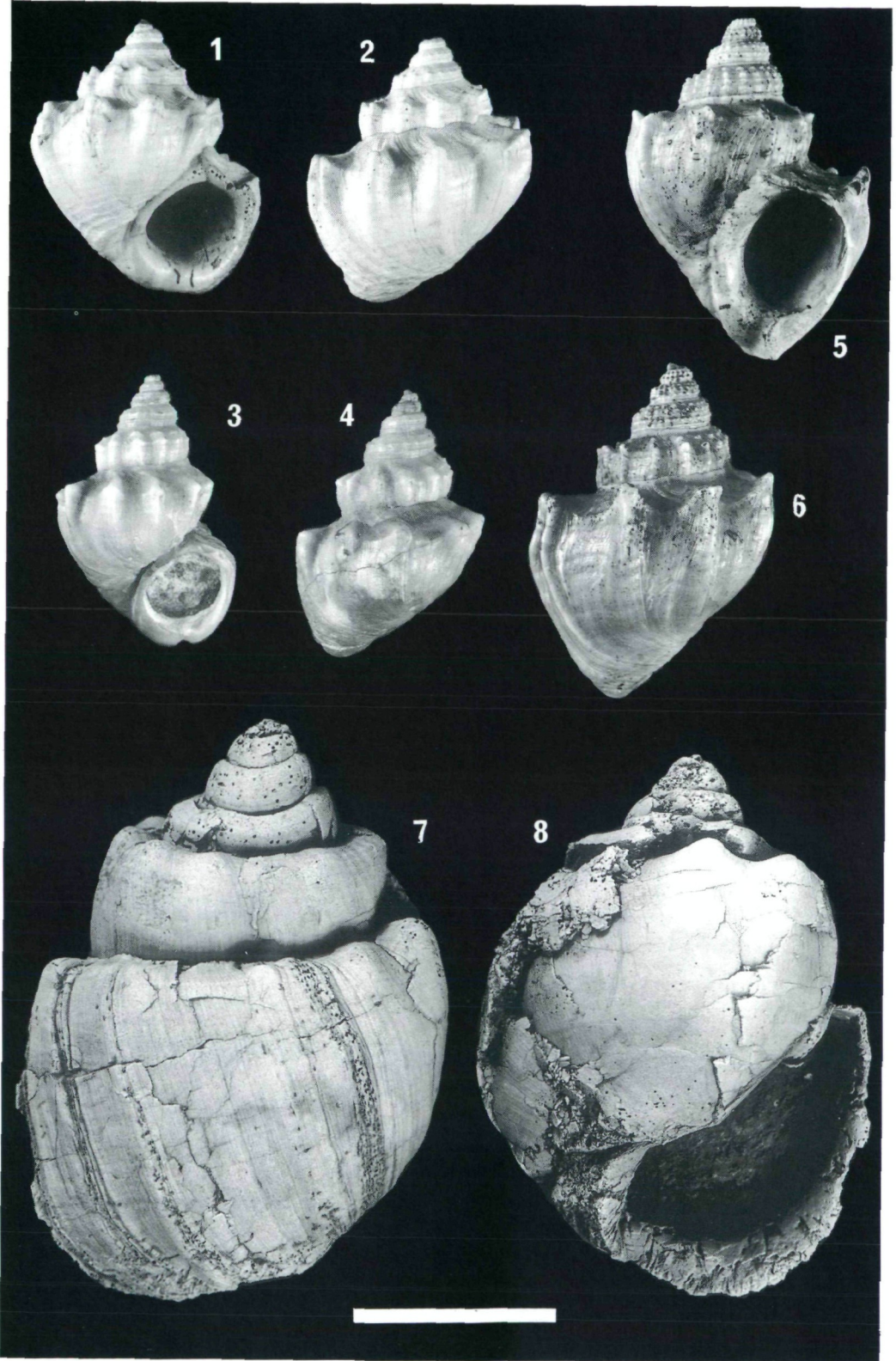
***Pyrgulifera* MEEK, 1872**

figs. 1–8: some variations of *Pyrgulifera*, NHMWien 1994/139–142. – Scale bar = 2 cm.

figs. 3–4: specimen similar to holotype of *Pyrgulifera humerosa*, NHMWien 1994/140.

figs. 7–8: "*Pyrgulifera*" *pannonica*, NHMWien 1994/142.





