Morphology and taxonomy of Late Badenian to Sarmatian *Mohrensternia* (Gastropoda: Rissooidea) of the Central Paratethys

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ABSTRACT:


The protoconch and teleoconch morphology of the Late Badenian and Sarmatian species of the genus *Mohrensternia* of the Central Paratethys are described and illustrated. Eight species of the genus are considered valid: *Mohrensternia inflata* HÖRNES, 1856, *M. sarmatica* FRIEDBERG, 1923, *M. pseudinflata* HILBER, 1897, *M. perinflata* FRIEDBERG, 1923, *M. angulata* (EICHWALD, 1830), *M. pseudangulata* HILBER, 1897, *M. banatica* JEKELIUS, 1944, and ? *M. friedbergi* sp. nov. A lectotype is designated for *Rissoa angulata* EICHWALD, 1830, the type species of *Mohrensternia* STOLICZKA, 1868. The type material of all species introduced by W. FRIEDBERG (1923) is revised and lectotypes are designated for *M. sarmatica*, *M. pseudosarmatica* and *M. perinflata*.

Key words: Gastropoda, Rissoidae, *Mohrensternia*, Shell morphology, Taxonomy, Miocene, Paratethys.

INTRODUCTION

The first studies of Late Badenian and Sarmatian rissoids of the Central Paratethys were the milestone works of EICHWALD (1830-1853), who described *Rissoa angulata*, later designated by NEVILL (1885) as the type species of the genus *Mohrensternia*. EICHWALD also described a few other *Rissoa*-like gastropods, characterised by thin-walled shell, strong axial ribs, aperture with indeterminate growth (sensu VERMEIJ & SIGNOR 1992, i.e. lacking a thickened outer lip) and slightly curved and lengthened base.

Subsequently HÖRNES (1856) contributed significantly to rissoid taxonomy, improving the nomenclature of all species of the genus then known in the European Miocene.

STOLICZKA (1868) erected the genus *Mohrensternia* for a few Miocene rissoid species (e.g. *Rissoa angulata* EICHWALD, 1830 and *R. inflata* HÖRNES, 1856), which occur in the semi-marine to brackish-water deposits of Central and Eastern Europe. Further new species of *Mohrensternia* were described by ANDRUSOV (1890) and HILBER (1897). FRIEDBERG (1911-1928) and KOLESNIKOV (1935) carried out detailed investigations of the Miocene rissoids (including *Mohrensternia*) from the Eastern Paratethys. KOLESNIKOV (1935) listed three Sarmatian species of *Mohrensternia*, whereas FRIEDBERG (1911-1928) recorded seven species from the Late Badenian and Sarmatian, three of which were described by him as new.

The genus *Mohrensternia* most likely evolved from *Rissoa* around the latest Oligocene/earliest Miocene. In the middle Miocene *Mohrensternia* became one of the most common components of the molluscan associations in the Paratethys (ANDRUSOV 1890, 1906; FRIEDBERG 1911-1928; KOLESNIKOV 1935; ZHIZHCHENKO 1936; ŠVAGROVSKÝ 1971; IŮNA 1979, 1993; ANISTRATENKO &
STADNICHENKO 1995; KOWALKE & HARZHAUSER 2004; ANISTRATENKO 2004). Its maximum diversity, both in the Central and Eastern Paratethys, coincides with the maximum transgression of the Sarmatian Sea. In the Eastern Paratethys it coincides with the Middle Sarmatian (i.e. Bessarabian substage according to the Eastern Paratethys chronostratigraphy) (KOLESNIKOV 1935; IL’INA 1998; ANISTRATENKO 2003, 2004), but in the Central Paratethys with the Early Sarmatian (i.e. Volhynian substage according to the Eastern Paratethys chronostratigraphy) (e.g. ŠVAGROVSKÝ 1971; KOWALKE & HARZHAUSER 2004) (Text-fig. 1).

In spite of a long period of research concerning the palaeogeography, palaeoecology and morphology of Mohrensternia, there are still some basic morphological and taxonomical problems to be solved.

The ornamentation and shape of the protoconch are now generally accepted as useful taxonomic characters, particularly in marine gastropods with a planktotrophic larva. The importance of embryonic, larval and juvenile shells for reconstruction of gastropod phylogeny is undoubted (e.g. BANDEL 1982, 1991; RIEDEL 1993; KOWALKE & HARZHAUSER 2004; KAÍM 2004). The characters of the protoconch gain a particular taxonomic importance when teleoconch characters are highly variable or too ambiguous to recognize phylogenetic relationships, as with the Middle to Late Miocene representatives of the genus Mohrensternia in the Eastern Paratethys.

In the present paper the taxonomy and shell morphology of Mohrensternia species which inhabited the Central Paratethys in the Late Badenian and Sarmatian are revised. Detailed descriptions and SEM images of all recognized species are presented. The results of detailed analysis of shell variability and the problem of dwarf species in Mohrensternia have been discussed elsewhere (ANISTRATENKO 2005).

MATERIAL AND METHODS

The present investigation is based mainly on the large collection of Wilhelm FRIEDBERG, housed in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences (Kraków, Poland). The collection studied includes Mohrensternia shells from the Late Badenian and Sarmatian of eastern Poland and western Ukraine (Text-fig. 2), collected between 1905 and the 1930s. The entire collection comprises almost 34 000 specimens, including 1 605 specimens of Mohrensternia attributable to seven species (see Appendix 1). The material has never been revised, although the taxonomical approach of FRIEDBERG (1923) became obsolete a long time ago.

![Stratigraphic correlation chart](image_url)

Fig. 1. Stratigraphic correlation chart of the standard scale with the Central Paratethys and the Eastern Paratethys (after RÖGL 1988). The horizons from which study material came from are indicated with grey belts.
Additional material came from field collecting during the period 1983-2004, mainly from outcrops in western Ukraine (Text-fig. 2); more than 2,000 specimens of *Mohrensternia* were identified in this material. This collection is housed in the Institute of Zoology NAS Ukraine (Kiev). One original specimen of EICHWALD, from the Late Badenian/Sarmatian of Zalešće (Ukraine), came from the Geological Museum of the State University in St Petersburg, Russia.

Shell characters were studied with an optical stereomicroscope. Standard dimensions for shell characters were measured. The apical angles also proved to be a simple and easy species-diagnostic parameter (e.g. KEEN 1960; CLARKSON 1987; see also ANISTRATENKO & STADNICHENKO 1995).

Morphological features of protoconchs were examined under SEM with special attention to shape, size and number of whorls, sculpture and character of the boundary with the early teleoconch. Four parameters are given for the protoconch: the maximum diameter and height of the protoconch shell, the number of whorls, and the width of the initial cap-like part of the embryonic shell (see Text-fig. 3).

Fig. 2. Source localities (and their chronostratigraphic range) in eastern Poland and western Ukraine
The SEM micrographs of specimens from FRIEDBERG’S collection were performed in the Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis, Institute of Geological Sciences, Jagiellonian University, Kraków (Poland). Shells were mounted on stubs, sputter-coated with carbon and then photographed using a Hitachi S-4700 scanning electron microscope.

Some additional SEM micrographs of specimen from the collection of the Institute of Zoology NAS Ukraine (Kiev) were made by Dr Andrzej KAIM at the Institute of Paleobiology, Polish Academy of Sciences (Warsaw, Poland). The shell was mounted on a stub, coated with platinum and examined with a PHILIPS XL 20.

One specimen from the collection of the Geological-Paleontological Department of the Natural History Museum, Vienna (Austria) was SEM photographed by Dr Jens HARTMANN, in the Geological-Paleontological Institute and Museum of the University of Hamburg (Germany). Here the shell was mounted on a stub and then photographed uncoated using a LEO 1455 VP.

ABBREVIATIONS

Repositories:
IZ NANO – Institute of Zoology NAS Ukraine (Kiev).
ZPAL Ga. 11/3 – Institute of Paleobiology, Polish Academy of Sciences, Warsaw (Poland).

GMSPU – Geological Museum of the St-Petersburg State University, St-Petersburg (Russia).
NHMV – Geological-Paleontological Department of Natural History Museum, Vienna (Austria).

Morphological terms for the shell description: HS – height of shell, WS – width of shell, HBW – height of last (body) whorl, HA – height of aperture, WA – width of aperture, NW – number of whorls, HP – height of protoconch, MD – maximum diameter of protoconch, WE – width of initial cap-like part of embryonic shell, No – number of lots according to Museum Catalogue.

