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Morphogenesis of Rissoidae in the Inland Basins of the Eastern Paratethys

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Abstract—Miocene rissoids from the heterochronous low-salinity seas of the Eastern Paratethys (Early Chokrakian, Karaganian, Late Konkian, Early Sarmatian, and Early Maeotian) were revised. The polyphyletic genus *Mohrensternia* is subdivided into several generic and subgeneric taxa. The new genus *Zhgentia* and the new subgenera *Rissoa (Turboellina)*, *R. (Pseudoturboellina)*, and *R. (Maeotia)* are established.

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Key words: Gastropoda, Rissoinae, Miocene, Eastern Paratethys, polyphyletic taxa, *Mohrensternia*.

DISCUSSION

The alternation of different basin types in the Miocene of the Pont-Caspian Region (Eastern Paratethys) depended on their isolation from the ocean waters. The salinity of the successive inland basins of the Eastern Paratethys primarily depended on connection or disconnection with the open waters. The salinity was almost normal while the connective channel was wide, and it reduced with the restriction of connection. In the completely closed basins a considerable desalination occurred and the salt composition changed from that of the open sea to that of the Caspian Sea (Nevesskaja et al., 2005).

The degree of isolation from the ocean waters closely controlled the bionomic features of the inland basin, a topic studied by N.I. Andrusov, L.Sh. Davitashvili, R.L. Merklin, L.A. Nevesskaja, and others. When closed, the sea gradually became desalinated and the taxonomic diversity of its fauna decreased. The marine stenobiontic forms disappeared, and the most eurybiontic species began to dominate. In the changing environment, these eurybiontic species evolved in different ways. The conservative eurybiontic species adapted to the new conditions without fundamental modifications and usually did not generate new taxa (Merklin, 1966). The progressive eurybiontic species "in the new conditions are capable of rapid and radical change and after some time they can give rise to clusters of new species and subspecies that are adapted to different facies" (Merklin, 1966, p. 186). This group of eurybiontic species dominated in the fauna of closing basins and gave rise to the explosion of species and forms in the process of adaptation to the vacated ecological niches.

In Miocene gastropods, intensive ecological and morphological modifications are known in representatives of the successful families Trochidae, Potamididae, Cerithiidae, Hydrobiidae, and especially Rissoidae. The peculiarities of species formation were traced for a group of species from the rissoid genus *Mohrensternia* in semi-marine basins existing at different times in the Eastern Paratethys (Andrusov, 1890; Zhizhchenko, 1936; Švagrovský, 1971; Iljina, 1979, 2001; Zhgenti, 1981; Anistratenko, 2003, 2004; Kowalke and Harzhauser, 2004; etc.). The study of the group was begun by Schwarz von Mohrenstern. In his monograph on rissoids he wrote: "I am obliged to refer preliminarily to this genus some fossils with the shell more or less resembling the shell of the true *Rissoa*. If there is no proof that they are degenerated species of the true *Rissoa*, they may constitute a separate group characterized by a thin-walled, fragile shell with a curved, downwardly elongated, and acute outer lip lacking thickening and, especially, by their distribution, restricted to brackish deposits" (Schwarz von Mohrenstern, 1864, p. 12). The author included four species into the group: *"Rissoa" inflata* Andrz., *"R." angulata* Eichw., *"R." zitteli* Schw., and *"R." dimidiata* Eichw. Andrusov, however, believed that *R. dimidiata* is "just a keeled *Hydrobia*" and, thus, should be excluded from the group (1905, p. 80).

Stoliczka (1868) distinguished this group as the subgenus *Mohrensternia* of the genus *Rissoa*, and later it was raised to a genus (Hilber, 1897; Friedberg, 1911–1928; Kolesnikov, 1935; Zhizhchenko, 1936; etc.). Korobkov (1955) suggested that the genus *Mohrensternia*, which had increased considerably by this time, should be ranked as a subfamily, Mohrensterniinae, with the following diagnosis: "Shell thin-walled, small, and fragile. Resembling *Rissoa* and *Rissoina* but lacking the thickening of the outer lip. Miocene–Pliocene. Brackish basins" (Korobkov, 1955, p. 175).

In recent years special attention was paid to the taxonomy and phylogeny of rissoids and especially of *Mohrensternia*. Kowalke and Harzhauser (2004) supported the subfamily rank of the group and noted that *Mohrensternia* protoconchs had embryonic shells ornamented with fine spiral threads. "The status of Mohrensterniinae as a subfamily of the Rissoidae is confirmed by the morphology of the low conical protoconch consisting of a fine spirally sculptured embryonic shell and a larval shell which is smooth except for growth lines" (Kowalke and Harzhauser, 2004, p. 111). However, they figured no ornamented protoconchs in their paper.

Anistratenko (2003) elevated this subfamily to a family, Mohrensterniidae Korobkov, 1955, with subfamilies Mohrensterniinae Korobkov, 1955; Coelacanthiinae Anistratenko, 2003; and Archascheniinae Zhgenti, 1991. He later rejected this idea, and now considers *Rissoa* Desmarest, 1814, *Mohrensternia*, *Archaschenia*, and *Coelacanthia* to be separate genera in the family Rissoidae (Anistratenko, 2004, p. 3). To confirm this conclusion, Anistratenko describes (but does not figure) the protoconchs of *Rissoa* and *Mohrensternia*. "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" (Anistratenko, 2004, p. 9).

The group of species that is usually assigned to *Mohrensternia* is known from the beginning of the Middle Miocene (Chokrakian) of the Eastern Paratethys. In the preceding Tarkhanian Sea, in which salinity was higher than in the Chokrakian Sea, the representatives of the group are unknown. The data on the presence of *Mohrensternia* in the Tarkhanian are probably erroneous (Kowalke and Harzhauser, 2004). These species are also unknown from the earliest Sakaraulian Sea with almost normal salinity (Early Miocene, Eastern Paratethys).

Thus, the species assigned to *Mohrensternia* are unknown from waters with normal salinity. Of rissoids, *Rissoa*, *Cingula*, *Manzonia*, and *Alvania* (family Alvaniidae by Golikov and Starobogatov, 1972) have inhabited and continue to inhabit the basins of this type. Species of the morphological group resembling *Mohrensternia* are known only from the semi-marine, partly or completely closed basins of the Eastern Paratethys: Early Chokrakian, Karaganian, Late Konkian, Early Sarmatian, and Early Maeotian. They inhabited the Wielicien (Middle Badenian) and Sarmatian seas of the Western (Central) Paratethys, where the salinity was also abnormal. Now it is generally agreed that this group of species originated from marine rissoids. Hilber (1897) erroneously thought that *Mohrensternia* originate from smooth *Hydrobia* species.