## Plate 11

***Szaboella* gen. nov. and *Melanopsis* FÉRUSSAC, 1807**

fig. 1: early ontogenetic whorls of *Szaboella* gen. nov., NHMWien 1994/143. – Scale bar = 0.5 mm.

fig. 2: magnification of the apex of *Szaboella* showing the wrinkled shell of the protoconch and the primary keel on the teleoconch, NHMWien 1994/143. – Scale bar = 0.2 mm.

figs. 3–4: *Szaboella ajkaensis*, NHMWien 1994/144. – Scale bar = 2 cm.

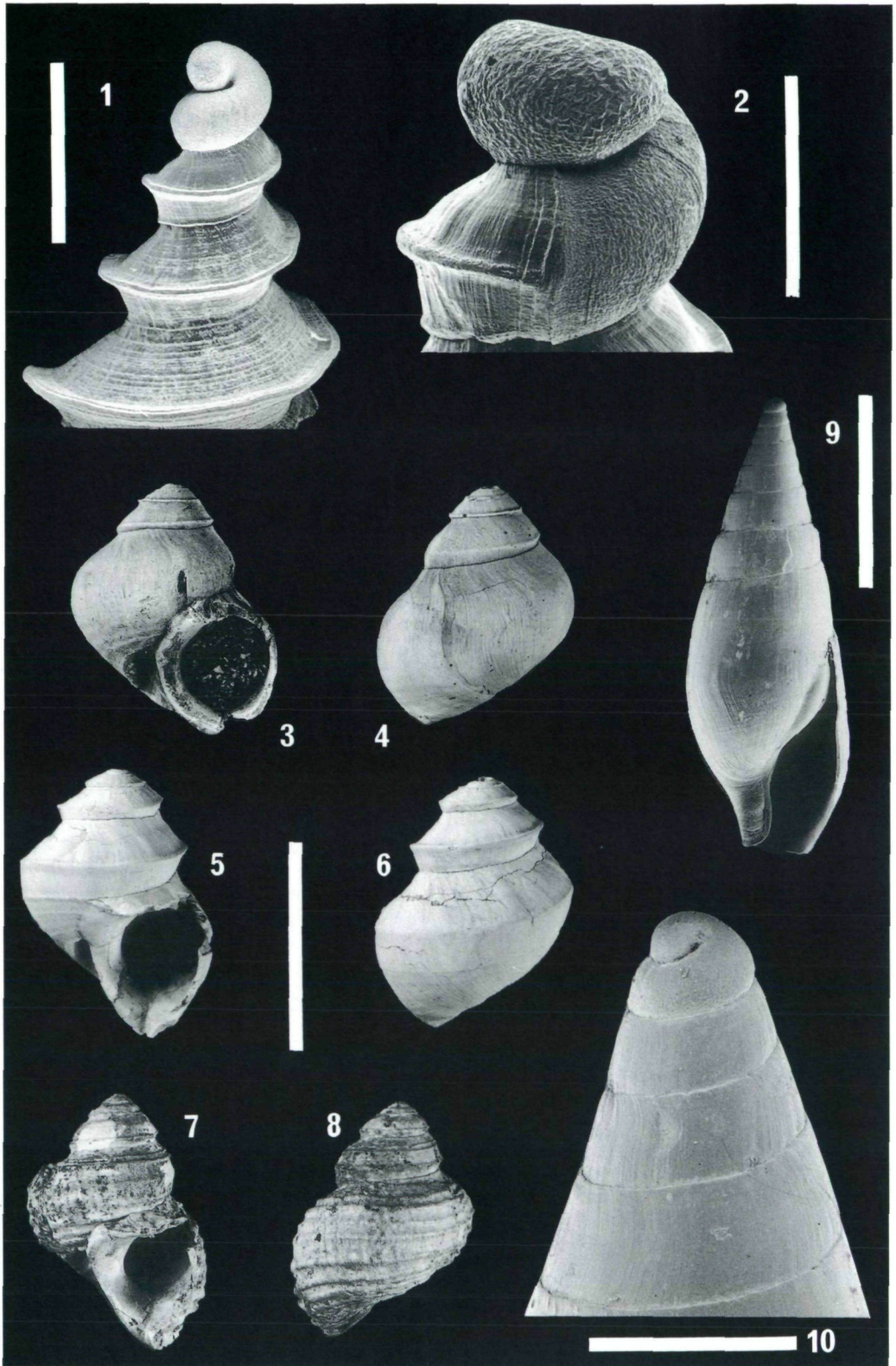
figs. 5–6: *Szaboella riethmuelleri*, NHMWien 1994/145. – Scale bar = 2 cm.