SYSTEMATIC PALAEONTOLOGY

Class Gastropoda CUVIER, 1797
Family Rissoidae GRAY, 1847
Genus Mohrensternia STOLICZKA, 1868

TYPE SPECIES: Rissoa angulata EICHWALD, 1830, by subsequent designation of NEVILL (1885). Miocene (Badenian and Sarmatian) of central and eastern Europe.

REMARKS ON THE GENUS: Teleoconch. Mohrensternia has a low conical to slender, high-spired shell which usually measures up to 8 mm in height [FRIEDBERG (1923) reported 9 mm] and up to 5 mm in width. The apical angle ranges from 21° to 69°.

The teleoconch consists of up to five inflated whorls, separated by moderately incised sutures. The sculpture usually consists of 10–14 axial ribs, which are usually slightly sinuously curved. In some cases the number of ribs is up to 20 per whorl (according to FRIEDBERG 1923) or exceptionally even up to 22 (KOWALKE & HARZHAUSER 2004, own observations). More or less strongly expressed spiral threads are commonly present in the gaps between the axial ribs. The aperture is broadly oval to round holostomate, with a thin peristome. The umbilicus is usually narrow and chink-like, or closed.

Some other aspects of the variability of the shell of Mohrensternia are discussed below.

Protoconch. Mohrensternia is characterised by an inflated conical protoconch, consisting of 2.15–2.75 whorls measuring 0.32–0.56 mm in maximum diameter and 0.30–0.55 mm in height. The embryonic shell is relatively small and the larval shell is much bigger and longer. The initial cap-like part of the embryonic shell ranges from 0.06 to 0.12 mm in diameter (exceptionally 0.20 mm by 1.5 whors in M. friedbergi sp. nov.). The embryonic
shell is ornamented by four to seven fine spiral rows of granules or threads, whereas the larval part of the protoconch is apparently smooth, with only growth lines visible. The protoconch shape, dimensions and proportions indicate indirect development with a free-living, feeding larval stage. The dimensions of the protoconch of Mohrensternia are given in Table 1.

Species (number of SEM micrographs) | NW | HP | MD | WE
--- | --- | --- | --- | ---
Mohrensternia inflata (1) | 2.75 | 0.42 | 0.55 | 0.06
M. perinflata (4) | 2.20-2.5 | 0.30-0.35 | 0.37-0.45 | 0.08-0.12
M. pseudoinflata (2) | 2.75 | 0.55 | 0.55-0.56 | 0.12
M. sarmatica (9) | 2.15-2.5 | 0.25-0.35 | 0.32-0.38 | 0.07-0.12
M. angulata (2) | 2.25-2.75 | 0.35 | 0.35-0.38 | 0.075
M. pseudangulata (3) | 2.25-2.75 | 0.35-0.40 | 0.36-0.40 | 0.08
M. banatica (4) | 2.25-2.75 | 0.40-0.55 | 0.37-0.44 | 0.09-0.11
?M. friedbergi sp.n. (1) | 1.5 | 0.31 | 0.36 | 0.20

Table 1. Protoconch dimensions of Mohrensternia (mm)

The protoconches and teleoconches of some Sarmatian Rissoa and Mohrensternia collected in Western Ukraine have recently been documented in detail (ANISTRATENKO 2004). This study revealed that the protoconches of both these genera have a quite similar shape and sculpture, viz. inflated conical, rounded protoconches, sculptured in Mohrensternia only by a few fine spiral rows of granules or threads (ANISTRATENKO 2004). At the same time KOWALKE & HARZHAUSER (2004) contributed similar data based on Badenian and Early Sarmatian Mohrensternia from the Central Paratethys. These authors concluded that Mohrensternia can be differentiated from other Rissoinae (I would say at least from Rissoa) by a very fine spirally sculptured embryonic shell and smooth larval whorls which usually bear only growth lines. Moreover, they claim that Rissoa, in contrast to Mohrensternia, bears two granulated spiral threads in the course of the second whorl of the protoconch (i.e. on its larval part) whereas their embryonic shells lack any ornamentation.

New data from the FRIEDBERG and IZ NANU collections confirmed that the embryonic part of the protoconch of Mohrensternia is ornamented by delicate spiral rows of granules or threads. Apparently the smooth embryonic shell of Rissoa in the material of KOWALKE & HARZHAUSER (2004) is an artefact, resulting from poor preservation of their material. At least a few specimens of Rissoa sp., which I examined from the Sarmatian of the Western Ukraine, show an ornamented embryonic shell very similar to that of Mohrensternia. A similar protoconch microsculpture is also shown by recent Rissoa species (e.g. PONDER 1985; WARÉN 1996). Therefore, no characters of the protoconch clearly differentiate these two genera (perhaps except slightly inclined spiral rows in Mohrensternia while they are parallel to the suture in Rissoa). Further studies are required to determine the morphological distinction and affinity between these two genera as indicated by their teleoconch and protoconch ornamentation. The problem will be discussed in detail elsewhere.

The taxonomically significant differences between Mohrensternia and Rissoa are rather in the teleoconch morphology. According to ANISTRATENKO (2004), in contrast to those of Rissoa, the shells of Mohrensternia are thinner (1), their aperture lacks the thickened outer lip (2), are slightly curved and elongated at the base (3) and their axial ribs express a tendency to form high sickle-shaped or half-moon-shaped scales (4).

To these characters of the teleoconch can be added that the protoconch of Rissoa is terminated by sinuous, closely spaced, thickened growth lines, whereas in Mohrensternia the transition from the protoconch to the teleoconch is only slightly thickened and commonly indistinct. The onset of the teleoconch in Mohrensternia can usually be determined by the beginning of wavy axial folds which grade into the axial ribs (Text-figs 4-7). In some cases, the transition from the larval shell to the teleoconch is sharp, indicated by a rim and the abrupt onset of the adult sculpture (see also KOWALKE & HARZHAUSER 2004). In Mohrensternia the boundary between the embryonic and the larval shells is only slightly thickened and often indistinct.

The genus Mohrensternia has recently been referred (ANISTRATENKO 2003; KOWALKE & HARZHAUSER 2004) to a separate subfamily Mohrensterniinae KOROBKOV, 1955 within the family Rissoidae. This subfamily was even raised to family rank (ANISTRATENKO 2003), and divided into the subfamilies Mohrensterniinae KOROBKOV, 1955, Coelacanthiinae ANISTRATENKO, 2003, and Archascheniinae ZHIGENTI, 1991. Subsequently, the Mohrensterniinae was considered as insufficiently substantiated (ANISTRATENKO 2004), since the protoconch morphology supports a close relationship between Mohrensternia and Rissoa. The morphological data available did not confirm their subfamilial status but suggest that they should be considered separate genera within a single family Rissoidae.

The concept of what is known today as Mohrensternia appeared long ago. It was HÖRNES (1856: 578) who recognized that “Rissoa” angulata and “R.” inflata formed a particular group within the genus Rissoa. This was also suggested by SCHWARZ von MOHRENSTERN.
(1864) in his monograph on rissoids, where he discussed several Miocene *Rissoa* (“*turrricula*”, “*angulata*”, “*inflata*” and “*zitteli*”). He noted peculiarities in the three last-named species, considering them as “the degenerated true *Rissoa*”, and recognized that they formed a special group (a section within the genus). A new genus *Mohrensternia* (not subgenus as some authors alleged, e.g. Badzohvili 1991) was later formally introduced by Stoliczka (1868). Stoliczka mentioned that species of *Mohrensternia* occur typically in brackish or fresh-water sediments of Central and Eastern Europe and gave as its generic diagnosis: “*Mohr. testa turrículata, tenui, semipellucida; anfractibus saepissime transversaliter costulatis; columella ad basin

