

A late Pleistocene gastropod fauna from the northern Caspian Sea with implications for Pontocaspian gastropod taxonomy

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Academic editor: M. Haase | Received 29 March 2018 | Accepted 20 May 2018 | Published 4 July 2018

<http://zoobank.org/4D984FDD-9366-4D8B-8A8E-9D4B3F9B8EFB>

Citation: Neubauer TA, van de Velde S, Yanina T, Wesselingh FP (2018) A late Pleistocene gastropod fauna from the northern Caspian Sea with implications for Pontocaspian gastropod taxonomy. ZooKeys 770: 43–103. <https://doi.org/10.3897/zookeys.770.25365>

Abstract

The present paper details a very diverse non-marine gastropod fauna retrieved from Caspian Pleistocene deposits along the Volga River north of Astrakhan (Russia). During time of deposition (early Late Pleistocene, late Khazarian regional substage), the area was situated in shallow water of the greatly expanded Caspian Sea. The fauna contains 24 species, of which 16 are endemic to the Pontocaspian region and 15 to the Caspian Sea. The majority of the species (13) belongs to the Pyrgulinae (Hydrobiidae), a group famous for its huge morphological variability in the Pontocaspian region. The phenotypic diversity has led to an inflation of genus and species names in the literature. New concepts are proposed for many of the genera and species found in the present material, with implications for the systematics and taxonomy of the entire Pontocaspian gastropod fauna. *Laevicaspia vinarskii* sp. n. is described as a new species. This contribution is considered a first step in revising the Pontocaspian gastropod fauna.

Keywords

biodiversity, endemism, long-lived lakes, non-marine Gastropoda, Quaternary

Introduction

The Caspian Sea is Earth's largest inland water body. With an area of 378,100 km² it covers about 40% of the world's continental surface water (Dumont 1998, Lehner and Döll 2004). The endorheic Caspian Basin is situated at the crossroads between Europe and Asia and borders Azerbaijan, Iran, Kazakhstan, Russia, and Turkmenistan. Today, its water balance is strongly controlled by the rivers Volga (Russia) and Ural (Kazakhstan) entering from the north and the Kura River (Azerbaijan) flowing in from the southwest and by evaporation from the sea and the adjacent Kara Bogaz Gol (Dumont 1998). The Caspian Sea is a mesohaline lake with an average salinity of about 12.8‰. Steep salinity gradients exist in the northern Caspian Sea from near freshwater conditions at the Volga River delta in the north to a maximum of 13.8‰ in the southeast (Dumont 1998).

During the Pleistocene, several major transgressive–regressive cycles caused recurrent connections between Black Sea and Caspian basins, which were accompanied by dramatic changes in lake size, salinity and biotic assemblages (e.g., Dumont 1998, Yanko-Hombach et al. 2007, Svitoch 2008, 2012, Shkatova 2010, Forte and Cowgill 2013, Van Baak et al. 2013, Yanina 2013, 2014, Taviani et al. 2014). In spite of the major environmental fluctuations over the geological past, the Caspian Sea Basin hosted a succession of anomalohaline to freshwater lakes since the late Pontian (late Messinian, late Miocene; Popov et al. 2006, Van Baak et al. 2013). The extensive duration facilitated the accumulation of diverse and highly endemic (“Pontocaspian”) biota in this long-lived lake (sensu Gorthner 1994), especially since the Early Pleistocene. As to the recent mollusk fauna, 92 species of gastropods and 35 species of bivalves are listed in latest systematic catalogues (e.g., Kantor and Sysoev 2005, 2006, Kantor et al. 2010, Vinarski and Kantor 2016). As for the gastropods, which are dominated by small-sized Hydrobiidae, 92.4% of them are endemic to the Caspian Sea (Neubauer et al. 2016a). Because of its high diversity, the Caspian Sea has been classified as a major biodiversity hotspot for anomalohaline gastropods (Neubauer et al. 2015a). However, the endemic mollusk fauna is at present severely suffering from the expansion of a number of invasive species (Kosarev and Yablonskaya 1994, Grigorovich et al. 2003, Orlova et al. 2005, Therriault et al. 2004, Riedel et al. 2006, Heiler et al. 2010, Albrecht et al. 2014). Since the early 20th century, human activity has led to a massive increase in the rate of establishment of non-indigenous aquatic species compared to preceding natural colonization (Grigorovich et al. 2003). Additional environmental pressure is exerted on the resident fauna by the increasing concentrations of heavy metals and pesticides (e.g., Agusa et al. 2004, Anan et al. 2005).

In order to predict future biodiversity loss as a response to natural or anthropogenically induced environmental change, it is vital to document and understand the species richness and development of the endemic fauna over longer temporal scales. For this purpose, a sound taxonomic framework is required. The extreme morphological variability of many of the described species complicates taxonomy and, thereby, hampers reliably diversity assessments. Preceding taxonomic studies carried out in the 19th and 20th century have produced a plethora of available species names, partly based on minor morphological deviations. Taxonomic works are hampered by (1) the inadequate



Figure 1. Geographic overview of the Pontocaspian region, with indication of the extent of the late Khazarian (early Late Pleistocene) transgression. The star marks Selitrennoye. Paleo-lake level was modeled in ESRI ArcGIS 10.4 based on Yanina (2014), who suggested an absolute lake level of 10 m b.s.l. at that time. Considering the present Caspian base level of 27 m b.s.l., this estimate corresponds to a lake level rise of 17 m. (Note that the model is restricted to the Pontocaspian catchment area and disregards potential topographic differences.) The bathymetry ranges are based on the GEBCO_2014 model (version 20150318) for present-day (Weatherall et al. 2015); shown isobaths equal to 100, 500 and 1000 m below current lake level.

nature of descriptions and illustrations, (2) the apparent loss of much of the material, (3) the few and hugely variable morphological characters in some of the groups, and (4) the apparent recent loss of many of the species, which makes combined morphological and molecular approaches impossible. Presently, the statuses of most Caspian endemic gastropods, especially of the numerous representatives of the Pyrgulinae (Hydrobiidae), are poorly resolved.

