Early ontogeny and palaeoecology of the Mid-Miocene rissoid gastropods of the Central Paratethys

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Kowalke, T. and Harzhauser, M. 2004. Early ontogeny and palaeoecology of the Mid-Miocene rissoid gastropods of the Central Paratethys. *Acta Palaeontologica Polonica* 49 (1): 111–134.

Twenty-six species of Rissoidae (Caenogastropoda: Littorinimorpha: Rissooidea) are described from the Badenian and Early Sarmatian of 14 localities in Austria and the Czech Republic (Molasse Basin, Styrian Basin, Vienna Basin) and from the Badenian of Coştei (Romania). For the first time, the early ontogenetic skeletal characters of these gastropods are described. Based on these features an indirect larval development with a planktotrophic veliger could be reconstructed for all investigated Mid-Miocene species. The status of Mohrensterniinae as a subfamily of the Rissoidae is confirmed by the morphology of the low conical protoconch, consisting of a fine spirally sculptured embryonic shell and a larval shell which is smooth except for growth lines. Transitions from embryonic shells to larval shells and from larval shells to teleoconchs are slightly thickened and indistinct. Whilst representatives of the subfamily Rissoinae characterise the marine Badenian assemblages, Mohrensterniinae predominate the Early Sarmatian faunas. We hypothesize that this take-over by the Mohrensterniinae was triggered by changes in the water chemistry towards polyhaline conditions. Consequently, the shift towards hypersaline conditions in the Late Sarmatian is mirrored by the abrupt decline of the subfamily. Four new species *Rissoa costeiensis* (Rissoinae) from the Badenian and *Mohrensternia hollabrunnensis*, *Mohrensternia pfaffstaettensis*, and *Mohrensternia waldhofensis* (Mohrensterniinae) from the Early Sarmatian are introduced.

Key words: Gastropoda, Rissoidae, Littorinimorpha, protoconch-morphology, Miocene, Badenian, Sarmatian, Paratethys.

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Introduction

The superfamily Rissooidea comprises minute littorinimorph gastropods, which settled various shallow to deeper normal marine and brackish-water habitats at least since Jurassic times (Gründel and Kowalke 2002). Rissoidae usually prefer shallow littoral habitats, where they either live on hard substrates as micro-algal grazers or on softer substrates as detritivores (see e.g., Bandel and Kowalke 1999). Most rissoid species are characterised by protoconchs that reflect a larval development. This includes a free-swimming larval stage with either feeding on the remaining embryonic yolk (lecithotrophic development) or on phytoplankton (planktotrophic development) (Thiriot-Quiévreux 1980; Ponder 1985; Warén 1996; Kowalke 1998; Harzhauser and Kowalke 2001). Both types of larval development facilitated a wide distribution of species and also enabled populations to massively settle temporary and extreme biotopes ("r-strategies"). This strategy has also been documented in other lower caenogastropods (cf. Kowalke 2001, 2003; Harzhauser and Kowalke 2002).

Littoral gastropod assemblages of the Central Paratethys were characterised by modern rissoid genera such as *Rissoa* and *Alvania* at least since the Eggenburgian, Early Miocene (Steininger 1963). The protoconch morphologies of Badenian species with planktotrophic development are very similar to their Recent Mediterranean and NE Atlantic congeners (cf. Thiriot-Quiévreux 1980; Ponder 1985; Kowalke 1998).

The evolution of the brackish-marine rissoid genus *Mohrensternia* is connected to the Sarmatian biogeographic history of the Paratethys. A conspicuous maximum diversity of *Mohrensternia* in the Central Paratethys coincides with the maximum transgression of the Early Sarmatian Sea. This phase is consequently termed the *Mohrensternia* Zone according to the ecostratigraphic zonation by Papp (1956). During the subsequent Mid-Sarmatian *Ervilia* Zone, the diversity of *Mohrensternia* drops distinctly, and in shallow coastal habitats the genus is apparently replaced by *Cerithium*-dominated assemblages in carbonate-oversaturated marine waters.

Coelacanthia Andrussov, 1890 and *Archaschenia* Zhgenti, 1981, restricted to the Eastern Paratethys, are distinguished from *Mohrensternia* by the formation of hollow spines on the teleoconch whorls (see e.g., Wenz 1938–1944: 597, fig. 1642). The genera co-occurred with *Mohrensternia*, e.g., during the Karaganian and Maeotian of the Eastern Paratethys, and could well be related to *Mohrensternia*, however, the protoconch morphology is unknown.

The rissoid genera *Rissoa*, *Alvania*, and *Manzonia* typically have a similar teleoconch morphology in Badenian assemblages, but could be differentiated from *Mohrensternia* based on protoconch morphology.

This study describes the protoconch morphology of Badenian and Early Sarmatian rissoid taxa in detail. The early ontogenetic shells of the species are described and figured for the first time. The palaeoecological context of the taxa and marked changes in ecological parameters in Paratethyan assemblages are discussed.

Material and methods

The investigated material mainly derives from the Badenian and Early Sarmatian of Central Paratethys Basins (Figs. 1, 2). The Badenian (early Middle Miocene) faunas were collected in the Vienna Basin (Steinebrunn, Baden/Sooß, Vöslau, Austria; Sedlec/Nový Rybník, Lednicé, Czech Republic). Additional material derives from the Badenian of Coştei (Romania). The Early Sarmatian (late Middle Miocene) material was found at Hollabrunn (Molasse Basin), Pfaffstätten, Siebenhirten (Vienna Basin) and Waldhof/Wetzelsdorf close to Graz (Western Styrian Basin). Recent material for comparison derives from the Adriatic Sea (Mediterranean Sea).

Special emphasis was placed on early ontogenetic shells. The investigated small to medium-sized gastropods were extracted from marly and silty sediment samples after processing with H_2O_2, drying and fractionating with sieves. Shells with preserved protoconchs were mounted on stubs, sputtered with gold and documented using scanning electron microscopy (digital scan "Leo 1525").

Protoconch dimensions were measured during the SEM investigations. Maximum height and diameter of the protoconchs are given. The dimensions (i.e. the width of the initial cap-like onset and the maximum diameter of the embryonic shell) and the ornament of the embryonic shell are described along with the morphology of the transition to the larval shell, if preserved. Larval sculptural patterns and the morphology of the transition to the teleoconch are also described. For terminology of early ontogenetic shells in gastropods see also Kowalke (1998).

Additional original material derives from the collection of A. Papp at the Natural History Museum, Vienna (NHMW) and from the Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB IG 23693). All figured specimens are deposited in the collection of the NHMW (NHMW 2002z0029/0001–2002z0029/0017; NHMW 2002z0030/0001–2002z0030/0019).

Palaeoecology

Badenian assemblages of the Vienna Basin, with large numbers of *Rissoa* and *Alvania,* also yield abundant pectinids, echinoderms, calcareous algae and various sharks, indicating normal marine conditions. Assemblages are very diverse, consisting of more than 250 species of molluscs each (Stur 1870; Karrer 1877; Vetters 1910). Rissoinae are commonly found in silt and fine to medium sand, but also occurred in limestones, e.g in Early Badenian limestones of the Styrian Basin (Schmid

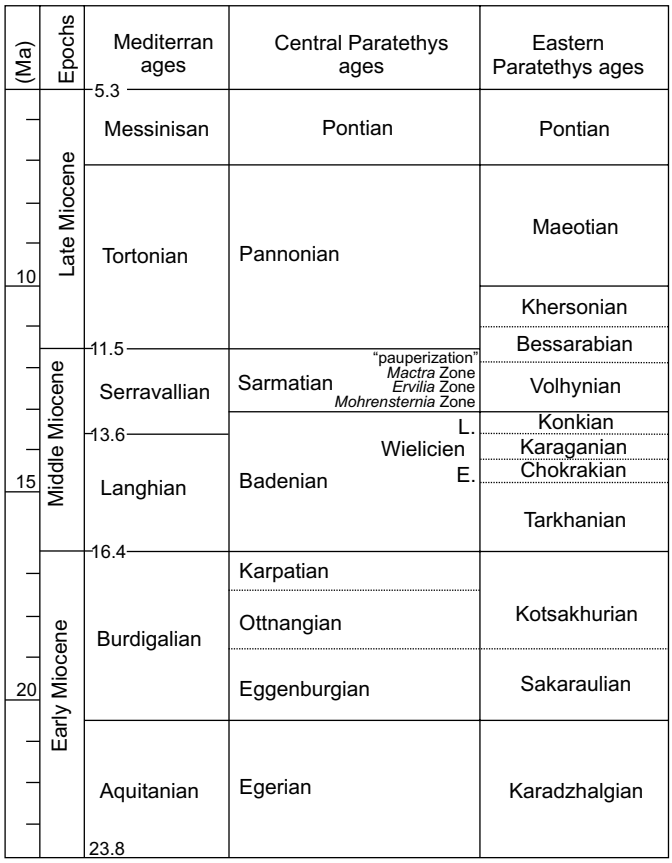

Fig. 1. Stratigraphic correlation chart of the standard scale with the Central Paratethys and the Eastern Paratethys; modified after Rögl (1998) and Studencka et al. (1998). The investigated faunas derive exclusively from the Badenian and Early Sarmatian of the Central Paratethys. Serravallian and Tortonian ages after Foresi et al. (2002) and Lirer et al. (2002).

et al. 2001: 11)—no distinct preference for siliciclastic or calcareous substrates can be stated. Diverse shallow marine habitats have been settled, like by their modern Mediterranean counterparts.

Mohrensterniinae, in contrast, are usually accompanied by few euryhaline taxa, indicating the "extreme" character of their habitats. Nonetheless, the protoconch morphology in all investigated species reflected a planktotrophic larval development. This indicates a connection of the habitats to the open sea. The Sarmatian Sea displayed its maximum extension during the *Mohrensternia* Zone of the Central Paratethys. The palaeogeographic position of the investigated sections was along the western margin of the Sarmatian Sea. The north-western-most section Hollabrunn in Lower Austria represents a flat shore of a small and shallow embayment; it reached about 40 km from the Vienna Basin to the west into the otherwise already dry Molasse Basin. This situation established a tidelands environment settled by large populations of solenid bivalves, which may still be found in situ in life position. Large numbers of potamidid and batillariid gastropods settled the mud flats. The narrow lough was probably strongly influenced by the waters of the surrounding drainage systems in the north and west, leading to vary-

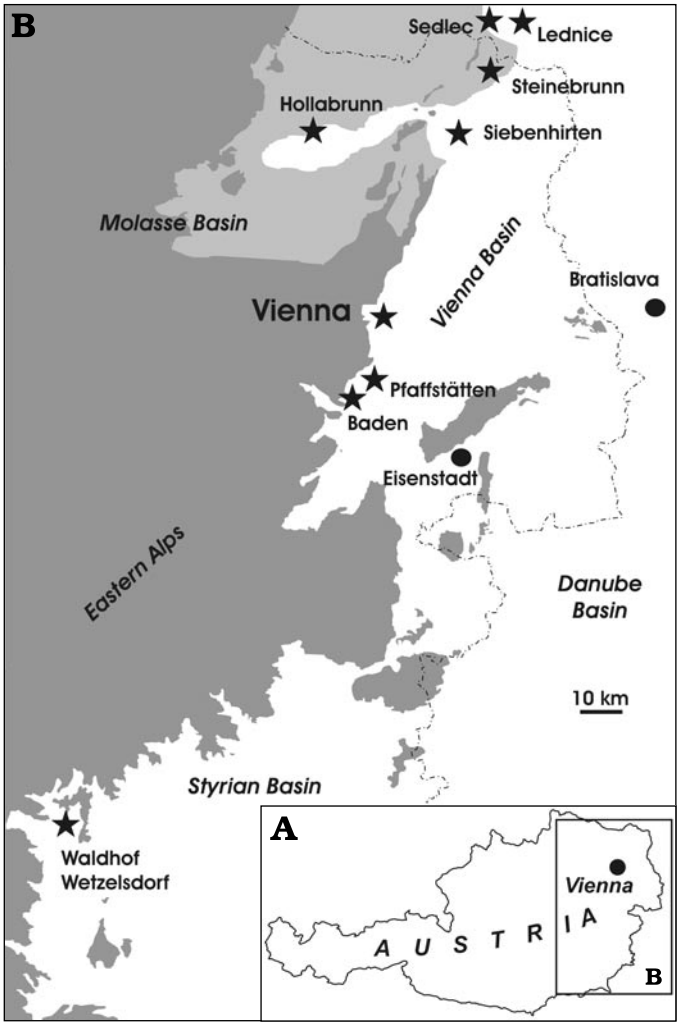

Fig. 2. General map of Austria (**A**) with position of the studied area i.e., Vienna Basin, the Styrian Basin and the Molasse Basin (**B**). Stars that indicate outcrops with Badenian and Sarmatian rissoid faunas are plotted on a tentative reconstruction of the Early Sarmatian shoreline (grey areas indicate land).

ing salinities. The occurrence of turritellids and naticids excludes a salinity drop far from polyhaline conditions. The situation was similar for the fauna of Waldhof/Graz in Styria. The Stallhofen Bay in the north-western part of the Western Styrian Basin was affected by the drainage systems from the Alps. To the east the small depression was protected from the open Sarmatian Sea by the Sausal Swell, allowing the establishment of very calm conditions.

Siliciclastic sedimentation predominated during this phase, and only rarely did autochthonous carbonate build-ups of serpulids and bryozoans occur; these were usually avoided by *Mohrensternia*. Representatives of the genus preferred a clay or fine to medium sand substratum. In the sandy conditions documented for Hollabrunn and Petronell in Austria, sedimentological features indicate littoral settings. Shells are often accumulated on the top of cross bedding sets together with cardiids. Typically, the co-occurring gastropod assemblage found in the sandy facies consisted of *Granulolabium bicinctum* (Brocchi, 1814), *Ocenebra striata* (Eichwald, 1853), and *Acteocina lajonkaireana* (Basterot, 1825) alongside various species of *Hydrobia* Hartmann, 1821. Rare shells of *Abra reflexa* (Eichwald, 1853) and *Plicatiforma pseudoplicata* (Friedberg, 1934) represented the typical bivalves. In the pelitic facies, the accompanying fauna changed towards a bivalve-dominated assemblage, characterised by high numbers of *Abra reflexa*, rare *Ervilia dissita*, *Modiolus incrassatus*, *Musculus sarmaticus*, and various thin-shelled cardiids. Among the gastropods, *Granulolabium bicinctum* and hydrobiids were still abundant. *Mohrensternia* is generally distinctly more common in the pelitic facies, hinting at a preference for the calm conditions which prevailed during the deposition of the dark clays.

Freshwater habitats, however, as erroneously reported by Stoliczka (1868) for *Mohrensternia*, were never settled by this genus. The rather careless comment by Stoliczka (1868) resulted from the very vague ideas on the Sarmatian palaeoenvironments at that time and should not be used as a reference for the palaeoecology of the Mohrensterniinae.

During the subsequent early *Ervilia* Zone, high-energy conditions along the coast of the Western Paratethys led to the formation of ooliths and thick coquina beds, indicating swift, agitated environments unsuitable for *Mohrensternia*. The genus nearly vanished after the Early Sarmatian of the Central Paratethys and the Volhynian of the Eastern Paratethys. Despite its abundance (up to 2/3 of all mollusc individuals), no gastropod in younger sediments definitively filled the vacant ecological niche. Hydrobiids and *Granulolabium* Cossmann, 1889 did not significantly change in abundance, whereas the abruptly diversifying *Dorsanum* Gray, 1847 represented a quite different ecological guild. Only the herbivorous *Cerithium rubiginosum* Eichwald, 1853 started to flourish in the *Ervilia* Zone, and even became rock forming.

Rissoa and *Alvania* in the Middle Miocene Paratethys

The evolution and development of *Rissoa* and *Alvania* during the Early Miocene of the Central Paratethys are largely unknown. This probably reflects poor preservation because the contemporaneous faunas of the Atlanto-Mediterranean Region yielded a considerably more diverse fauna (Sacco 1895; Cossmann and Peyrot 1919). Three species each are described from the Eggenburgian (early Early Miocene) of Austria and Bavaria (Steininger 1963; Hölzl 1973) and from the Carpathian (late Early Miocene) of the Korneuburg Basin in Lower Austria (Harzhauser 2002).

Badenian (early Middle Miocene) faunas, however, indicate a marked increase in diversity.

Representatives of *Rissoa* display their acme in the Central Paratethys during the Badenian. Aside from the discussed species *Rissoa turricula*, *R. clotho* and *R. acuticosta*, additional taxa are described in the literature: *R. sulzeriana* Risso, 1826, *R. sobieskii* Friedberg, 1923, *Turboella conoi-*

dea Baluk, 1975, *T. dilemma* (Boettger, 1906), *T. hebes* (Boettger, 1906), *T. johannae* Boettger, 1901, *T. inconspicua* Aldrovandi, 1648 (invalid name), *T. podhorcensis* (Friedberg, 1923), *T. perparva* (Friedberg, 1923), and *T. dubiosa* (Friedberg, 1923). The validity of these literature-based species may be debatable in certain cases. *Rissoa turricula* is the only species distributed throughout the Central Paratethys. Sarmatian representatives were described as *Rissoa soceni* Jekelius, 1944, *R. banatica* Jekelius, 1944, *R. certa* Svagrovský, *R. gracilis* Svagrovský, *R. mucronata* Svagrovský, and *R. rugosa* Svagrovský (Svagrovský 1971). This high number of taxa probably reflects oversplitting. In fact most of the "species" may represent morphs of *Rissoa turricula* (cf. discussion in the systematic part). In the Eastern Paratethys, representatives of *Rissoa* are still mentioned from the Maeotian—*Rissoa subinflata* (Andrusov, 1890), *R. ventricosa* (Desmarest, 1814), and *R. subangulata* (Andrusov, 1890) (Iljina et al. 1976).