Fig. 4. Three species of *Mohrensternia* Stoliczka, 1868. A. *Mohrensternia inflata* (Hörnes, 1856). Specimen (ZNG PAN A-I-50/1162) from the Sarmatian of Chlebów, Ukraine (A₁). Lateral view of the protoconch of the same specimen as in A₁ (A₂). B. *Mohrensternia pseudoinflata* Hilber, 1897. Specimen (ZPAL Ga. 11/3) from the Late Badenian of Varovtsy, Ukraine (B₁). Detailed apical view of the embryonic shell of the same specimen as in B₁ (B₂). Close-up of the embryonic shell of the same protoconch as in B₁ (B₃). The embryonic shell is ornamented by fine spiral threads. C, D. *Mohrensternia perinflata* Friedberg 1923. Specimen (ZNG PAN A-I-50/1180) from the Sarmatian of Rydoml, Ukraine (C₁); illustrated in pl. 23, fig. 13 of Friedberg’s monograph (1911-1928). Apical view of the protoconch of the same specimen as in C₁ (C₂). Lectotype of *Mohrensternia perinflata* Friedberg 1923, specimen (ZNG PAN A-I-50/1187) from the Late Badenian of Zborów, Ukraine (D); illustrated in pl. 23, fig. 14 of Friedberg’s monograph (1911-1928)
Mohrensterna inflata (Hörnes, 1856)
(Text-fig. 4A)

nec 1792. Bulimus turricula n. sp.; Bruguère.
1850. Rissoa turricula Eichwald; Eichwald, pp. 129-130, pl. 10, fig. 9.
1853. Rissoa turricula Eichwald; Eichwald, p. 267, pl. 10, fig. 9.
1831. Melania roppii n. sp.; Du Bois de Montpèreme, p. 45, pl. 3, fig. 32-33.
1850. Rissoa turricula var. striata n. var.; Eichwald, pp. 129-130, pl. 10, fig. 9*.
non 1850. Rissoa angulata var. striata n. var.; Eichwald, p. 130, pl. 10, fig. 10*.
 nec 1833. Rissoa striata n. sp.; Andrzejowski, p. 447, pl. 11, fig. 3.
nec 1833. Rissoa striata n. sp.; Quoy & Gaimard, p. 443.
1835. Rissoa semicostata; nomen nudum.; Andrzejowski in Deshayes, p. 321.
1848. Rissoa tenuis; nomen nudum.; M. Hörnes, p. 23.
1856. Rissoa inflata Andrzejowski; M. Hörnes, p. 576, pl. 48, fig. 22a-22b.

MATERIAL: Seven specimens from Chlebów, Ukraine, ZNG PAN A-I-50/1165, 1162, 1182; sixty-nine specimens from Zaleśce, Ukraine, ZNG PAN A-I-50/1164, 1184, IZ PANU; six specimens from Żolobki, Ukraine, ZNG PAN A-I-50/1166, 1183; seventeen specimens from Rydomył, Ukraine, ZNG PAN A-I-50/1167, 1168.2, 1181; one specimen from Ślupcza, Poland, ZNG PAN A-I-50/1170; four specimens from Dwikozy, Poland, ZNG PAN A-I-50/1171, thirteen specimens from Chmielnik, Poland, ZNG PAN A-I-50/1165, 1185. Samples from Zaleśce are of Late Badenian/Sarmatian age, all others are from the Sarmatian.

DESCRIPTION: The species has a thin-walled, compar-
In 1856 Hörnès stated that Eichwald’s “turricula” was a junior secondary homonym (ICZN Art. 53.3) of Bulimus turricula Bruguère, 1792 and referred Eichwald’s species to “Rissoa inflata Andrzejowski, 1835”. The latter name was first published by Deshayes (1835), in a faunal list from Podolia; however, Andrzejowski’s species was never described or figured. Andrzejowski had just sent shells to Deshayes with a label “Rissoa inflata”, and the name is a nomen nudum. Other names, Rissoa semicostata Andrzejowski, 1835 and Rissoa tenuis Hörnès, 1848, quoted by Hörnès (1856) are also nomina nuda.

The name “Rissoa inflata” was made available by Hörnès, who provided its description and illustration (Hörnès 1856, p. 576; pl. 48, fig. 22 a, b). Hörnès stated that his material was identical to the material sent by Andrzejowski to Deshayes. Based on Eichwald’s synotypes, he put “Rissoa inflata” into synonymy of Eichwald’s “Rissoa turricula”, albeit noting that Eichwald’s specimens differed from the Vienna material in possessing a thicker shell and a thickened apertural margin. The authorship and date of Rissoa inflata have thus to be attributed to M. Hörnès, 1856 (ICZN Art. 50.1).

As the name Rissoa inflata was intended by Hörnès (1856) as a replacement name for the preoccupied Rissoa turricula Eichwald 1830, Article 72.7 of the present Code applies, i.e. the name-bearing types of the two nominal species are the same. It is irrelevant, for the purpose of this Article, that Hörnès regarded the name “inflata” available from Andrzejowski, 1835, and that he implicitly did not consider Eichwald’s material as the “typical” form. Unfortunately Hörnès (1856) failed to include in the synonymy of his “Rissoa inflata” Trochus detritus and Melania roppii, described by Du Bois de Montpéréux (1831), although this synonymy was recognized already by Eichwald (1850 and 1853).

Nevertheless, because Du Bois’ names have not been utilized as valid names after 1899, probably on the authority of M. Hörnès and Schwarz von Mohrenstern, the conditions of Article 23.9.1 for the conservation of prevalent use are fulfilled (see the List of references – Appendix 2); the older synonyms are therefore here declared as nomina oblitae and Rissoa inflata is declared a nomen protectum (ICZN Art. 23.9.2).

Schwartz von Mohrenstern (1864) remarked on the shells of “R. turricula”, which had been sent to him by Eichwald, that these shells conformed neither to the description nor to the image of this species published by Eichwald (1830, 1850, 1853). He stated also that Eichwald’s shells disagreed with the description and image of Melania roppii Du Bois de Montpéréux, 1831, considered as a synonym of R. turricula by Eichwald. That is why Schwartz von Mohrenstern (1864) suggested the use of the name “R. inflata” for the shells with a sharp and non-thickened outer lip of the aperture and the name “R. turricula” Eichwald, 1830, for shells with a thickened outer lip. This proposal, however, is incorrect under the present Code as the two nominal species “inflata” and “turricula” are objective synonyms, as discussed above. If indeed two species have to be distinguished, as Schwartz von Mohrenstern assumed, the form with a thickened outer lip has to be named M. inflata, and the other M. detrita or M. roppii.

The repository of the type material for Rissoa inflata is unknown and its knowledge is based exclusively on the original description by Hörnès (1856, p. 576; pl. 48, fig. 22 a, b). Hörnès’ figures 22 show two different specimens, which belong to rather different conchological forms. One specimen (his fig. 22a) has a distinct spiral sculpture covering axial ribs, whereas the other one (fig. 22 b) is ornamented only with well-developed axial ribs. It has already been stated above that spiral ornamentation on the shell of M. inflata shows a wide variability and could be present or absent. Therefore it should not to be considered as a reliable character for species diagnosis. The original measurements can be used as a more reliable character. According to Hörnès (1856, p. 576), one of the figured specimens is 2 lines high and 1 line wide (4.2 mm and 2.1 mm respectively). The only specimen figured in fig. 22b agrees well with these measurements. This specimen represents Rissoa inflata sensu stricto (sensu Hörnès, 1856), but according to the foregoing only Eichwald’s syntypes of his Rissoa turricula are syntypes of Rissoa inflata Hörnès.

REMARKS: In the collection of Prof. Friedberg a mixture of several species is labelled M. inflata (see Appendix 1). The most variable character of M. inflata is the degree of axial rib development. The ribs are sometimes very sharp and strong but sometimes weak and/or almost absent, especially on the body whorl. Axial ribs are usually sickle-shaped or wavy. The outline of the spire is more or less slender, the whorls flattened or convex. The wide variability of all these features was the reason for introducing several varieties of M. inflata (e.g. Hilber 1897), but the material studied has not confirmed their validity, because all of them are characterized by identical or very similar protoconch dimensions.

M. inflata differs from other known Mohrensternia species in its small cap-like initial part of the embryonic shell. From M. pseudinflata, which has a similar shape, it differs in its lower protoconch and straight or even slightly convex tangent-line; in M. pseudinflata the tangent-line
is usually slightly concave, which results in a somewhat mammillated spire.

In the Early Sarmatian of Podolia M. hydrobioïdes HILBER, 1897 (HILBER 1897, p. 199, figs 12-14; KOLESNIKOV 1935, p. 213, pl. 27, figs 7, 8) commonly occurs. This species closely resembles M. inflata, differing from it merely in very weak sculpture on the last whorl – it is sometimes completely smooth or covered by very fine spiral threads. Since the variability of M. inflata is very wide M. hydrobioïdes falls possibly into its synonymy.