The present contribution details a diverse gastropod fauna from upper Khazarian (Upper Pleistocene) deposits from the northwestern part of the Caspian Basin, at that time witnessing a major transgressive event (Svitoch 2012; Fig. 1). We provide descriptions, illustrations and comparisons of the so far mostly poorly known species, and suggest nomenclatural and taxonomic rectifications. Since we could examine little of the type material of the discussed species (mostly because the whereabouts are

unknown), we limit our conclusions on former concepts and potential synonymies to taxa that have been thoroughly described and/or adequately illustrated (e.g., Kantor and Sysoev 2006). One particular focus of the present work is the revision of genus concepts that have been applied to Pontocaspian Hydrobiidae.

Materials and methods

The studied mollusk fauna derives from deposits exposed near the small village of Selitrennoye (also as Selitrennoe; *Russ.* СЕЛИТРЕННОЕ) along the left bank of the Akhtuba River, a tributary of the Volga River (Russia) (Fig. 1). The locality is situated about 100 km NNW of the city of Astrakhan in the administrative division of the same name (47°10'21.19"N, 47°26'25.41"E, WGS84). The investigated section of 14 m height spans the upper Khazarian to Khvalynian regional substages, which correlates to the early Late Pleistocene (Svitoch 2012, Yanina 2013, 2014). The base of the Quaternary outcrop, which lies 19 m below sea level, is formed by 2.5 m of upper Khazarian sands with common dispersed shells, including shell lenses (Fig. 2). This layer contains the here described gastropod fauna and several species of Lymnardiinae bivalves. Upsection follows a 1-m-thick interval of horizontally alternating sandy and silty layers containing a diverse assemblage of bivalves of the genera *Monodacna*, *Didacna*, and *Dreissena*. Above it, 4 m of clays containing siltstones and sand layers were deposited. Overlying the interval, 3 m of lower Khvalynian sands are present, containing species of *Didacna* and *Dreissena*, followed by 1 m of brown silty clays ("chocolate clays"). The top of the Pleistocene deposits is marked by 1 m of upper Khvalynian sands and sandy loams barren of fossils, topped by a late Holocene soil complex rich in archeological remains.

Approximately 5 kg of sediment were collected by F.W. in September 2015 and were washed over a 0.5 mm sieve before sorting. All material is stored at the Faculty of Geography of the Moscow State University under collection numbers LV 201501–201530 and 201731–201750 and at the Naturalis Biodiversity Center, Leiden, The Netherlands, under collection numbers RGM 1309784–1309793, 1309797–1309856, 1310190–1310249, and 1310252–1310258.

Macro-photographs of the specimens were taken with a Leica M165 C stereomicroscope with attached DFC420 camera, using the focus stacking function of the Leica Application Suite software v. 4.4.0 at the Naturalis Biodiversity Center, Leiden. SEM images were acquired on a JEOL JSM-6480LV at the same institute. Specimens were coated with a 20 nm thick platinum-palladium alloy in a Quorum Q150T S coater.

For every species, a number of specimens was measured as representatives of its morphological spectrum. Shell measurements for *Theodoxus* are given as height × largest width (perpendicular to height) × second-largest width (perpendicular to both other axes); for all other species, measurements are given as height × width. Counting of protoconch whorls follows the method used by Verduin (1977) (Fig. 3). Descriptions and information on the whereabouts of type material are only indicated for Pontocaspian species; a brief account on the non-indigenous species detected herein is provided



Figure 2. Geographic position and log of the sampled section at Selitrennoye village. The star marks the layer of which the fauna derives. The stratigraphy was established based on the occurrence of *Lymnocardinae* bivalves, following the biostratigraphic scheme of Yanina (2013).

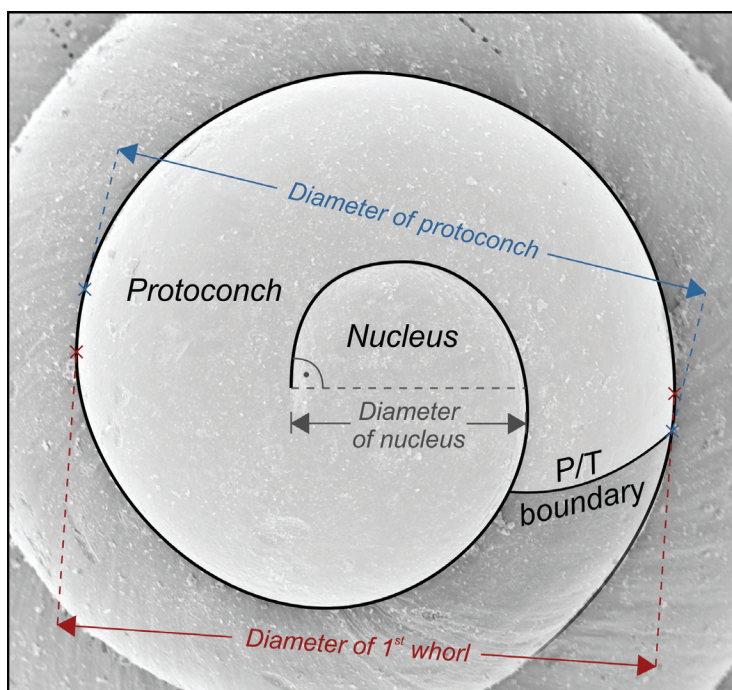


Figure 3. Sketch of the measurements made on the protoconch. The method for counting whorls follows Verduin (1977).