Twenty-eight species of *Alvania* are described from the Badenian of the Central Paratethys. In addition to the species described in this paper there occur: *Alvania* (*Alvania*) *alta* Bałuk, 1975, *A.* (*A.*) *brachia* Boettger, 1901, *A.* (*A.*) *helenae* Boettger, 1901, *A.* (*A.*) *productilis* Boettger, 1906, *A.* (*A.*) *sublaevigata* Boettger, 1906, *A.* (*A.*) *tenuicosta* Bałuk, 1975, *A.* (*A.*) *trochiformis* Csepreghy-Meznerics, 1950, *A.* (*A.*) *holubicensis* Friedberg, 1923, and *A.* (*A.*) *veliscensis* Reuss, 1867. Further species mentioned in the literature are: *Alvania* (*Alvinia*) *alexandrae* (Boettger, 1901), *A.* (*Alvinia*) *convexispira* (Boettger, 1901), *A.* (*Alvinia*) *ellae* (Boettger, 1901), *A.* (*Alvinia*) *hungarica* (Bohn-Havas, 1973), *A.* (*Alvinia*) *kowalewskii* (Bałuk, 1975), *A.* (*Alvinia*) *subzetlandica* (Boettger, 1901), *Alvania* (*Acinus*) *reticulata* (Montagu, 1803), *Alvania* (*Arsenia*) *punctura* (Montagu, 1803), *Alvania* (*Turbona*) *giselae* (Boettger, 1901), *Alvania* (*Turbona*) *subclavata* (Boettger, 1906), and *Alvania* (*Turbona*) *subcrenulata* (Schwartz von Mohrenstern, 1864). The subgeneric affiliation of these taxa was not checked within the frame of this paper.

The maximum diversity was achieved during the Early Badenian, as represented by the extraordinarily rich faunas of Korytnica (Poland), Coştei, and Lăpugiu (Romania). At that time the diversity of *Alvania* seems to have been considerably lower in the Eastern Paratethys, where only *Alvania (Alvania) gontsharovae* Iljina, 1993 and *Alvania* (*A.*) *montagui* Iljina, 1993 (non Payraudeau, 1826) were described from the Tarkhanian to Konkian of southern Russia/Eastern Paratethys (Iljina 1993).

None of the manifold Badenian *Alvania* spp. passes the Badenian/Sarmatian boundary in the Central or the Eastern Paratethys. Whilst the environments of Lake Pannon (cf. Harzhauser et al. 2002) in the former Central Paratethys excluded any resettlement by *Alvania* during the Late Miocene, at least two species managed to enter the Eastern Paratethys in the contemporaneous Maeotian: *Alvania* (*A.*) *montagui* (Payraudeau, 1826), *Alvania pseudalvania pseudalvania* (Andrusov, 1905), and *Alvania pseudalvania raricostata* Iljina, 1976 from Southern Russia and Ukraine (Iljina et al. 1976).

The history of *Mohrensternia* and its biostratigraphic constraints

The first occurrence of *Mohrensternia* dates to the early Middle Miocene (Fig. 3), when *Mohrensternia subprotogena* (Zhizhchenko, 1936), *Mohrensternia nitida* (Zhizhchenko, 1936), and *Mohrensternia protogena* (Andrusov, 1890) are recorded from the Tarkhanian and Tshokrakian of the Eastern Paratethys (Zhizhchenko 1936; Iljina 1993). Also, *Mohrensternia angulata* (Eichwald, 1853) is known from the Badenian of the Central Paratethys (Kókay 1966). In the latter area, *Mohrensternia* represents an extremely rare element throughout the Badenian. Aside from *M. angulata*, only *Mohrensternia pseudosarmatica* (Friedberg, 1923) occurs here. Both species extend beyond the marine Badenian into the Sarmatian. In contrast, the Eastern Paratethyan lineages underwent a first marked radiation during the Karaganian, when at least five species are documented from southern Russia by Iljina (1993): *Mohrensternia barboti* (Andrusov, 1890), *M. grandis* (Andrusov, 1890), *M. gratiosa* Zhizhchenko in Iljina, 1993, *M. karaganica* Zhgenti, 1981, and *M. subglobosa* Zhgenti, 1981. This bloom correlates well with a phase of total isolation of the Eastern Paratethys from the Mediterranean, which caused aberrant salinities (Rögl 1998). Correspondingly, the Karaganian Crises are also reflected in the evolution of several endemics among the bivalves (Studencka et al. 1998). This regional stage is tentatively correlated herein with the Early Serravallian sea level drop of TB2.4/TB2.5 (Haq et al. 1988). In the Central Paratethys the same event seems to be reflected in the Wielician substage of the Middle Badenian, when thick evaporites were deposited in the foredeep from Poland to Romania. After that first acme, the genus declined distinctly in the again fully marine Konkian, when only *Mohrensternia pseudoinflata* Hilber, 1897 inhabited the Eastern Paratethys.

These data show that *Mohrensternia* preferred aberrant salinities because it is rare during all normal marine stages in both the Central and the Eastern Paratethys. The catastrophic change in water chemistry in the Early Sarmatian re-installed the conditions favoured by *Mohrensternia*. About 20 Sarmatian species of *Mohrensternia* in the Central Paratethys bear witness to an extraordinary diversity. *Mohrensternia* is therefore the name-giving taxon for the ecostratigraphic Early Sarmatian *Mohrensternia* zone in the Central Paratethys. Only three of these species are rooted in the Badenian/Konkian faunas. The *Mohrensternia* Zone is followed by the *Ervilia* Zone, which coincides with the spreading of a thick-shelled mollusc fauna. The abrupt change in biofacies usually allows a clear separation of both mollusc zones. The genus strongly declined after the Early Sarmatian in the Central Paratethys and became extinct in the brackish to freshwater environments of Lake Pannon (Rögl 1998; Harzhauser et al. 2002). In the Eastern Paratethys, however, *Mohrensternia* attained its last acme during the Late Miocene Maeotian stage. Six taxa are documented by Iljina et al. (1976) from that stage: *Mohrensternia acuta* Iljina in Ilyina et al. 1976, *M. carinata* Andrusov, 1905, *M. gupii* Iljina in Ilyina et al., 1976, *M. nasyrica* Iljina in Ilyina et al., 1976, *M. multicostata multicostata* (Senes, 1953), and

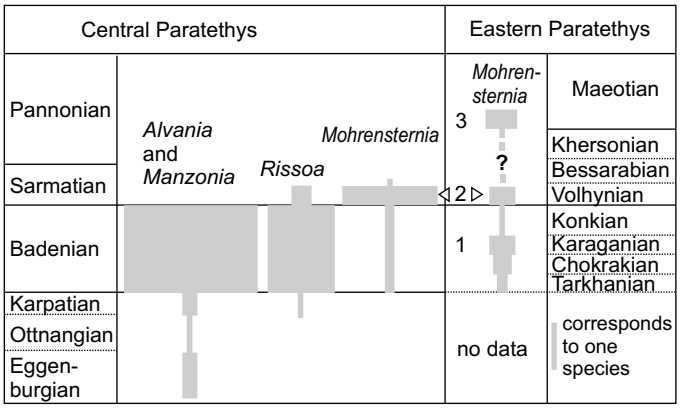

Fig. 3. Stratigraphical distribution of *Alvania, Manzonia*, *Rissoa*, and *Mohrensternia* in the Central Paratethys compared with the distribution of the Mohrensterniinae in the Eastern Paratethys. The data document the extraordinary bloom of the *Alvania* and *Rissoa* during the Badenian of the Central Paratethys. In contrast, *Mohrensternia*, although already present, is only of subordinate importance. The extinction of *Alvania* at the Badenian/Sarmatian boundary is followed by a spectacular radiation of the Mohrensterniinae, which might have conquered environments formerly settled by *Alvania*. The abrupt decline of the genus in the Central Paratethys during the Mid-Sarmatian can only be explained by another drastic change in the water chemistry of the Sarmatian Sea. In the Eastern Paratethys, *Mohrensternia* already experienced its first radiation during the Karaganian Crises and displays a third, post-Sarmatian bloom during the Maeotian (see text for references).

M. multicostata kerchensis Iljina, 1976. Of these, only *M. multicostata multicostata* can be traced back to the Sarmatian faunas of the Central Paratethys. Another Late Miocene species assigned to *Mohrensternia* is described as *M. inflata* (Hörnes, 1856) and *M. inflata cristulatolaevis* (Sacco, 1895). This alleged occurrence from Montegibbio in Northern Italy may represent the sole non-Paratethyan distribution of the otherwise endemic genus.

Systematic palaeontology

Class Gastropoda Cuvier, 1797
Subclass Caenogastropoda Cox, 1959
Order Littorinimorpha Golikov and Starobogatov, 1975
Superfamily Rissooidea Gray, 1847
Family Rissoidae Gray, 1847
Subfamily Rissoinae Gray, 1847
Genus *Rissoa* Desmarest, 1814

Type species: *Rissoa ventricosa* Desmarest, 1814, Recent, from the Mediterranean Sea.

Remarks.—*Rissoa parva* from the NE Atlantic and Mediterranean Sea has frequently been regarded as the type species of *Turboella* Leach in Gray (1847). Ponder (1985) reported that the anatomical, radular, and protoconch characters exhibit no differences compared to *Rissoa*, and that the general appearance of the teleoconch is extremely similar. The diagnosis presented by Nordsieck (1972) does not support a separation of *Turboella*. Wenz (1938–1944) regarded *Mohrensternia* Stoliczka, 1865 as a synonym of "*Turboella*", which is herein rejected (see discussion of Mohrensterniinae).

Rissoa turricula Eichwald, 1853

Fig. 4A.

Rissoa turricula sp. nov. Eichwald 1853: 267–268 (pro parte, non text ad 9*), pl. 10: 9 (non 9*).
Rissoa soceni sp. nov. Jekelius 1944: 68, pl. 14: 9–10.
Rissoa soceni Jekelius; Papp 1954: 32, pl. 5: 36–37.
Rissoa turricula Eichwald; Strausz 1966: 69, pl. 45: 20, pl. 46: 1–5.
Rissoa soceni Jekelius; Svagrovský 1971: 258, pl. 37: 1–9, pl. 38: 1–4.
Rissoa turricula Eichwald; Bohn-Havas 1973: 1039, pl. 3: 3–4.

Material.—Five specimens from the Early Sarmatian of Waldhof/Styria, Austria, from the collection of A. Papp, NHMW 2002z0030/0001.

Description.—The low conical to slender oval shell usually measures up to 6 mm in height—up to 8 mm according to Strausz (1966). The width amounts to slightly more than half of the height. The shell comprises up to six only slightly rounded whorls separated by moderately incised sutures. Sculpture of the teleoconch whorls consists of 10–12 prominent, slightly rounded axial ribs. The last whorl forms 60–70% of total shell height. The large, inclined, rounded triangular aperture is characterised by a broad, slight basal notch and by a pointed parietal edge. The thick outer lip is rounded. The thin columellar and parietal lip is bent.

The protoconch comprises 2.25 rounded whorls measuring 0.3 mm in height and 0.35 mm in maximum diameter. Sculpture is not preserved. The first whorl measures 0.03–0.04 mm in the width of the initial cap and 0.15 mm in maximum diameter. The protoconch is terminated by a thickened rim on the shell.

Remarks.—Morphology and dimensions of the protoconch indicate an indirect development with inclusion of a planktotrophic larval stage.

Slightly more slender morphs from the Early Sarmatian have been described as *R. soceni* by Jekelius (1944). A comparison with the material from Styria reveals no conchological differences warranting a separation from the generally variable *R. turricula*. Svagrovský (1971), who presented a very strict species concept for the Sarmatian representatives of *Rissoa*, treated the morphs from Waldhof/Styria as a separate species, based on the less slender outline. Other distinguishing features mentioned by Svagrovský (1971), such as the shallow sutures and the less convex whorls, display considerable variability and range well within the variability of *Rissoa turricula* from Romania and Slovakia. Rather than separating the Styrian shells from *Rissoa turricula,* we consider them to merely be a stout morph. Following the concept of Svagrovský (1971), the Styrian specimens with regard to shell shape might be considered as closely related to *Rissoa certa* Svagrovský, 1971 and *Rissoa rugosa* Svagrovský, 1971, which could be distinguished by their additional spiral teleoconch sculpture.

The species has commonly been described from Badenian sediments of the Central Paratethys in the Polish foredeep, Hungary, and Austria (Meznerics 1933; Bohn-Havas 1973). It is also documented from the Early Sarmatian of Austria, Ro-

mania, and Slovakia (Papp 1954; Svagrovský 1971). At least in Austria, *Rissoa turricula* settled the same environments as *Mohrensternia* spp.

Modern representatives of *Rissoa* from the Mediterranean Sea and from the North Atlantic are characterised by a protoconch morphology very similar to *R. turricula* (Warén 1996; Kowalke 1998). Closest are *R. membranacea* (J. Adams, 1800) from the North Atlantic coasts as figured by Warén (1996: fig. 9) and Ponder (1985: fig. 77C, D), and *R. guerini* Récluz, 1843 from the Mediterranean Sea (Kowalke 1998: pl. 9: 6). They have nearly the same protoconch dimensions, but are distinguished by larger, more bulbous embryonic shells measuring about 0.17–0.18 mm in maximum diameter (*versus* only 0.15 mm in *R. turricula*), reflecting a yolk-rich embryogenesis. The protoconch of the type species differs by its smaller dimensions, including a considerably smaller embryonic shell, and by its slender shape, which is higher than wide (Thiriot-Quiévreux 1980; Kowalke 1998).

Rissoa acuticosta (Sacco, 1895)

Fig. 4C.

Rissoa Lachesis Basterot; Hörnes 1856: 572, pl. 48: 16.
Turbella [sic!] *acuticosta* sp. nov.; Sacco 1895: 23.
Turboella acuticosta Sacco; Meznerics 1933: 329, pl. 13: 7a, b.
Rissoa turricula acuticosta (Sacco); Strausz 1966: 69–70, pl. 46: 6, 7.
Rissoa acuticosta Sacco; Bohn-Havas 1973: 1039, pl. 3: 7.
Turboella (*Turboella*) *acuticosta* (Sacco); Bałuk 1975: 69, pl. 8: 9–11.
Turboella (*Turboella*) *acuticosta* (Sacco); Svagrovský 1981: 121, pl. 37: 8, 9.
Turboella acuticosta (Sacco); Iljina 1993: 41, pl. 3: 27–30.

Material.—145 specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0003.

Description.—The small egg-shaped shell with acute apex comprises 5–6 slightly rounded low whorls. It measures slightly more than 3 mm in height. Teleoconch sculpture consists of 14–16 prominent, straight axial ribs and 10–15 subordinated, flat spiral threads, which are most strongly developed on the abapical half of the whorls. The last whorl forms 60–70% of total shell height. The base is ornamented by three spiral threads. The aperture is drop-shaped. It is holostomatous and only slightly thickened. The parietal portion is slightly pointed.

The protoconch (n = 9) comprises 2.5–2.6 slightly rounded whorls measuring 0.38–0.4 mm in height and in maximum diameter. The first whorl measures 0.03–0.04 mm in the width of the initial cap and 0.13–0.14 mm in maximum diameter. The transition from the embryonic shell to the larval shell is indistinct, indicated by a slight thickening of the shell. In the course of the second whorl of the protoconch, two granulated spiral threads are visible just above the abapical suture. The protoconch is terminated by sinuous, closely spaced, thickened growth lines. The beginning of the teleoconch is indicated by the formation of fine, regular growth lines and by the onset of the adult sculpture.

