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PHYLOGENETIC RELATIONSHIPS OF *COELACANTHIA* AND *ARCHASCENIA*, TWO SPINOSE RISSOIDS (MOLLUSCA, GASTROPODA) FROM THE MIOCENE OF THE EASTERN PARATETHYS

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Phylogenetic Relationships of *Coelacanthia* and *Archascenia*, Two Spinose Rissoids (Mollusca, Gastropoda) from the Miocene of the Eastern Paratethys. Anistratenko V. V. — The Miocene rissoids *Archascenia* Zhgenti, 1981 and *Coelacanthia* Andrusov, 1890 are not directly related, but have common ancestors in the *Mohrensternia* Stoliczka, 1868 lineage. They have evolved from the different species of *Mohrensternia*, which immigrated into the Ponto-Caspian area of the Eastern Paratethys from the Mediterranean. *Archascenia merklini* Zhgenti, 1981 and *A. iljinae* Zhgenti, 1981 have evolved from *Mohrensternia barboti* Andrusov, 1890 or a related species during the Karagianian, whereas *Coelacanthia quadrispinosa* Andrusov, 1890 evolved from *Mohrensternia subinflata* Andrusov, 1890 during the Maeotian. The morphological data available suggest that *Rissoa* Desmarest, 1814, *Mohrensternia*, *Archascenia* and *Coelacanthia* should be considered as separate genera within the family Rissoidae. The recently introduced for these taxa (Anistratenko, 2003) family Mohrensterniidae Korobkov, 1955 (with the subfamilies Mohrensterniinae Korobkov, 1955, Coelacanthiinae Anistratenko, 2003 and Archasceniinae Zhgenti, 1991) is considered as insufficiently substantiated.

Key words: Gastropoda, Rissooidea, phylogeny, taxonomy, Miocene, Paratethys.

Филогенетические отношения *Coelacanthia* и *Archascenia*, двух родов «шипастых» риссоид (Mollusca, Gastropoda) из миоцена Восточного Паратетиса. Анистратенко В. В. — Миоценовые риссоиды родов *Archascenia* Zhgenti, 1981 и *Coelacanthia* Andrusov, 1890 не связаны друг с другом непосредственным родством, однако имеют общих предков в эволюционной ветви рода *Mohrensternia* Stoliczka, 1868. Они произошли от разных видов *Mohrensternia*, которые проникали в Понто-Каспийскую область Восточного Паратетиса из Средиземноморья. *Archascenia merklini* Zhgenti, 1981 и *A. iljinae* Zhgenti, 1981 произошли от *Mohrensternia barboti* Andrusov, 1890 или близкого вида в карагане, тогда как вид *Coelacanthia quadrispinosa* Andrusov, 1890 обособился от *Mohrensternia subinflata* Andrusov, 1890 в мэотисе. Имеющиеся морфологические данные убеждают, что *Rissoa* Desmarest, 1814, *Mohrensternia*, *Archascenia* и *Coelacanthia* должны рассматриваться как особые роды в пределах семейства Rissoidae. Недавнее установление для этих групп (Анистратенко, 2003) семейства Mohrensterniidae Korobkov, 1955 (с подсемействами Mohrensterniinae Korobkov, 1955, Coelacanthiinae Anistratenko, 2003 и Archasceniinae Zhgenti, 1991) признается теперь излишним.

Ключевые слова: Gastropoda, Rissooidea, филогения, систематика, миоцен, Паратетис.

Introduction

The Rissooidea is one of the largest and most diversified gastropod groups worldwide. It occupies full marine to fresh-water habitats (Wenz, 1938–1944; Ponder, 1985; Anistratenko, Starobogatov, 1994). The Miocene fossil record of Paratethys reveals a wide range of rissoid morphologies, which are usually related to different ecological conditions. During this time many endemic lineages have evolved, of which the best known one is the *Mohrensternia* Stoliczka, 1868 lineage. The gastropods of this genus became one of most common components of the semi-marine to brackish-water gastropod associations in the Paratethys (Stoliczka, 1867–1868; Andrusov, 1890, 1906; Friedberg, 1911–1928; Kolesnikov, 1935; Zhizhchenko, 1936; Svagrovsky, 1971; Il'ina, 1972 a, b, 1979; Il'ina et al., 1976).