at the end of the Systematic Paleontology section. Synonymy lists comprise original descriptions, records providing illustrations and entries in systematic catalogues referring to Caspian records (e.g., Kantor and Sysoev 2006, Vinarski and Kantor 2016). The systematic classification follows Bouchet et al. (2017) and MolluscaBase (2017).

Abbreviations used are:

P/T	protoconch/teleoconch;
MSU	Moscow State University, Moscow, Russia, Faculty of Geography;
RGM	Naturalis Biodiversity Center, Leiden, The Netherlands, coll. Fossil Mollusca (formerly Rijksmuseum van Geologie en Mineralogie);
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Systematic paleontology

We tried to locate the depository of type specimens for all identified species, but this was successful only for a part of the fauna. In particular, much of the type material of the species described by Logvinenko and Starobogatov (1969) could not be located, since these authors did not provide information on the depository of the types or the localities they were retrieved at. According to Kantor et al. (2010), the types should be stored in ZIN but few have been found, since large parts of Starobogatov's collection have not been entirely inventoried as yet.

Class Gastropoda Cuvier, 1795

Subclass Neritimorpha Golikov & Starobogatov, 1975

Order Cycloneritimorpha Frýda, 1998

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Subfamily Neritinae Poey, 1852

Genus *Theodoxus* Montfort, 1810

Type species. *Theodoxus lutetianus* Montfort, 1810 [currently considered as a synonym of *Theodoxus fluviatilis* (Linnaeus, 1758)]; by original designation. Recent; Europe.

Theodoxus pallasii Lindholm, 1924

Fig. 4A–F

1838 *Neritina liturata* m. Eichwald: 156–157 [non *Neritina liturata* Schultze, 1826].
 1841 *Neritina liturata* m. – Eichwald: 258–260, pl. 38, figs 18–19 [non Schultze, 1826].
 1855 *Neritina liturata* m. – Eichwald: 307–308 [non Schultze, 1826].

- 1887 *Neritina liturata* Eichw. sp. – W. Dybowski: 56–60 [non Schultze, 1826].
- 1888 [*Neritina*] *liturata* Eichw. – W. Dybowski: 79, pl. 2, fig. 10 [non Schultze, 1826].
- * 1924 *Theodoxus pallasi* nom. nov.; Lindholm: 33, 34.
- 1952 *Theodoxus pallasi* Lindh. – Zhadin: 208–209, fig. 124.
- 1969 *Theodoxus pallasi* Ldh. – Logvinenko & Starobogatov: 343, pl. 5, figs 5–6, text-fig. 356.
- 1994 *Theodoxus atrachanicus* Starobogatov in Starobogatov et al.: 8–9, fig. 1 (1–2).
- 1994 *Th.[eodoxus] pallasi* Ldn. – Starobogatov et al.: 8–9, fig. 1 (3–4).
- 2006 *Theodoxus pallasi* Lindholm, 1924. – Kantor & Sysoev: 45, pl. 20, fig. C.
- 2006 *Theodoxus atrachanicus* Starobogatov in Starobogatov et al., 1994. – Kantor & Sysoev: 44, pl. 21, fig. C
- 2009 *Theodoxus pallasi* Lindholm, 1924. – Filippov & Riedel: 70, 72, 74, 76, figs 4g–i.
- 2011 *Theodoxus astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova et Pirogov, 1994. – Anistratenko et al.: 54–55, fig. 1 (6).
- 2012 *Theodoxus pallasi* Lindholm, 1924. – Welter-Schultes: 29, unnumbered textfig.
- 2016 *Theodoxus (Theodoxus) astrachanicus* Starobogatov in Starobogatov et al., 1994. – Vinarski & Kantor: 155–156.
- 2016 *Theodoxus (Theodoxus) pallasi* (Lindholm, 1924). – Vinarski & Kantor: 156–157.
- 2017 *Theodoxus pallasi* Lindholm, 1924. – Anistratenko et al.: 221, figs 4, 7, 10, 11 [cum syn.].

Material. 294 specimens (RGM 1309841, RGM 1309843, RGM 1310190–1310193, LV 201510).

Type material. Lectotype: ZIN 54547/63, designated by Starobogatov et al. (1994).

Type locality. “Inter Fucos littoris Derbendensis viva” (living among algae on the shores of Derbent), Dagestan, Russia.

Dimensions. $5.95 \times 6.62 \times 4.81$ mm (RGM 1310191, Fig. 4A–C); $4.52 \times 5.59 \times 4.05$ mm (LV 201510, Fig. 4D–F); $6.62 \times 7.31 \times 5.30$ mm (RGM 1310192, Fig. 4I); $6.63 \times 7.53 \times 4.99$ mm (RGM 1310190).