However, *Mohrensternia* is possibly not a monophyletic genus but comprises morphologically similar species that originated at different times from different (although related) ancestors. There is no certainty of the succession of species of this group from the heterochronous seas of the Eastern and Western (Central) Paratethys.

Many of my previous papers have pointed out that, with changes in the hydrologic regime (usually reduced salinity), variability and the rate of formation of species and varieties of the surviving rissoids increased abruptly (Iljina, 1966, 1979; Iljina et al., 1976; Nevesskaja et al., 1986). This is readily illustrated by the history of Late Quaternary and subfossil rissoids in the Black Sea Basin (Iljina, 1966).

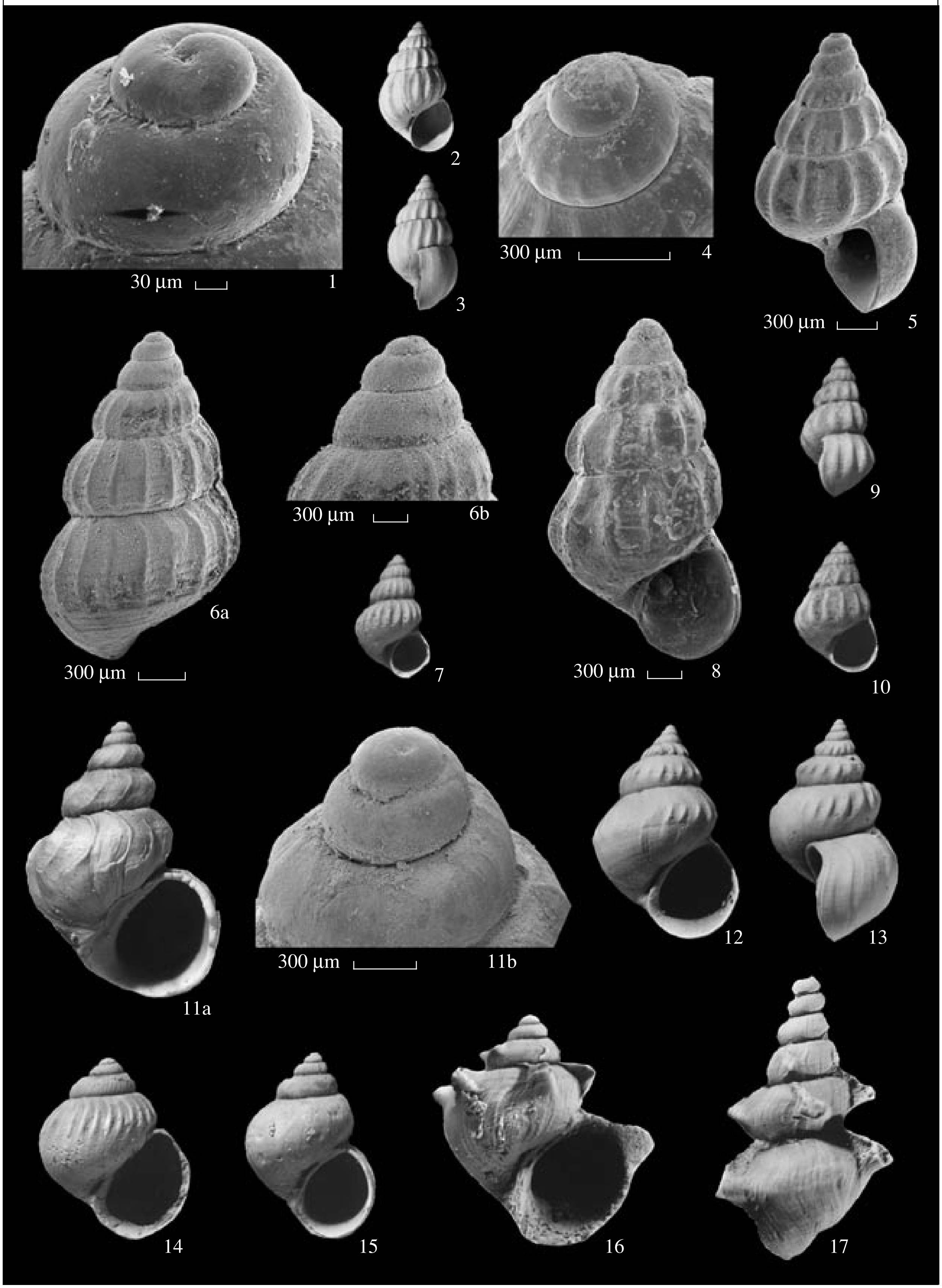
Almost all of the Late Quaternary species of the Black Sea are more or less variable, but the maximum variability is observed in the widely distributed species, including rissoids such as *Rissoa (Turboella) parva* (Costa) (Pl. 6, figs. 1–3). Having migrated to the Black Sea from the Mediterranean Sea, this species changed its shell form, size, and sculpture. The shell form varies from oviform conical to widely conical and from oviform conical to oviform elongated. These varieties are so different that they would be regarded as different species rather than just varieties of a polymorphic species if it were not for transitional forms. *Rissoa (Turboella) parva* also varies in the strength of ornamentation. This feature is obviously connected with ecological variability. Based on this feature two ecomorphs α and β, connected with transitional forms, are distinguished (Iljina, 1966). Morph α has well-pronounced axial ribs and sometimes spiral threads. Thickening of the outer lip may also be developed. Morph α is restricted to open, higher salinity parts of the sea (Caucasian coast and southern coast of the Crimea).

Morph β inhabits regions with lower salinity of the Black Sea (Odessa, Karkinit, and Taman' bays). Unlike morph α, it either virtually or completely lacks axial ribs and has a larger and relatively thin-walled shell; the lip thickening is reduced. *R. (T.) parva* from the Black Sea differs from the typical representatives of this species from the Atlantic, and off the English coast in particular (Forbes and Hanley, 1853). The largest difference is observed in the smooth representatives of morph β. The shells of morph α also differ in the slightly greater number of ribs and in the less acute apex.