Remarks.—*R. acuticosta* has frequently been regarded as a species of *Turboella*, which represents a synonym of *Rissoa* (see remarks to the genus *Rissoa*). *R. acuticosta* from the Badenian of Várpalota (West Hungary) has been assigned to the genus *Rissoa* as a subspecies of *R. turricula* by Strausz (1966). The protoconch of *R. acuticosta* differs by its larger size, comprising about a quarter of a larval whorl more and

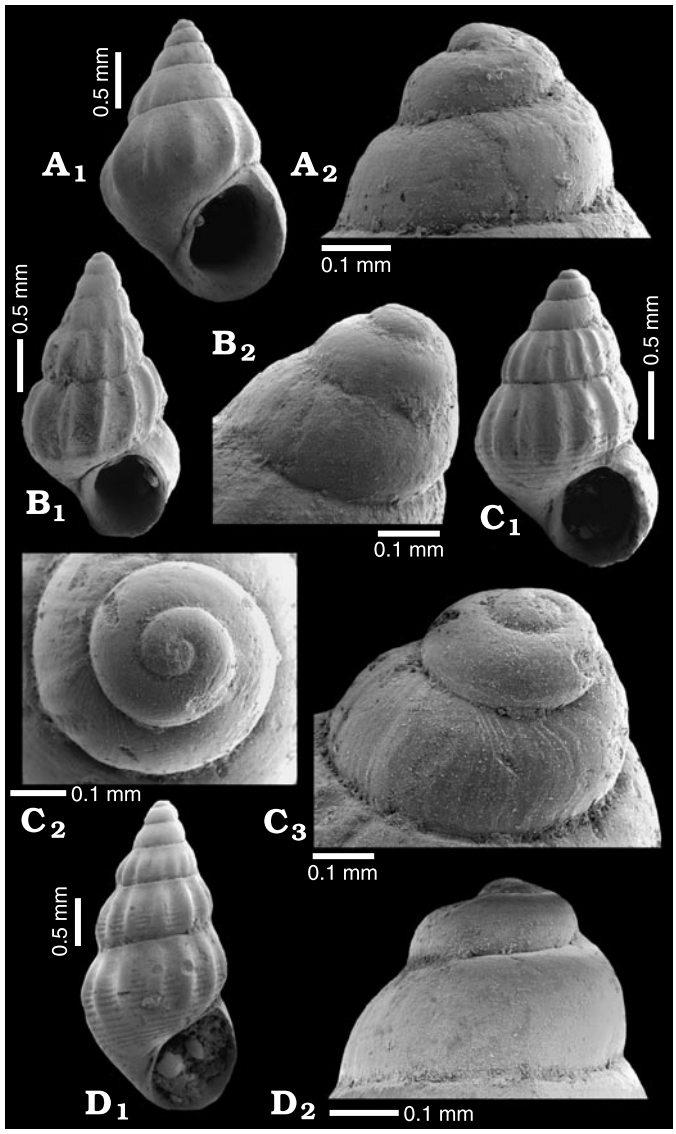

Fig. 4. Four species of *Rissoa* Desmarest, 1814. **A**. *Rissoa turricula* Eichwald, 1853. Specimen (collection A. Papp, NHMW 2002z0030/0001) from the Early Sarmatian of Waldhof/Styria (A_1). Protoconch of the same specimen in lateral view (A_2). The protoconch is terminated by a thickened rim, reflecting the thickened apertural margin of the veliger ready for metamorphosis. **B**. *Rissoa parva* (Da Costa, 1778). Specimen (NHMW 2002z0030/0002), Recent, from the Northern Adriatic Sea (B_1). Protoconch of the same specimen in lateral view (B_2). The protoconch is terminated by a prominent slightly sinuous, thickened rim. **C**. *Rissoa acuticosta* (Sacco, 1895). Specimen (NHMW 2002z0030/0003) from the Badenian of Steinebrunn, Lower Austria (C_1). Apical and lateral view of the protoconch of the same specimen (C_2, C_3). The protoconch is terminated by sinuous, closely spaced, thickened growth lines. **D**. *Rissoa clotho* Hörnes, 1856. Specimen (NHMW 2002z0030/0004) from the Badenian of Steinebrunn, Lower Austria (D_1). Protoconch of the same specimen in lateral view (D_2). The protoconch is terminated by an indistinct, very fine thickened rim on the shell. Regular closely spaced growth lines indicate the onset of the teleoconch.

measuring up to 0.4 mm in height and in maximum diameter. The transition to the teleoconch is indicated by closely spaced, thickened growth lines (versus straight, thickened rim in *R. acuticosta*). The protoconch of *R. clotho* is of about the same size and slightly wider than high, whereas the protoconch of *R. turricula* is higher than wide.

The protoconch indicates an indirect development with inclusion of a free planktotrophic larval stage. The characteristic larval sculpture is similar to that of Recent rissoids from the North Atlantic and from the Mediterranean Sea. Warén (1996) described the protoconch-morphology of *R. parva* from the Swedish west coast. Ponder (1985) described a specimen from Plymouth, England, with well-preserved protoconch. This modern species (Fig. 4B) differs from the Badenian congener *R. acuticosta* with very similar teleoconch morphology by its larger protoconch comprising about 0.4 larval whorls more. The acute conical protoconch of *Pusillina dolium* from the Mediterranean Sea is characterised by a similar sculptural pattern (see Kowalke 1998: pl. 9: 7). *P. dolium* differs by its more slender and considerably smaller protoconch, which measures only 0.26 mm in height.

R. acuticosta occurred in the Badenian of Poland, Hungary, Romania, the Czech Republic, and Austria but is also known from the Miocene of SW France (Cossmann and Peyrot 1919). During the Late Badenian it invaded also the Eastern Paratethys, where it was described from the Konkian by Ilyina (1993).

Rissoa clotho Hörnes, 1856

Fig. 4D.

Rissoa clotho sp. nov.; Hörnes 1856: 574–575, pl. 48: 20 a, b.
Alaba (*Gibborissoa*) *clotho* Hörnes; Meznerics 1933: 328
Turboella (*Turboella*) *clotho* (Hörnes); Bałuk 1975: 70, pl. 8: 8.

Material.—Nine specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0004.

Description.—The small, elongated egg-shaped shell comprises six regularly increasing, moderately rounded whorls separated by deep sutures. It measures slightly more than 3 mm in height. Sculpture of the teleoconch whorls consists of 12 regularly rounded straight ribs and 10 subordinated flat spiral threads, which are most strongly developed on the abapical half of the whorls. The last whorl forms about 50–60% of total shell height. The drop-shaped, holostomatous aperture is slightly thickened and is characterised by a pointed parietal portion. The base is sculptured by 4–5 flat spiral threads about equally as strong as the threads sculpturing the whorls.

The protoconch comprises 2.25 slightly rounded whorls measuring 0.3 mm in height and 0.33 mm in maximum diameter. The first whorl measures 0.03–0.04 mm in the width of the initial cap and 0.14–0.15 mm in maximum diameter. The transition from the embryonic to the larval shell is not preserved. In the course of the second whorl, larval sculpture consisting of two granulated fine spiral threads just above the abapical suture is evident; these threads decrease in the course of the last quarter whorl of the protoconch. The protoconch is terminated by an indistinct, very fine thickening on the shell. The onset of the teleoconch is indicated by the formation of regular, closely spaced growth lines and by the formation of the regular adult sculpture.

Remarks.—*R. clotho* is similar to the syntopic *R. acuticosta*, but differs by its more slender shell, with a sculpture of fewer but well-rounded ribs causing a more angulate shell outline. The spiral sculpture is more strongly developed and the aperture is less thickened in *R. clotho*. The protoconch of *R. clotho* differs by comprising 0.25 whorls less. It is slightly smaller in height and in maximum diameter, whereas the first whorl is slightly larger. The transition to the teleoconch is indistinct, not indicated by the formation of thickened growth lines as in *R. acuticosta*.

Rissoa clotho is known from Poland, Austria, the Czech Republic, and Romania (Boettger 1901; Bałuk 1975).

Rissoa costeiensis sp. nov.

Fig. 5B.

Derivation of the name: Named after the type locality (spelling according to Studencka et al. 1998).

Type horizon and locality: Grey clay from the Early Badenian of Coştei in western Romania; Banat Region, 50 km W of Deva, northern slopes of the Poiana Ruscă Moutains (see Studencka et al. 1998 for references and further data).

Material.—The holotype (NHMW 2002z0030/0006) and four paratypes (NHMW 2002z0030/0007) from the Badenian of Coştei, Romania.

Diagnosis.—Small, slender *Rissoa* with whorls narrowing towards the aperture; prominent, sickle-shaped axial ribs crossed by fine spiral threads; small, rounded to subangular aperture; large protoconch with prominent subsequent incision of early teleoconch.

Description.—The small, slender shell comprises five rounded whorls measuring up to 3 mm in height. The whorls narrow towards the aperture and are separated by moderately deep sutures. Sculpture consists of 12–16 prominent, sickle-shaped axial ribs which are crossed by 12–14 fine spiral threads. The base is sculptured by 8–10 fine spiral threads. The last whorl forms 50–60% of total shell height. The small aperture is rounded to subangular. It is characterised by a thin peristome whose columellar portion is slightly bent. A very narrow slit-like umbilicus is present.

The large protoconch has three rounded whorls measuring up to 0.55 mm in height and up to 0.5 mm in maximum diameter. The width of the initial cap amounts to 0.03 mm and the first whorl measures 0.13–0.14 mm in maximum diameter. The transition from the embryonic to the larval shell is not obvious. The second whorl is characterised by remains of two very fine, granulated spiral threads above the abapical suture. The protoconch is terminated by closely spaced, sinuous, thickened growth lines. A subsequent incision of the whorl and the formation of regular adult growth lines indicate the onset of the teleoconch.

Remarks and differences.—*R. costeiensis* sp. nov. differs from the Recent Mediterranean species *R. similis* (fig. 5A) by its smaller size, the teleoconch sculpture having more axial ribs,

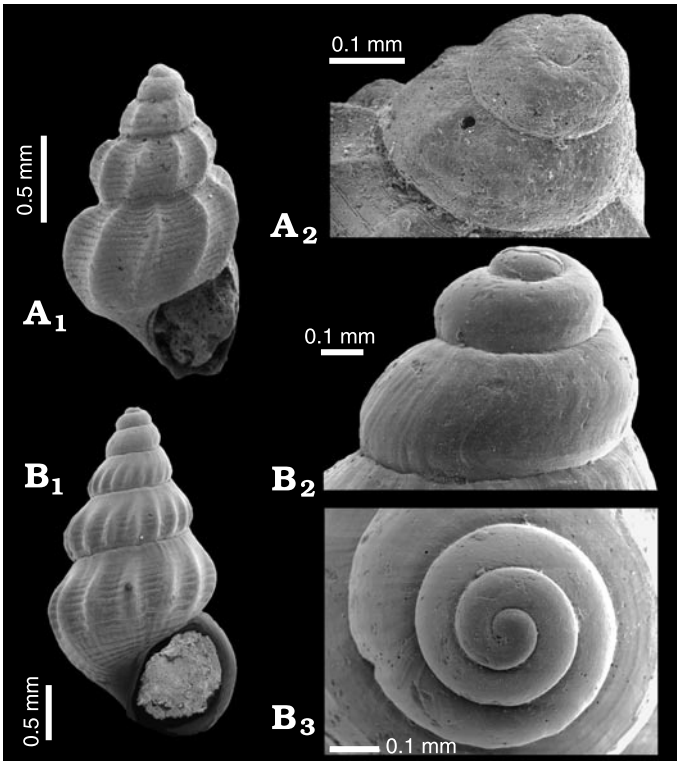

Fig. 5. Two species of *Rissoa* Desmarest, 1814. **A**. *Rissoa similis* Scacchi, 1836. Specimen (NHMW 2002z0030/0005), Recent, from the Adriatic Sea (A_1). Protoconch of the same specimen in lateral view (A_2). **B**. *Rissoa costeiensis* sp. nov. Holotype (NHMW 2002z0030/0006) from the Badenian of Coştei, Romania (B_1). Protoconch of the same specimen in lateral and apical views (B_2, B_3). The protoconch is terminated by closely spaced, sinuous, thickened growth lines. The onset of the teleoconch is indicated by a prominent incision of the whorl.

and by its larger protoconch comprising one larval whorl more. Ferrero Mortara et al. (1984) reported *Apicularia angulatacuta* Sacco, 1895 and *A. guerini* var. *antiqua* Schwartz v. Mohrenstern, 1864 from the Pliocene of Italy, which are distinguished by more slender shells. According to the figure in Ferrero Mortara et al. (1984: pl. 38: 5a), *Rissoa angulatacuta* appeared to be a direct developer, without a free planktonic veliger stage during its early ontogeny.

The Badenian species *Rissoa acuticosta* from Steinebrunn/Austria is characterised by a similar protoconch as *R. costeiensis*, but it is distinguished by comprising only 2.6 whorls measuring only up to 0.4 mm in height and in maximum diameter. It furthermore lacks the prominent subsequent incision following the sinusigera terminating the protoconch. The teleoconch of *R. acuticosta* differs by lacking the characteristic elongated shape, and by the teleoconch whorls narrowing towards the aperture.

Genus *Alvania* Risso, 1826

Remarks.—*Alvania* was regarded as belonging to its own subfamily Alvaniinae by Golikov and Starobogatov in Golikov and Scarlato (1972) and by Nordsieck (1972). Golikov and Starobogatov (1975) even elevated this taxon to family rank within their superfamily Alvanioidea. As indicated by Ponder (1985), however, the teleoconch sculpture, operculum and radular characters are similar to *Rissoa*. The protoconch morphology and sculpture exhibit a coarser larval sculpture in most species with planktotrophic development, with frequently occurring zigzag-shaped spiral striae. Nonetheless, the pitted sculpture and even weakly sculptured, rather smooth protoconchs hardly distinguish *Alvania* from Rissoinae on a suprageneric level.

Subgenus *Alvania* Risso, 1826

Type species: *Turbo cimex* Linnaeus, 1758 from the Mediterranean Sea and NE Atlantic.

Alvania (*Alvania*) *curta* (Dujardin, 1837)

Fig. 6C.

Rissoa curta sp. nov.; Dujardin 1837: 279, pl. 19: 5.
Rissoa curta Dujardin; Hörnes 1856: 571, pl. 48: 15 a, b.
Alvania curta Dujardin var. *cristatocosta* Sacco 1895: 23.
Alvania curta Dujardin; Meznerics 1933: 330.
Rissoa (*Alvania*) *curta* Dujardin; Strausz 1966: 71–72, pl. 46: 8, 9.
Alvania curta (Dujardin); Bohn-Havas 1973: 1038, pl. 2: 27.
Alvania (*Alvania*) *curta* (Dujardin); Bałuk 1975: 78, pl. 9: 11.
Alvania (*Alvania*) *curta* (Dujardin); Svagrovský 1981: 117, pl. 37: 1, 2.
Alvania (*Alvania*) *curta* (Dujardin); Atanackovic 1985: 87, pl. 20: 13, 14.
Alvania (*Alvania*) *curta* (Dujardin); Gürs and Weinbrecht 2001: 80, fig. 2.4, pl. 1: 6.

Material.—Five specimens from the Early Badenian of Sedlec/Nový Rybník (formerly Porz) 6 km SE Mikulov, Czech Republic, NHMW 2002z0030/0010.

Description.—The egg-shaped, thick shell comprises 5–6 slightly rounded low whorls measuring up to 2.5 mm in height. The last whorl forms about 60–70% of total shell height and is elongate, whereas the spire is conical. The teleoconch sculpture consists of 16 prominent, straight to slightly prosocline axial ribs and 10 spiral threads; these form a reticulate pattern on the early teleoconch and are subordinated on the last two whorls. The base is sculptured by 3 spiral threads. The thickened aperture has an elongate drop shape. It is characterised by a faint, broad anterior notch and by an acute parietal edge. The columellar lip is bent. The interior portion of the outer lip is characterised by 4 weak teeth.

The protoconch comprises three slightly rounded whorls measuring 0.46 mm in height and 0.44 mm in maximum diameter. The first whorl measures 0.06 mm in the width of the initial cap and 0.16–0.17 mm in maximum diameter. Embryonic ornament and the transition from the embryonic shell to the larval shell are not preserved. Remains of tuberculate spiral threads sculpture the larval shell and are apparently concentrated on the abapical half of the whorls. The protoconch is terminated by a well-developed sinusigera notch. The onset of the teleoconch is indicated by the formation of the regularly reticulate adult sculpture.

Remarks.—The protoconch indicates an indirect development including a free planktotrophic larval stage. The similar Recent Mediterranean species *Alvania* (*Alvania*) *montagui* (Payraudeau, 1826) (fig. 6B) differs by its slightly larger aperture and by deeper sutures separating the whorls. The

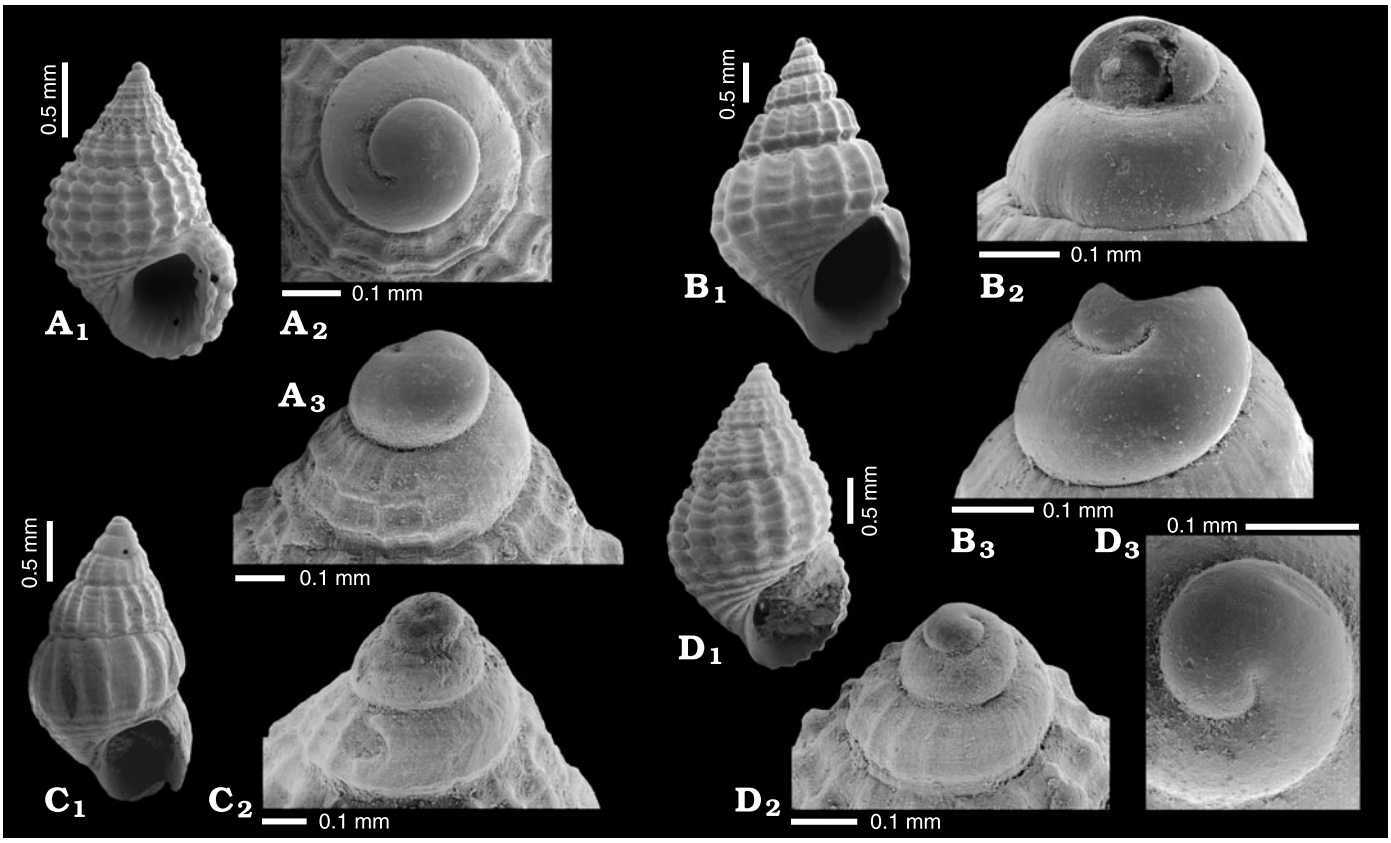

Fig. 6. Four species of *Alvania* (*Alvania*) Risso, 1826. **A**. *Alvania* (*Alvania*) *mamillata* (Risso, 1826). Specimen (NHMW 2002z0030/0008), Recent, from the Adriatic Sea (A_1). Apical and lateral views of the protoconch of the same specimen (A_2, A_3). Thickened, closely spaced growth lines are terminating the protoconch. The onset of the teleoconch is indicated by the formation of a regular reticulate sculpture. **B**. *Alvania* (*Alvania*) *montagui* (Payraudeau, 1826). Specimen (NHMW 2002z0030/0009), Recent, from the Adriatic Sea (B_1). Lateral views of the protoconch of the same specimen (B_2, B_3). The protoconch is terminated by a slightly thickened sinuous rim and a subsequent slight incision. **C**. *Alvania* (*Alvania*) *curta* (Dujardin, 1837). Specimen (NHMW 2002z/0030/0010) from the Early Badenian of Sedlec/Nový Rybník, Czech Republic (C_1). Protoconch of the same specimen in lateral view (C_2). The protoconch is terminated by a well-developed sinusigera notch. **D**. *Alvania* (*Alvania*) *ampulla* (Eichwald, 1853). Specimen (NHMW 2002z0030/0011) from the Badenian of Steinebrunn, Lower Austria (D_1). Lateral view of the protoconch of the same specimen as in D_1 (D_2). The protoconch is terminated by a sinusigera notch which is thickened in its adapical portion. Detailed apical view of the embryonic shell of the same protoconch as in D_2 (D_3). The embryonic shell is sculptured by fine spiral threads and it is terminated by an indistinct rim on the shell.