Description. Near globular shell with up to 2.7 whorls. Protoconch consists of about half a whorl; diameter of about 570 μ m; nucleus measures ca. 250 μ m in diameter; surface mostly corroded; P/T transition indistinct, marked by onset of growth lines. Apex weakly raised. Last whorl passes from upper suture over weakly inclined ramp with shallow concavity into broadly, regularly rounded flank that is near semi-circular in profile; relative length of ramp increases with ontogeny. Aperture inclined, regularly semicircular. Callus moderately thickened, glossy, edentate; right margin bulging, symmetrically sinuate, with near straight-sided lower and upper thirds and broad, shallow indentation in central third; left margin extends sinuate over base of penultimate whorl, with small adapical indentation, formed by slightly protruding peristome margin. Peristome sharply edged throughout ontogeny from adapical tip to where it passes into callus margin at base of penultimate whorl. Adapically, peristome margin forms steep crest towards callus, sometimes accompanied by thin, shallow furrow at the transition. Color pattern already starts on early teleoconch as widely spaced,

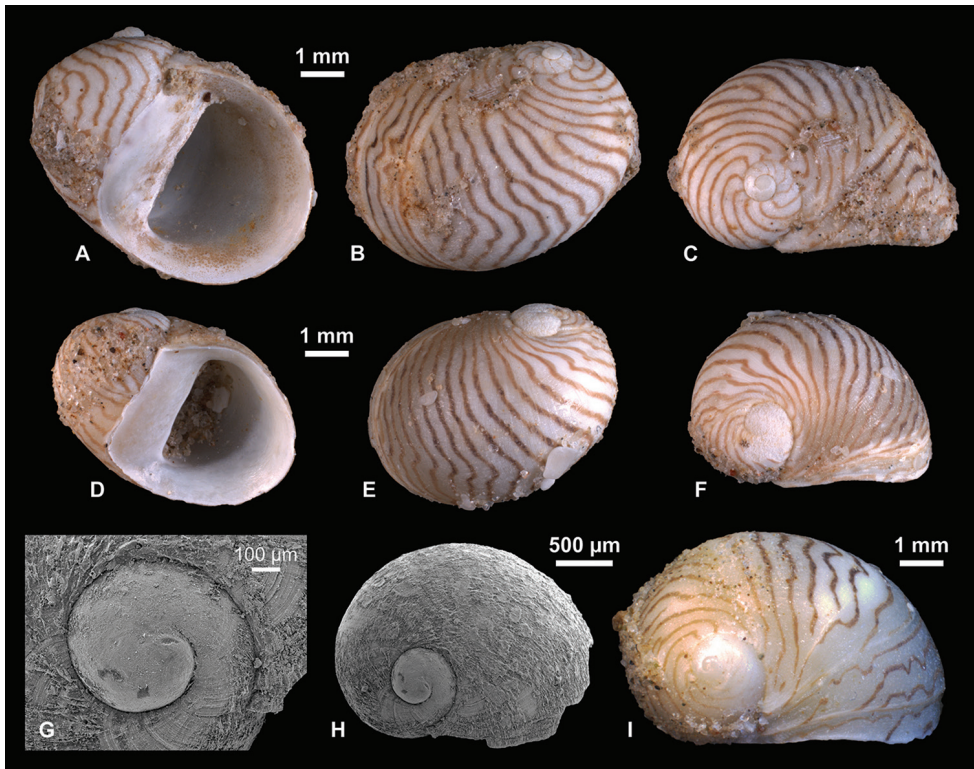


Figure 4. Neritidae. **A–C** *Theodoxus pallasi* Lindholm, 1924, RGM 1310191 **D–F** *T. pallasi*, LV 201510 **G, H** *T. pallasi*, RGM 1309843 **I** *T. pallasi*, RGM 1310192.

dark yellow to brown curved lines, which pass into slightly irregular zigzag lines with partly dichotomizing branches on last whorl; line width, density, amplitude, color and raggedness varies among specimens and partly within the same individual.

Discussion. The regular, widely spaced zigzag pattern is characteristic of the species. Comparable patterns occur in *T. danubialis* (Pfeiffer, 1828) and occasionally in *T. fluviatilis* (Linnaeus, 1758), but in these species lines are finer and more closely spaced. They furthermore differ in their less elongated shells. Similarly, *T. euxinus* (Clessin, 1886) from the Black Sea is more globular and shows a much denser and finer color pattern (Kantor and Sysoev 2006, Welter-Schultes 2012). *Theodoxus schultzei* (Grimm, 1877) has traditionally been distinguished from *T. pallasi* by its rounder shell and the massively expanded aperture (Zettler 2007). Currently, the whole group is under study using genetic data. Preliminary results suggest that both *T. pallasi* and *T. schultzei* may be grouped with the Armenian species *T. major* Issel, 1865, and possibly a major name change for *T. pallasi* is due (A.F. Sands, pers. commun. 05/2018).

Theodoxus astrachanicus Starobogatov in Starobogatov et al., 1994 from the Azov Sea and Volga delta is claimed to differ from *T. pallasi* in size and rate of whorl expansion (Starobogatov et al., 1994). However, both species correspond well in terms of shell shape and, in particular, the typical zigzag pattern (see also Kantor and Sysoev

2006). We therefore agree with Anistratenko et al. (2017) to treat *T. astrachanicus* as a junior synonym of *T. pallasii*.

Distribution. Presently living in the Caspian Sea, the Sea of Azov and the Aral Sea; records from Armenia and the Ural River need confirmation (Anistratenko et al. 2017). In the Pleistocene, the species also dwelled in river deltas entering the Black Sea, where it probably became extinct during the Neoeuxinian/late Pleistocene (Anistratenko et al. 2017).