However, the transitional forms prevented the establishment of a new taxon in the Black Sea (even if ranked as low as a subspecies) based on these characters. The most likely reason is the time factor and not the absence of isolating barriers. The seven or eight thousand years that have elapsed since the strait of the Bosporus emerged were probably insufficient to transform the intraspecific differentiation of *R.(T.) parva* into speciation.

R. (T.) parva is the type species of the subgenus *Turboella* (Leach) Gray, 1847. The rank of this taxon is questionable. In the present paper I support the opinion

Plate 6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that *Turboella* is a subgenus of the genus *Rissoa* (Wenz, 1938–1944; *Fundamentals…*, 1960; etc.), but I disagree with the opinion that this taxon (either a subgenus or genus) is a synonym of the genus *Mohrensternia* Stoliczka, 1868 (Golikov and Starobogatov, 1972).

The subgenus *Turboella* includes some Miocene species. One of them, *Rissoa (Turboella) acuticosta* (Sacco) (Pl. 6, figs. 4, 5), resembles the recent *R. (T.) parva* in the shell shape and teleoconch sculpture. The former is known from the Middle Miocene of the Mediterranean, Western (Central) Paratethys, and Eastern Paratethys. This species has a small (about 3 mm high), oviform conical shell comprising six slightly convex whorls separated by a slightly incised suture. The protoconch consists of two or two and a half smooth and convex whorls (Pl. 6, fig. 4). The teleoconch is ornamented with well-pronounced, almost straight axial ribs that are as wide as the gaps between them. The number of ribs on the penultimate whorl is from 12 to 15. The intercostal spaces and the base of the last whorl bear fine spiral threads. The aperture is rounded oval and slightly compressed upwards. The outer lip is smooth on the inside and thickened outside by wide varix (Iljina, 1993).

The Chokrakian species *"Rissoa (Mohrensternia)" protogena* Andrus resembles the *Rissoa (Turboella) acuticosta* in shape (Pl. 6, figs. 6, 7). The former species has a 4.0-mm-high shell comprising six or six and a half convex whorls. As in the former species, the protoconch also consists of two or two and a half translucent smooth whorls (Pl. 6, fig. 6b). The teleoconch is also ornamented with up to sixteen axial ribs that reach only the periphery of the whorl. When well-preserved, the intercostal spaces and the base of shell bear spiral threads (Iljina, 1993). These species differ in the absence of lip thickening. This sculptural element does not develop in rissoids in the conditions of reduced salinity.

The morphological affinity of the Chokrakian species and *Rissoa (Turboella) acuticosta* suggests that the former species is an ancestor of the Chokrakian species, especially as the *Turboella* variability in the conditions of reduced salinity (as it was indicated for the Late Quaternary *Rissoa (Turboella) parva*) leads to the thinning of the shell wall, lost of the sculpture elements and the lip thickening, sometimes to the enlargement of the shell (Iljina, 1966).

The differences between the Chokrakian species and its ancestral species are not very significant; however, during the 0.5 million years (Early Chokrakian) they became well established. This species cannot be assigned to the genus *Mohrensternia* (as it was suggested by Andrusov, 1890), since the latter only appeared three million years later and belongs to a different (although closely related) genetic stock (this point will be discussed below).

I believe that the Chokrakian forms should be assigned to a separate endemic subgenus of the genus *Rissoa* and named *Turboellina* L. Iljina, subgen. nov. with the type species *Rissoa (Turboellina) protogena* (Andrus.) (Pl. 6, figs. 6, 7). The subgenus includes two more Chokrakian endemics: *R. (T.) subprotogena* (Zhizh.) and *R. (T.) nitida* (Zhizh.). The latter may be nothing more than an extreme variant of the *R. (T.) subprotogena* varieties (Iljina, 1993). Another Chokrakian species, *"Mohrensternia" reticulata* (Zhg.) (Zhgenti, 1981), does not belong to this group and is most likely a member of the genus *Alvania*.

The Chokrakian Sea was replaced by the closed Karaganian Basin (except the Varnian Episode). In the Early Karaganian (Arkhashenian), this basin with

Explanation of Plate 6

Figs. 1–3. *Rissoa (Turboella) parva* (Costa): (1) specimen PIN, no. 1953/66, protoconch; (2) specimen PIN, no. 1953/65, apertural view, ×6; (3) specimen PIN, no. 1953/67, lateral view, ×6; Late Quaternary, Dzhemete Layers; Anapa Region.

Figs. 4 and 5. *Rissoa (Turboella) acuticosta* (Sacco): (4) specimen PIN, no. 4450/81, protoconch (SEM); Konkian; western Ciscaucasia, region of the small town of Tul'skii; (5) specimen no. 4450/A (L. Artin collection), lateral view (SEM); Lower Badenian; Romania, village of Kostei.

Figs. 6 and 7. *Rissoa (Turboellina) protogena* (Andrus.), ×5: (6) specimen PIN, no. 4450/84: (a) view from the side opposite the aperture; (b) protoconch; (7) specimen PIN, no. 4450/83, apertural view; Chokrakian; western Ciscaucasia, region of the small town of Tul'skii.

Figs. 8–10. *Rissoa (Pseudoturboellina) laskarevi* (Liver): (8) specimen PIN, no. 4450/91, apertural view (SEM); (9) specimen PIN, no. 4450/366, lateral view, ×6; Konkian, Veselyankian Layers; central Ciscaucasia, Mt. Dubrovaya; (10) specimen PIN, no. 4450/89, apertural view, ×5; Konkian, Veselyankian Layers; Transcaspian, Mt. Zheltau.

Fig. 11. *Zhgentia grandis* (Andrus.): specimen PIN, no. 4450/97: (a) apertural view, ×5; (b) protoconch (SEM); Karaganian; Kerch Peninsula, Uzmyak area.

Figs. 12 and 13. *Zhgentia barboti* (Andrus.), ×5: (12) specimen PIN, no. 4450/92, apertural view; (13) specimen PIN, no. 4450/94, lateral view; Karaganian; Ustyurt Plateau, collective farm Akbulak.

Fig. 14. *Zhgentia karaganica* (Zhg.): specimen PIN, no. 4450/100, apertural view, ×5; Karaganian; Georgia, village of Gorisa.