protoconch of *A*. (*A*.) *montagui* differs by reflecting a lecithotrophic larval development. A second Mediterranean morph assigned to *A*. (*A*.) *montagui* with multispiral protoconch but identical teleoconch morphology probably represents another species. Solving this problem, however, will require further anatomical studies because several species pairs of *Alvania* and *Rissoa* only differing in reproductive mode and thus in protoconch morphology exist in the Mediterranean Sea as well as in Northern Europe (Oliverio 1994, 1996; Warén 1996).

A. (*A*.) *curta* has been described from the Badenian of Várpalota in Hungary (Strausz 1966), Poland (Bałuk 1975), Slovakia (Hörnes 1856; Svagrovský 1981), Bosnia and Ukraine (Atanackovic 1985). Gürs and Weinbrecht (2001) mentioned its occurrence in Miocene deposits of the North Sea Basin (Northern Germany). The alleged occurrences from the Middle Miocene of the Loire Basin (Glibert 1949) and from the Burdigalian of the Aquitaine (Cossmann and Peyrot 1919) are considered as synonyms of *Alvania lachesis* (Basterot, 1825) by Lozouet et al. (2001).

Alvania (*Alvania*) *ampulla* (Eichwald, 1853)

Fig. 6D.

Rissoa ampulla Eichwald 1853: 274, pl. 10: 16.
Rissoa Montagui Payraudeaux; Hörnes 1856: 569, pl. 48: 13.
Alvania (*Alvania*) *montagui* var. *miocaenica* Sacco 1895: 23.
Alvania miocaenica Sacco; Meznerics 1933: 330, pl. 13: 2a, b.
Alvania (*Alvania*) *montagui ampulla* Eichwald; Steininger 1963: 44, pl. 13: 2.
Rissoa (*Alvania*) *montagui miocaenica* Sacco; Strausz, 1966: 74, pl. 46: 19, 20.
Alvania (*Alvania*) *montagui ampulla* Eichwald; Bałuk 1975: 79, pl. 9: 9.
Alvania (*Alvania*) *montagui miocaenica* Sacco; Svagrovský 1981: 114, pl. 35: 5–7.
Alvania (Alvania) *montagui miocaenica* Sacco; Atanackovic 1985: 86, pl. 20: 9, 10.

Material.—Nine specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0011.

Description.—The ovate shell comprises six slightly rounded whorls measuring about 3.5 mm in height. Sculpture consists of 16 prominent axial ribs crossed by 6 spiral cords, which are about as strong as the axial ribs on the early teleoconch whorls

and which slightly decrease on the last two whorls. The base is sculptured by 5 strong spiral cords. The last whorl forms about 60–70% of total shell height. The slightly thickened aperture has an elongate drop shape. It is characterised by a faint anterior notch and by a pointed parietal portion. The columellar edge is bent.

The protoconch comprises two rounded whorls measuring 0.27–0.28 mm in height and 0.26–0.27 mm in maximum diameter. The embryonic shell has one whorl measuring 0.03–0.04 mm in the width of the initial cap and 0.15–0.16 mm in maximum diameter. It is ornamented by remains of fine spiral threads. The embryonic shell is terminated by an indistinct rim on the shell. The subsequent larval shell is sculptured by remains of 6 rows of coarse granules. The protoconch is terminated by a sinusigera notch which is thickened in its adapical portion. The onset of the teleoconch is indicated by the formation of the regular adult sculptural pattern.

Remarks.—The protoconch, reflecting a planktotrophic larval development, closely resembles that of the Recent Mediterranean species *Alvania* (*Alvania*) *punctura* (Montagu, 1803), which is slightly larger, comprising half a larval whorl more (Kowalke 1998: pl. 9: 9). The Recent Mediterranean species *Alvania* (*A.*) *mamillata* (Risso, 1758) (fig. 6A), with similar teleoconch morphology, differs by its thicker shell. The protoconch morphology, however, facilitated a clear separation of the taxa: *A.* (*A.*) *mamillata* is characterised by a lecithotrophic development, including a very short larval stage following a yolk-rich embryogenesis as indicated by a bulbous embryonic shell.

Two available names for this taxon are reported in the literature. *Rissoa ampulla* Eichwald was introduced for specimens from Poland, whereas *Alvania montagui miocaenica* Sacco referred to shells from the Vienna Basin in Austria. As already argued by Steininger (1963), both occurrences yield conspecific specimens and thus *Rissoa ampulla* gains priority.

Alvania (*Alvania*) *ampulla* is documented during the entire Badenian. Occurrences are known from Bosnia, Austria, Poland, Ukraine, Bulgaria, Hungary, and Slovakia. Its earliest occurrence in the Paratethys was reported by Steininger (1963) from the Eggenburgian of Lower Austria. Shells from the Tarkhanian to Konkian of the Eastern Paratethys affiliated with *Alvania montagui* (Payraudeau) by Iljina (1993: pl. 3: 24, 25) probably represent another species based on their regularly reticulate sculpture.

Alvania (*Alvania*) *oceani* (d'Orbigny, 1852)

Fig. 7A.

Rissoa oceani sp. nov.; d'Orbigny 1852: 28, nr. 368.
Rissoa Moulinsi d'Orbigny; Hörnes 1856: 570, pl. 48: 14.
Alvania curta? var. *rotundulina* Sacco 1895: 24 (pars).
Alvania oceani d'Orbigny; Meznerics 1933: 330, pl. 13: 8a, b.
Rissoa (*Alvania*) *oceani* d'Orbigny; Strausz 1966: 72, textfig. 40.
Alvania (*Alvania*) *oceani* (d'Orbigny); Bałuk 1975: 82, pl. 9: 17.
Alvania (*Alvania*) *oceani* (d'Orbigny); Svagrovský 1981: 116, pl. 36: 1–3.
Alvania (*Alvania*) *oceani* (d'Orbigny); Atanackovic 1985: 86, pl. 20: 11, 12.

Material.—Fifteen specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0012.

Description.—The small, elongate, egg-shaped shell comprises 5–6 slightly rounded whorls measuring up to 3 mm in height. The last whorl forms about 60–70% of total shell height. Teleoconch sculpture consists of 20 straight axial ribs crossed by 6 about equally strong spiral cords, forming a very regularly reticulate pattern. The base is sculptured by 6 spiral cords. The thickened, egg-shaped aperture is characterised by a faint anterior notch and by a pointed posterior portion. The columellar edge is bent.

The protoconch comprises 2.5 slightly rounded whorls measuring 0.33 mm in height and 0.35 mm in width. Sculpture is not preserved. The first whorl measures about 0.04 mm in the width of the initial cap and 0.15 mm in maximum diameter. The transition from the embryonic shell to the larval shell is indistinct due to the poor preservation. The protoconch is terminated by a slightly thickened, fractionated sinusigera notch.

Remarks.—*Alvania* (*Alvania*) *oceani* differs from the similar species *A.* (*A.*) *venus* by its finer sculpture, comprising 4 axial ribs more, and by its considerably smaller protoconch which in addition comprises 0.25 whorls less.

A. (*A.*) *oceani* is commonly found in the Badenian of the entire Central Paratethys and was variously mentioned from Poland, Hungary, Ukraine, Bosnia, Slovakia, and Austria. Outside the Paratethys the species is described by Cossmann and Peyrot (1919) from the Early Miocene of SW France. There, also the oldest occurrence was mentioned from the Late Oligocene by Lozouet (1986).

Alvania (*Alvania*) *perregularis* (Sacco, 1895)

Fig. 7B.

Rissoa Mariae d'Orbigny; Hörnes 1856: 563, pl. 48: 9a, b.
Alvania Mariae? var. *perregularis*; Sacco 1895: 25.
Alvania (*Acinus*) *perregularis* Sacco; Meznerics: 331, pl. 13: 9a, b.
Alvania perregularis Sacco; Bohn-Havas 1973: 1037, pl. 3: 1, 2.
Alvania (*Turbona*) *perregularis* (Sacco); Bałuk 1975: 85, pl. 9: 13–15.
Alvania (*Turbona*) *perregularis* (Sacco); Svagrovský 1981: 118, pl. 36: 4.
Alvania (*Alvania*) *perregularis* (Sacco), Atanackovic 1985: 87, pl. 20: 17, 18.

Material.—Nine specimens from the Badenian of Sedlec/Nový Rybník (formerly Porz) 6 km SE of Mikulov, Czech Republic, NHMW 2002z0030/0013.

Description.—The elongated, egg-shaped shell consists of 6 flat whorls measuring up to 3 mm in height. The last whorl forms about 70% of total shell height. The teleoconch sculpture consists of a very regular reticulate pattern of 24–30 straight to slightly prosocline axial ribs crossed by 8–10 spiral cords. Nodes form in the points of intersection of the axial and spiral sculpture. The large aperture has a drop shape. It is characterised by a faint, broad anterior notch and by a pointed, slightly incised parietal portion. The interior portion of the outer and basal lip bears 10–11 coarse teeth.

The protoconch comprises 2.75 slightly rounded whorls measuring 0.46 mm in height and 0.45 mm in maximum diameter. The embryonic shell consists of one inflated whorl measuring 0.06 mm in the width of the initial cap and 0.17 mm in

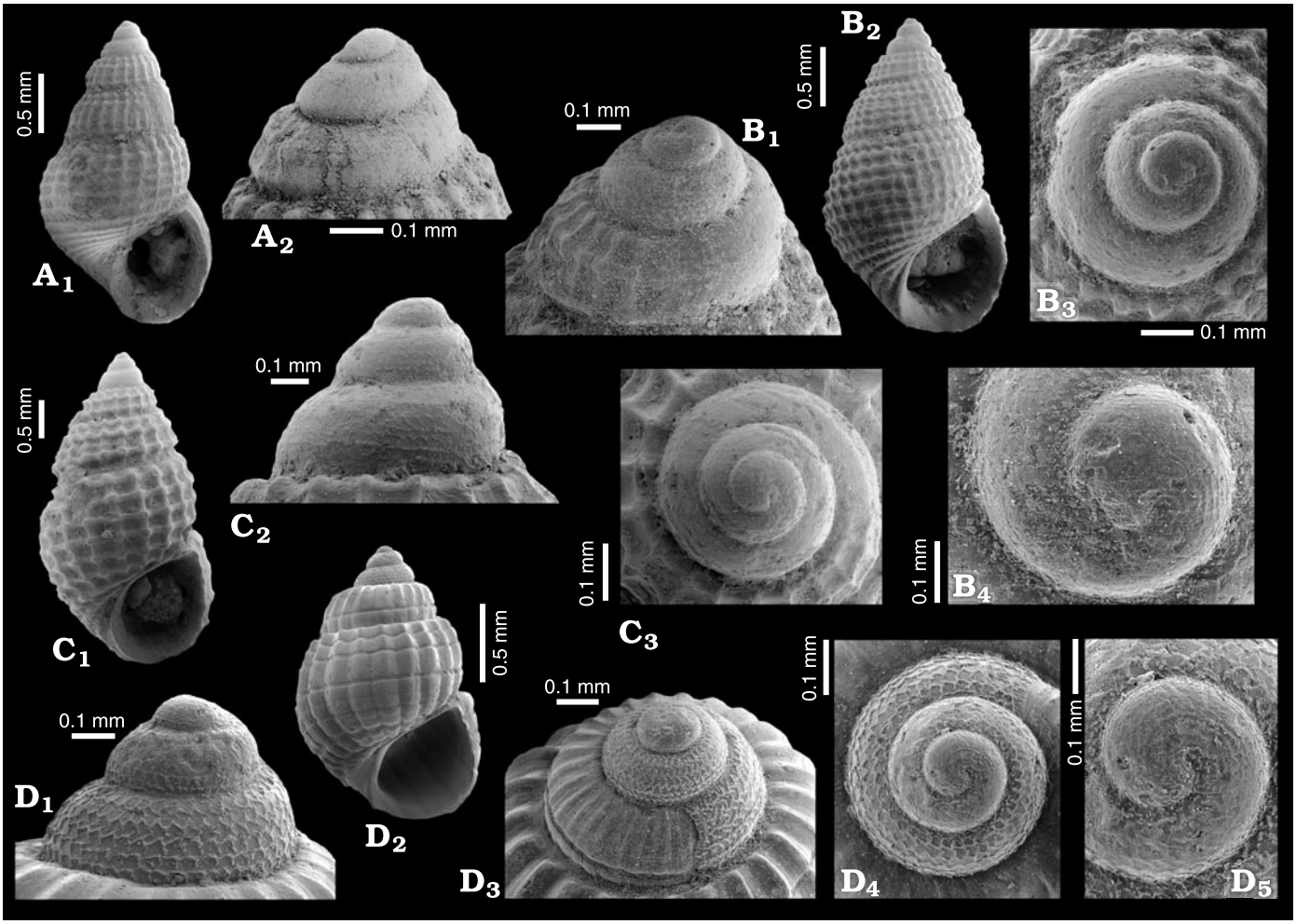

Fig. 7. Four species of *Alvania* (*Alvania*) Risso, 1826. **A**. *Alvania* (*Alvania*) *oceani* (d'Orbigny, 1852). Specimen (NHMW 2002z0030/0012) from the Badenian of Steinebrunn, Lower Austria (A_1). Protoconch of the same specimen as in A_1 in lateral view (A_2). The protoconch is terminated by a slightly thickened, fractionated sinusigera notch. **B**. *Alvania* (*Alvania*) *perregularis* (Sacco, 1895). Specimen (NHMW 2002z0030/0013) from the Early Badenian of Sedlec/Nový Rybník, Czech Republic (B_2). Lateral and apical view of the protoconch of the same specimen as in B_2 (B_1, B_3). The protoconch is terminated by a sinusigera notch. Detailed apical view of the initial whorl of the same protoconch as in B_3 (B_4). The embryonic shell consists of one inflated whorl, which is terminated by a thickened rim, reflecting the thickened apertural margin of the hatchling. **C**. *Alvania* (*Alvania*) *transiens* (Sacco, 1895). Specimen (NHMW 2002z0030/0014) from the Badenian of Steinebrunn, Lower Austria (C_1). Protoconch of the same specimen as in C_1 in lateral and apical view (C_2, C_3). The larval shell is sculptured by spiral rows of tubercles. It is terminated by a well developed sinusigera notch. **D**. *Alvania* (*Alvania*) *schwartzi* (Hörnes, 1865). Specimen (NHMW 2002z0030/0015) from the Badenian of Steinebrunn, Lower Austria (D_2). Lateral and apical views of the protoconch of the same specimen as in D_2 (D_1, D_3, D_4). The protoconch is terminated by a well developed sinusigera notch. Detailed view of the initial whorl of the same protoconch as in D_4 (D_5). The embryonic shell is demarcated from the subsequent larval shell by a thickened rim.

maximum diameter. Embryonic sculpture consists of 10 rows of granulated spiral threads. The transition to the subsequent larval shell is indicated by a thickened rim on the shell. The larval shell is characterised by remains of 8 rows of coarse granules and is terminated by a sinusigera notch. The onset of the teleoconch is indicated by the formation of the regular adult sculpture.

Remarks.—The protoconch resembles that of *Alvania* (*Alvania*) *ampulla* regarding the sculpture of the larval shell, but differs by its much larger size and by comprising 0.75 larval whorls more. Additionally, the embryonic sculpture is much coarser in the case of *A. perregularis*.

Alvania (*Alvania*) *perregularis* represents an ubiquitous species during the Badenian of the Central Paratethys. Literature data cover an area from Poland and Ukraine, via Austria, Hungary, and Romania south to Bosnia and Bulgaria (see Strausz 1966; Atanackovic 1985).