Although the genus *Mohrensternia* is well known to West European readers (see review by Kowalke, Harzhauser, 2004), other related gastropods have been studied only by paleontologists of the former USSR.

The subfamily Mohrensteriinae was introduced by Korobkov (1955), but its taxonomy and generic/specific content have not been adequately evaluated (Badzoshvili, 1991; Zhgenti, 1981, 1991; Il'ina, 1993).

The aim of this paper is to discuss possible taxonomic significance of shell morphological characters of some *Mohrenstermia*-related gastropods and to trace their possible phylogenetic relationships. A review of the poorly known homeomorphic genera *Coelacanthia* Andrusov, 1890 and *Archaschenia* Zhgenti, 1981 is provided and the systematic position of these taxa is evaluated.

Material and methods

The present investigation is mainly based on large collections of Miocene gastropods, which are housed at the Institute of Geological Sciences of the National Academy of Sciences of the Ukraine and at the Schmalhausen Institute of Zoology NAS of Ukraine (Kyiv). The material comes from natural outcrops and borehole of Sarmatian deposits in western Ukraine. More than 3 000 specimens of the *Mohrenstermia* and *Rissoa* Desmarest, 1814 identified in studied samples. Also I examined three specimens of *Coelacanthia quadrispinosa* Andrusov, 1890 from the type collection of Andrusov (1890). Andrusov collected this material from Maeotian deposits near Pavlovsky Cape on Kerch Peninsula (fig. 1). These samples quite possibly are paralectotypes for this species as Il'ina (2001) designated the lectotype from the same locality.

An optical stereoscopic microscope (MBS-9) and a simple "drawing tube" were used for studying and drawing the shell characters. The SEM micrographs were made at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw (Poland), abbreviated ZPAL Ga. 11/1; the illustrated specimen is housed there.