Fig. 15. *Zhgentia subglobosa* (Zhg.): specimen PIN, no. 4450/103, apertural view, ×5; Karaganian; Mangyshlak, town of Fort-Shevchenko.

Fig. 16. *Archaschenia merklini* Zhg.: holotype no. P16/25, apertural view, ×20, Karaganian, Varnian Layers; Georgia, Arkhashenistskali River (Zhgenti, 1981, pl. 6, fig. 1).

Fig. 17. *Archaschenia ilyinae* Zhg.: holotype VG 13/19, view from the side opposite the aperture, ×20; Karaganian, Varnian Layers; Georgia, Arkhashenistskali River (Zhgenti, 1981, pl. 5, fig. 1).

abnormal hydrological regime gave rise to new endemics *"Mohrensternia" grandis* Andrus., *"M." barboti* Andrus., *"M." subglobosa* Zhg., *"M." karaganica* Zhg., and *"M." gratiosa* Zhizh. (Iljina, 1993), which are probable descendants of the subgenus *Turboellina*.

These species differ from the Chokrakian *Rissoa* (*Turboellina*) in the larger (up to 8–10 mm), egg-shaped conical or egg-shaped rounded shell, high (Hlw/H is up to 0.80) and rounded in the periphery last whorl with convex base, and oval aperture with thin and usually curved outer lip (Pl. 6, figs. 11–15).

Based on the above-mentioned characters, this group of Karaganian species can be assigned to a new endemic genus, *Zhgentia* L. Iljina, gen. nov., with the type species *Zhgentia grandis* (Pl. 6, fig. 11). In the closed Karaganian Basin *Zhgentia* could descend only from the Chokrakian *Turboellina*, although no transitional forms have been found.

In the Middle Karaganian a short-lived Varnian ingression changed somewhat the hydrological regime of the basin and thus affected rissoids. Two very similar species, *Zhgentia grandis* and *Z. barboti*, were then widely distributed and showed variability higher than in the Chokrakian rissoids. The sculpture was especially variable. Different whorls of the shell were sometimes differently ornamented, and even scales and spines could develop on the periphery of the last whorls. Zhgenti has shown that scales and spines are characteristic morphological features of the new forms evolved in the Karaganian Sea. She united these species into a separate genus, *Archaschenia* Zhgenti (Zhgenti, 1981), with the type species *A. merklini* Zhg. (Pl. 6, fig. 16). The genus includes one more species, *A. ilyinae* Zhg. (Pl. 6, fig. 17). The main diagnostic features of the genus are triangular scales or spines convoluted into tubules that are usually present on the last two or three whorls. It is worth noting that Zhgenti believed that *"Mohrensternia" barboti* (=*Zhgentia barboti*) rather than *Zhgentia grandis* was the ancestor of *Archaschenia*.

At this point the eco- and morphogenesis of rissoids of the early Middle Miocene was discontinued. In the Kartvelian Sea rissoids and other gastropods were absent. In the Early Konkian a prochoresis of mollusks from the western open waters into the Eastern Paratethys occurred; thus, *Rissoa (Turboella) acuticosta* again penetrated into the basin.

In the Late Konkian (Veselyankian), when the sea salinity reduced, a new endemic species *"Mohrensternia" laskarevi* Liver. appeared. Earlier I erroneously believed that this species was a synonym of the species *Mohrensternia pseudoinflata* Hilb. (Iljina, 1993), which I also defined mistakenly. The Veselyankian species resembles the Chokrakian *Rissoa* (*Turboellina*) quite closely. Zhizhchenko (1936) also noted this fact in his description of a new Chokrakian species, *"Mohrensternia" nitida.* He included the Konkian forms that had been named by the earlier authors *"Mohrensternia (Rissoa) inflata* var." (Sokolov, 1899) and *"Mohrensternia inflata"* (Laskarev, 1902) into the synonymy of this species. Liverovskaya considered the first species to be a synonym of her new Konkian species, *Mohrensternia laskarevi* (1935). The Konkian species is known from several localities of the Eastern Paratethys (Konka River, Central Ciscaucasia, Mt. Dubrovaya, Transcaspian, Mts. Aksengir and Zheltau, etc). It is undoubtedly close to *Rissoa (Turboella) acuticosta* from which it is probably descended. But it cannot be referred to the closely related Chokrakian subgenus *Turboellina*. To adhere the principle of the common standard of the taxonomic isolation, I suggest the placement of the Konkian species into a separate monotypic subgenus, *Pseudoturboellina* L. Iljina, subgen. nov. of the genus *Rissoa*. The diagnosis of the subgenus is similar to that of *Rissoa (Turboellina)*. *R. (Pseudoturboellina) laskarevi* has a small (less than 4.0 mm high) shell that varies in shape from low to high oviform conical (Pl. 6, figs. 8–10).

Thus, the Middle Miocene species *Rissoa (Turboella) acuticosta* gave rise to a phylogenetic branch that includes the successively appearing *Mohrensternia*-like forms: Chokrakian *Rissoa* (*Turboellina*) (*protogena*, *subprotogena*, etc.), Arkhashenian *Zhgentia* (*grandis*, *barboti*, etc.), Varnian *Archaschenia* (*merklini* and *ilyinae*), and Late Konkian (Veselyankian) *Rissoa (Pseudoturboellina) laskarevi*. All of them are dead-end specific branches (Fig. 1).

About 13.0–13.7 million years ago the connection between the Paratethys and the Mediterranean Tethys broke and the wide semi-marine Sarmatian Sea formed in the Paratethys Region (Chumakov, 1993; Rögl, 1998). The change of hydrological regime (reduced salinity) affected the Sarmatian biota and led to new eco- and morphogenesis of rissoids. New species of *Mohrensternia* Stoliczka, 1868 with the type species *M. inflata* (M. Hoernes) established by Sacco (1895) appeared and settled in the basin (Pl. 7, figs. 3, 4). Because of the confusion with Eichwald specimens (Andrusov, 1890), I accept the name *Mohrensternia inflata* as it was used by Schwarz von Mohrenstern (1864). Like the majority of researchers I agree with Schwarz von Mohrenstern that *M. inflata* descended from the Middle Miocene *Rissoa turricula* Eichw.