DISTRIBUTION: Mohrensternia inflata is a typical (sometimes abundant) and widespread species in Late Badenian and Sarmatian sediments of the Eastern Paratethys (e.g. Eastern Poland and Western Ukraine). It is also well-known from coeval deposits of the Central Paratethys (FRIEDBERG 1911-1928; ŠVAGROVSKÝ 1971; KOWALKE & HARZHAUSER 2004).

Mohrensternia perinflata FRIEDBERG, 1923
(Text-fig. 4C, D)

1923. Mohrensternia pseudoinflata HILBER; FRIEDBERG, pp. 390-391, pl. 23, fig. 13.

MATERIAL: Four specimens from Chlebów, Ukraine, ZNG PAN A-I-50/1162; one specimen from Krzemieniec, Ukraine, ZNG PAN A-I-50/1163; seven specimens from Zaleśce, Ukraine, ZNG PAN A-I-50/1164, 1184; nine specimens from Żolobki, Ukraine, ZNG PAN A-I-50/1166, 1180, 1181; three specimens from Chmielnik, Poland, ZNG PAN A-I-50/1185; seven specimens from Zborów, Ukraine ZNG PAN A-I-50/1187, 1188. Samples from Zaleśce and Zborów are of Late Badenian/Sarmatian age; all others are from the Sarmatian.

DESCRIPTION: The shell is comparatively large, stout, low conical to egg-shaped, moderately thin. It comprises 6-7 rounded, regularly expanding, strongly convex whorls, which are separated by deeply incised and slightly inclined sutures. The shell measures up to 7.80 mm in height and up to 4.75 mm in width. The sculpture consists of closely spaced, wavy growth lines and 16-18 weak, sickle-like thin axial ribs with narrow gaps between them. Spiral sculpture is usually not evident. The last whorl of strongly inflated forms comprises 0.65-0.70 of the total shell height. Aperture large, irregularly oval, with a thin outer lip and an indistinct parietal angle. Umbilical chink usually almost completely covered by the columellar margin of the aperture. The apical angle is about 54–56° (rarely up to 69°); the tangent-line is straight.

The conical protoconch consists of 2.2–2.5 regularly expanding whorls measuring 0.30–0.35 mm in height and 0.37-0.45 mm in maximum diameter. The initial cap-like part of the embryonic shell is 0.08–0.12 mm wide. The embryonic shell is separated from the subsequent larval part of the protoconch by a slightly thickened rim. The indistinct demarcation from the teleconch is marked only by an appearance of wavy axial folds. The ornamentation of the embryonic shell is the same as in M. inflata, composed of 4–6 delicate, slightly inclined, spiral threads or fine rows of grains. The larval part of the protoconch is smooth.

MEASUREMENTS (in mm): First is the lectotype, followed by paralectotypes:

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<td>4.75</td>
<td>-</td>
<td>3.5</td>
<td>2.4</td>
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</table>

REMARKS: This species is housed in FRIEDBERG’s collection under different names (see Appendix 1). The specimen collected in Zborów, Ukraine (ZNG PAN A-I-50/1187) (see Text-fig. 4D), described and illustrated by FRIEDBERG (1923, p. 391, pl. 23, fig. 14), is designated here as lectotype of Mohrensternia perinflata FRIEDBERG, 1923. Six other specimens from this collection (ZNG PAN A-I-50/1188) are paralectotypes.

Some authors (e.g. ŠVAGROVSKÝ 1971) considered that M. perinflata simply represented specimens of M. inflata with slightly sickle-shaped axial ribs. Also KOWALKE & HARZHAUSER (2004) treated M. perinflata as a probable synonym of M. inflata. The material studied from FRIEDBERG’s collection exhibits clear distinctions from that species, not only in the features of its teleconch but also in protoconch shape and dimensions.

The shell shape and ornament are the most variable features of M. perinflata (see Text-fig. 4C, D), with, e.g. axial ribs number ranging from 16–18 up to 24 per body whorl. Nonetheless, the material studied showed quite similar protoconch structure and dimensions in all forms.
**Mohrensternia perinflata** is quite similar to *Mohrensternia inflata* in shell shape but differs from the latter and other *Mohrensternia* species in a far greater variability of the apical angle (resulting in the widest and lowest shells with the maximum apical angles known in *Mohrensternia*), and comparatively weak sculptural patterns. *Mohrensternia perinflata* differs also from *Mohrensternia inflata* in having a much larger (1.5–2 times) cap-like initial part of the embryonic shell, and in a lower and less wide protoconch.

**DISTRIBUTION:** *Mohrensternia perinflata* is apparently rare in the Late Badenian and Sarmatian of the East Central Paratethys (e.g. FRIEDBERG 1923, see also Appendix 1), but probably its restricted distribution represents an artefact caused by attributing this species to intraspecific variants of *Mohrensternia inflata* or similar *Mohrensternia* species.

**Mohrensternia pseudoinflata** HILBER, 1897  
(Text-fig. 4B)


**MATERIAL:** Two specimens from the Late Badenian/Sarmatian of ZaleÊce, Ukraine, ZNG PAN A-I-50/1164; one specimen from the Sarmatian of Žolobki, Ukraine, ZNG PAN A-I-50/1166; five specimens from the Sarmatian of Dwikozy, Poland, ZNG PAN A-I-50/1186; one specimen from the Late Badenian of Varovtsy, Ukraine, ZPAL Ga. 11/3.

**DESCRIPTION:** The small, low conical to medium conical, moderately thin shell, comprising up to 6–7 whorls, measures up to 4.6 mm in height and up to 2.7 mm in width. The rounded convex whorls are separated by deep and slightly inclined sutures. The whorls are sculptured by 14–16 slightly wavy axial ribs per whorl, about as broad as the gaps between them. Spiral sculpture is usually well-developed. The last whorl occupies 0.60–0.65 of total shell height. The holostomate aperture is oval to round, with a thin peristome. The umbilical chink is usually almost completely covered by the columellar margin of the aperture. The apical angle is about 55–57°; the tangent-line is straight to slightly concave, resulting in a somewhat mammillated shape of the spire.

The conical protoconch comprises 2.75 slightly rounded, slowly expanding whorls measuring 0.55 mm in height and 0.56 mm in maximum diameter. The initial cap-like part of the embryonic shell measures 0.12 mm in width. The transition from the embryonic to the larval shell is not evident. The indistinct demarcation from the teleoconch is indicated by the appearance of weak axial folds that grade into regular axial ribs. The embryonic shell is ornamented by 4–6 fine, slightly inclined spiral threads (Text-fig. 4B). The larval part of the protoconch is smooth.

**MEASUREMENTS** (in mm):

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<td>2.5</td>
<td>1.5</td>
<td>1.2</td>
<td>6.0</td>
</tr>
</tbody>
</table>

**REMARKS:** *Mohrensternia pseudoinflata* differs from all other *Mohrensternia* species in its large protoconch. It is distinguished from *Mohrensternia inflata*, which has a similar shape, by its smaller size (having the same number of whorls), slender shell and somewhat mammillated spire.

FRIEDBERG (1923: 392) considered *Mohrensternia graecensis* a synonym of *Mohrensternia inflata*, which cannot be confirmed. Based on shell shape and sculptural resemblance, *Mohrensternia graecensis* HILBER, 1897 is considered here a synonym of *Mohrensternia pseudoinflata*. Since HILBER (1897) described *Mohrensternia pseudoinflata* and *Mohrensternia graecensis* in the same publication one name needs to be assigned priority. Because the name *Mohrensternia graecensis* has been used extremely rarely (e.g. ŠVAGROVSKÝ 1971), the name *Mohrensternia pseudoinflata*, which has been used more frequently (e.g. FRIEDBERG 1911-28; JEKELIUS 1944 and many others), is chosen here. The shape, proportion and ornament of specimens of *Mohrensternia graecensis*, described and illustrated by HILBER (1897, p. 202, fig. 19), correspond fully to the specimens studied herein. In most cases the incorrect spelling “pseudoinflata” has been used for the species discussed here (e.g. FRIEDBERG 1923; JEKELIUS 1944; ŠVAGROVSKÝ 1971; IČINA 1993, 1998) whereas the original spelling is “pseudo-inflata” (HILBER 1897, p. 202), and there is no nomenclatural reason to change it.