figs. 7–8: holotype of *Szaboella barthai* gen. et sp. nov., NHMWien 1994/146. – Scale bar = 2 cm.

fig. 9: fully grown *Melanopsis ajkaensis*, NHMWien 1994/147. – Scale bar = 2 mm.

fig. 10: apical whorls of same specimen as in fig. 9. – Scale bar = 0.5 mm.





## Plate 12

***Melanopsis* FÉRUSSAC, 1807 and *Esperiana* BOURGUIGNAT, 1877**

fig. 1: apex of *Melanopsis ajkaensis*, NHMWien 1994/147. – Scale bar = 0.2 mm.

figs. 2–3: holotype of *Melanopsis pauli* sp. nov., NHMWien 1994/148, showing the typical preservation. – Scale bar = 3 mm.

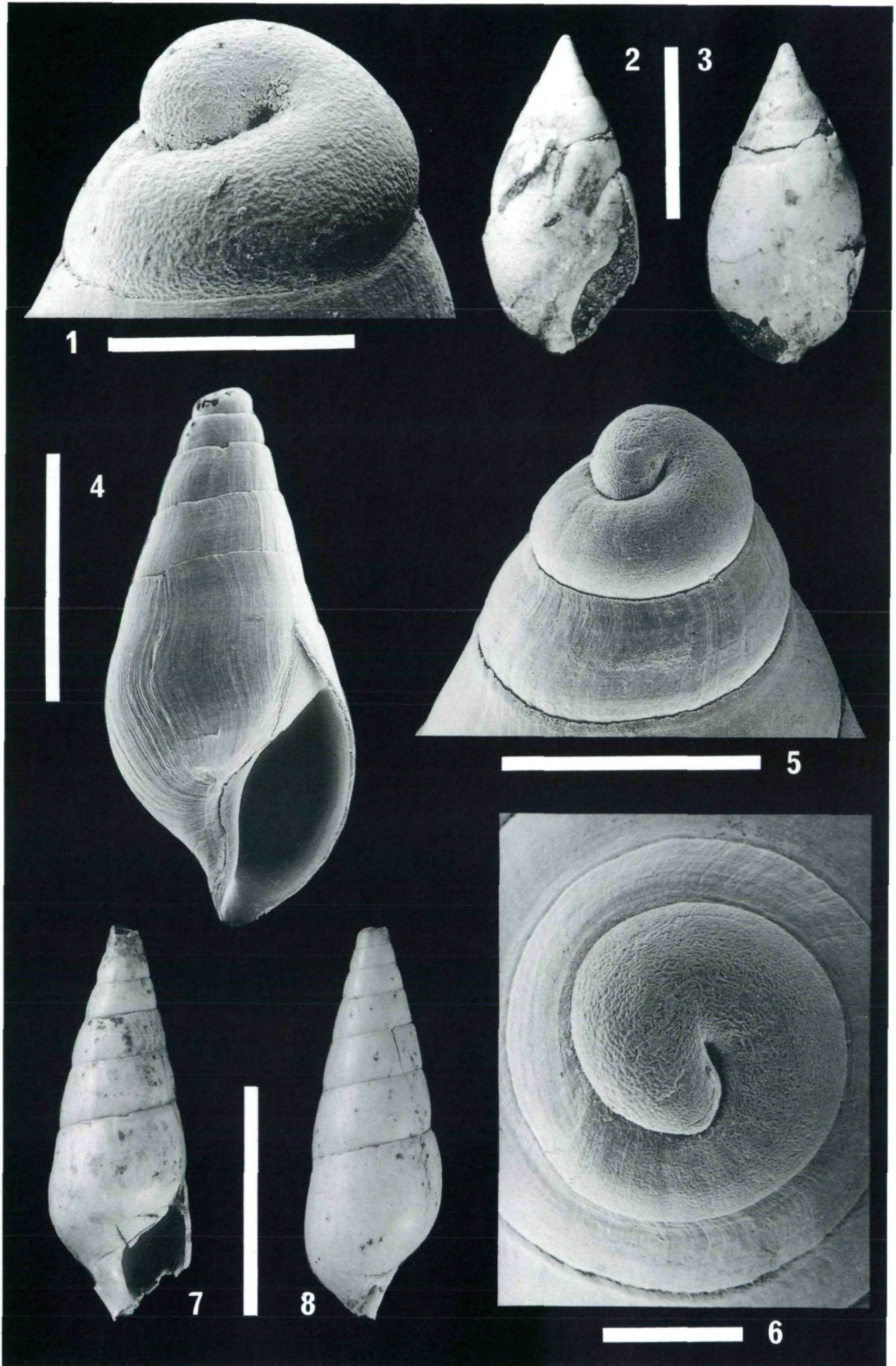
fig. 4: juvenile *Melanopsis pauli* sp. nov., NHMWien 1994/149, showing characteristic apertural features; paratype. – Scale bar = 1 mm.