Rissoa (Rissoa) turricula belongs to the nominative subgenus with the type species *Rissoa ventricosa* Desmarest, 1814 from the Mediterranean Sea (Pl. 7, fig. 1). *Rissoa turricula* is common in the Badenian of the Central (Western) Paratethys and is also known from the Early Sarmatian of Austria (Kowalke and Harzhauser, 2004). The recent *Rissoa (Rissoa) splendida* (Eichwald) from the Black Sea is closely related to *Rissoa (Rissoa) ventricosa*. The variability of *R. splendida* species in the reduced salinity consisted in the change of the shell form (from oviform conical to elongated oval) and size, convexity of the whorls, and strength of axial ornamentation and lip thickening. Thus, ecological morphs α and β formed, which are connected by a

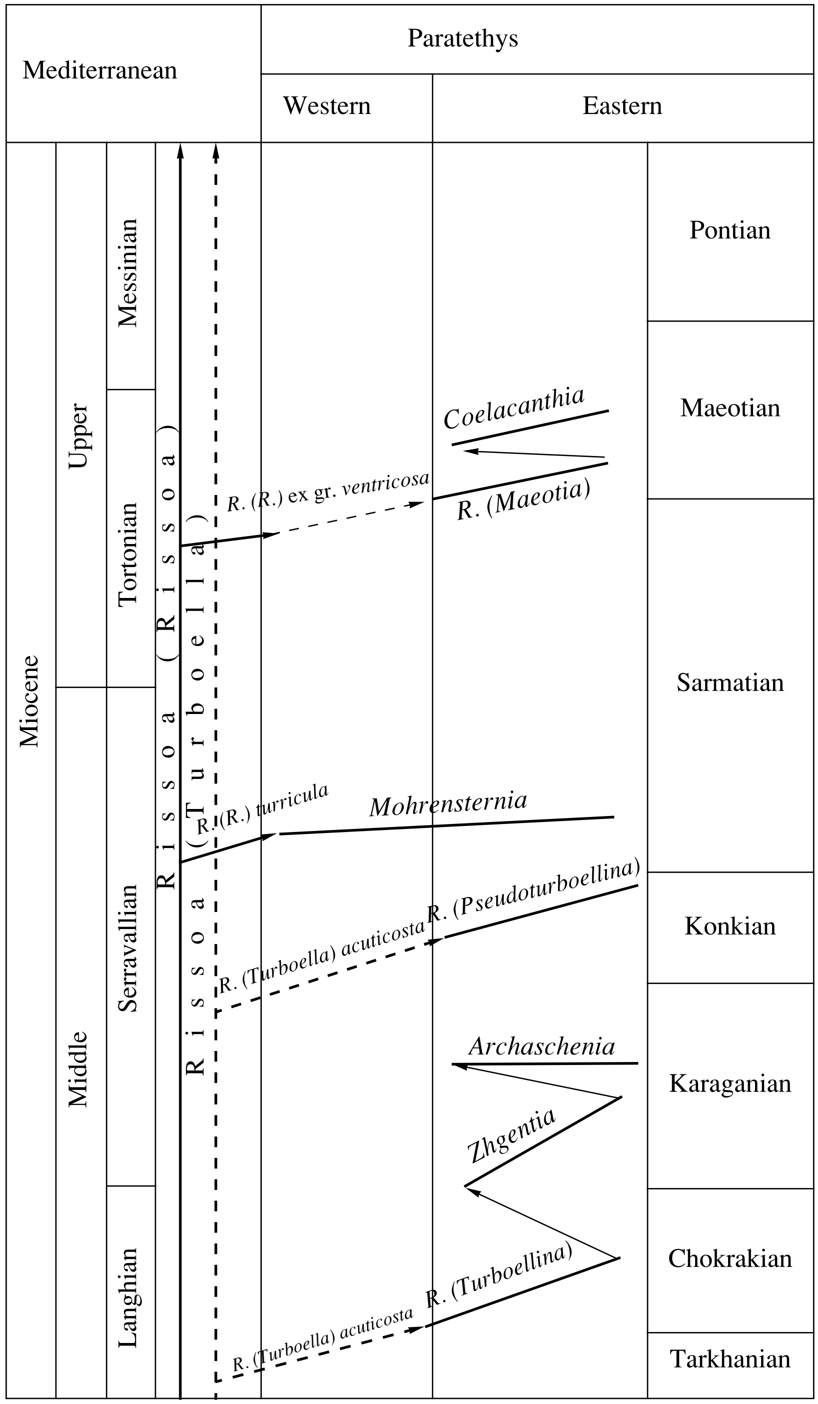


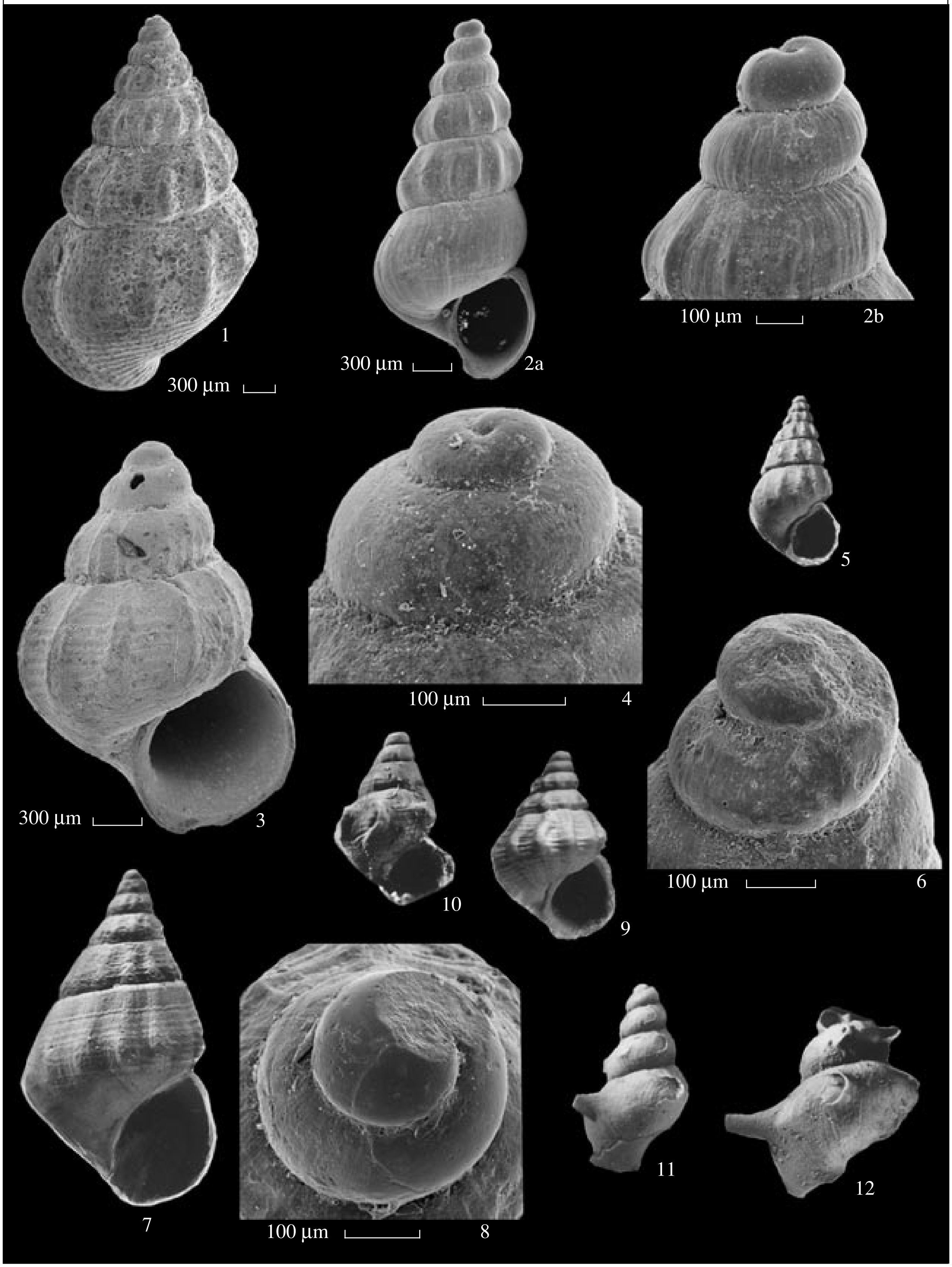
Fig. 1. Phylogeny of the Miocene rissoids of Paratethys.

series of transitional forms (Iljina, 1966). The ecological morph α had well-developed axial ribs and lip thickening and inhabited open parts of the basin. Morph β had poorly developed axial ornamentation and inhabited the northwestern region of the Black Sea.

The eco- and morphogenesis of *R. turricula* in the Early Sarmatian Sea may possibly resemble that of the Black Sea *R. splendida* and could have given rise to a taxon of the species or genus rank, such as *Mohrensternia* Stoliczka. This genus differs from the true *Rissoa* in the thin-walled shell, poorly ornamented teleoconch, and absence of thickening of the outer lip.

Kowalke and Harzhauser (2004) provided the diagnosis of *Mohrensternia* with data on the protoconch morphology: “Protoconchs are characterised by fine spirally sculptured embryonic shells” (Kowalke and

Plate 7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Harzhauser, 2004, p. 125), but no such ornamentation can be seen on the figures of the *Mohrensternia* species in the cited paper. I also did not see this feature in the specimens of *Mohrensternia* from my collection.