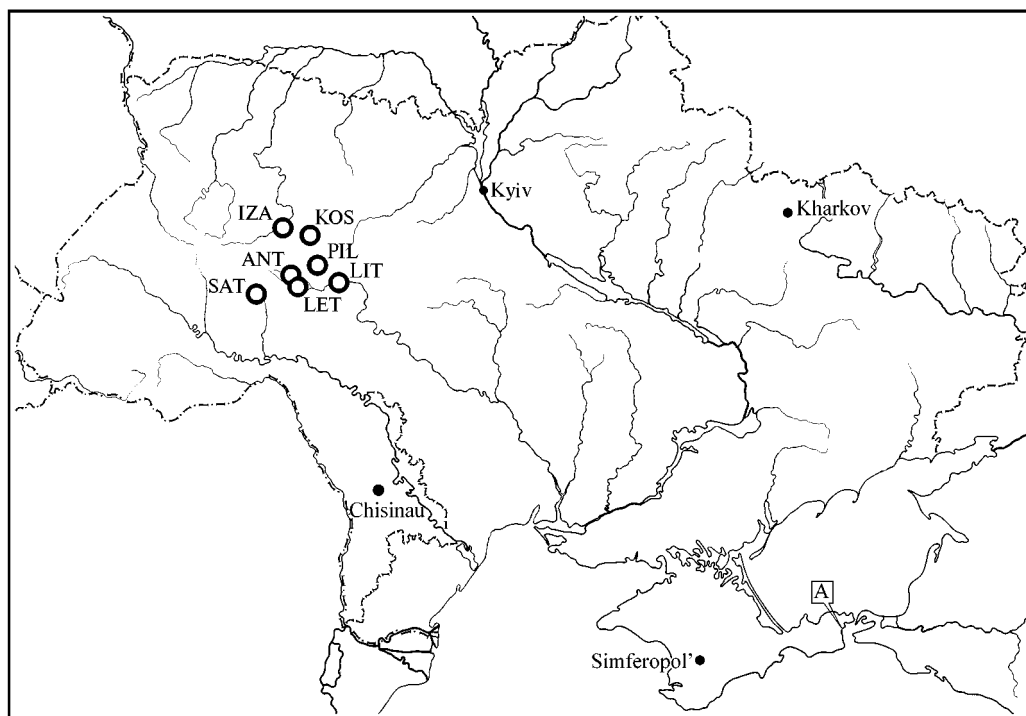


Fig. 1. Location of the outcrops and borehole in the western Ukraine and on Kerch peninsula: PIL — outcrop between Pilyava and Ivankovcy villages, Staraya Sinyava district, Khmelnytsky region; KOS — outcrop between Kos'kov and Grycev villages, Shepetovka district, Khmelnytsky region; LIT — borehole 1529 near Litinka village, Litin district, Vinnitsky region; ANT — outcrop near Antonovka village, Letichev district, Khmelnytsky region; LET — outcrop near Letichev, Khmelnytsky region; SAT — outcrop near Satanov town, Khmelnytsky region; IZA — precipice on the bank of river Goryn, vicinity of Izyaslav town, Khmelnytsky region; A — Andrusov's (1890) record of *Coelacanthia quadrispinosa* in Kertsch peninsula — type locality.

Рис. 1. Местонахождение обнажений и скважин в западной части Украины и на Керченском п-ве: PIL — обнажение между селами Пилява и Иванковцы, Старосинявский р-н, Хмельницька обл.; KOS — обнажение между селами Коськов и Грицев, Шепетовський р-н, Хмельницька обл.; LIT — скважина 1529 возле с. Литинка, Литинський р-н, Вінницька обл.; ANT — обнажение возле с. Антоновка Летичевского р-на., Хмельницька обл.; LET — обнажение возле Летичева, Хмельницька обл.; SAT — обнажение возле г. Сатанов, Хмельницька обл.; IZA — береговой обрыв р. Горынь в окр. г. Изяслав, Хмельницька обл.; А — место обнаружения *Coelacanthia quadrispinosa* Андрусовым (1890) на Керченском п-ове — типовое местонахождение.

Results and discussion

The genus *Mohrensternia* was erected by Stoliczka (1868) for a few Miocene rissoid species (*Rissoa angulata* Eichwald, 1830, *R. inflata* Hörnes, 1856 and others), which occur in the brackish or fresh-water deposits of central and Eastern Europe. Since that time the number of species classified in *Mohrensternia* has increased significantly (Andrusov, 1890, 1906; Zhizhchenko, 1936; Zhgenti, 1981) although some of them were transferred later to morphologically similar genus *Rissoa* (Il'ina, 1979; Badzoshvili, 1991). The shell of *Mohrensternia* differs from *Rissoa* one by having relatively thin walls and not thickened outer lip of aperture; the ornament consists of delicate spiral threads and strong usually curved axial ribs.

The fossil record of *Mohrensternia* strongly suggests that the genus has evolved from *Rissoa* as early as latest Oligocene/earliest Miocene (Andrusov, 1890; Zhizhchenko, 1936; Korobkov, 1955). In the middle part of Miocene *Mohrensternia* is already well diversified. For instance the Tarkhanian and Chokrakian seas were inhabited by *Mohrensternia protogena* (Andrusov, 1890), *M. subprotogena* Zhizhchenko, 1936, *M. nitida* Zhizhchenko, 1936, *M. pseudosarmatica* Friedberg, 1923. In Karaganian Sea lived the *Mohrensternia grandis* (Andrusov, 1890), *M. barboti* (Andrusov, 1890), *M. subglobosa* Zhgenti, 1981, *M. karaganica* Zhgenti, 1981, *M. gratiosa* Zhizhchenko in Il'ina, 1993. From Sarmatian deposits are known the *Mohrensternia angulata* (Eichwald, 1830), *M. inflata* (Hörnes, 1856), *M. hydrobioides* Hilber, 1897, *M. pseudoinflata* Hilber, 1897. At last the Maeotian Sea was inhabited by the *Mohrensternia carinata* (Andrusov, 1890), *M. subangulata* (Andrusov, 1890) and *M. subinflata* (Andrusov, 1890). Actually these are only our preliminary survey, because the exact faunal composition is still incomplete, and is a subject for discussions and contradictions.

The decrease of the salinity in the Ponto-Caspian basins forced *Mohrensternia* to adapt these conditions. As a result the homeomorphic genera *Archaschenia* and *Coelacanthia* have developed in two different time horizons (Karaganian and Maeotian respectively) independently.