Alvania (*Alvania*) *transiens* (Sacco, 1895)

Fig. 7C.

Rissoa venus d'Orbigny; Hörnes 1865: 565–566, pl. 48: 10 a, b.

Alvania sculpta? var. *transiens* Sacco 1895: 27.

Alvania venus d'Orbigny var. *danubiensis* Cossmann and Peyrot; Mezzerics 1933: 331.

Alvania (*Alvania*) *venus* (d'Orbigny); Steininger 1963: 43, pl. 13: 1.

Rissoa venus danubiens Cossmann and Peyrot; Strausz 1966: 72–73, pl. 48: 17, 18.

Alvania venus danubiensis Cossmann and Peyrot; Bohn-Havas 1973: 1037.

Alvania (*Acinulus*) *venus transiens* Sacco; Bałuk 1975: 86, pl. 9: 18, 19.

Material.—Eight specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0014.

Description.—The elongate, egg-shaped shell comprises 6 flat to slightly rounded whorls separated by deep sutures. The shell measures up to 3 mm in height. The teleoconch sculpture consists of 16 straight axial ribs crossed by 6 about equally strong spiral cords forming a very regular reticulate pattern. Nodes are developed in the points of intersection of the axial and spiral sculptural elements. The last whorl forms about 70% of total shell height. It is elongate cylindrical, whereas the spire is conical. The aperture has a drop shape with pointed parietal portion. A faint, broad anterior notch is present. The columellar lip is bent. The interior portions of the outer and basal lip are characterised by more or less strongly developed teeth.

The conical protoconch comprises 2.75 slightly rounded whorls measuring 0.48 mm in height and 0.43 mm in maximum diameter. The embryonic shell comprises one whorl measuring about 0.05 mm in the width of the initial cap and 0.13–0.14 mm in maximum diameter. Remains of fine spiral threads are present on the embryonic shell. It is terminated by a slightly thickened rim on the shell. The larval shell bears 10 spiral rows of coarse tubercles. It is terminated by a well-developed sinusigera notch.

Remarks.—The shells have usually been treated as *Alvania venus* (d'Orbigny, 1852) or as a subspecies thereof. Indeed, the Paratethyan specimens differ considerably in their less convex whorls, the more angulated aperture and the characteristic, deep, angulated suture which separates the penultimate whorl strongly from the body whorl. *Alvania venus* from the Aquitanian of France, illustrated by Lozouet et al. (2001), clearly documents these differences and furthermore reveals a much coarser sculpture with rather pointed nodes. In contrast, the protoconchs of both discussed species are very similar (see protoconch of *Alvania venus* in Lozouet et al. 2001: pl. 13: 5b, c).

Cossmann and Peyrot (1919) correctly recognised the differences of the Paratethyan species from *Alvania venus* and consequently introduced the new name *Alvania venus* var. *danubiensis*. Twenty-four years earlier, however, the same conclusions already prompted Sacco (1895) to separate the Paratethyan shells as var. *transiens*.

Alvania (*Alvania*) *transiens* resembles *Alvania* (*Alvania*) *perregularis*, but differs by its coarser teleoconch sculpture and by an acute conical protoconch, which is higher than wide, whereas the protoconch of *Alvania* (*A*.) *perregularis* is about as wide as high. The embryonic shell of *Alvania* (*A*.) *transiens* is considerably smaller than that of *A*. (*A*.) *perregularis. Alvania anabaptizata* Boettger, 1901, and the specimens described as *Alvania sculpta* (Philippi, 1836) by Boettger (1901) from the Early Badenian of Romania are considered as synonyms of *Alvania transiens* by Bałuk (1975). *Alvania transiens* appears in the Central Paratethys during the Early Miocene (Eggenburgian) and is an ubiquitous Paratethyan species up to the Late Badenian.

Alvania (Alvania) schwartzi (Hörnes, 1856)

Fig. 7D.

Rissoa Schwartzi Hörnes 1856: 573, pl. 48: 18.
Rissoa (*Alvania*) *schwartzi* Hörnes; Strausz 1966: 75, pl. 46: 14–16.
Alvania (?*Galeodinopsis*) *schwartzi* (Hörnes); Bałuk 1975: 89, pl. 9: 3.

Material.—Ten specimens from the Badenian of Baden and five specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0015.

Description.—The small stout shell comprises 5 flat to slightly rounded whorls measuring up to 2.1 mm in height and up to 1.4 mm in width. Sculpture consists of 16 straight axial ribs which are incised by 5–6 spiral grooves. The last whorl forms about 70% of total shell height. The base is sculptured by indistinct spiral threads. The large aperture has a drop shape, with a broad basal notch and a pointed parietal edge. It is characterised by a thickened outer lip which may bear indistinct teeth in its interior portion, and by a thin bent parietal and columellar lip.

The protoconch comprises 2.75 slightly rounded whorls measuring 0.45 mm in height and 0.42–0.43 mm in maximum diameter. The embryonic shell comprises one whorl, which measures 0.04 mm in the width of the initial cap and 0.16 mm in maximum diameter and which is well demarcated from the subsequent larval shell by a thickened rim on the shell. Embryonic ornament consists of dense, wavy spiral folds. The larval shell is sculptured by 6 prominent, zigzag-shaped spiral threads which are connected by very short axial threads. The protoconch is terminated by a well-developed sinusigera notch.

Remarks.—The protoconch is indicative of an indirect development including a free planktotrophic larval stage. The species is documented from the Badenian of Austria, Romania, Hungary, and Poland (Meznerics 1933; Bałuk 1975). In Austria, *Alvania* (*Alvania*) *schwartzi* typically occurred in pelitic, offshore facies but is hardly recorded from sandy, littoral deposits, pointing to a preference for deeper-water environments.

Genus *Manzonia* Brusina, 1870

Subgenus *Manzonia* Brusina, 1870

Type species: *Turbo crassus* Kanmacher in J. Adams, 1798 from the West Mediterranean and NE Atlantic.

Remarks.—The subgenus *Manzonia* differs from the subgenus *Alvinia* by teleoconch whorls narrowing towards the aperture, thus separated by deep sutures and by a teleoconch sculpture of prominent, rounded, strongly opisthocline axial ribs crossed by much weaker spirals.

Manzonia (*Manzonia*) *crassa* (Kanmacher in J. Adams, 1798)

Fig. 8C.

Manzonia costata Adams var.; Friedberg 1923: 385, pl. 23: 5.
Manzonia costata (J. Adams); Wenz 1938–1944: 614, fig. 1707.
Folinia (*Manzonia*) *costata* (Adams); Iljina 1966: 91, pl. 4: 2.
Folinia (*Manzonia*) *costata* (Adams); Bałuk 1975: 74, pl. 8: 12.

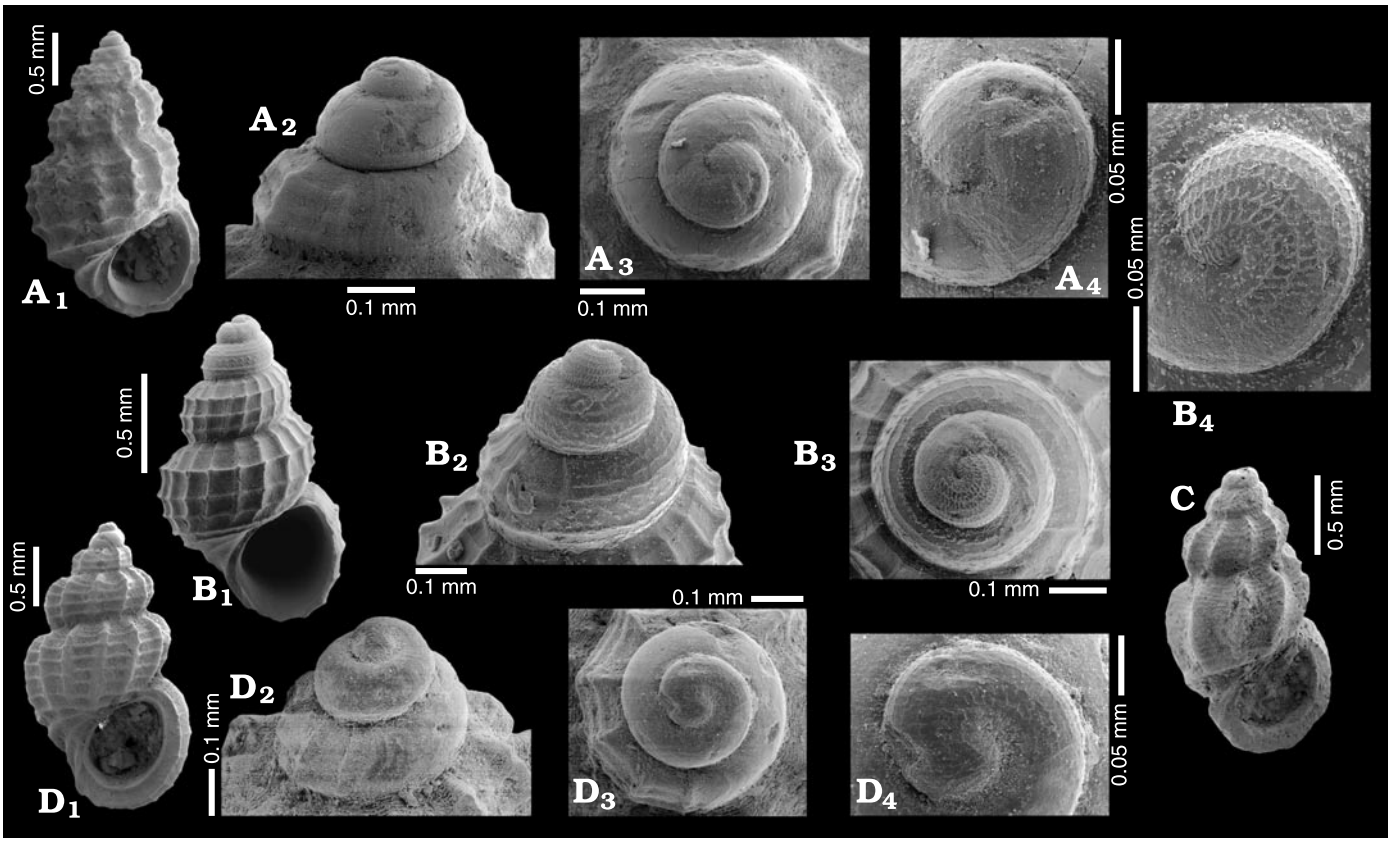

Fig. 8. Two species of *Manzonia* (*Alvinia*) Monterosato, 1884 and two of *Manzonia* (*Manzonia*) Brusina, 1870. **A**. *Manzonia* (*Alvinia*) *miocrassicosta* (Sacco, 1895). Specimen (NHMW 2002z0030/0016) from the Badenian of Steinebrunn (A_1). Lateral and apical view of the protoconch of the same specimen (A_2, A_3). The protoconch is terminated by a short sinusigera notch. Detailed view of the initial whorl of the same protoconch as in A_3 (A_4). The embryonic shell is demarcated from the subsequent larval shell by a well developed thickened rim. **B**. *Manzonia* (*Alvinia*) *partschi* (Hörnes, 1856). Specimen (NHMW 2002z0030/0017) from the Badenian of Baden/Sooß, Lower Austria (B_1). Lateral and apical view of the protoconch of the same specimen as in B_1 (B_2, B_3). The protoconch is terminated by a short, slightly thickened sinusigera notch. Detailed view of the initial whorl of the same protoconch as in B_3 (B_4). The embryonic shell is strongly sculptured and terminated by a slightly sinuous rim. **C**. *Manzonia* (*Manzonia*) *crassa* (Kanmacher in J. Adams, 1798), specimen (NHMW 2002z0030/0018) from the Badenian of Niederleis, Lower Austria. **D**. *Manzonia* (*Manzonia*) *scalaris* (Dubois, 1831). Specimen (NHMW 2002z0030/0019) from the Badenian of Steinebrunn, Lower Austria (D_1). Lateral and apical view of the protoconch of the same specimen as in D_1 (D_2, D_3). The protoconch is terminated by a well developed sinusigera notch. Detailed view of the initial whorl of the same protoconch as in D_3 (D_4). The transition to the larval shell is indicated by a thickened rim.

Manzonia (*Manzonia*) *crassa* (Kanmacher in J. Adams); Ponder 1985: fig. 99A–F.

Material.—Three specimens from the Badenian of Niederleis, Lower Austria, NHMW 2002z0030/0018.

Description.—The small, elongated conical to spindle-shaped shell has 5 low whorls measuring up to 2.5 mm in height and up to 1.4 mm in width. Whorls are separated by deep sutures. Sculpture consists of 8–10 prominent opisthocyrt axial ribs, crossed by numerous very fine spiral threads. The base is sculptured by 2 strong spiral keels. The last whorl forms 60–70% of total shell height. The large thickened, holostomatous aperture is rounded to egg shaped.

The protoconch is heavily corroded. It comprises about two rounded whorls measuring 0.33 mm in height and in maximum diameter. The transition to the teleoconch is indicated by the formation of the regular adult sculpture.

Remarks.—Although *M.* (*M.*) *crassa* represents a Recent species, it is not possible to distinguish our material based on conchological features from the Mediterranean representatives. Recent *M. costata* has a protococh of about the same dimensions as the material described here (Ponder 1985: fig. 99 B). *M.* (*M.*) *crassa* is described from the Badenian of Poland, Austria, Hungary, and Romania. Glibert (1949) mentioned *Manzonia costata falunica* (Morgan, 1915) from the Langhian –Early Serravallian of the Loire Basin, whereas Cossmann and Peyrot described *Manzonia costata minuta* (Dollfus and Dautzenberg, 1886) from the Burdigalian of SW France. The species is not recorded from the Miocene of the Eastern Paratethys but appears along the Black Sea coasts during the Quaternary (Iljina 1966). In the modern seas, *M.* (*M.*) *crassa* ranges from the Black Sea and the Mediterranean Sea and along the Atlantic coast as far north as Scandinavia (Nordsieck 1972). *Manzonia miocristata* Sacco, 1895 from the Late Miocene of Italy differs by its more slender shell and by having fewer but more strongly developed axial ribs, which additionally differ by their stronger opisthocyrt course (Ferrero Mortara et al. 1984: pl. 39: 8a–c).

Manzonia (*M.*) *scalaris* (Dubois, 1831)

Fig. 8D.

Cyclostoma scalare Dubois de Montpereux 1831: 47, pl. 3: 40, 41.
Rissoa scalaris Dubois; Hörnes 1856: 567, pl. 48: 12.
Rissoa (*Manzonia*) *scalaris* Dubois; Strausz 1966: 77: 42.
Alvania (*Taramellia*) *scalaris* (Dubois); Bałuk 1975: 75, pl. 8: 13, 14.

Material.—Seven specimens from the Badenian of Steinebrunn, NHMW 2002z0030/0019.

Description.—Dimensions of the teleoconch correspond to *M. costata*. Twelve axial ribs are present, crossed by 8 weaker spirals. The protoconch comprises 2.25 slightly rounded whorls measuring 0.38–0.39 mm in height and 0.36 mm in maximum diameter. The embryonic shell comprises one whorl measuring 0.06 mm in the width of the initial cap and 0.17–0.18 mm in maximum diameter. Sculpture consists of 6 spiral threads connected by short axial ribs. The transition to the larval shell is indicated by a thickened rim. The subsequent larval shell is sculptured by 2 weak spirals on the abapical half of the whorls. The protoconch is terminated by a well-developed sinusigera notch.

Remarks.—The protoconch indicates an indirect development including a free planktotrophic larval stage. *M. scalaris* differs from *M. crassa* by more but weaker-developed axial ribs, as well as by fewer and stronger-developed spirals. The protoconch differs by its larger size and by comprising about 0.25 whorls more. This widespread species is known from the Badenian of the Central Paratethys from Poland, Austria, Hungary, and Romania.

Subgenus *Alvinia* Monterosato, 1884

Type species: The recent species *Alvania weinkauffi* (Mohrenstern ms.) Weinkauff, 1868 from the Mediterranean.

Remarks.—*Flemellia* Nordsieck, 1972, which had been introduced as a new name for *Taramellia* Seguenza, 1903, *Seguenziella* Sacco, 1904 and *Flemingia* Jeffreys, 1884 with the type species *Turbo zetlandicus* Montagu, 1803, Recent, from the NE Atlantic (Wenz 1938-1944: 616, fig. 1717), represents a synonym. *Alvinia* differs from *Alvania* by its well-rounded base and by the roundish, thickened aperture with duplicated peristome lacking interior teeth. Ponder (1985) mentioned that *M.* (*Alvinia*) probably had diverged from *Alvania* in the Paleogene, because species from the Eocene of the Paris Basin are similar to recent congeners from the eastern Atlantic and from the Mediterranean, and only differed in peristome morphology, which was not duplicated.

Manzonia (*Alvinia*) *miocrassicosta* (Sacco, 1895)

Fig. 8A.

Rissoa zetlandica Montagu; Hörnes 1856: 566, pl. 48: 11.
Manzonia zetlandica var. *miocrassicosta* Sacco 1895: 30.
Manzonia (*Taramellia*) *zetlandica* Montagu; Meznerics 1933: 332.
Flemingia zetlandica var. *miocrassicosta* Sacco; Ferrero Mortara et al. 1984: pl. 39: 6.

Material.—Fifty-three specimens from the Badenian of Steinebrunn, Lower Austria, NHMW 2002z0030/0016.