These authors pay special attention to the structure of the protoconch of Rissoidae, describing its form, height, maximum diameter, number and shape of whorls, borders between the embryonic and larval shells and teleoconch, and the absence or presence of microornamentation. These are undoubtedly good additional features for identification of taxa; however, the common traditional diagnostic features of genera and species, i.e., the size and shape of the shell, number and form of the whorls, ratios of different shell parts, form and size of the last whorl and aperture, sculpture, etc. are more than sufficient for the present.

In the Early Sarmatian Basin *Mohrensternia* produced an outbreak of speciation, especially in the western parts of the Paratethys (Viennian–Pannonian and Dacian basins, Gulfs of Galicia and Borysthenes), where the reduction in salinity was not as marked as in the eastern regions. In the Eastern Paratethys (southern Ukraine, Georgia) *Mohrensternia* was rare. From the Central (Western) Paratethys 15–16 species of *Mohrensternia* are known (Švagrovský, 1971) and in the Eastern Paratethys no more than three species have been found (Iljina, 1998). *Mohrensternia* seems to be unable to survive considerable desalination, which may explain its apparent absence from the Middle and Late Sarmatian. The data on the presence of *M. inflata* at the beginning of the Middle Sarmatian of Moldavia (Roshka, 1987) need to be confirmed.

Thus, *Mohrensternia* descended from the Middle Miocene *Rissoa (R.) turricula* and existed for about one and a half million years during the Early Sarmatian in the Paratethys. From the beginning of the Middle Sarmatian and up to the end of the Late Sarmatian (from 12.2 to 9.3 million years ago (Chumakov, 1993)) *Mohrensternia* is unknown. No refugia in which *Mohrensternia* could have survived during this three million year period are known. Thus, the *Mohrensternia*-like rissoids that appeared in the Early Maeotian in the Eastern Paratethys cannot be the descendants of the Sarmatian *Mohrensternia* and need to be given their own generic name.

Because of the incompleteness of the fossil data it is hard to establish the genetic stock of a newly evolved taxon. But the Maeotian species should be related to the genetic line *Rissoa (Rissoa) turricula–R. (R.) ventricosa* (Fig. 1). For the subgenus of the genus *Rissoa* that appeared in the Early Maeotian I suggest the name *Maeotia* L. Iljina, subgen. nov. with the type species *"Mohrensternia" subinflata* Andrus.