The question of affinity and distinction between *Mohrensternia* and *Rissoa*, *Mohrensternia* and *Archaschenia*, and also *Mohrensternia* and *Coelacanthia* were widely discussed in the literature (Stoliczka, 1868; Il'ina, 1972 a, b; Zhgenti, 1981, 1991; Badzoshvili, 1991). Zhgenti (1991) provided the hypothesis on the origin of *Archaschenia* while phylogenetic relationships between *Mohrensternia* and *Coelacanthia* have been postulated by Il'ina et al. (1976).

The monotypic genus *Coelacanthia* was established by Andrusov (1890) for *C. quadrispinosa* from Maeotian deposits of Kerch Peninsula. Later Andrusov (1906) repeated the original description of the species, which he supplemented by three drawings and one photograph of the shells. Although these images are of rather poor quality they allow nevertheless to note the main diagnostic characters. The shell of *C. quadrispinosa* is characterized by very thin walls, conical shape and lacking both spiral and axial ornamentation. Apart from fine growth lines it bears also spine-like projections with a narrow slit along their posterior side (fig. 2, 3). Andrusov (1890, 1906) classified *Coelacanthia* with some doubts in the family Rissoidae and its systematic position is still not fully understood (Wenz, 1938–1944; Starobogatov, 1970). In the original description of the species as well as in the formal diagnosis of the genus, Andrusov (1890, 1906) has emphasized the distinctiveness of the *Coelacanthia* sculpture elements and supposed that the spines are the outer lip projections sealed by the following whorls.

C. quadrispinosa has spines that are highly modified axial ribs (such ribs are always present at the *Mohrensternia* species), which were inflected into strongly stretched projections and not outer lip through projections (as e. g., in *Typhis* Montfort, 1810 or *Murex* Linnaeus, 1758). They form a semiclosed cone narrowing towards its end (fig. 2, 3). Only the outer layers of the shell (i. g., periostracum and outer layer of ostracum)

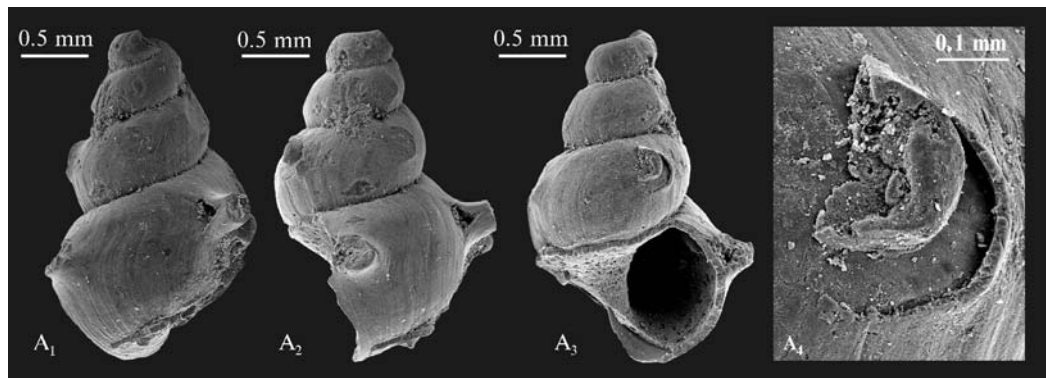


Fig. 2. Shell of paralectotype of *Coelacanthia quadrispinosa* in different position showed the characteristics of sculpture (A₁–A₃) and base part of a broken spine (A₄).

Рис. 2. Раковина паралектотипа *Coelacanthia quadrispinosa* в различных положениях; показаны особенности скульптуры (A₁–A₃) и базального участка отломившегося шипа (A₄).

were engaged in forming the spines (as in the forming of the axial ribs of *Rissoa* and *Mohrensternia*). The aperture of adult *C. quadrispinosa* is simple, holostomous without any channel extended into the spine as it was mentioned in the original description of Andrusov (1890).

All these facts strongly suggest that *Coelacanthia* belongs to Rissoidae, not to Hydrobiidae or Pyrgulidae (= Micromelaniidae) as it was suggested by some authors (Wenz, 1938–1944; Starobogatov, 1970; Badzoshvili, 1991).