fig. 5: lateral view of apical whorls of *Melanopsis pauli* sp. nov., same specimen as in fig.4. – Scale bar = 0.3 mm.

fig. 6: apical view of early ontogenetic whorls of *Melanopsis pauli* sp. nov. showing the demarcation of the protoconch and the onset of spiral striation, same specimen as in fig.4. – Scale bar = 0.1 mm.

figs. 7–8: fully grown conch of *Esperiana obeloides*. – Scale bar = 1 cm.



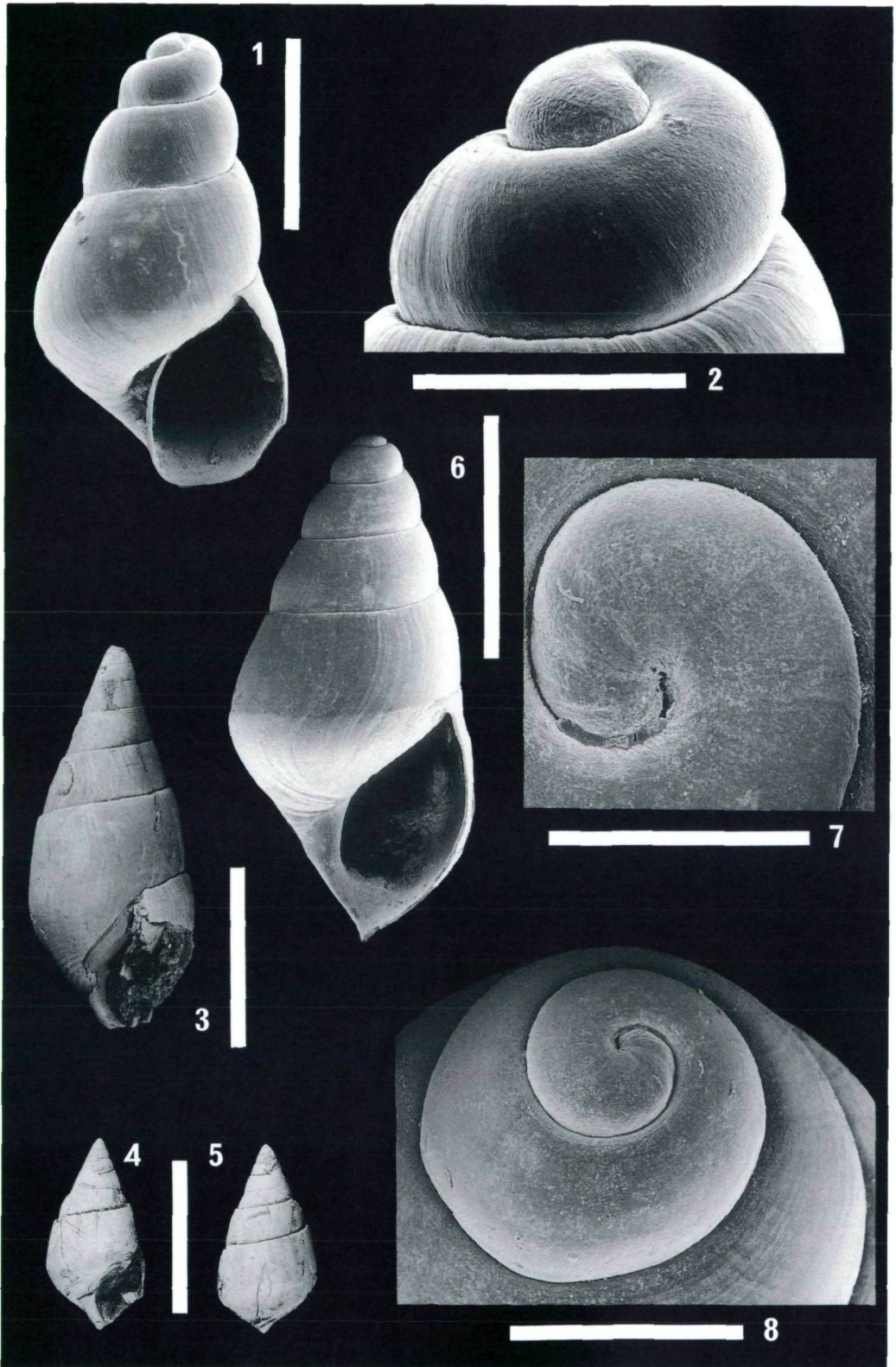


## Plate 13

***Esperiana* BOURGUIGNAT, 1877 and *Campylostylus* SANDBERGER, 1870**

- fig. 1: juvenile shell of *Esperiana obeloides*, NHMWien 1994/151. – Scale bar = 0.5 mm.
- fig. 2: magnification of the apex of *Esperiana obeloides* showing the faint ornamentation of the protoconch, same specimen as in fig. 1. – Scale bar = 0.2 mm.
- fig. 3: fully grown conch of *Campylostylus heberti*, NHMWien 1994/152. – Scale bar = 2 cm.
- figs. 4–5: juvenile conchs of *Campylostylus heberti*, NHMWien 1994/153. – Scale bar = 2 cm.
- fig. 6: early ontogenetic shell of *Campylostylus heberti*, NHMWien 1994/154. – Scale bar = 2 mm.
- fig. 7: nuclear whorl of *Campylostylus heberti*, same specimen as in fig. 6. – Scale bar = 0.2 mm.
- fig. 8: apical whorls of *Campylostylus heberti* showing the onset of ornamentation, same specimen as in fig. 6. – Scale bar = 0.4 mm.