Rissoa (Maeotia) subinflata has a strong, rounded conical shell up to 6.5–7.0 mm high, comprising 5 or 6 whorls (Pl. 7, figs. 7–9). The protoconch consists of two smooth and convex whorls (Pl. 7, fig. 8). The last whorl is large and subangular in the periphery. The aperture is widely oval and slightly angular upwards. The outer lip is thin and lacks thickening. The teleoconch is ornamented with variously developed axial ribs, which usually do not extend to the base, and dense fine spiral threads. *R. (Maeotia) subinflata* is highly variable, especially in some shell parameters and the ornamentation of the outer surface. "Some forms have well-developed axial ribs and fine spiral threads (pl. 3, figs. 1, 2). Others have smoothed axial ornamentation or lack it (pl. 3, fig. 8), while the spiral ornamentation may be better (pl. 3, fig. 3) or poorly (pl. 3, figs. 4–8) developed. Some shells bear axial ribs, which are weakly pronounced in the upper parts of the whorls and exaggerated to node-like swellings in the periphery of the whorls (pl. 3, figs. 5–7). The shell shape … also varies from low conical to elongated conical" (Iljina, 1979, p. 36). Because of the shell shape and sculpture, *Rissoa (Maeotia) subinflata* resembles representatives of the type subgenus of the genus *Rissoa*. In the Early Maeotian two indigenous species arose from *R. (M.) subinflata*. They are probably *R. (M.) subangulata* (Andrus.) (Pl. 7, figs. 5, 6) and possibly *R. (M.) maeot-*

Explanation of Plate 7

Fig. 1. *Rissoa (Rissoa) turricula* Eichw.: specimen PIN, no. 1467/1356G, view from the side opposite the aperture (SEM); Badenian; western Ukraine, village of Tsikhovka.

Fig. 2. *Mohrensternia* ex. gr. *angulata* (Eichw.): specimen PIN, no. 1467/2398 (SEM): (a) apertural view; (b) protoconch; Lower Sarmatian; Moldova, village of Bursuk.

Figs. 3 and 4. *Mohrensternia inflata* (M. Hoernes): (3) specimen PIN, no. 2392/G, apertural view (SEM); Lower Sarmatian; western Ukraine, village of Zalestsy; (4) specimen no. 4304-X (Švagrovský collection), protoconch (SEM); Lower Sarmatian; eastern Slovakia.

Figs. 5 and 6. *Rissoa (Maeotia) subangulata* (Andrus.): (5) specimen PIN, no. 2220/1101, apertural view, ×6; Lower Maeotian; Azerbaijan, region of the village of Marazy; (6) specimen PIN, no. 2220/427, protoconch (SEM); Lower Maeotian; Georgia, Galidzga River, near the village of Gedzhiri.

Figs. 7–9. *Rissoa (Maeotia) subinflata* (Andrus.): (7) specimen PIN, no. 2220/1083, apertural view, ×10; (8) specimen PIN, no. 2220/432, protoconch (SEM); (9) specimen PIN, no. 2220/490, apertural view, ×10; Lower Maeotian; Kerch Peninsula, village of Arshintsevo.

Figs. 10–12. *Coelacanthia quadrispinosa* Andrus., ×10: (10) specimen PIN, no. 2220/491, apertural view; transitional form combining features of *Mohrensternia subinflata* (axial ribs on one of the upper whorls, tubercle-like projection in the periphery of the last whorl, spiral threads) and new features such as hollow spines (broken in this specimen; only bases preserved as arc-like scales); (11) specimen PIN, no. 2220/497, broken shell, view from the side opposite the aperture; (12) specimen PIN, no. 2220/498, fragment of the lower part of the shell with spines, side opposite the aperture; Lower Maeotian; Kerch Peninsula, village of Arshintsevo.

ica (Badz.). The latter species possibly gave rise to *R. (M.) carinata* (Andrus.). *Rissoa (Maeotia) subangulata* differs from *R. (M.) subinflata* in the slender and elongated shell (width to height ratio is about 0.49), and ratios (Hlw/H is about 0.61 and Ha/H is about 0.37). These two species have a number of transitional forms. *R. (M.) maeotica* has an elongated, slender shell comprising five or six whorls with well-developed keel in the middle of whorls. The keel bears clearly defined tubercles (Badzoshvili, 1979, pp. 80–81, pl. 17, figs. 1–4). This species might not originate directly from *R. (M.) subinflata* but from *R. (M.) subangulata*, whose shell is also highly conical.

Rissoa (Maeotia) carinata is genetically close to *R. (M.) maeotica*. They differ in the shorter shell and weakly developed axial ornamentation in *R. (M.) carinata*. *R. (M.) carinata* resembles *"Mohrensternia" zitteli* (Schwarz v. Mohr.) from the Pleistocene of the Island of Rhodes (Greece); however, this similarity is homeomorphic as well as the similarity with the Early Sarmatian *Mohrensternia pseudoangulata* Hilb.

A representative of a new distinctive genus, another unusual species *Coelacanthia quadrispinosa* Andrus., 1890, evolved from the highly variable *Rissoa (Maeotia) subinflata* in the Early Maeotian (Pl. 7, figs. 10–12). It has small (about 5.0 mm high), elongated conical, and usually thin-walled shell comprising 5.5 or 6 moderately convex whorls. The whorls are usually separated by a clearly defined and slightly oblique suture. The protoconch consists of two smooth whorls. The last whorl with a moderately convex base is more than half the shell height. The aperture is oval, and the peristome is solid. The outer lip is thin and lacks notch or sinuses. The outer surface of the upper whorls is smooth. The periphery of the other whorls has rare, elongated and hollow spines, with a usually healed slit in the front side.

Coelacanthia was included into the family Rissoidae (Iljina, 1972, 1979, 2001; Iljina et al., 1976) and descended directly from *Rissoa (Maeotia) subinflata*. This species (and genus) evolved as the result of the almost sudden detachment of the extreme variants of variability of *R. (M.) subinflata*. The transitional forms between *R. (M.) subinflata* and typical *C. quadrispinosa* have shells that simultaneously contain remains of the axial ribs in the shape of tubercles in the periphery of the whorls, poorly developed spiral threads, and spines in the shape of arc-like scales that constitute the bases of broken spines (Pl. 7, fig. 10).

Coelacanthia quadrispinosa strikingly resembles the Karaganian *Archaschenia*, which existed about five million years earlier. The possible reason for such similarity between taxa that evolved from related species (rissoids) in the basins existed at different times is homeomorphic development (Iljina, 1979; 2001). Although *Archaschenia* and *Coelacanthia* are almost identical in morphology, I believe that they should not be united into a single taxon (Badzoshvili, 1986), since they originated from different (although related) groups: *Archaschenia* evolved from *Zhgentia* and *Coelacanthia* evolved from *Rissoa* (*Maeotia*).