Description.—The small, thick, egg-shaped shell has 5–6 slightly rounded whorls measuring up to 3 mm in height. The last whorl forms about 70% of total shell height. The teleoconch sculpture consists of 12 strongly developed straight axial ribs, crossed by 4 slightly weaker spiral keels. The points of intersection of the axial and spiral sculpture are slightly thickened. The base is sculptured by two prominent spiral keels. The thickened, holostomatous aperture is rounded to egg shaped. It is characterised by a slightly pointed posterior portion and by a prominent circular pad.

The protoconch comprises 2.4 slightly rounded whorls measuring 0.3 mm in height and 0.36 mm in maximum diameter. The embryonic shell comprises nearly one inflated whorl measuring 0.06–0.07 mm in the width of the initial cap and 0.16–0.17 mm in maximum diameter. Sculpture consists of 6 tuberculate spiral threads. The embryonic shell is well demarcated from the subsequent larval shell by a thickened rim. The larval shell is sculptured by remains of tuberculate spiral threads. The protoconch is terminated by a short sinusigera notch. The onset of the teleoconch is indicated by the formation of the regularly reticulate adult sculpture.

Remarks.—The protoconch indicates indirect development including a free planktotrophic larval stage. The inflated embryonic shell reflects a yolk-rich embryogenesis. The protoconch is very similar to that of Recent *Alvania* spp., especially to *A.* (*A.*) *punctura* with similar dimensions, which differs by weaker-developed embryonic sculpture, but stronger-developed larval sculpture (see Kowalke 1998: pl. 9: 9). The type species *Manzonia* (*Alvinia*) *weinkauffi* differs by its direct mode of early ontogenetic development and by its teleoconch sculpture of more but weaker-developed axial ribs (Ponder 1985: fig. 102A, B). *Manzonia* (*Alvinia*) *miocrassicosta* differs from Recent *M.* (*A.*) *zetlandica* by having less but slightly stronger-developed axial ribs (see Ponder 1985: fig. 100D). The shell shape is additionally less acute than that of *M.* (*A.*) *zetlandica*. A species with very similar protoconch, described as *Flemingia zetlandica* var. *perraricincta* Sacco, 1895 from the Early Pliocene of Italy, differs by having fewer but more strongly developed axial ribs; they form short spines in the points of intersection with the spiral sculpture (Ferrero Mortara et al. 1984: pl. 39: 7a, b).

Manzonia (*Alvinia*) *miocrassicosta* is known so far from the Central Paratethys only from the Vienna Basin (Austria, Czech Republic) and Romania. Specimens from the Tortonian of the Mediterranean as described by Ferrero Mortara et al. (1984) could not be differentiated from *M.* (*A.*) *miocrassicosta* based on conchological considerations.

Manzonia (*Alvinia*) *partschi* (Hörnes, 1856)

Fig. 8B.

Rissoa partschi sp. nov.; Hörnes 1856: 573–574, pl. 48: 19 a, b.
Manzonia partschi (Hörnes); Meznerics 1933: 332.
Rissoa (*Manzonia*) *partschi* (Hörnes); Strausz 1966: 77, pl. 46: 23.
Alvania (*Manzonia*) *partschi* (Hörnes); Bohn-Havas 1973: 1038, pl. 3: 8.
Alvania (*Taramellia*) *partschi* (Hoernes); Gürs and Weinbrecht 2001: 82, fig. 2.10, pl. 1: 11.

Material.—Fourteen specimens from the Badenian of Baden/Sooß, Lower Austria, NHMW 2002z0030/0017.

Description.—The slender, conical shell comprises 6 rounded whorls measuring up to 5 mm in height. The last whorl forms about 60% of total shell height. Sculpture consists of 20 weak, straight to slightly opisthocyrt axial ribs, which are crossed by 4 about equally strong spiral keels forming a very regular reticulate pattern. The points of intersection of axial and spiral sculptural elements are thickened. Nodes to very short spines are formed. The base is sculptured by two prominent spiral keels. The large, rounded, egg-shaped, holostomatous aperture is characterised by a circular pad.

The protoconch has 2.5 slightly rounded whorls measuring 0.41–0.43 mm in height and 0.39–0.43 mm in maximum diameter. The embryonic shell comprises nearly one inflated whorl measuring 0.06–0.07 mm in the width of the initial cap and 0.15–0.16 mm in maximum diameter. It is strongly sculptured by 7 spiral threads connected by weak short axial threads. The embryonic shell is terminated by a slightly sinuous rim. The subsequent larval shell is sculptured by 8 spiral threads which may be disconnected, building rows of elongated nodes. The rows are strongest developed in the median portion of the whorls. The protoconch is terminated by a short, slightly thickened sinusigera notch.

Remarks.—The protoconch points to indirect development including a free planktotrophic larval stage. *Manzonia* (*Alvinia*) *partschi* differs from *M.* (*A.*) *miocrassicosta* by its larger, slender, less thickened shell and by its weaker-developed sculpture of more but delicate axial ribs. The protoconch differs by its considerably larger size and stronger-developed embryonic and larval sculpture. *M.* (*A.*) *partschi* is very similar to the type species but differs by its slightly weaker sculpture and by its indirect mode of early ontogenetic development. *M.* (*A.*) *partschi* is a rather rare species which is known in the Central Paratethys from Hungary, Austria, and Romania. Janssen (1984) and Gürs and Weinbrecht (2001) described this species from the Miocene of the North Sea Basin.

Subfamily Mohrensterniinae Korobkov, 1955

Diagnosis (supplement).—Mohrensterniinae are characterised by low-conical protoconchs usually comprising 2–2.75 whorls measuring 0.3–0.5 mm in maximum diameter with small embryonic shells (only species with indirect development are known). Protoconchs are characterised by fine spirally sculptured embryonic shells and larval shells which are smooth except for growth lines. The transitions from the embryonic shell to the larval shell and from the larval shell to the teleoconch are only slightly thickened and often indistinct. No marked sinusigera notch is present.

The monogeneric subfamily Mohrensterniinae ranges stratigraphically from the early Middle Miocene (Early Badenian, Tarkhanian) to the early/mid Late Miocene (Maeotian).

Differences.—Mohrensterniinae differ from Rissoinae with similar teleoconch in their protoconch morphology, by lacking any larval sculpture aside from growth lines and by lacking a marked thickened sinusigera notch in transition to the teleoconch. This transition is often indistinct, only indicated by the successive onset of the adult sculpture. If a rim terminates the protoconch, this is only slightly thickened and slightly sinuous in course. Rissoininae differ by lacking embryonic sculpture in the case of indirect development; this sculpture is present in Mohrensterniinae. Mohrensterniinae differ from Hydrobiidae and Assimineidae by lacking a groove-ridge pattern ornamenting the embryonic shell and by lacking spiral larval sculpture (cf. Kowalke 1998).

Genus *Mohrensternia* Stoliczka, 1868

Type species: *Rissoa angulata* Eichwald, 1856 from the Badenian and Early Sarmatian of Central and East Europe.

Remarks.—The designation of *Rissoa inflata* Hörnes, 1856 as the type species according to Sacco (1895), as frequently cited in the literature, is incorrect. The earlier designation by Nevill (1885) is valid (see Ponder 1985).

Mohrensternia angulata (Eichwald, 1853)

Fig. 9A, B.

Rissoa angulata sp. nov.; Eichwald 1853: 268–269, pl. 10: 10.
Rissoa angulata Eichwald; Hörnes 1856: 577–578 (partim), pl. 48: 23 a.
Mohrensternia angulata (Eichwald); Friedberg 1923: 392, pl. 23: 15, 16.
Mohrensternia angulata (Eichwald); Jekelius 1944: 71, pl. 15: 7, 8.
Mohrensternia angulata (Eichwald); Papp 1954: 35–36, pl. 5: 27.
Rissoa (*Mohrensternia*) *angulata angulata* Eichwald; Boda 1959: 707, pl. 24: 12–16.
Mohrensternia angulata (Eichwald); Svagrovský 1971: 294–296, pl. 46: 1–9.

Material.—Thirteen specimens from the Early Sarmatian of Lednicé (formerly Eisgrub) E of Mikulov, Czech Republic, NHMW 2002z0029/0001.

Description.—The slender shell comprises up to 7 rounded whorls measuring up to 6 mm in height and up to 2.5 mm in width. Whorls slowly increase, separated by incised sutures. Sculpture consists of 10 broad orthocline to slightly opisthocyrt axial ribs whose intensity may decrease in the course of the last whorl. Slender morphs with regularly curving ribs exist alongside those with ribs increasing in thickness in the mid to abapical portion of the whorls. The last whorl forms 50–60% of total shell height. The holostomatous aperture is broad oval to rounded and is characterised by a very thin peristome.

The protoconch has 2.25–2.3 rounded whorls, which appear to be smooth. It measures 0.35–0.36 mm both in maximum diameter and in height. The first whorl measures 0.14–0.15 mm in maximum diameter and 0.03–0.04 mm in the width of the initial cap-like onset. The transition to the teleoconch is indistinct. The onset of the teleoconch is indicated by the formation of wavy axial folds which grade into axial ribs.

Remarks.—The dimension of the protoconch indicates an indirect development with inclusion of a free veliger stage. The veliger spent a brief period of probably one or two weeks within the plankton, feeding on phytoplankton.

Mohrensternia angulata is a typical and widespread species during the Early Sarmatian of the Vienna Basin and the Styrian Basin and is also known from Sarmatian deposits of

the Mid Danube Basin (Jekelius 1944), the Carpathian Foredeep (Friedberg 1923), Slovakia (Svagrovský 1971), and South-East Europe, e.g., Bulgaria and Romania (Kolesnikov 1935; Iljina 1998). Svagrovský (1971) noted a certain variability of the shell, with more or less slender outline and variable strength of the axial ribs; this was confirmed by the investigation of our material. Its roots reach back to the Badenian, when it is a rare element throughout the Central Paratethys, documented from Hungary, Poland, and Romania (Csepreghy-Meznerics 1950; Kokay 1966; Friedberg 1923).

Mohrensternia banatica (Jekelius, 1944)

Fig. 9C.

Mohrensternia pseudoangulata banatica var. nov.; Jekelius 1944: 72, pl. 15: 16–18.

Mohrensternia banatica (Jekelius); Papp 1954: 36–37, pl. 5: 30–33.

Mohrensternia banatica (Jekelius); Svagrovský 1971: 301–303, pl. 49: 1–12.

Material.—Four specimens from the Early Sarmatian of Eichkogel/Mödling, Austria (Vienna Basin), NHMW 2002z 0029/0002.

Description.—The small, high-spired shell comprising up to seven regularly increasing whorls measures up to 4 mm in height and up to 1.5 mm in width. The rounded whorls are separated by moderately deep sutures. Whorls are sculptured by 14 delicate, closely spaced, slightly wavy to sickle-shaped axial ribs, which regularly curve in the course of the whorls' flanks. Weaker spiral sculpture is more or less developed. The last whorl forms about 40% of total shell height. The holostomatous aperture is rounded to oval. It is characterised by a thin peristome.

The low conical protoconch comprises 2.25 rounded whorls measuring 0.36–0.37 mm both in height and in maximum diameter. The apparently smooth embryonic shell comprises one whorl, measuring 0.14–0.15 mm in maximum diameter and 0.03 mm in the width of the initial cap. It is well separated from the larval shell by a marked incision and a subsequent thickened rim. The larval shell is smooth and is terminated by a slightly thickened rim.

Remarks.—The protoconch indicates an indirect development with inclusion of a free planktonic larval stage. Size and dimensions of the protoconch closely resemble those of *Mohrensternia angulata*. *Mohrensternia banatica* differs, however, by a distinct demarcation of the embryonic shell from the subsequent larval shell with an incision and a thickened rim, indicating the thickened apertural margin of the hatchling. The transition from the larval shell to the teleoconch is sharp in the case of *M. banatica*, indicated by a rim of the aperture of the pediveliger ready for metamorphosis and the abrupt onset of the adult sculpture, whereas in *M. angulata* this transition is indistinct.

According to Papp (1954) this species was also found in the Early Sarmatian of the drilling St. Marx in the Vienna Basin. Svagrovský (1971) mentioned its occurrence in the Sarmatian of Slovakia, but remarked its absence from the Pannonian Basin, the Carpathian Foredeep, and from the Sarmatian of South-East Europe, whereas Iljina (1998) mentioned it from the Early Sarmatian of Hungary.

Mohrensternia hollabrunnensis sp. nov.

Fig. 9D.

Derivation of the name: Named after the type locality.

Type horizon and locality: Early Sarmatian silt at Hollabrunn (Molasse Basin/Lower Austria).

Material.—Only the holotype (NHMW 2002z0029/0003) is known.

Description.—The broad-conical shell comprises six slightly rounded whorls separated by deeply incised sutures. The holotype measures 4 mm in height and 2.16 mm in width. Sculpture consists of 20–22 straight axial ribs about as broad as the gaps between them. The last whorl forms 70% of total shell height. The large oval aperture is slightly inclined to the main axis of the shell.

The low-conical protoconch comprises 2.2 slightly rounded whorls measuring 0.21–0.22 mm in height and 0.34 mm in maximum diameter. The first whorl measures 0.17 mm in maximum diameter and 0.04–0.05 mm in the width of the initial cap. Transitions from the embryonic to the larval shell and sculpture are not evident. The transition to the teleoconch is indistinct. The onset of the adult shell is indicated by the formation of weak axial folds that grade into regular axial ribs.

Remarks and differences.—The protoconch indicates a free larval stage during early ontogeny. The large initial whorl may indicate a yolk-rich embryogenesis, probably with a subsequent lecithotrophic larval stage.

Mohrensternia hollabrunnensis has a similar sculpture as *M. hydrobioides*, but differs by a protoconch that is wider than high, by a larger embryonic shell, and by a broader teleoconch; the latter is sculptured by more but thinner axial ribs that do not decrease in the course of the last teleoconch whorls. *Mohrensternia hollabrunnensis* is distinguished from *M. inflata*, which has a similar teleoconch shape, by its smaller larval shell but larger embryonic shell and by its teleoconch sculpture of more but thinner axial ribs.

Mohrensternia hydrobioides Hilber, 1897

Fig. 9E, F.

Mohrensternia hydrobioides sp. nov.; Hilber 1897: 199, pl. 1: 12–14.

Mohrensternia hydroboides [sic!] Hilber; Papp 1954: 35; pl. 5: 22, 23.

Rissoa (*Mohrensternia*) *inflata hydrobioides* Hilber; Boda 1959: 706, pl. 23: 15–23.

Mohrensternia hydrobioides Hilber; Svagrovský 1971: 289–292, pl. 45: 1–8.

Material.—Two specimens (original material in Papp 1954: pl. 5: 22, 23) and four specimens from the Early Sarmatian of Waldhof, Styria/Austria, NHMW 2002z0029/0004.

Description.—The shell comprises six regularly increasing, slightly rounded whorls measuring up to 5.5 mm in height and up to 3.2 mm in width. Whorls are separated by distinct, moderately deep sutures. Sculpture consists of 14–16 straight axial ribs about as broad as the gaps between them. The ribs are most strongly developed on the initial two whorls of the

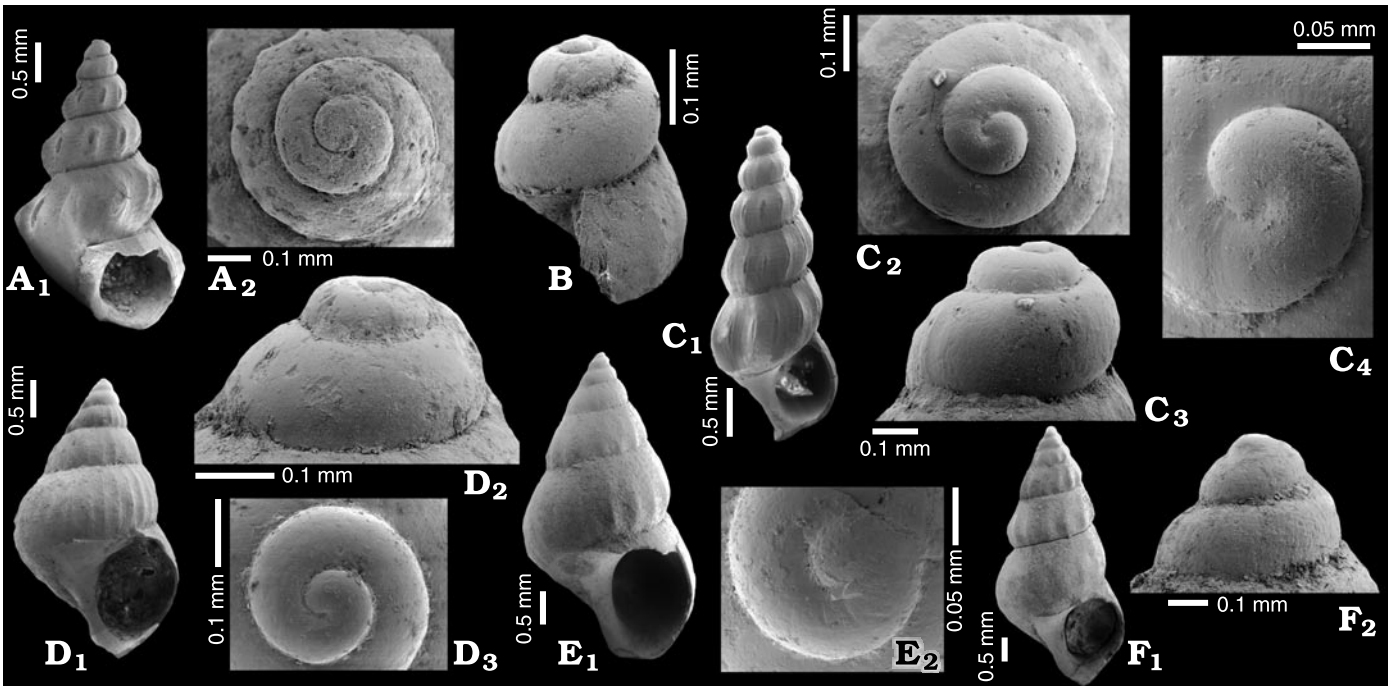

Fig. 9. Four species of *Mohrensternia* Stoliczka, 1868. **A**, **B**. *Mohrensternia angulata* Eichwald, 1853. Specimen (NHMW 2002z0029/0001) from the Early Sarmatian of Lednicé, Czech Republic (A_1). Protoconch of the same specimen as in A_1 in apical view (A_2). The onset of the teleoconch is indicated by the formation of wavy axial folds which grade into axial ribs. **B**. Apex fragment of the specimen (NHMW 2002z0029/0001) from the Early Sarmatian of Lednicé, Czech Republic. **C**. *Mohrensternia banatica* (Jekelius, 1944). Specimen (NHMW 2002z0029/0002) from the Early Sarmatian of Eichkogel/Mödling, Vienna Basin (Austria) (C_1). Apical and lateral view of the protoconch of the same specimen as in C_1 (C_2, C_3). The protoconch is terminated by a slightly thickened rim. Detailed view of the embryonic shell of the same protoconch as in C_3 (C_4). The embryonic shell is well separated from the larval shell by a marked incision and a subsequent thickened rim. **D**. *Mohrensternia hollabrunnensis* sp. nov. Holotype (NHMW 2002z0029/0003) from the Early Sarmatian of Hollabrunn (Molasse Basin, Lower Austria) (D_1). Lateral and apical view of the protoconch of the same specimen (D_2, D_3). **E**, **F**. *Mohrensternia hydrobioides* Hilber, 1897. Specimen (NHMW 2002z0029/0004) from the Early Sarmatian of Waldhof, Styria/Austria (E_1). Apical view of the initial whorl of the same specimen (E_2). **F**. Specimen (collection A. Papp, NHMW 2002z0029/0004) from the Early Sarmatian of Siebenhirten (F_1). Protoconch of the same specimen in lateral view (F_2).

teleoconch, and they decrease on later whorls. The last two whorls are smooth in some individuals (Svagrovský 1971). The last whorl forms 50–60% of total shell height. The small holostomatous aperture is rounded to oval. The peristome is very thin.