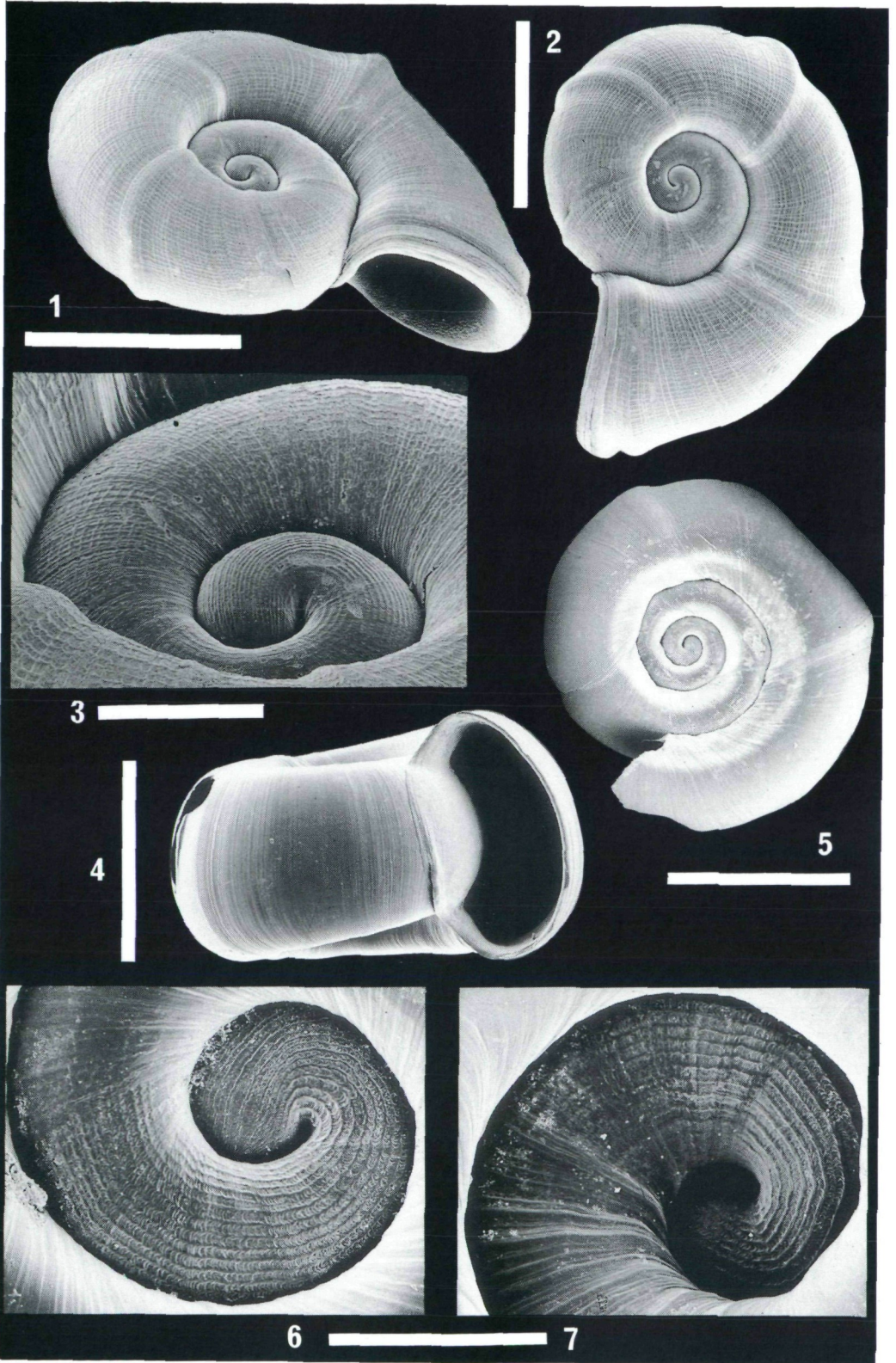


## Plate 14

*Ariomphalus* gen. nov.

- fig. 1: apertural view of fully grown *Ariomphalus varicatus*, NHMWien 1994/155. – Scale bar = 1 mm.
- fig. 2: apical view of same specimen as in fig. 1. – Scale bar = 1 mm.
- fig. 3: magnification of apical whorls of *Ariomphalus varicatus* revealing the ornamentation, same specimen as in fig. 1. – Scale bar = 0.2 mm.
- fig. 4: apertural view of *Ariomphalus involutus*, NHMWien 1994/156. – Scale bar = 1 mm.
- fig. 5: apical view of *Ariomphalus involutus* showing angulation of whorls, same specimen as in fig. 4. – Scale bar = 1 mm.
- fig. 6: magnification of apex of *Ariomphalus involutus* showing the typical valvatid sculpture, same specimen as in fig. 4. – Scale bar = 0.2 mm.
- fig. 7: magnification of umbilicus of *Ariomphalus involutus*, same specimen as in fig. 4. – Scale bar as in fig. 4.