Subclass Caenogastropoda Cox, 1960

Order Littorinimorpha Golikov & Starobogatov, 1975

Superfamily Truncatelloidea Gray, 1840

Family Hydrobiidae Stimpson, 1865

Subfamily Caspiinae B. Dybowski, 1913

Discussion. The genus *Caspia* has been widely used for species with small ovoid shells, occasionally with spiral or reticulate teleoconch sculpture. Based on the expression of sculpture, some authors have divided the species among the (sub)genera *Caspia* s.s., with a single spiral line below the suture, and *Clathrocaspia* Lindholm, 1930, exposing a reticulate pattern (e.g., Anistratenko and Prisyazhniuk 1992, Anistratenko 2013, Boeters et al. 2015, Büyükmeriç and Wesselingh 2018). Species lacking teleoconch sculpture were grouped under the new taxon *Ulskia* by Logvinenko and Starobogatov (1969). While those authors considered it a subgenus of *Pyrgula*, W. Dybowski (1887) originally treated its type species (*Caspia ulskii* Clessin & W. Dybowski in W. Dybowski, 1887, see below) as a sculpture-less form of *Caspia*.

Ulskia ulskii is available in the present material, and we have investigated the type species of *Clathrocaspia* (*Caspia pallasii* Clessin & W. Dybowski in W. Dybowski, 1887) obtained from Holocene deposits of the northern and southern Caspian Sea. However, the type species of *Caspia*, *Caspia baerii* Clessin & W. Dybowski in W. Dybowski, 1887, is unknown to us. The original description suggests that it is similar to *Ulskia* and *Clathrocaspia* in terms of size and shape, yet to differ in the presence of a single line below to suture, demarcating a narrow subsutural ramp. All three genera are probably closely related, which is also suggested by the similar protoconchs of *Ulskia* and *Clathrocaspia* (pers. obs. T.A.N.). Since *Ulskia* and *Clathrocaspia* can be easily distinguished based on the presence of sculpture, we propose to treat them as distinct genera. The status of *Caspia* remains doubtful until the type species is properly re-investigated.

The *Caspia*–*Clathrocaspia*–*Ulskia* species group can be well delimited from the larger, elongate-conical or -ovoid *Turricaspia* auct. and *Pyrgula* auct. Moreover, unpublished molecular data suggest that the group is unrelated to Pyrgulinae (T. Wilke, pers. comm. 04/2018). We follow Anistratenko (2013) and Bouchet et al. (2017), who listed the Caspiinae as separate subfamily.

Genus *Ulskia* Logvinenko & Starobogatov, 1969

Type species. *Caspia ulskii* Clessin & W. Dybowski in W. Dybowski, 1887; by original designation. Caspian Sea, Recent.

Ulskia ulskii (Clessin & W. Dybowski in W. Dybowski, 1887)

Fig. 5A–K

*1887 *Caspia Ulskii* nob.; W. Dybowski: 38–39.

1888 [*Caspia*] *Ulskii* n. sp. – W. Dybowski: 79, pl. 3, fig. 8.

1952 *Caspia ulskii* W. Dyb., 1888. – Zhadin: 205, fig. 205.

1969 *Pyrgula* [(*Ulskia*)] *nana* Logvinenko & Starobogatov: 379, fig. 367 (12).

1969 *Pyrgula* [(*Ulskia*)] *schorygini* Logv. et Star. sp. n.; Logvinenko & Starobogatov: 379, fig. 367 (11).

1969 *Pyrgula* [(*Ulskia*)] *ulskii* (Cless. et W. Dyb.). – Logvinenko & Starobogatov: 379, figs 367 (10).

2006 *Pyrgula nana* Logvinenko et Starobogatov, 1968. – Kantor & Sysoev: 101, pl. 47, fig. D.

2006 *Pyrgula schorygini* Logvinenko et Starobogatov, 1968. – Kantor & Sysoev: 103, pl. 45, fig. E.

2006 *Pyrgula ulskii* (Clessin et W. Dybowski in W. Dybowski, 1888). – Kantor & Sysoev: 104, pl. 45, fig. F.

2016 *Pyrgula nana* Logvinenko et Starobogatov, 1968. – Vinarski & Kantor: 240–241.

2016 *Pyrgula schorygini* Logvinenko et Starobogatov, 1968. – Vinarski & Kantor: 242.

2016 *Pyrgula ulskii* (Clessin et W. Dybowski in W. Dybowski, 1888). – Vinarski & Kantor: 244.

Material. 19 specimens (RGM 1309790, RGM 1309810, RGM 1309856, RGM 1310208, LV 201506).

Type material. “Probable syntype”: ZIN 4608/1. Holotype of *P. schorygini*: ZIN 4357/1. Holotype of *P. nana* not traced.

Type locality. “Kaspi-See” (Caspian Sea, no further details mentioned). Type locality of *P. schorygini*: Caspian Sea; off Apsheron Peninsula, 40°07.5'N, 50°57.5'E, WGS84, 88 m (after Vinarski and Kantor 2016). Type locality of *P. nana*: western part of the Caspian Sea, 70–120 m.

Dimensions. 2.05 × 1.13 mm (RGM 1309810, Fig. 5A, F, H, I); 2.16 × 1.16 mm (LV 201506, Fig. 5B, C, G); 2.12 × 1.10 mm (RGM 1309856, Fig. 5D, E); 2.12 × 1.23 mm (RGM 1309790, Fig. 5J, K).