This species is deposited in FRIEDBERG’s collection under different names (see Appendix 1). Probably it has sometimes been confused with *Mohrensternia inflata* or other *Mohrensternia* species.

**DISTRIBUTION:** Although not abundant, *Mohrensternia pseudoinflata* is quite common in the Late Badenian and Sarmatian sediments of the Eastern and Central Paratethys (FRIEDBERG 1923; JEKELIUS 1944). IČINA (1993, 1998) mentioned it from the Late Badenian and Early Sarmatian of west Ukraine and from the Late Badenian (=Konkian) of the Central Subcaucasus and south Ukraine. It is also known from the equivalent deposits of the Central Paratethys (e.g. HILBER 1897; ŠVAGROVSKÝ 1971; KOWALKE & HARZHAUSER 2004).
Mohrensternia sarmatica FRIEDBERG, 1923
(Text-fig. 5A-C)

1923. Mohrensternia sarmatica n. sp.; FRIEDBERG, p. 389, pl. 23, fig. 8-10.
1923. Mohrensternia pseudosarmatica n. sp.; FRIEDBERG, p. 389-390, pl. 23, fig. 11-12.

MATERIAL: Two hundred and twenty-four specimens from Rydmol, Ukraine, ZNG PAN A-I-50/1168.1, 1168.2, 1175.1, 1175.2; two specimens from Miechoin, Poland, ZNG PAN A-I-50/1169; forty-five specimens from Słupca, Poland, ZNG PAN A-I-50/1170; four specimens from Dwikozy, Poland, ZNG PAN A-I-50/1171; three hundred and twenty-six specimens from Zaleśce, Ukraine, ZNG PAN A-I-50/1172, 1178, IZ NANU; one specimen from Chlebów, Ukraine, ZNG PAN A-I-50/1174; eight specimens from Słupca, Poland, ZNG PAN A-I-50/1176; five specimens from Chmielnik, Poland, ZNG PAN A-I-50/1177; seven specimens from Żółbki, Ukraine, ZNG PAN A-I-50/1179; Samples from Zaleśce are of Late Badenian/Sarmatian age; all others are from the Sarmatian.

DESCRIPTION: The small, moderately slender, conical shell consists of 7–8 moderately convex whorls. The maximum convexity of the whorls is in their median part, causing an angulated outline of the shell. According to FRIEDBERG (1923), the shell measures 3.0 mm in height and 1.5 mm in width. The material studied included shells up to 4.5 mm high and 2.7 mm wide (see measurements). The whorls are separated by deep sutures. The sculpture consists of 12–14 (exceptionally 10) strongly developed, orthocline (not sickle-shaped) axial ribs, which diminish or sometimes even disappear on the basal half of the last whorl, similar to those individuals of M. inflata named M. hydrobioides by HILBER (1897). The last whorl occupies about 0.5 or slightly more of the total shell height. The holostome aperture is broad-oval to round, with a thin peristome and slightly prominent parietal portion. The umbilical chink is usually completely covered by the col- umellar margin of the aperture. The apical angle is about 43–47°; the tangent-line is straight.

The protoconch comprises about 2.15–2.5 whorls measuring 0.25–0.35 mm in height and 0.32–0.38 mm in maximum diameter. The initial cap-like part of the embryonic shell measures 0.07–0.12 mm in width. The boundary of the embryonic shell with the subsequent larval part of the protoconch is distinct, marked by a thickened rim. The transition from the larval shell to the teleoconch is also distinct. The onset of the adult shell is indicated by the formation of weak axial folds that grade into regular axial ribs. The ornamentation of the embryonic shell is composed of 5–7 fine but (under higher magnification) clearly visible spiral rows of grains or threads, which are slightly inclined. The larval part of the protoconch is smooth.

MEASUREMENTS (in mm): First is the lectotype, followed by paralectotypes (2-4):

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<td>0.95</td>
<td>0.5</td>
<td>0.5</td>
<td>6.0</td>
</tr>
</tbody>
</table>

REMARKS: This species is housed in FRIEDBERG’s collection under different names (see Appendix 1). The type series of Mohrensternia sarmatica comprises 197 syntypes collected from the Sarmatian of Rydmol, Ukraine (ZNG PAN A-I-50/1168.1 and 1168.2). Three of these specimens (ZNG PAN A-I-50/1168.1) were originally described and illustrated by FRIEDBERG (1923, p. 389, pl. 23, figs 8-10). One of them (Text-fig. 5A) is designated here as the lectotype.

The type series of Mohrensternia pseudosarmatica FRIEDBERG, 1923 comprises 33 syntypes collected from the Sarmatian of Rydmol, Ukraine (ZNG PAN A-I-50/1175.1 and 1175.2). Two of these specimens (ZNG PAN A-I-50/1175.1) were originally described and illustrated in FRIEDBERG’s work (FRIEDBERG 1923, p. 389, pl. 23, figs 11, 12). One of the syntypes is designated here as the lectotype of Mohrensternia pseudosarmatica FRIEDBERG, 1923 and the SEM micrographs of it are presented in Text-fig. 5C.

The detailed study of the type material of M. sarmatica and M. pseudosarmatica has shown that the variability of both species overlaps [the variability of both morphotypes (including type material) is shown by ANISTRATENKO (2005)]. Even FRIEDBERG (1923, p. 390) himself, in the original description of M. pseudosarmatica, mentioned that both species were very close one to another and differed only in the slightly less slender shell in M. pseudosarmatica. I consider Mohrensternia pseudosarmatica FRIEDBERG, 1923 a subjective synonym of Mohrensternia sarmatica FRIEDBERG, 1923.

From M. pseudangulata, which has a similar outline, M. sarmatica differs in its slightly shorter protoconch, broader teleoconch, and smaller size of the shell at the
Fig. 5. Two species of Mohrensternia STOLICZKA, 1868. A – C. Mohrensternia sarmatica FRIEDBERG, 1923. Lectotype, specimen (ZNG PAN A-I-50/1168.2) from the Sarmatian of Rydoml, Ukraine (A1). Lateral and apical views of the protoconch of the same specimen as in A1 (A2, A3). Specimen (ZNG PAN A-I-50/1170) from the Sarmatian of Slupcza, Ukraine (B1). Lateral and apical views of the protoconch of the same specimen as in B1 (B2, B3). Close-up of the embryonic shell of the same protoconch as in B1 (B4); arrows show the fine spiral threads on the surface of the embryonic shell. Lectotype of Mohrensternia pseudosarmatica FRIEDBERG, 1923, specimen (ZNG PAN A-I-50/1175.2) from the Sarmatian of Rydoml, Ukraine (C1). Lateral and apical views of the protoconch of the same specimen (C2, C3). D, E. Mohrensternia angulata (EICHWALD, 1830). Specimen (ZNG PAN A-I-50/1190) from the Sarmatian of Chlebów, Ukraine (D1). Lateral and apical views of the protoconch of the same specimen as in D1 (D2, D3). Specimen (ZNG PAN A-I-50/1201) from the Sarmatian of Chmieleń, Poland (E1). Lateral and apical views of the protoconch of the same specimen as in E1 (E2, E3).
same number of whorls. From all other species of *Mohrensternia, M. sarmatica* differs in its significantly smaller (about 1.5 times) shell at the same number of whorls. Although there are several hypotheses devoted to the causes of dwarfism – connecting it either with sudden freshening or hypersalinity of the basin (see review in Belokry 1963), – the nature of the phenomenon of dwarfism in *M. sarmatica*, as well as in some other Sarmatian molluscs is still unresolved.

**DISTRIBUTION:** *Mohrensternia sarmatica* is a widespread and abundant species in the Late Badenian and Sarmatian of the East and Central Paratethys (Friedberg 1911-1928; Kolesnikov 1935; Švagrovský 1971; Kowalke & Harzhauser 2004).

**Mohrensternia angulata** (Eichwald, 1830)
(Text-fig. 5D-E, 6A-B)

1850. *Rissoa angulata* EICHWALD; EICHWALD, p. 130, pl. 10, fig. 10.