The conical protoconch comprises two rounded whorls. It measures 0.36 mm in height and in maximum diameter. The first whorl measures 0.14–0.15 mm in maximum diameter and 0.03–0.04 mm in the width of the initial cap. Transitions of the embryonic to the larval shell and sculpture are not evident. The transition to the adult shell is indistinct. The onset of the teleoconch is indicated by the formation of axial folds that grade into ribs.

Remarks.—The protoconch is indicative of an indirect development including a free planktonic veliger stage. According to Papp (1954), *Mohrensternia hydrobioides* closely resembles *M. inflata*, but differs by its smaller, more slender shell. The "transitional" morphs he also mentioned could not be confirmed by our investigations. *Mohrensternia hydrobioides* is well distinguished from *M. inflata* by its smaller protoconch, comprising about 0.5 whorls less, and by its considerably broader teleoconch. Svagrovský (1971) mentioned the variability of *M. hydrobioides*, with the occurrence of phenotypes having a slender shell outline and of those with broad conical shape and a higher body whorl. These are most probably represented by *Mohrensternia hollabrunnensis* sp. nov., which is distinguished by its flattened protoconch with bulbous embryonic whorl and by its broad, conical teleoconch with a sculpture of more and weaker axial ribs.

Papp (1954) mentioned *Mohrensternia hydrobioides* also from the Early Sarmatian of Siebenhirten in the northern Vienna Basin. According to Svagrovský this species occurred in several South-East European localities (see also Kolesnikov 1935; Iljina 1998).

Mohrensternia inflata (Hörnes, 1856)

Fig. 10A, B.

Rissoa inflata; Andrzejowsky in Deshayes 1835: 321, nomen nudum.
Rissoa inflata Andrzejowsky; Hörnes 1856: 576, pl. 48: 22b.
Mohrensternia inflata (Andrzejowsky); Jekelius 1944: 69, pl. 14: 14–18.
Mohrensternia inflata (Andrzejowsky); Papp 1954: 34, pl. 5: 12–17.
Mohrensternia inflata (Andrzejowsky); Korobkov 1955: 155, pl. 21: 8a, b.
Rissoa (*Mohrensternia*) *inflata inflata* Andrzejowsky; Boda 1959: 705, pl. 23: 6–11.
Mohrensternia inflata (M. Hoernes); Svagrovský 1971: 282–285, pl. 43: 1–12.
Mohrensternia inflata (Andrzejowsky); Ponder 1985: 77G.

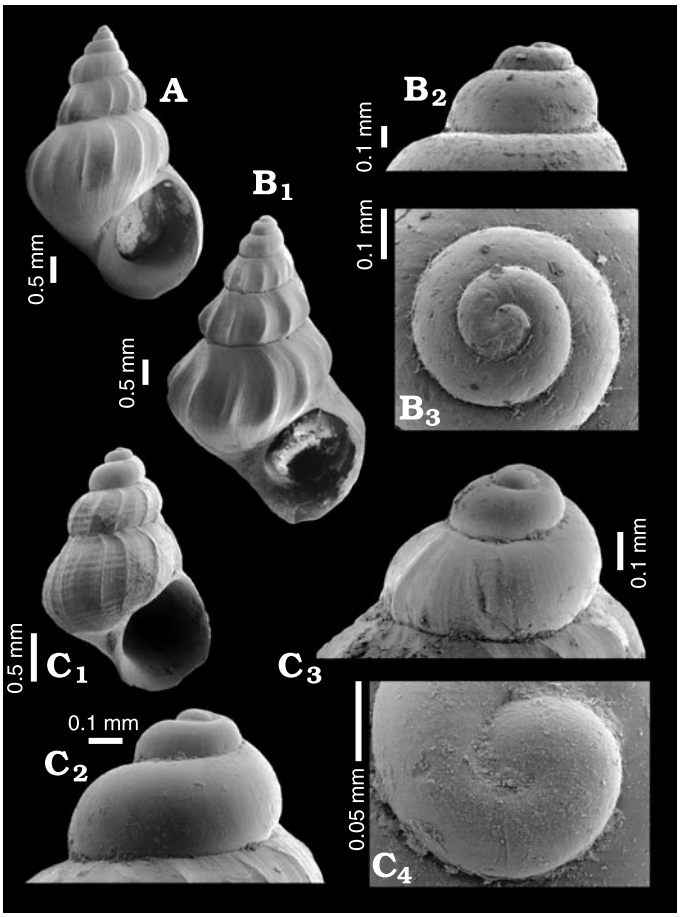

Fig. 10. Two species of *Mohrensternia* Stoliczka, 1868. **A**, **B**. *Mohrensternia inflata* (Hörnes, 1856). **A**. Specimen (NHMW 2002z0029/0005) from the Early Sarmatian of Hollabrunn. **B**. Specimen (NHMW 2002z0029/0006) from the Early Sarmatian of Vienna-Nußdorf. Protoconch in lateral (B_2) and apical (B_3) views. The embryonic shell is separated from the subsequent larval shell by a slightly thickened rim. The onset of the teleoconch is indicated by the formation of weak axial folds, grading into regular axial ribs. **C**. *Mohrensternia moesinensis* Jekelius, 1944. Specimen (collection A. Papp, NHMW 2002z0029/ 0008) from the Early Sarmatian of Eichkogel (C_1). Lateral views of the protoconch of the same specimen as in C_1 (C_2, C_3). The protoconch is terminated by a slightly projecting rim, which is slightly thickened in its adapical portion. Detailed apical view of the initial whorl of the same protoconch as in C_3 (C_4). The embryonic shell has fine spiral sculpture and it is terminated by a slightly thickened rim.

Material.—Five specimens from Hollabrunn, Lower Austria (Molasse Basin), NHMW 2002z0029/0005; four specimens from Vienna-Nußdorf, Austria (Vienna Basin), NHMW 2002z0029/0006; six specimens from Vienna-Ottakring, Austria (Vienna Basin), NHMW 2002z0029/0007.

Description.—The comparatively large, thin shell has a broad, conical shape. It measures up to 8 mm in height and up to 5 mm in width, comprising 5–6 rounded, regularly increasing whorls with maximum convexity in the abapical half of the whorls. These are separated by distinct, moderately incised sutures. Twelve rounded orthocline to slightly opisthocyrt axial ribs are present, regularly following the outline of the whorls, with more or less broad gaps between them. Additional sculpture consists of regular, closely spaced, sinuous growth lines. Spiral sculpture is not evident. The last whorl forms about 60% of total shell height. The large holostomatous aperture is broad-oval and is characterised by a very thin peristome. The parietal portion is slightly pointed.

The large, conical, smooth protoconch comprises 2.5 rounded whorls measuring 0.43–0.44 mm in height and 0.4–0.42 mm in maximum diameter. The embryonic shell comprises 0.8–0.9 whorls measuring 0.15–0.16 mm in maximum diameter and 0.03–0.04 mm in the width of the initial cap; it is separated from the subsequent larval shell by a slightly thickened rim on the shell. The transition from the larval shell to the teleoconch is indistinct. The onset of the adult shell is indicated by the formation of weak, indistinct axial folds that grade into regular axial ribs.

Remarks.—Specimens with slightly sickle-shaped axial ribs have been described by Friedberg (1923) and have been assigned to *Mohrensternia perinflata* Friedberg, which most probably represents a synonym of *M. inflata* (Svagrovský, 1971). Our material from the Vienna Basin exhibits several specimens with opisthocyrt course of the axial ribs, but with identical protoconch and teleoconch dimensions fully corresponding to specimens with orthocline ribs.

Mohrensternia inflata differs from *M. angulata* ,which has a similar sculpture, by its considerably larger protoconch and by a broader teleoconch. It is distinguished from *M. hollabrunnensis* sp. nov. with similar outline by its considerably larger protoconch, which is higher than wide (versus wider than high in *M. hollabrunnensis*). The latter differs furthermore by its teleoconch sculpture of more and weaker axial ribs.

Papp (1954) also described *Mohrensternia inflata* from Early Sarmatian deposits of Heiligenstadt, Pfaffstätten, and Siebenhirten (Vienna Basin, Austria). According to Svagrovský (1971) this species is widespread in Early Sarmatian deposits of the Mid Danube Basin and of the Carpathian Foredeep. Iljina (1998) mentioned its occurrence in Early Sarmatian deposits of SE Europe and in Middle Sarmatian deposits of Georgia.

Mohrensternia moesinensis Jekelius, 1944

Fig. 10C.

Mohrensternia moesinensis sp. nov.; Jekelius 1944: 72, pl. 15: 19–22.
Mohrensternia moesinensis Jekelius; Papp 1954: 36, pl. 5: 34–35.
Mohrensternia moesinensis Jekelius; Svagrovský 1971: 310–311, pl. 52: 7–13.

Material.—Two specimens (original material in Papp 1954: pl. 5: 34, 35) from the Early Sarmatian of Eichkogel, Vienna Basin, NHMW 2002z0029/0008.

Description.—The small, stout, rather egg-shaped shell comprises five slightly rounded whorls which are separated by moderately incised sutures. The shell measures up to 3 mm in height and up to 1.7 mm in width. The last two whorls are characterised by rather flat sides. Sculpture consists of closely spaced, sinuous growth lines and 10–12 weak, thin axial ribs with broad gaps between them, crossed by 8–10 more or less

strongly developed spiral threads. The last whorl forms about 70–75% of total shell height. The holostomatous aperture is broad-conical to rounded. The parietal portion is pointed. A very narrow, slit-like umbilicus is present.

The large, conical protoconch comprises 2.75 slightly rounded whorls measuring 0.47 mm both in height and in maximum diameter. The embryonic shell comprises one whorl measuring 0.14–0.15 mm in maximum diameter and 0.03–0.04 mm in the width of the initial cap. Three very fine spiral stripes are visible. The embryonic shell is terminated by a slightly thickened rim. The subsequent larval shell appears to be smooth. It is terminated by a slightly projecting rim, which is slightly thickened in its adapical portion. The onset of the teleoconch is indicated by the formation of regular growth lines and axial ribs.

Remarks.—According to Svagrovský (1971), *Mohrensternia moesinensis* occurred in the Sarmatian of the Mid Danube Basin. Similar but larger-sized, broad-conical shells with more flattened whorls restricted to the Mysla Beds, Slovakia, have been described as *Mohrensternia rectecostata* by Svagrovský (1971).

Mohrensternia pseudoangulata politioanei Jekelius, 1944

Fig. 11A.

Mohrensternia pseudoangulata politioanei n. var.; Jekelius 1944: 72, pl. 15: 11–15.
Mohrensternia pseudoangulata politioanei Jekelius; Svagrovský 1960: 76, pl. 5: 5.
Mohrensternia pseudoangulata politioanei Jekelius; Svagrovský 1971: 299–301, pl. 48: 1–7.

Material.—Four specimens from the Early Sarmatian of Waldhof, Styrian Basin, NHMW 2002z0029/0009; two specimens from Siebenhirten, Vienna Basin, NHMW 2002z0029/0010; 3 specimens from Hollabrunn, Molasse Basin, NHMW 2002z0029/0011 (all Early Sarmatian).

Description.—The slender shell comprises 6–7 regularly increasing whorls measuring up to 7 mm in height and up to 2.8 mm in width. The rounded whorls are separated by deep sutures. Sculpture consists of 10–12 strongly developed orthocline axial ribs with broad gaps between them, crossed by 12 fine spiral threads. The last whorl forms 50% of total shell height. The holostomatous aperture has an inclined, oval shape. It is characterised by a thin peristome and by a pointed anterior and posterior portion.

The protoconch comprises 2.25–2.3 rounded whorls measuring 0.34–0.35 mm in height and 0.35–0.36 mm in maximum diameter. The embryonic shell comprises 0.8–0.9 whorls measuring 0.12–0.13 mm in maximum diameter and 0.04–0.05 mm in the width of the initial cap. The transition to the larval shell is indicated by a slight rim on the shell. The larval shell appears to be smooth. The transition to the teleoconch is indistinct. The onset of the adult shell is indicated by the formation of weak axial folds that grade into strong axial ribs.

Remarks.—The protoconch is indicative of an indirect development including a free planktonic veliger stage. *M. pseudoangulata politioanei* differs from *M. pseudoangulata pseudoangulata* Hilber, 1897 by its considerably less slender shell. It furthermore differs by its less angular outline. It differs from *M. banatica* by its slightly smaller protoconch but slightly larger cap-like onset of the embryonic shell, and by its less slender shell with less strongly developed axial ribs, which not orthocline in course. *Mohrensternia pseudoangulata politioanei* is distinguished from the similar *M. angulata* by its slightly smaller embryonic shell, but slightly larger initial cap, and by the lack of spiral sculpture on the teleoconch whorls.

Mohrensternia sarmatica Friedberg, 1923

Mohrensternia sarmatica sp. nov.; Friedberg 1923: 389, pl. 23: 8–10.
Mohrensternia sarmatica Friedberg; Papp 1954: 35.
Mohrensternia sarmatica Friedberg; Korobkov 1955: pl. 21: 10.
Rissoa (*Mohrensternia*) *inflata sarmatica* Friedberg; Boda 1959: 705, pl. 23: 12–14.
Mohrensternia sarmatica Friedberg; Svagrovský 1971: 306–308, pl. 51: 1–10.

Material.—Four specimens from Siebenhirten, Lower Austria, IRSNB IG 23693.

Description.—The small, not very slender, conical shell consists of 5–6 regularly increasing, rounded whorls with a maximum convexity in the median portion of the whorls or just below, causing an angulated shell outline. The shell measures up to 4.8 mm in height and up to 3 mm in width. Whorls are separated by marked, deep sutures. Sculpture consists of 12 strongly developed, stout, orthocline axial ribs, which diminish on the lower half of the last whorl. The base appears to be smooth. The last whorl forms about 50–60% of total shell height. The very thin aperture has a broad-oval to roundish outline with a prominent, pointed parietal portion.

The protoconch is not well preserved. It comprises about 2.5 well-rounded whorls and measures 0.38–0.4 mm in height and in maximum diameter. The diameter of the corroded initial whorl amounts to about 0.14 mm. The onset of the teleoconch is indicated by the less rounded, wavy outline of the whorls and by the formation of the adult sculpture of axial ribs.

Remarks.—According to Papp (1954), *Mohrensternia sarmatica* is closely related to *M inflata* and differs by a slightly more slender shell with fewer but more strongly developed ribs, causing a more angulate outline of the whorls. The axial ribs are orthocline, not sickle-shaped as in *M. inflata*. *Mohrensternia sarmatica* also differs in protoconch morphology (slightly smaller protoconch). In contrast to the interpretation of Papp (1954), who treats *Mohrensternia soceni* Jekelius, 1944 (p. 71, pl. 15: 4–6) as closely related with *M. sarmatica*, the latter differs distinctly by its smaller, more slender shell, comprising more and regularly increasing whorls, which are more strongly convex. The aperture of *M. sarmatica* is not detached from the spire and its protoconch is considerably smaller.

Mohrensternia sarmatica occurred in the Sarmatian of the Vienna Basin, the Styrian Basin, the Carpathian Foredeep, the Mid Danube Basin and in the Sarmatian of South-East Europe (Svagrovský 1971).

Mohrensternia soceni Jekelius, 1944

Fig. 11B.

Mohrensternia soceni sp. nov.; Jekelius 1944: 71; pl. 15: 4–6.
Mohrensternia soceni Jekelius; Svagrovský 1971: 315–317, pl. 53: 1–5.

Material.—Four specimens from Siebenhirten, Vienna Basin, NHMW 2002z0029/0013; two specimens from Hollabrunn, Molasse Basin, NHMW 2002z0029/0012 (all Early Sarmatian).