Description. Slender ovoid shell with up to 4.7 whorls. Protoconch broad, low dome-shaped, comprising 1.25 whorls that measure 365 µm; nucleus is ca. 105 µm wide; protoconch surface finely but strongly malleate; pattern irregular on initial part and only partly present on nucleus; P/T transition marked by thin axial line and slight

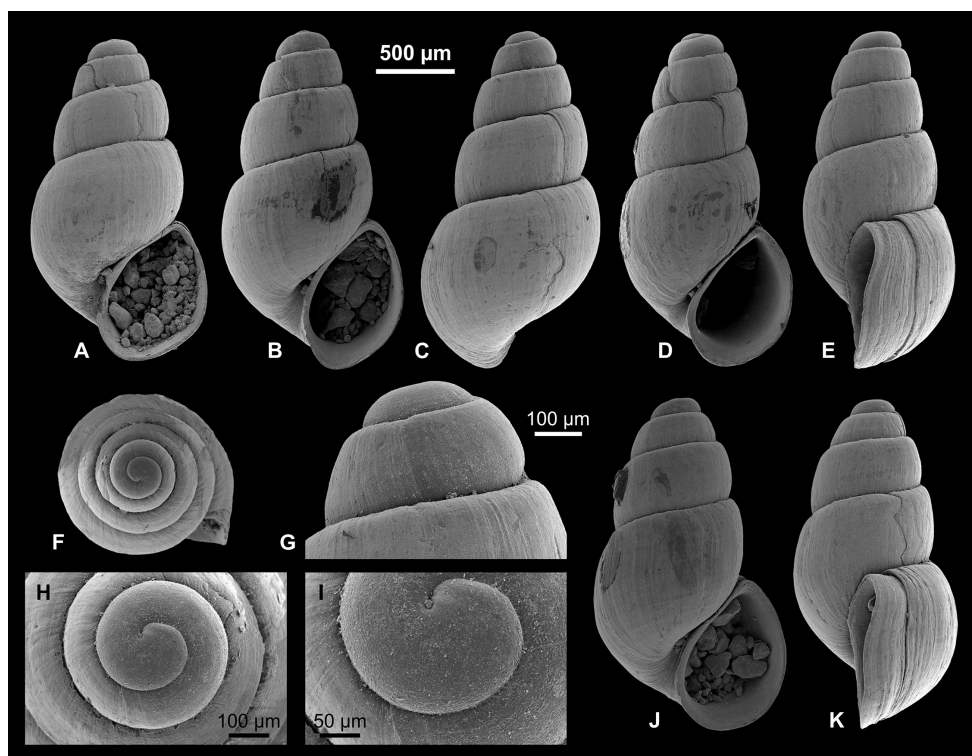


Figure 5. Caspiinae. **A, F, H, I** *Ulskia ulskii* (Clessin & W. Dybowski in W. Dybowski, 1887), RGM 1309810 **B, C, G** *U. ulskii*, LV 201506 **D, E** *U. ulskii*, RGM 1309856 **J, K** *U. ulskii*, RGM 1309790.

step in the upper suture. Teleoconch whorls slightly ton-shaped, weakly convex in abapical half and straight-sided or almost so in adapical half, followed by pronounced convexity at upper suture, producing slightly stepped spire. Last whorl attains ca. 61–66%, descends into steep, straight base. Aperture slender ovoid, slightly inclined, with faint adapical notch at contact to penultimate whorl. Peristome slightly thickened and expanded. In lateral view, outer lip exposes marked adapical indentation and very weak abapical indentation; columellar lip straight. Umbilicus narrow but always open. Growth lines weak but distinctly sigmoidal, with opisthocyrt upper half and prosocline lower half. In addition, faint spiral threads are visible on some shells.

Discussion. *Pyrgula schorygini* Logvinenko & Starobogatov, 1969 and *P. nana* Logvinenko & Starobogatov, 1969, both of which were also originally included in the subgenus *Ulskia*, closely resemble this species. Logvinenko and Starobogatov (1969) did not discuss similarities or differences among the species involved, but their descriptions suggest they considered minor differences in whorl profile and suture depth sufficient to discriminate species. A similar range of variability is present in our sample as well and might rather reflect intraspecific variation. We thus consider the three species synonymous.

Two more species were attributed to the subgenus *Ulskia* by Logvinenko and Starobogatov (1969). The shell of *Caspia derzhavini* (Logvinenko & Starobogatov,

1969) is more slender and has more whorls. *Caspia behningi* (Logvinenko & Starobogatov, 1969) differs in its broader and distinctly conical shape.

Distribution. Endemic to the Caspian Sea, reported from water depths between 45 and 120 m (Logvinenko and Starobogatov 1969).

? Subfamily Horatiinae Taylor, 1966

Genus *Andrusovia* Brusina in Westerlund, 1902a

Type species. *Andrusovia dybowskii* Brusina in Westerlund, 1902a; by original designation. Caspian Sea, Recent.

Discussion. The subfamily placement of the genus follows Vinarski and Kantor (2016: 214) and is based on the resemblance with species of the genus *Horatia* Bourguignat, 1887 (see also discussion in Starobogatov 2000). A recent molecular phylogeny including the Hydrobiidae suggests the Horatiinae to be distinct from the Belgrandiinae (Wilke et al. 2013; see also Bank 2017). We follow Starobogatov (2000) and regard *Caspiohoratia* Logvinenko & Starobogatov, 1969 as a junior synonym of *Andrusovia*.