**MATERIAL:** One specimen from Krzemieniec, Ukraine, ZNG PAN A-I-50/1163; one hundred and fifteen specimens from Zalešće, Ukraine, ZNG PAN A-I-50/1164, 1194, 1203, IZ NANU, GMSPU, NHMV - 1843/IX/26; nine specimens from Rydomy, Ukraine, ZNG PAN A-I-50/1167, 1195, 1205, 1206; twelve specimens from Chlebów, Ukraine, ZNG PAN A-I-50/1189, 1190, 1197, 1198; sixteen specimens from Białózurka, Ukraine, ZNG PAN A-I-50/1196; three specimens from Chmielnik, Poland, ZNG PAN A-I-50/1201; twelve specimens from Żółobki, Ukraine, ZNG PAN A-I-50/1204.

Samples from Zalešće are of Late Badenian/Sarmatian age; all others are from the Sarmatian.

**DESCRIPTION:** The small, slender high-conical shell comprises up to 6.5–7.5 rounded, regularly increasing whorls measuring up to 5 mm in height and up to 2.5 mm in width. Distinct and incised sutures separate the whorls, which have a maximum convexity in their abapical half. The sculpture consists of 10–12 usually strongly developed, orthocline to opisthocyrt axial ribs about as wide as the gaps between them. The last whorl occupies 0.55–0.6 of the total shell height. The aperture is broad-oval to rounded and is characterized by a very thin outer lip. The umbilical chink is narrow or completely covered by the columellar margin of the aperture. The apical angle is about 35–40°; the tangent-line is straight or slightly curved.

The protoconch comprises about 2.25–2.75 whorls measuring 0.35 mm in height and 0.35–0.38 mm in maximum diameter. The initial cap-like part of the embryonic shell is 0.075 mm wide. The transition from the embryonic to the larval shell is not evident. The boundary with the teleoconch is indistinct and indicated by the appearance of weak axial folds that grade into regular axial ribs. The ornamentation of the embryonic shell consists of 4–5 fine, slightly inclined spiral threads. The larval part of the protoconch is smooth.

**MEASUREMENTS** (in mm):

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</table>

**NOMENCLATURE:** Two syntypes of *Rissoa angulata* EICHWALD, 1830, are known and have been studied to date. One of them is specimen 3/486, the original to EICHWALD (1850, pl. 10, fig. 10), and according to the original (?Eichwald’s) label, is from the Schipilowa Mount in Zalisce (Ukraine), from the Late Badenian/Sarmatian. The specimen is housed in the Geological Museum of the State University in St-Petersburg, Russia. Obviously this specimen was used by EICHWALD for the original description of *Rissoa angulata* (EICHWALD 1830, p. 218) and was subsequently figured (EICHWALD 1850, p. 130, pl. 10, fig. 10; 1853, p. 268, pl. 10, fig. 10). This syntype was already figured by Anistratenko & Starobogatov (1994, p. 44, fig. 2 c), and by Anistratenko & Stadniczenko (1995, p. 72-73, fig. 47) but, unfortunately, only as a drawing (see the reproduction in Text-fig. 6B). The measurements of this specimen...
are as follows (in mm): height of shell – 5.4 (apex partially corroded); width of shell – 2.8; height of last whorl – 3.0; height of aperture – 1.8; width of aperture – 1.4; number of whorls approximately 6.5 (only preserved whors counted). The shell is ornamented by sharp axial ribs; the space between them is covered by spiral threads clearly visible under higher magnification.

The second syntype has recently been found in the Natural History Museum of Vienna, Austria, thanks to the kind assistance of Dr Mathias HARZHAUSER. He provided the information that in the inventory book of this Museum is a remar that a single specimen of Rissoa angulata from “Salisze” was given to the Imperial collection by custodian PARTSCH in 1836, together with a large collection of Neogene molluscs from all over Europe. In 1843 it was given the inventory number 1843/IX/26.

It is quite possible that EICHWALD had connections with PARTSCH in these years; however, there is no direct indication that the specimen was a gift from EICHWALD, although this cannot be excluded. The supposition that this specimen belongs to the type series of Rissoa angulata is based mainly on HÖRNES’ (1856) remark that the “imperial collection” in Vienna had Rissoa angulata from Salisze, received from EICHWALD.

This specimen has been examined with aid of the SEM (Text-fig. 6A) and is relatively better preserved than the above-mentioned syntype. Therefore, this specimen is hereby designated as lectotype and the other shell becomes a paralectotype (ICZN Art. 74). The reason for the lectotype designation is that, in the Miocene of the Eastern Paratethys (including the Late Badenian/Sarmatian deposits of Zalešće, which is the type locality of Rissoa angulata), several more or less similar but distinct species of Mohrensternia occur. Designation of a lectotype will allow confident identification of M. angulata. This is important because the original description of the species could apply to more than one of the Miocene Mohrensternia species (see EICHWALD 1830: 218, 1850: 130, 1853: 268).

REMARKS: Several lots of the FRIEDBERG collection contain M. angulata under different names (see Appendix 1). All these specimens conform to the lectotype and paralectotype in shape and sculpture. M. angulata differs from M. pseudangulata in a less slender shell.

**DISTRIBUTION:** Mohrensternia angulata is one of the most widespread and abundant species that occurs in the Late Badenian and Sarmatian of the East and Central Paratethys (FRIEDBERG 1911-1928; KOLENOK 1935; ŠVAGROVSKY 1971; IČIĆA 1998; KOWALKE & HARZHAUSER 2004).

**Mohrensternia pseudangulata HILBER, 1897**

(Text-fig. 7A-C)

1850. Rissoa angulata var. striata n. var.; EICHWALD, p. 130, pl. 10, fig. 10*.

non 1850. Rissoa turricula var. striata n. var.; EICHWALD, pp. 129-130, pl. 10, fig. 9*.

nc 1833. Rissoa striata n. sp.; ANDRZEJOWSKI, p. 447, pl. 11, fig. 3.

nc 1833. Rissoa striata n. sp.; QUOY & GAIMARD, p. 443.


1897. Mohrensternia styriaca n. sp.; HILBER, p. 202, fig. 11. part 1944. Mohrensternia pseudangulata var. politoanei n. var.; JUKELIUS, p.72, pl. 15, fig. 11, 12.

**MATERIAL:** Ten specimens from Dwikozy, Poland, ZNG PAN A-I-50/1192, 1199; sixty-seven specimens from Zalešće, Ukraine, ZNG PAN A-I-50/1194, 1203, IZ NANU; thirty-one specimens from Chlebów, Ukraine, ZNG PAN A-I-50/1198; ten specimens from Słupca, Poland, ZNG PAN A-I-50/1200; twelve specimens from Żolobki, Ukraine, ZNG PAN A-I-50/1204; seven specimens from Rydomyl, Ukraine, ZNG PAN A-I-50/1206. Samples from Zalešće are of Late Badenian/Sarmatian age; all others are from the Sarmatian.

**DESCRIPTION:** The small, slender shell comprises up to 6.5–7.5 rounded, usually strongly developed, orthocline to opisthocyrt axial ribs per whorl. The spiral ornamentation consists of distinct threads. The last whorl occupies 0.53–0.62 of total shell height. The aperture is broad-oval to rounded, with a thin outer lip. The umbilical chink is narrow or
MORPHOLOGY AND TAXONOMY OF \textit{MOHRENSTERNIA} OF THE CENTRAL PARATETHYS
completely covered by the columellar margin. The apical angle is about 32–37°; the tangent-line is straight.

The protoconch comprises 2.25-2.75 whorls measuring 0.35–0.40 mm in height and 0.36–0.40 mm in maximum diameter. In its initial cap-like part the embryonic shell is 0.08 mm wide. The transition from the embryonic to the larval shell is indistinct. The boundary with the teleoconch is indicated by the appearance of wavy axial folds that grade into regular axial ribs. The embryonic shell is ornamented by 4–6 fine spiral threads. The larval part of the protoconch is smooth.

MEASUREMENTS (in mm):

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</table>

REMARKS: Mohrensternia pseudangulata differs from M. angulata, which has a similar outline, in its slightly more slender shell. From M. sarmatica, the species differs in its slightly larger protoconch, more slender outline and a larger size of shell at the same number of whorls.

Eichwald (1850) named a form similar to “Rissoa angulata”, but which bears both spiral and axial sculpture, “var. striata” whereas Hilber (1897) established for it a new species “pseudangulata”. Many authors consider M. pseudangulata as an intraspecific form of the variable M. angulata.

In fact this species is very widely-variable in many characters. Nevertheless, M. pseudangulata differs from M. angulata in its slightly more slender shell (apical angle 32-37° cf. 35-40° in M. angulata).