The fossil record suggests also that *C. quadrispinosa* has evolved from a species of Maecotian *Mohrensternia*, most probably *M. subinflata* (Andrusov, 1890). The transformation of the *Mohrensternia* axial ribs into spines of *Coelacanthia* is quite simple from the morphological point of view (see the reconstruction of those projections on fig. 3, A₁–A₄). The collection of Andrusov, deposited at the Paleontological Institute of Russian Academy of Sciences (Moscow) consists also of some intermediate forms (specimens were collected from the same strata) showing the continuous transformation *M. subinflata* into *C. quadrispinosa* (fig. 3, B–D). It is clearly visible, that the intermediate forms differ from typical smooth *Coelacanthia* by its wider and thickened shell ornamented with fine spiral threads and remnants of axial ribs (fig. 2, 3). This ornamentation is similar to the one present among *M. subinflata* specimens but the presence of the spines and more slender shell shape are typical of *C. quadrispinosa*. Although the intermediate forms between *M. subinflata* and *C. quadrispinosa* are known nevertheless the transformation was so fast, that it might be considered as “instantaneous”. *M. subinflata*, when evolved towards *C. quadrispinosa*, lost the axial and spiral sculpture but acquired spines and thinner-walled shell instead.

These transformations seem to be connected with a rapid change of habitat, which probably had an impact on their mode of life. *Mohrensternia* most probably lived in sea grass meadows similarly to many modern species of the *Rissoa* (Fretter, Graham, 1963; Anistratenko, Stadnichenko, 1995). The long and fragile spines cannot be regarded as adaptive to such conditions. The thin-walled shells and spines of *Coelacanthia* suggest that the mollusks inhabited most likely a rather soft substratum (И’ина, 1979).

A similar scenario as with *Coelacanthia* led probably to the development of *Archaschenia merklini* Zhgenti, 1981 and *Archaschenia iljinae* Zhgenti, 1981, the Karagian rissoids of the Crimean-Caucasian region of the Paratethys. These gastropods are known only from the Varnensky substage of the Karagian and, according to Zhgenti (1991), are derived from *Mohrensternia barboti* (Andrusov, 1890). Also in this case a sequence of intermediate forms (from the same strata) is known (fig. 3, E–G).

Shell of *Archaschenia* differs from *Coelacanthia* one practically only by lower spire and having an extremely fragile periostracal plate that covers the slit which is along the spine-like projections.

An much harder task is to solve the problem of demarcation between *Mohrensternia* and *Mohrensternia*-derived *Archaschenia* and *Coelacanthia*. The fossil record of both



Fig. 3. The sculptural elements of *Coelacanthia quadrispinosa* (A₁–A₄) and reconstructions of the morphological lineage *Mohrensternia subinflata* (B) — *Coelacanthia quadrispinosa* (C, D₁, D₂) and *Mohrensternia barboti* (E) — *Archaschenia merklini* (F, G). B–D after Il'ina et al., 1976, modified; E–G after Zhgenti, 1991, modified.

Рис. 3. Элементы скульптуры *Coelacanthia quadrispinosa* (A₁–A₄) и реконструкции морфолого-эволюционных рядов *Mohrensternia subinflata* (B) — *Coelacanthia quadrispinosa* (C, D₁, D₂) и *Mohrensternia barboti* (E) — *Archaschenia merklini* (F, G). B–D по Ильиной и др., 1976, с изменениями; E–G по Жгенти, 1991, с изменениями.

cases is complete enough to trace continuous lineages. The evolution of these gastropods may be divided into four stages as follows.

1. Typical *Mohrensternia* ornamented with strong axial ribs.
2. Shells with sinusoidal and relatively weaker but wider ribs.
3. Shells with clamp-shaped ribs, which express a tendency to form high half-moon-shaped scales. Both features (clamp-shaped ribs and sinusoidal ribs) can be noted sometimes even on the same shell.
4. Shells with both half-moon-shaped scales and spines typical of *Archaschenia* and *Coelacanthia*.

The shells, which have axial ribs with half-moon-shaped scales, even low and not inflected into incipient spines, have to be excluded from *Mohrensternia*. Spines and scales as modifications of the sculpture are typical of *Archaschenia* and *Coelacanthia* and gastropods with such features should be classified in those genera.