Andrusovia brusinai Starobogatov, 2000

Fig. 6F–K, M–N

*2000 *Andrusovia brusinai* Starobogatov, sp. nov.; Starobogatov: 41, fig. 1C.

2006 *Andrusovia brusinai* Starobogatov, 2000. – Kantor & Sysoev: 83, pl. 40, fig. C.

2016 *Andrusovia brusinai* Starobogatov, 2000. – Vinarski & Kantor: 214.

Material. 39 specimens (RGM 1309839, RGM 1309840, RGM 1310206, LV 201509).

Type material. Holotype: ZIN (no number).

Type locality. Eastern part of the middle Caspian Sea (42°42.5'N, 51°32.5'E, WGS84), at 80 m.

Dimensions. 1.52 × 1.44 mm (RGM 1309840, Fig. 6F, G); 1.54 × 1.55 mm (LV 201509, Fig. 6H, K, N); 1.81 × 1.80 mm (RGM 1309839, Fig. 6I, J, M); 1.71 × 1.52 mm; 1.67 × 1.69 mm; 1.83 × 1.55 mm; 1.64 × 1.51 mm.

Description. Shell broad trochiform, about as high as wide, with up to 4 whorls. Rarely specimens with slightly elevated spire occur. Protoconch high domical, about semicircular in profile; initial part immersed; consists of 1.1 whorls, measures 300 µm in diameter; nucleus about 90 µm wide; protoconch surface finely but strongly malleate near lower suture, rest appears to be irregularly granulate, but that might be due to poor preservation; P/T boundary sharp, marked by massive growth constrictions near lower suture. Teleoconch whorls highly convex, with maximum convexity in adapical half, producing slightly stepped spire. Last whorl attains 74–81% of shell height. Aperture broadly drop-shaped, slightly inclined, with faint adapical notch at

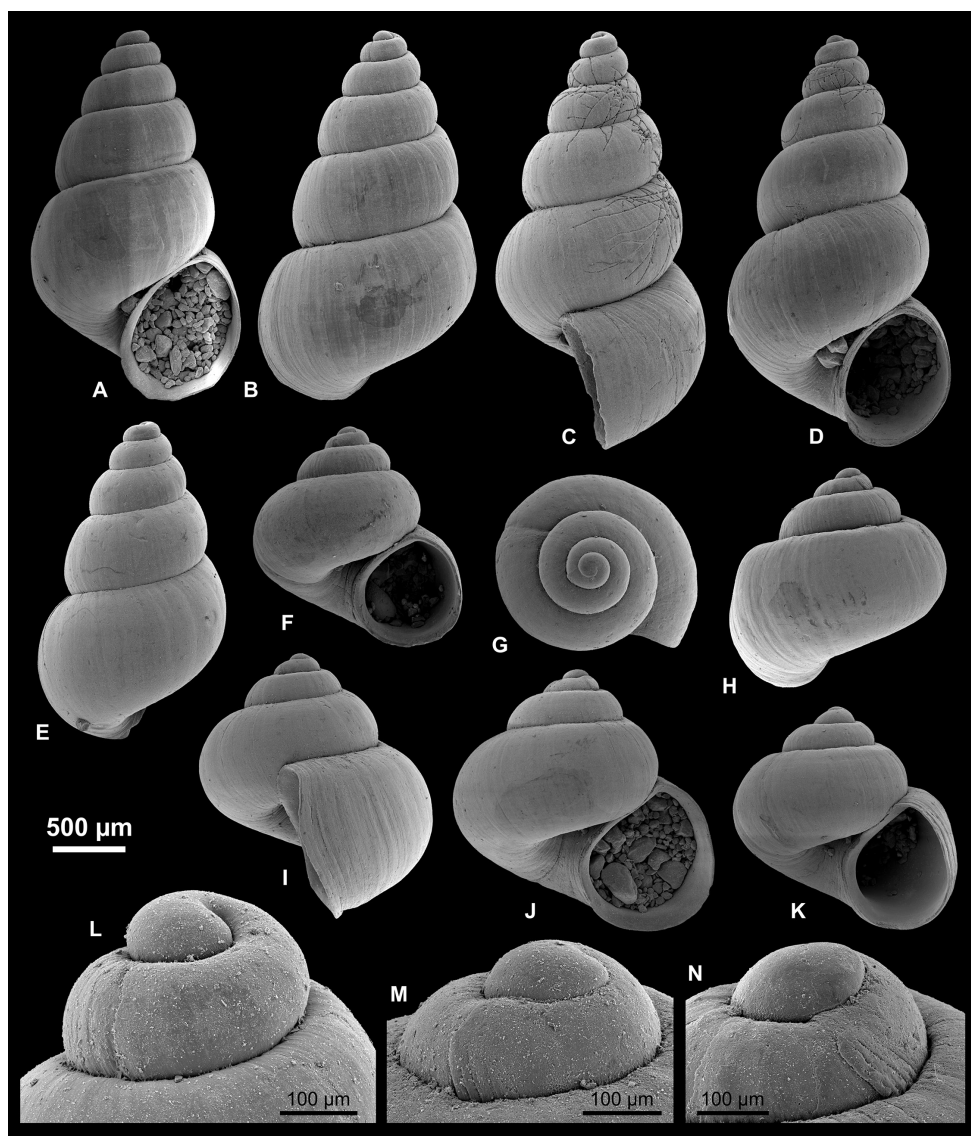


Figure 6. Hydrobiinae and Horatiinae. **A, B, L** *Ecribia* cf. *grimmi* (Clessin in W. Dybowski, 1887), LV 201508 **C, D** *E. cf. grimmi*, RGM 1309845 **E** *E. cf. grimmi*, RGM 1309847 **F, G** *Andrusovia brusinai* Starobogatov, 2000, RGM 1309840 **H, K, N** *A. brusinai*, LV 201509 **I, J, M** *A. brusinai*, RGM 1309839.

contact to penultimate whorl. Peristome slightly thickened and expanded at columella and base; sinuate in lateral view, with weakly protruding central part and weak adapical indentation. Umbilicus wide, deep. Fine prosocline growth lines cover shell. On one specimen, traces of spiral threads occur on base.