The shape, proportion and sculptural characters of M. styriaca Hilber 1897 as originally illustrated (Hilber 1897, p. 202, fig. 11) fall within the wide range of variability of M. pseudangulata in its present concept. It is concluded that the name Mohrensternia styriaca Hilber, 1897 has to be considered a synonym of Mohrensternia pseudangulata Hilber, 1897. Since Hilber (1897) described both M. pseudangulata and M. styriaca simultaneously, one name has to be given preference. Friedberg (1923, p. 394) was the first to treat M. styriaca as a subjective synonym of M. pseudangulata; this act is a valid determination of precedence according to Article 24.2 of the ICZN; it was subsequently accepted by Jekelius (1944) and others. Nevertheless, some authors (e.g. ŠVagrovský 1971; Il’ina 1998; Kowalke & Harzhauser 2004) treat M. styriaca as a separate species, distinguishing it from M. pseudangulata by its proportions and shell outline.

The senior synonym Rissoa angulata striata Eichwald, 1850 is a multiple junior objective homonym. It was published simultaneously with the name Rissoa turricula striata Eichwald, 1850. As first revising author (ICZN Art. 24.2), I assign precedence of the name Rissoa turricula striata Eichwald, 1850 over the name Rissoa angulata striata Eichwald, 1850. This action renders the latter invalid as a junior objective homonym. Its subjective synonym M. pseudangulata Eichwald, 1897 becomes therefore the valid name for the species in question. Sometimes the incorrect spelling “pseudoangulata” is used (e.g. Jekelius 1944; Švagrovsky 1971), although the correct original spelling is “pseudangulata” (Hilber 1897, p. 202), which should be maintained.

DISTRIBUTION: Mohrensternia pseudangulata occurs widely in the Late Badenian and Sarmatian of the East and Central Paratethys (Hilber 1897; Friedberg 1911-1928; Jekelius 1944; Švagrovsky 1971; Il’ina 1998).

Mohrensternia banatica Jekelius, 1944
(Text-fig. 7D-E)
1944. Mohrensternia pseudoangulata var. banatica n. var.;
Jekelius, p. 72, pl. 15, figs 16-18.
part 1944. Mohrensternia pseudoangulata var. politioanei n. var.;
Jekelius, p. 72, pl. 15, figs 13-15.
1944. Mohrensternia pseudoangulata Hilber; Jekelius, p. 71, pl. 15, figs 9-10.

MATERIAL: Three specimens from Chmielnik, Poland, ZNG PAN A-I-50/1177, 1201; two specimens from Chlebów, Ukraine, ZNG PAN A-I-50/1190; one specimen from Dmosice, Poland, ZNG PAN A-I-50/1191; two specimens from Zwierzyniec, Poland, ZNG PAN A-I-50/1193, 1202; twenty-five specimens from Zaleśce, Ukraine, ZNG PAN A-I-50/1194, 1203; two specimens from Rydomyl, Ukraine, ZNG PAN A-I-50/1195; thirteen specimens from Žolobki, Ukraine, ZNG PAN A-I-50/1204. Samples from Zaleśce and Dmosice are of Late Badenian/Sarmatian age; all others are from the Sarmatian.

DESCRIPTION: The small, high-spired shell, comprising up to 7.5 rounded, regularly increasing whorls, measures up to 4.0 mm in height and up to 1.5 mm in width. The rounded whorls increase slowly, separated by distinct and moderately deep sutures. Whorls are sculptured by 14–16 closely spaced, slightly wavy to sickle-shaped axial ribs per whorl and fine spiral threads. The last whorl occupies 0.43-0.48 of total shell height. The holostomate aperture is rounded-oval to rounded with a
thin outer lip. The umbilical chink is narrow or completely covered by the columellar margin of the aperture. The apical angle is about 21–28°; the tangent-line is straight.

The conical protoconch comprises 2.25–2.75 whorls measuring 0.40–0.55 mm in height and 0.37–0.44 mm in maximum diameter. The initial cap-like part of the embryonic shell is 0.09–0.11 mm wide. Its boundary with the subsequent larval part of protoconch is well marked by a distinct incision and a slightly thickened rim. The transition from the larval shell to the teleoconch is also distinct. The onset of the adult shell is indicated by the formation of weak axial folds that grade into regular axial ribs. The ornamentation of the embryonic shell is composed of 4–6 fine but (under higher magnification) clearly visible spiral rows of grains or threads, which are slightly inclined. The larval part of the protoconch is smooth.

MEASUREMENTS (in mm):

<table>
<thead>
<tr>
<th>No</th>
<th>HS</th>
<th>WS</th>
<th>HBW</th>
<th>HA</th>
<th>WA</th>
<th>NW</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZNG PAN A-I-50/1172</td>
<td>2.4</td>
<td>1.65</td>
<td>1.6</td>
<td>1.0</td>
<td>0.75</td>
<td>5.25</td>
</tr>
</tbody>
</table>

REMARKS: *Mohrensternia banatica* differs from other known species of *Mohrensternia* in its slenderer shell outline. The species is also one of the most conservative regarding shell shape variability. According to my own observations, the most variable character of the *M. banatica* shell is the strength of development of the axial sculpture. *M. pseudangulata*, which has a quite similar protoconch differs, however, from *M. banatica* in its considerably less slender shell: the apical angle in *M. pseudangulata* is 32–37° compared to 21–28° in *M. banatica*.

**DISTRIBUTION:** *Mohrensternia banatica* is widespread in Late Badenian and Sarmatian deposits of the Eastern and Central Paratethys (HILBER 1897; JEKELIUS 1944; ŠVAGROVSKÝ 1971; IL'INA 1998; KOWALKE & HARZHAUSER 2004).

**TYPE HORIZON AND LOCALITY:** Late Badenian/ Sarmatian sands near the village of Zaleśce, Zbarazhsky district, Khmelnitsky region, Ukraine (Central Paratethys).

**MATERIAL:** The holotype (ZNG PAN A-I-50/1172) from Zaleśce, Ukraine.

**DESCRIPTION:** The shell is comparatively small in size, with a stout, broad conical shape. It comprises at least 5.25 (most likely more) rounded, strongly inflated and regularly increasing whorls separated by deep, distinctly but moderately incised and inclined sutures. The holotype measures 2.4 mm in height and 1.70 mm in width (having 5.25 whorls).

The teleoconch whorls have a maximum convexity in the middle of their height. The ornament consists of up to twenty rounded, strong orthoclinal axial ribs per whorl, with narrow gaps between them (gaps are approximately as wide as the ribs). Additional sculpture consists of regular, closely spaced, sinuous growth lines. The space between the axial ribs is smooth, lacking even delicate spiral ornamentation. The body whorl is strongly inflated, occupying 0.66 of the total shell height. The aperture is large, broad-oval with a thin outer lip. The parietal portion is slightly prominent. The apical angle is about 60°; the tangent-line is straight.

The small conical protoconch comprises 1.5 whorls measuring 0.31 mm in height and 0.36 mm in maximum diameter. The initial cap-like part of the embryonic shell is very large and bulbous, measuring 0.20 mm in width. The embryonic shell as well as the whole protoconch is covered by reticulate micro-ornamentation which stops at the transition from the protoconch to the teleconch. The transition is quite sharply marked by a thickened sinuigera notch on the shell. The onset of the adult shell is indicated by the formation of weak axial folds that grade into regular axial ribs of adult sculptural pattern.

**MEASUREMENTS (in mm):** Holotype only:

<table>
<thead>
<tr>
<th>No</th>
<th>HS</th>
<th>WS</th>
<th>HBW</th>
<th>HA</th>
<th>WA</th>
<th>NW</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZNG PAN A-I-50/1172</td>
<td>2.4</td>
<td>1.65</td>
<td>1.6</td>
<td>1.0</td>
<td>0.75</td>
<td>5.25</td>
</tr>
</tbody>
</table>

REMARKS: The specimen designated here as holotype was labelled *Mohrensternia sarmatica* in FRIEDBERG’s collection. In shell geometry (shape, proportions, apical angle) and characters of ornamentation this species very closely resembles *M. inflata*. However the protoconch morphology enables a clear separation of *M. friedbergi* sp. nov. from all known species of *Mohrensternia*. *M. friedbergi* sp. nov. is characterised by a paucispiral proto-
conch with a bulbous embryonic shell that evidently indicates a lecithotrophic (yolk-rich) embryogenesis, possibly followed by a very short free-living larval stage.