## Plate 15

***Leopoldium* gen. nov. and *Auriculinella* TAUSCH, 1886**

fig. 1: juvenile specimen of *Leopoldium balatonicum*, NHMWien 1994/157. – Scale bar = 1 mm.

fig. 2: apical view of same specimen as in fig.1. – Scale bar = 0.5 mm.

fig. 3: lateral view of protoconch of *Leopoldium balatonicum*, same specimen as in fig. 1. – Scale bar = 0.1 mm.

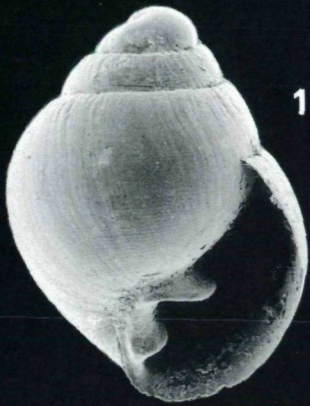
fig. 4: same protoconch as in fig. 3, apical view. – Scale bar = 0.2 mm.

fig. 5: portion of *Auriculinella whitei*, the youngest two whorls are missing, NHMWien 1994/158. – Scale bar = 0.5 mm.

fig. 6: same specimen as in fig. 5, apical view. – Scale bar = 0.5 mm.

fig. 7: same specimen as in figs. 5–6, magnification of the apex showing the development of ornamentation. – Scale bar = 0.3 mm.





1



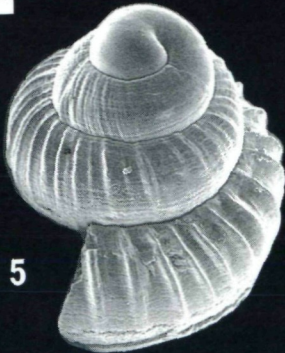
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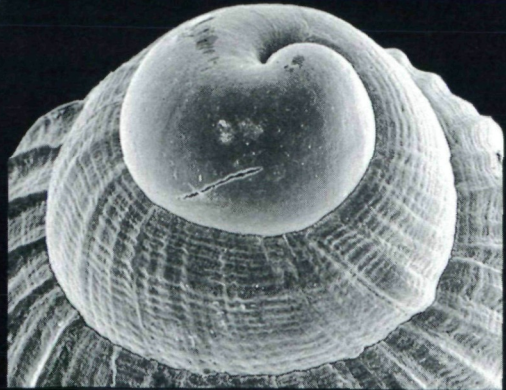
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6



7

## Plate 16

*Ancylina* gen. nov. and *Gastrobulimus* WENZ, 1940

- fig. 1: lateral view of *Ancylina cretacea*, NHMWien 1994/159. – Scale bar = 1 mm.
- fig. 2: magnification of posterior portion of same specimen as in fig. 1. – Scale bar = 1 mm.
- fig. 3: apical view of *Ancylina cretacea* showing the oval shape and the excentric apex, same specimen as in fig. 1. – Scale bar = 1 mm.
- fig. 4: magnification of the apex of same specimen as in fig. 3. – Scale bar = 0.1 mm.
- fig. 5: apertural view of teleoconch of *Gastrobulimus munieri*, NHMWien 1994/160. – Scale bar = 1.5 cm.
- fig. 6: same specimen (and scale bar) as in fig. 5, showing the ornamentation.
- fig. 7: apical whorls of *Gastrobulimus munieri* showing the transition from protoconch to teleoconch, NHMWien 1994/161. – Scale bar = 2 mm.
- fig. 8: magnification of same specimen as in fig. 7 demonstrating the diameter of the embryonic shell. – Scale bar = 1 mm.