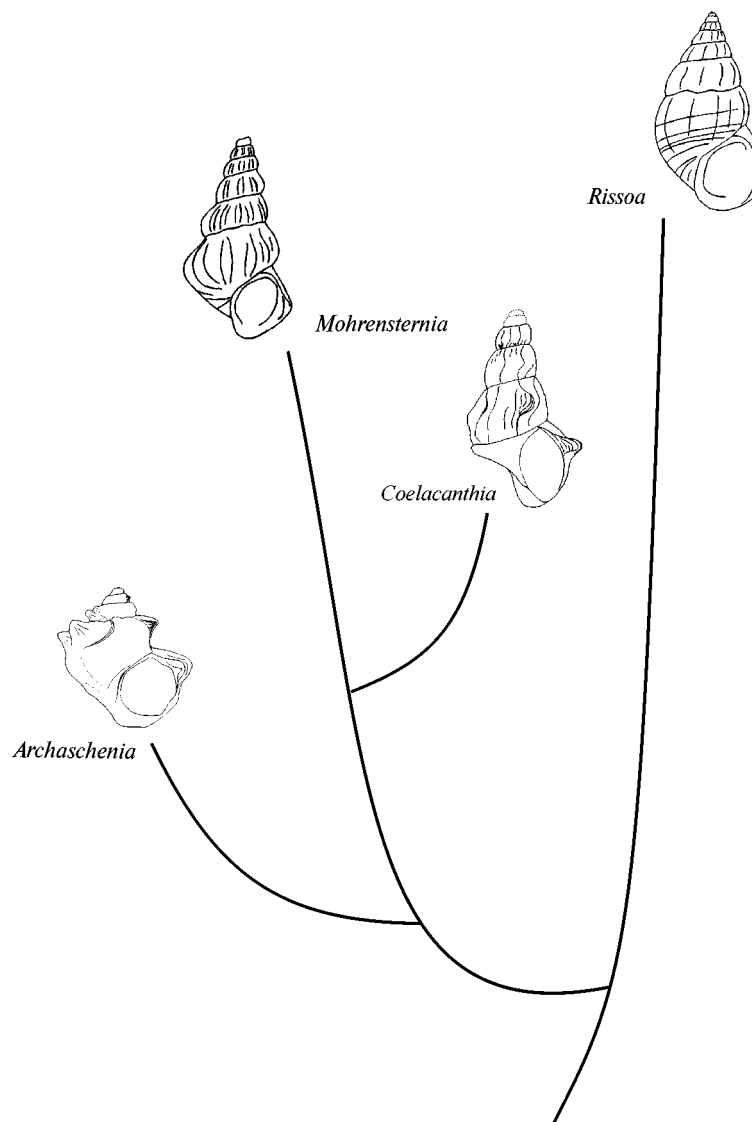


Fig. 4. The hypothetical scheme of the phylogenetic relationships of some Miocene rissoids.

Рис. 4. Предполагаемая схема филогенетических отношений некоторых миоценовых риссоид.

In result *Archaschenia* and *Coelacanthia* although strikingly similar are only heterochronous homeomorphic taxa developed in two different time horizons from two different species of *Mohrensternia*, which immigrated repeatedly from the Mediterranean into the Ponto-Caspian area of the Eastern Paratethys (Anistratenko, 2001). Thus the position of these genera among Rissoidae is doubtless. The hypothetical scheme of the phylogenetic relationships of mentioned taxa is presented in figure 4.

The Rissoidae in broad sense is a conglomerate of families, which are united into the superfamily Rissooidea (Ponder, 1985; Anistratenko, Starobogatov, 1994). Karaganian *Archaschenia*, Maeotian *Coelacanthia* and also their ancestor group *Mohrensternia* should be considered as separate genera. Taking into consideration mainly the unusual characteristics of the adult shell (namely lacking of spiral and axial ornamentation and bearing the spine-like projections instead of), the level of their distinctiveness was recently evaluated to merit subfamily rank (Anistratenko, 2003). This decision has been made in a similar way as the taxonomic treatment of the recent Rissoiformes, based on a complex evaluation of conchological, anatomical and other characters (Golikov, Starobogatov, 1975, 1989; Ponder, 1985; Anistratenko, Starobogatov, 1994; Anistratenko, Stadnichenko, 1995).