The shell of *Mohrensternia friedbergi* sp. nov. is also significantly smaller than in specimens of *Mohrensternia inflata* with the same number of whorls. Taking into consideration these differences, the species described here can only provisionally be attributed to the genus *Mohrensternia*.

**DISTRIBUTION:** This species is known only from the type locality – the Late Badenian/Sarmatian deposits near Zaleśce village (Zbarazhsky district Khmelnitsky region) in the Western Ukraine (Central Paratethys).

**CONCLUSIONS**

The newly examined material confirmed that certain characters of the protoconch and teleconch of Sarmatian *Mohrensternia* and *Rissoa* species are quite similar to each other. Both genera have inflated conical, rounded protoconchs ornamented by delicate spiral rows of granules or threads. This protoconch morphology supports a close relationship between *Mohrensternia* and *Rissoa*; the protoconch characters do not enable these two genera to be clearly distinguished, except for slightly inclined spiral rows in *Mohrensternia*, and spiral rows parallel to the suture in *Rissoa*.

The morphological data available do not justify classification of *Mohrensternia* in a subfamily Mohrensterniinae of the Rissooidae, but suggest rather that both *Mohrensternia* and *Rissoa* should be maintained as independent genera within the family Rissooidae *sensu stricto*.

The taxonomically significant differences between *Mohrensternia* and *Rissoa* lie in teleconch morphology. The shells of *Mohrensternia* are relatively thinner (1), they have indeterminate growth, while *Rissoa* has determinate growth and develops a thickened outer lip (2), the aperture of *Mohrensternia* is slightly curved and elongated abapically (3), the axial ribs of *Mohrensternia* tend to form high sickle-shaped or half-moon-shaped scales, while this is absent at *Rissoa*.

Due to the highly variable shell shape and sculpture, *Mohrensternia* species require the complex of all available characters and dimensions for their diagnoses.

An unexplained morphological phenomenon is the existence of dwarf *Mohrensternia* species (e.g. *M. sarmatica*), in which the shell is about two-thirds the height of other species at the same number of whorls. Although there are several hypothesis devoted to the causes of dwarfism, the nature of dwarfism phenomena in *M. sarmatica* and some other Sarmatian molluses is still unknown.

Comparison of the species lists of *Mohrensternia* known from coeval Late Badenian/Sarmatian sediments from the central and eastern parts of the Central Paratethys shows that within the central part considerably more species are recorded than within its eastern part. *Kowalke & Harzhauser* (2004) listed 12 in the central part while in the eastern part no more than seven to eight species are known (*Friedberg* 1923; *Kolesnikov* 1935; present data). Some authors, e.g. *Jekelius* (1944), recognize more taxa including subspecies, which have been treated as synonyms in this study and by others.

*Mohrensternia* flourished in the Central Paratethys during the maximum transgression of the Sarmatian Sea. In the central part of the Central Paratethys its bloom occurred in the Early Sarmatian substage, whereas in its eastern part it was in the Middle Sarmatian. In both cases, the species of the genus preferred marine conditions with reduced salinity.

According to this study, practically the same species of *Mohrensternia* inhabited the Late Badenian and Sarmatian basins in western Ukraine and eastern Poland.

The taxonomic position of the new described species (*Mohrensternia friedbergi* sp. nov.) is still somewhat uncertain and it is only provisionally included in the genus *Mohrensternia*. In *Mohrensternia friedbergi* sp. nov. protoconch dimensions, proportions and shape clearly indicate lecithotrophic development. Within the Badenian and Sarmatian of the central part of the Central Paratethys no representative with this type of development has been documented to date (*Kowalke & Harzhauser* 2004).

**Acknowledgements**

I am deeply indebted to Barbara Kietlinska-Michalik (Geological Museum of the Institute of Geological Sciences of the Polish Academy of Sciences, Kraków, Poland), who helped me so much during my stay in the Museum. The SEM micrographs were performed by Anna Latkiewicz, Laboratory of Field Emission Scanning Electron Microscopy and Microanalysis at the Institute of Geological Sciences of the Jagiellonian University, Kraków (Poland). Photographs of one specimen from the Natural History Museum, Vienna (Austria) have been provided by Dr. Jens Hartmann, Geological-Paleontological Institute and Museum of the University of Hamburg (Germany). The visits to Kraków and work on the rissoids from the W. Friedberg collection were made possible due to a four-month Scholarship from the Polish Fund of Assistance for Science (Kasa im. Józefa Mianowskiego) in 2004. The field expedition was partly supported by the Paleontological Society International Research Program – Sepkoski Grants 2003.
REFERENCES

ANDRUSOV, N.I. 1890. Kerch limestone and its fauna. Zapisiki Sankt-Peterburgskogo Mineralogicheskogo Obshchestva, Ser. 2 (26), 193-345. [In Russian, with extended summary in German]


*Manuscript submitted: 10th March 2005
Revised version accepted: 20th October 2005*
### Appendix 1.

The List of Late Badenian to Sarmatian occurrences of *Mohrensternia* species deposited in the Geological Museum of the IGS PAS (Kraków, Poland). Total amount 1605 samples in 46 lots

<table>
<thead>
<tr>
<th>Number of lots according to Museum Catalogue</th>
<th>Species name according to FRIEDBERG (1911-1928)</th>
<th>Pages, No of Tables and figures in the FRIEDBERG’S monograph 1911-1928</th>
<th>Locality</th>
<th>Species name, adopted in the present paper</th>
</tr>
</thead>
<tbody>
<tr>
<td>1161</td>
<td><em>Mohrensternia inflata</em> Hörn.</td>
<td>387 23 7 Chlebów</td>
<td>1</td>
<td><em>Mohrensternia inflata</em></td>
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<tr>
<td>1162</td>
<td><em>-</em></td>
<td>387 - - Chlebów</td>
<td>8</td>
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</tr>
<tr>
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<td><em>-</em></td>
<td>387 - - Krzemieniec</td>
<td>2</td>
<td><em>Mohrensternia perinflata, M. angulata</em></td>
</tr>
<tr>
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<td><em>-</em></td>
<td>387 - - Zalesie</td>
<td>23</td>
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<td><em>-</em></td>
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<td><em>Mohrensternia inflata, M. perinflata, M. pseudinflata</em></td>
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<td>387 - - Rydoml</td>
<td>13</td>
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<tr>
<td>1168.1</td>
<td><em>M. sarmatica</em> Friedb.</td>
<td>389 23 8-10 Rydoml</td>
<td>3</td>
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</tr>
<tr>
<td>1168.2</td>
<td><em>-</em></td>
<td>389 - - Rydoml</td>
<td>194</td>
<td><em>M. sarmatica</em> (including the lectotype), <em>M. inflata</em></td>
</tr>
<tr>
<td>1169</td>
<td><em>-</em></td>
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<td>2</td>
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</tr>
<tr>
<td>1170</td>
<td><em>-</em></td>
<td>389 - - Słupeč</td>
<td>51</td>
<td><em>M. sarmatica, M. inflata</em></td>
</tr>
<tr>
<td>1171</td>
<td><em>-</em></td>
<td>389 - - Dwikozy</td>
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<tr>
<td>1172</td>
<td><em>-</em></td>
<td>389 - - Zalesie</td>
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<td><em>M. sarmatica, M. inflata, M. friedbergi sp.n.(the holotype only)</em></td>
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<tr>
<td>1181</td>
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<tr>
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</tr>
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<td>1189</td>
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<tr>
<td>1191</td>
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<tr>
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<tr>
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</tr>
<tr>
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<td><em>Mohrensternia (?)</em> sp. indet.</td>
<td>395 23 19 Rydoml</td>
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<tr>
<td>1206</td>
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<td>395 - - Rydoml</td>
<td>11</td>
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</tr>
</tbody>
</table>
Appendix 2.
The list of 25 works in the last 50 years by at least 10 different authors encompassing a span of not less than 10 years, where the name *Mohrensternia inflata* (HÖRNES, 1856) has been used as a valid name.

3. BONČEV, E. 1960. *Geologia na Bolgaria. 2.*, pp. 1-163; *Nauka i Izkustvo*; Sofia. [In Bulgarian]
4. MOLIJKOV, G.I. 1960. *Neogen pivdna Ukrainy*, pp. 1-208; *Akademia Nauk USSR*; Kiev. [In Ukrainian]
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