All of the preceding suggests that those marine rissoids that had to live under the conditions of inland basins with abnormal salinity at different times in the Neogene and Quaternary experienced directed morphological changes. Apart from ecology, the changes depended on the time of isolation of the basin from the open-sea waters. While the conditions were acceptable for the species' existence, the variability in the *Rissoa* representatives (*R. splendida*, Recent, Black Sea; *R. turricula*, Badenian, beginning of the Sarmatian) grew and the ecological morphs formed in different regions of the sea (morph α near the open shores and morph β in the more desalinized regions). The latter forms had shells with thinner walls and poorly developed ornamentation. However, morphs with a number of transitional forms were not taxonomically isolated. In the half opened basins that existed for a long period, such features as thin-walled shell, reduced sculpture, and disappearance of the aperture thickening became firmly established in evolution. This allows new species and subgenera to be established in the absence of transitional forms: *R.* (*Turboellina*), *R.* (*Pseudoturboellina*), and *R.* (*Maeotia*). During subsequent evolution features unusual in marine rissoids could form, such as the enlargement of the shell and of the last whorl in the Karaganian *Zhgentia* and appearance of spines and scales in the Karaganian *Archaschenia* and Maeotian *Coelacanthia*. This resulted in the formation of new species, subgenera, and even genera.

The attempt to create a natural classification of some Rissoinae based on their phylogeny sometimes comes into conflict with the classification of individual taxa based on their morphological features. However, even if sometimes it is hard or even impossible to identify taxa and establish differences between them, the researcher should try to build a natural classification of organisms reflecting relationships between different groups in the light of their phylogeny.

SYSTEMATIC PALEONTOLOGY

Order Littorinimorpha

Family Rissoidae Gray, 1847

Subfamily Rissoinae Gray, 1847

Genus *Rissoa* Desmarest, 1814

Subgenus *Turboellina* L. Iljina, subgen. nov.

T y p e s p e c i e s. *Rissoa (Mohrensternia) protogena* Andrusov, 1890; Kerch Peninsula; Chokrakian.

D i a g n o s i s. Shell small, low conical, with convex and sometimes slightly angular whorls. Last whorl with convex base. Sculpture of straight or slightly curved axial ribs usually developed on the last two or three whorls and abruptly terminating in the periphery of the last whorl or sometimes passing into its base.

Spiral threads may be absent. Outer lip thin, sometimes slightly curved.

Composition. *Rissoa (Turboellina) protogena* (Andrus.), *R. (T.) subprotogena* (Zhizh.), and *R. (T.) nitida* (Zhizh.).; Middle Miocene, Chokrakian; Kerch Peninsula, Ciscaucasia, Transcaucasia, and Transcaspian.

Comparison and remarks. The new subgenus differs from the subgenera *Turboella* and *Rissoa* in the absence of the thickening of the outer lip. The differences from the Konkian *Pseudoturboellina* and Maeotian *Maeotia* see in their descriptions. *Turboellina* differs from *Mohrensternia* in the more slender shell with better pronounced ribs and axial ribs that can never be destroyed by weathering.

Subgenus *Pseudoturboellina* L. Iljina, gen. nov.

Type species. *Mohrensternia laskarevi* Liverovskaja, 1935; Central Ciscaucasia, Mt. Dubrovaya; Konkian (Veselyanka Layers).

Diagnosis. Shell small, from low to high conical. Last whorl with rounded or subangular periphery and slightly convex base. Sculpture usually present on the last three whorls and consists of massive, straight, rarely slightly oblique axial ribs. Ribs usually abruptly terminate in the periphery of the last whorl. Dense spiral threads in intercostal spaces and on the base.

Composition. Type species.

Comparison. The new subgenus differs slightly from the closely related Chokrakian subgenus *Turboellina* in the more slender shell, rare axial ribs that never pass onto the base of the last whorl. It differs from the subgenus *Turboella* in the absence of the thickening of the outer lip. *Pseudoturboellina* differs from *Maeotia* in the absence of keels on the whorls that are developed in some species of the latter.

Subgenus *Maeotia* L. Iljina, gen. nov.

Type species. *Mohrensternia subinflata* Andrusov, 1890; Kerch Peninsula; Maeotian (Bagerian Horizon).

Diagnosis. Shell strong, from tiny to small, usually conical, and consisting of moderately convex whorls. Protoconch of two or two and a half smooth whorls. Last whorl large and subangular in the periphery. Base slightly convex. Aperture oval and pointed upwards. Outer lip acute and lacking thickening. Ornamentation usually of thickened axial ribs (sometimes reduced) and fine spiral threads. Sometimes (*Maeotia maeotica*) with well-developed keel in middle of whorls. Keel with tubercles that are more or less preserved remains of axial ribs.

Composition. *Rissoa (Maeotia) subinflata* (Andrus.), *R. (M.) subangulata* (Andrus.), *R. (M.) maeotica* (Badz.), *R. (M.) carinata* (Andrus.), *R. (M.) nasyrica* L. Il., and *R. (M.) acuta* L. Il.; Upper Miocene, Maeotian, Bagerian Horizon; Northern Black Sea Region, Kerch Peninsula, Ciscaucasia, Transcaucasia, Transcaspian.

Comparison. The new subgenus differs from the subgenera *Rissoa* and *Turboella* in the absence of thickening of the outer lip. It differs from *Turboellina* and *Pseudoturboellina* in the more conical shell and sometimes in the presence of well-developed keel and tubercle-like ribs.

Genus *Zhgentia* L. Iljina, gen. nov.

Type species. *Rissoa (Mohrensternia) grandis* Andrusov, 1890, Kerch Peninsula; Karaganian.

Diagnosis. Shell up to 10 mm high, from oviform conical to wide oviform consisting of convex and rapidly increasing whorls. Protoconch smooth. Last whorl very large (Hlw/H is about 0.70–0.80) with convex base. Aperture oval with thin and acute outer lip. Variable sculpture usually of short and curved axial ribs, sometimes of axially elongated tubercles. Spiral threads poorly developed or absent.

Composition. *Zhgentia grandis* (Andrus.), *Z. barboti* (Andrus.), *Z. subglobosa* (Zhg.), *Z. karaganica* (Zhg.), and *Z. gratiosa* (Zhizh.); Kerch Peninsula, Ciscaucasia, Transcaucasia, and Transcaspian; Middle Miocene, Karaganian.

Comparison. The new genus differs from other Middle and Upper Miocene genera from the Eastern Paratethys in the considerably larger shell with large last whorl. It differs from *Mohrensternia* in the indestructible axial ornamentation and from *Archaschenia* and *Coelacanthia* in the absence of spines.

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