Homeomorphy, so common in different groups of gastropods, may be present among species of the same or closely related genera but commonly also different genera (e. g. *Archaschenia* and *Coelacanthia*) or even families. The latter has been exemplified by Anistratenko (1998). It was shown that species of the recent genera *Haurakia* Iredale, 1915 and *Mutiturbella* Nordsieck, 1972 (Haurakiidae) are very similar conchologically to *Rissoa* and *Benzia* Nordsieck, 1972 (Rissoidae); *Thalassobia* Bourguignat in Mabilie, 1877 (Cochliopidae Tryon, 1866 [syn. Littoridinidae Thiele, 1928]) is analogous to *Hydrobia* Hartmann, 1821 (Hydrobiidae). Anatomically all these pairs of genera differ enough to place them in easy distinguishable families — more detail see Ponder (1985) and Anistratenko, Stadnichenko (1995).

When the higher level taxonomic units of any group are defined it is important to follow certain principles. One of the most important, the principle of a uniform level of taxonomical distinctiveness, requires that all taxa of the same rank have to be based on the same level of distinctiveness (Mayr, 1971; Golikov, Starobogatov, 1989). Morphological characters of three reviewed genera were considered as sufficiently distinct to place them in three different monotypic subfamilies (Mohrensterniinae Korobkov, 1955, Coelacanthiinae Anistratenko, 2003 and Archascheniinae Zhgenti, 1991) and to unite them in the separate family Mohrensterniidae Korobkov, 1955 within Rissooidea (Anistratenko, 2003) (see Appendix).

Some data on protoconch characters of Sarmatian *Rissoa* and *Mohrensternia* from West Ukraine (author's collection) were recently obtained using the SEM. These are unpublished data obtained in summer 2003 jointly with Dr. Andrzej Kaim (Institute of Paleobiology, Polish Academy of Sciences, Warsaw). Unfortunately, the studied shells condition was not good, and the SEM micrographs are not proper enough for publication. Nevertheless, the main characters of protoconch and teleoconch both of *Rissoa* and *Mohrensternia* could be evaluated from those SEM micrographs. They suggest to change the taxonomy significantly. The detailed documentation of Sarmatian *Mohrensternia* and *Rissoa* from West Ukraine shows the following: 1) the structure and characteristics of *Rissoa* and *Mohrensternia* protoconchs are quite similar i. e., both genera have inflated, rounded protoconchs sculptured only by a few (2–4) fine spiral threads; 2) among the Sarmatian *Mohrensternia* at least a few distinct species (*M. angulata*, *M. inflata*, etc.), which lived sympatrically, could be recognized. They are similar on protoconch characters, but distinguished enough on shell geometry, i. e., Raup's parameters (Raup, 1966).

The taxonomically significant differences between *Mohrensternia* and *Rissoa* are: in *Mohrensternia* the shell is relatively thinner; the outer lip is not thickened, and is slight-

ly curved and lengthened on the base. Also the axial ribs of *Mohrensternia* express the tendency to form high half-moon-shaped scales. *Archaschenia* as well *Coelacanthia* usually lack the thickness of the outer lip which *Rissoa* has.

Thus the significant morphological similarities suggest a close relationship between *Mohrensternia* and *Rissoa*. The peculiarities of *Archaschenia* and *Coelacanthia* suggest their distinctiveness, although they are definitely connected with *Mohrensternia*.

Unfortunately we have no specimen of *Coelacanthia* or *Archaschenia* preserved well enough to study the protoconch structure. Therefore our proposed taxonomy is still quite provisional (Anistratenko, 2003). It follows from the preceding taxonomic interpretation that the separation of *Mohrensternia*, *Archaschenia* and *Coelacanthia* into three separate monogeneric subfamilies as well as establishing the family Mohrensterniidae was a premature decision (Anistratenko, 2003). Data available suggest that all mentioned taxa (*Rissoa*, *Mohrensternia*, *Archaschenia* and *Coelacanthia*) should be considered as independent genera within the family Rissoidae.

Conclusion

1. The species of *Archaschenia* lived in the Eastern Paratethys during the Karaganian, whereas the species of *Coelacanthia* lived only in the Early Maeotian. These taxa have a very similar morphology, with the resemblance of their sculpture elements being most conspicuous. The sculptural features are undoubtedly homologous, and they were generated independently at different times. The morphological similarity is so strong, that some authors (Badzoshvili, 1986) regard them as species of one genus or even as one species.