Description.—The not very slender shell measuring up to 6 mm in height and up to 3 mm in width comprises up to seven regularly increasing whorls. Sculpture consists of 10 prominent axial ribs with about equally broad gaps between them. The axial ribs reach a maximum convexity on the lower half of the whorls, near the abapical suture, causing an angulated outline of the whorls. Spiral sculpture is absent. The last whorl forms 50–60% of total shell height. The aperture, which is slightly detached from the spire, has a rounded oval shape. It is characterised by a very thin peristome.

The protoconch comprises 2.5 rounded whorls measuring 0.45 mm in height and in maximum diameter. The embryonic shell amounts to 0.9 whorls measuring 0.15–0.16 mm in maximum diameter and 0.03–0.04 mm in the width of the initial cap. It is demarcated from the subsequent larval shell by a slightly thickened rim followed by a slight incision of the shell. The larval shell appears to be smooth. It is terminated by an indistinct rim. The onset of the teleoconch is indicated by the formation of axial folds, causing a wavy outline of the shell.

Remarks.—This species was originally described by Jekelius (1944) from the Early Sarmatian of Romania (Banat). According to Svagrovský (1971) it also occurred in the Sarmatian of Slovakia.

Mohrensternia styriaca Hilber, 1897

Mohrensternia Styriaca sp. nov.; Hilber 1897: 202, pl. 1: 11.
Mohrensternia styriaca Hilber; Papp 1954: 36, pl. 5: 24–26, 28, 29.
Rissoa (*Mohrensternia*) *angulata styriaca* Hilber; Boda 1959: 707, pl. 24: 17–21.
Mohrensternia styriaca Hilber; Svagrovský 1971: 303–306, pl. 50: 1–7.

Material.—Three specimens from the Early Sarmatian of Siebenhirten, Lower Austria, IRSNB IG 23693.

Description.—The slender, quite large shell is characterised by rounded whorls separated by deep sutures. It measures up to 6.2 mm in height and up to 3 mm in width. Sculpture consists of 10–12 strong axial ribs with broad and deep gaps. The ribs are strongly angulate in the mid portion, causing the angulate shell outline. Axial elements are crossed by distinct spiral threads. The last whorl amounts to about 50% of total shell height. The holostomatous aperture is roundish to oval with slightly pointed anterior and posterior portion.

The protoconch is not well preserved. It comprises about 2.25 well-rounded whorls measuring 0.35–0.36 mm in height and maximum diameter. The diameter of the first whorl is 0.16–0.17 mm. The onset of the teleoconch is indicated by the formation of axial folds, causing a wavy outline of the whorl.

Remarks.—Differs from the similarly slender morphs of *M. pseudoangulata politioanei* (which has strongly developed axial ribs) due to the larger last whorl and to its angular shell outline. The protoconch of *M. styriaca* differs by having a considerably larger initial whorl. The shell is similar to *M. angulata*, but is sculptured with axial ribs becoming larger in the mid portion of the whorls, causing a strongly angulated outline of the whorls.

According to Papp (1954), *M. styriaca* is common in the Early Sarmatian of Hollabrunn (Molasse Basin), Pfaffstätten (Vienna Basin), and Waldhof/Styria (Styrian Basin). According to Svagrovský (1971) and Iljina (1998) it co-occurred in the Sarmatian of the Pannonian Basin and of Slovakia.

Mohrensternia pfaffstaettensis sp. nov.

Fig. 11C.

Derivation of the name: Named after the type locality.
Type horizon and locality: Early Sarmatian silty marls of Pfaffstätten, Vienna Basin/Lower Austria.

Material.—The holotype (NHMW 2002z0029/0014) and three paratypes (NHMW 2002z0029/0015) from Pfaffstätten, Vienna Basin/Lower Austria are present.

Description.—The small, slender shell comprises six regularly increasing, rounded whorls separated by deep sutures. The holotype measures 2.43 mm in height and 1.06 mm in width. Teleoconch whorls are sculptured by 14 sickle-shaped axial ribs which diminish in their abapical portion on the last whorl. Additional sculpture consists of about ten more or less distinct, granulated spiral threads, which appear to be strongest in the mid portion of the whorls. The last whorl forms about 50% of total shell height. A slit-like umbilicus is indicated. The inclined, egg-shaped aperture is characterised by a broad anterior notch and by a slightly pointed posterior portion.

The protoconch comprises 2.5 rounded whorls measuring 0.37 mm in height and 0.36 mm in maximum diameter. The embryonic shell has about one whorl. It measures 0.04 mm in the width of the initial cap and 0.13–0.14 mm in maximum diameter. Three very finely granulated spiral threads sculpture the embryonic shell. It is terminated by a very fine but distinct, slightly sinuous rim on the shell. The subsequent larval shell is smooth except for growth lines. It is terminated by a slightly sinuous rim. The onset of the teleoconch is indicated by the formation of the adult sculpture of strong axial ribs and subordinated spiral threads.

Remarks and differences.—The protoconch points to an indirect development including a free planktotrophic larval stage. *Mohrensternia pfaffstaettensis* sp. nov. differs from the similar *M. banatica* by its smaller shell with higher body whorl and by a sculpture consisting of more and sickle-shaped ribs. The protoconch of *M. pfaffstaettensis* has about the same size, but comprises 0.25 larval whorls more, and it lacks the prominent incision characterising the onset of the larval shell in *M. banatica*. The rim terminating the embryonic shell is less thickened than in *M. banatica*. *M. pfaffstaettensis* differs from *M. pseudangulata politioanei* by its much weaker ribs and less angular shell outline, by the higher body whorl, by its proto-

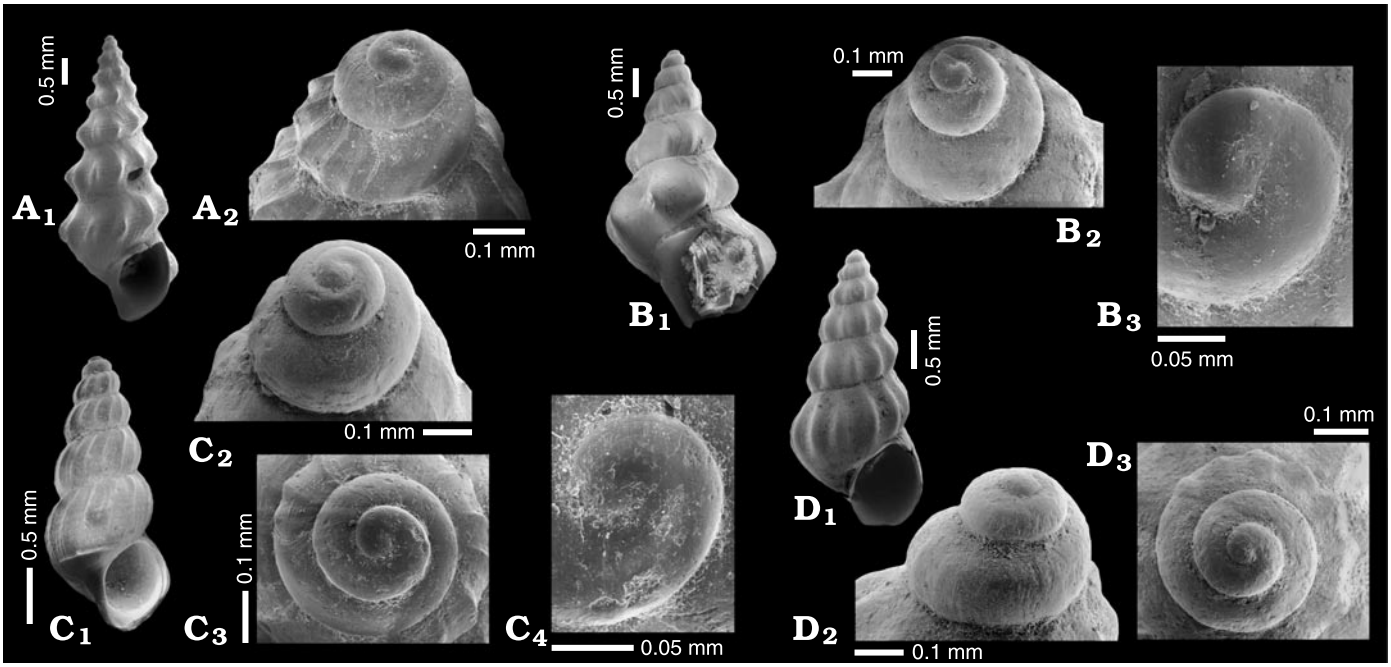

Fig. 11. Four species of *Mohrensternia* Stoliczka, 1868. **A**. *Mohrensternia pseudoangulata politioanei* Jekelius, 1944. Specimen (NHMW 2002z0029/0009) from the Early Sarmatian of Waldhof, Styria/Austria (A_1). Protoconch of the same specimen in lateral view (A_2). The onset of the teleoconch is indicated by the formation of weak axial folds, grading into axial ribs. **B**. *Mohrensternia soceni* Jekelius, 1944. Specimen (NHMW 2002z0029/0012) from the Early Sarmatian of Hollabrunn (B_1). Protoconch of the same specimen as in B_1 in lateral view (B_2). The onset of the teleoconch is indicated by the formation of axial folds. Detailed apical view of the initial whorl of the same protoconch as in B_2 (B_3). The embryonic shell is demarcated from the subsequent larval shell by a slightly thickened rim followed by an incision of the shell. **C**. *Mohrensternia pfaffstaettensis* sp. nov. Holotype (NHMW 2002z0029/0014) from the Early Sarmatian of Pfaffstätten, Vienna Basin/Lower Austria (C_1). Lateral and apical view of the protoconch of the same specimen as in C_1 (C_2, C_3). The protoconch is terminated by a slightly sinuous rim. The onset of the teleoconch is indicated by the formation of strong axial ribs and subordinated spiral threads. Detailed view of the initial whorl of the same protoconch as in C_3 (C_4). The embryonic shell has a finely granulated spiral sculpture. It is terminated by a slightly sinuous rim. **D**. *Mohrensternia waldhofensis* sp. nov. Holotype (NHMW 2002z0029/0004) from the Early Sarmatian of Waldhof, Styria/Austria (D_1). Lateral and apical view of the protoconch of the same specimen (D_2, D_3). The transition to the teleoconch is indicated by a thickened rim which is not projecting.

conch comprising about 0.25 whorls more, and by its larger embryonic shell but slightly smaller initial cap. *Mohrensternia pfaffstaettensis* is distinguished from *M. waldhofensis* sp. nov. by its smaller, less angular shell, and weaker sculpture of sickle-shaped ribs; its protoconch, however, is larger, slightly higher than wide (*versus* considerably wider than high in *Mohrensternia waldhofensis*).

Mohrensternia waldhofensis sp. nov.

Fig. 11D.

Derivation of the name: Named after the type locality.

Type horizon and locality: Early Sarmatian, silty to marly brackish water clay at Waldhof near Wetzelsdorf, Styria/Austria.

Material.—The holotype (NHMW 2002z0029/0016) and two paratypes (NHMW 2002z0029/0017) are present from the Early Sarmatian of Waldhof, Styria.

Description.—The small, moderately slender, turreted shell comprises up to seven slightly rounded whorls separated by moderately incised sutures. The holotype measures 3.42 mm in height and 1.64 mm in width. Sculpture consists of 12 regularly rounded, broad axial ribs, about as broad as the gaps between them. Indistinct, subordinated spiral striae cross the axial ribs. The last whorl forms about 50% of total shell height. The oval aperture is thin, holostomatous and is characterised by a slightly pointed posterior portion. A very narrow, slit-like umbilicus is present.

The broad, barrel-shaped protoconch comprises 2.25 slightly rounded whorls measuring 0.34 mm in height and 0.29 mm in maximum diameter. The first whorl measures 0.12–0.13 mm in maximum diameter and 0.04 mm in the width of the initial cap. The transition from the embryonic shell to the larval shell is indistinct. The transition from the larval shell to the teleoconch is indicated by a straight, thickened rim, which is not projecting.

Remarks and differences.—The protoconch indicates an indirect development including a free planktonic larval stage. *Mohrensternia waldhofensis* sp. nov. differs from *M. banatica* (which has a similar size and outline) by the higher body whorl and the coarser sculpture of fewer but stronger axial ribs. The protoconch of *M. waldhofensis* is higher than wide, whereas it is as high as wide in *M. banatica*, which is furthermore distinguished by a well-demarcated embryonic shell. *Mohrensternia waldhofensis* differs from *M. angulata* (with similar sculpture) by its smaller shell and by the oval aperture, which is more rounded in *M. angulata*. The protoconch differs in being higher than wide in *M. waldhofensis* (as high as wide in *M. angulata*).

Discussion and conclusions

Rissoidae most probably derived from palaeorissoinid-like ancestors that had a strong larval sculpture of collabral axial ribs and additional weaker spirals (Harzhauser and Kowalke 2001; Gründel and Kowalke 2002). The disintegration of this strong larval sculpture could have led to the tuberculate and zigzag-shaped spiral sculpture present in modern Rissoidae, especially in the genus *Alvania*. The Recent Mediterranean species *A. mamillata* and *A. montagui* are characterised by a lecithotrophic development including a free larval stage; during this stage, larvae feed on remaining embryonic yolk rather than phytoplankton, as indicated by the bulbous protoconch whorls and a larval shell only comprising about one whorl. These species are easily distinguishable from similar fossil and Recent Mediterranean species with planktotrophic development.

Within the Badenian of the Central Paratethys, the modern genera *Rissoa*, *Alvania*, and *Manzonia* are represented by species with indirect development. No lecithotrophic development is documented. Badenian representatives closely resemble the Recent representatives of the genera, which settle littoral marine habitats of the Mediterranean Sea and of the adjacent Atlantic Ocean (Thiriot-Quiévreux 1980; Ponder 1985; Kowalke 1998). As indicated by protoconch morphologies, the species were distributed by planktotrophic larvae that spent a few weeks within the plankton. *Alvania* and *Manzonia* differ from *Rissoa* in the morphology of both the teleoconch and protoconch: usually, stronger embryonic and larval sculptures are present. Closely spaced spiral threads and rows of tubercles are arranged all over the embryonic and larval shells, whereas *Rissoa* spp. exhibit only few fine spiral threads or rows of granules on the abapical half of the larval shells. The separation of a subfamily Alvaniinae, as suggested by Nordsieck (1972) and Golikov and Starobogatov in Golikov and Scarlato (1972), could not be followed because the anatomy, operculum and radula morphology exhibit no significant differences (cf. Ponder 1985). Moreover, the stronger embryonic and larval sculpture present in many species of *Alvania* do not justify the status of a separate subfamily because species with few spiral threads sculpturing the larval shell and rare species with very weak larval sculpture, e.g. of the subgenus *Punctulum*, exist.

Mohrensterniinae are well separated from the Rissoinae and Rissoininae by their protoconch morphology, and their status as a separate subfamily of the Rissoidae could be confirmed (see supplement to the subfamily diagnosis in the systematic part). Ponder (1985) mentioned the similarity of *Mohrensternia* with *Rissoa* and also with some hydrobiids regarding teleoconch morphology, but had not described the protoconch of *Mohrensternia* in any detail. An assignment to Hydrobiidae was in his opinion supported by their brackish and freshwater habitats. The palaeoecological interpretation was based on descriptions of Neogene deposits of Central and Eastern Europe by Stoliczka (1868). Mohrensterniinae in fact never occurred in freshwater, but might have preferred brackish conditions.

The distribution of the Miocene species of Rissoinae does not indicate any north/south trend within the Badenian of the Central Paratethys. Similarly, the distribution of several Miocene species along the Atlantic shores as far north as the North Sea Basin (Janssen 1984; Gürs and Weinbrecht 2001) documents that climate was not a major limiting factor in the distribution of Rissoinae, as it is in Recent times. For the distribution of recent species, see e.g., Warén (1996). Thus, the abrupt extinction of *Alvania* and the strong decrease of *Rissoa* in the Early Sarmatian was most probably triggered solely by changes in the water chemistry and not by climate shifts. This drastic change in faunal compositions was followed by the Mohrensterniinae taking over all shallow marine habitats formerly predominated by Rissoinae. The faunal impoverishments and the euryhaline character of the accompanying faunal elements indicates an extreme character of the *Mohrensternia* habitat.

Mohrensternia was already established in the Badenian faunas. Therefore it might have been expected to have experienced its first bloom in the Central Paratethys during the Wielician substage, when hypersaline conditions prevailed from Poland to Romania. Nevertheless, there is no evidence for any *Mohrensternia* acme during this phase. In contrast, *Mohrensternia* flourished during the Karaganian and Maeotian in the Eastern Paratethys. Thus, we interpret the genus to have favoured reduced marine, but not hypersaline conditions. This also agrees well with the fact that *Mohrensternia* became nearly extinct in the Central Paratethys at the beginning of the *Ervilia* Zone. Here, oolithic sediments, the growth of foraminifera bioherms and the considerable increase of shell thickness in the mollusc fauna point to a shift towards marine to hypersaline waters oversaturated in $CaCO_3$.

Acknowledgements

Annie Dhondt provided material from the Institut Royal des Sciences Naturelles de Belgique, Brussels. Renate Walter, Zoological Institute and Museum, Hamburg, assisted with SEM. Michael Stachowitsch, Vienna, improved the English. Willy J.M. Sleurs, Brussels, Friedrich Strauch, Münster, and an anonymous reviewer gave helpful comments on the manuscript. Investigations of the evolution of European Caenozoic brackish-water faunas were supported by the Deutsche Forschungsgemeinschaft (DFG, grants KO 2066/ 1-1, KO 2066/3-1) and the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich (FWF, grant P 13745 Bio). To all these persons and institutions we express our sincere thanks.

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