2. Although *Archaschenia* and *Coelacanthia* are not directly related, they have common ancestors in the *Mohrensternia* lineage. These taxa have evolved from the different species of *Mohrensternia*, which is known to have immigrated into the Ponto-Caspian area of the Eastern Paratethys from the Mediterranean.

3. *Archaschenia* has evolved from *Mohrensternia barboti* or a related species during the Karaganian, whereas *Coelacanthia quadrispinosa* evolved from *Mohrensternia subinflata* during the Maeotian. The homeomorphic similarity of those taxa was due to convergence in development of homologous structures because of similar ecological pressures related to episodes of paleogeographic isolation and lowering of the salinity of the Eastern Paratethys sea.

4. All taxa mentioned (*Rissoa*, *Mohrensternia*, *Archaschenia* and *Coelacanthia*) should be considered as separate genera within the family Rissoidae.

I wish to thank to Dr. L. B. Il'ina (Paleontological Institute RAS, Moscow) for the donation of three specimens of *Coelacanthia quadrispinosa*. I am greatly indebted to Dr. Andrzej Kaim (Institute of Paleobiology PAS, Warsaw) for making the SEM micrographs and for his effort to improve this manuscript. Dietrich Kadolsky (Great Britain) kindly helped in the proof-reading of the manuscript and provided helpful suggestions, for which I am very grateful.

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Appendix

The systematics of *Mohrensternia*, *Coelacanthia* and *Archaschenia* recently reviewed (Anistratenko, 2003). As this paper was published in Russian, the taxonomic proposals are summarized here in English.

Superfamily Rissooidea Gray, 1847
Family Mohrensterniidae Korobkov, 1955

Type genus: *Mohrensternia* Stoliczka, 1868

Diagnosis. Shell small, oval to ovate or conical. The ornament consists of fine spiral threads and commonly strong axial ribs. In some cases spine-like sculptural projections with a narrow slit along their posterior side are present. The aperture is rounded, holostomous. Umbilicus is absent.

Distribution. Miocene (and Pliocene?) of Europe.
Content. The family includes three subfamilies.

Subfamily Mohrenstermiinae Korobkov, 1955

Diagnosis. Shell with relatively thin walls, the outer lip not thickened. The ornament consists of delicate spiral threads and strong usually curved axial ribs.

Distribution. Miocene (and Pliocene?) of Europe.
Content. Monogeneric.

Genus *Mohrensternia* Stoliczka, 1868

Type species: *Rissoa angulata* Eichwald, 1830, by subsequent designation by Nevill, 1885.

Diagnosis. As for the subfamily.

Distribution. Miocene (and Pliocene?) of Europe.
Content. Approximately 15–20 species.

Subfamily Coelacanthiinae Anistratenko, 2003

Type genus: *Coelacanthia* Andrussov, 1890, by original designation.

Diagnosis. Shell very thin-walled. The shell usually lacks spiral and axial ornamentation apart from fine growth lines and spine-like projections with narrow slit along their posterior side.

Distribution. Miocene (Maeotian) of Eastern Europe.
Content. Monogeneric.

Genus *Coelacanthia* Andrussov, 1890

Type species: *Coelacanthia quadrispinosa* Andrussov, 1890, by monotypy.

Diagnosis. As for the subfamily.

Distribution. Miocene (Maeotian) of Eastern Europe.
Content. Only the type species.

Subfamily Archascheniinae Zhgenti, 1991
(proposed as tribe Archascheniini Zhgenti, 1991)

Type genus: *Archaschenia* Zhgenti, 1981.

Diagnosis. Shell thin-walled, conical in shape. Spiral and axial ornamentation are absent. The surface usually bears spine-like projections with narrow slit along their posterior side. The slit is covered by an extremely fragile periostracal plate.

Distribution. (Middle Miocene) Karaganian of East Europe.
Content. Monogeneric.

Genus *Archaschenia* Zhgenti, 1981

Type species: *Archaschenia merklini* Zhgenti, 1981, by original designation.

Diagnosis. As for the subfamily.

Distribution. Middle Miocene (Karaganian, Varnensky horizon) of Kerch Peninsula and Transcaucasia.
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