Discussion. The Caspian congeners *Andrusovia dybowskii* Brusina in Westerlund, 1902a (sensu Starobogatov 2000) and *A. andrusovi* Starobogatov, 2000 differ from

the present species in their much lower spires. *Andrusovia marina* (Logvinenko & Starobogatov, 1969) is smaller and has a shorter spire. Starobogatov (2000) based the distinction from *A. brusinai* on minor differences in shell ratios but these are strongly affected by the varying number of whorls and shell size; it might well be that *A. marina* and *A. brusinai* are just different growth stages of the same species. Since we have not seen the type material of Logvinenko and Starobogatov (1969), we tentatively accept the distinction of both taxa by Starobogatov (2000). Further comparison with the Logvinenko and Starobogatov material is essential to assess whether the two names refer indeed to distinct species.

Andrusovia brusinai resembles several recent species of *Horatia* Bourguignat, 1887, *Hauffenia* Pollonera, 1898 and *Islamia* Radoman, 1973 in terms of shell shape and protoconch surface. These differ from the present species in the either straight-sided (*Hauffenia*, *Islamia*; Arconada and Ramos 2006, Erőss and Petro 2008) or abapically (instead of adapically) sinuated peristome (*Horatia*; Szarowska 2006, Szarowska and Falniowski 2014). Shells of several species of *Pontohoratia* Vinarski, Palatov & Glöer, 2015 and *Motsametia* Vinarski, Palatov & Glöer, 2015 resemble *Andrusovia* species in terms of size and shape. They all differ in the more regularly shaped protoconchs, which show large nuclei and lack the massive growth constrictions.

Distribution. Endemic to the Caspian Sea, reported from middle and south Caspian Sea at depths between 47 and 311 m (Starobogatov 2000).

Subfamily Hydrobiinae Stimpson, 1865

Genus *Ecrobia* Stimpson, 1865

Type species. *Turbo minutus* Totten, 1834; by original description. United States, Recent.

Ecrobia cf. *grimmi* (Clessin in W. Dybowski, 1887)

Fig. 6A–E, L

cf. * 1887 *Hydrobia Grimmi* Cless.; W. Dybowski: 55–56.

cf. 1888 [*Hydrobia*] *Grimmi* Clessin. – W. Dybowski: 79, pl. 3, fig. 2.

cf. 1952 *Hydrobia grimmi* (Clessin) W. Dyb., 1888. – Zhadin: 225, fig. 147.

cf. 1969 *Pyrgohydrobia grimmi* (Cless. et W. Dyb.) – Logvinenko & Starobogatov: 249, fig. 358 (11).

cf. 2006 *Caspiohydrobia grimmi* (Clessin in W. Dybowski, 1888). – Kantor & Sysoev, 91–92, pl. 43, fig. E.

cf. 2009 *Caspiohydrobia grimmi* (Clessin et Dybowski, 1888). – Filippov & Riedel: 70–72, 74–76, figs 4a–d.

cf. 2016 *Caspiohydrobia grimmi* (Clessin et W. Dybowski in W. Dybowski, 1888). – Vinarski & Kantor: 229.

Material. 345 specimens (RGM 1309845, RGM 1309847, RGM 1310207, LV 201508).

Type material. Not traced.

Type locality. “Kaspi-See” (Caspian Sea, no further details mentioned).

Dimensions. 2.56×1.45 mm (LV 201508, Fig. 6A, B, L); 2.83×1.54 mm (RGM 1309845, Fig. 6C, D); 2.19×1.30 mm (RGM 1309847, Fig. 6E); 3.88×2.26 mm; 3.48×1.97 mm; 3.77×1.99 mm; 3.50×1.89 mm; 3.26×1.79 mm; 3.33×1.66 mm.

Description. Shell shape highly variable, ranging from broad ovoid to slender conical, comprising up to 6.5 whorls. Protoconch consisting of about one whorl, with nucleus immersed; initial part slightly raised, producing acute apex; surface weakly granular to malleate; P/T transition clear. Protoconch and teleoconch whorls highly convex, sometimes slightly flattened centrally in later whorls; suture deep. Size of last whorl varies between 55–62%, descends into straight-sided base. Aperture regularly ovoid, slightly inclined, touching base of penultimate whorl, leaving wide umbilicus. Peristome simple, sometimes weakly expanded. Surface smooth except for very fine prosocline growth lines.

Discussion. The shells of *Ecrobia* can only be reliably identified on the species-level using molecular data (Haase et al. 2010). Therefore, we tentatively assign the detected specimens to *Ecrobia grimmi*, which is the only *Ecrobia* species occurring in the Caspian Sea today (Haase et al. 2010).

Most of the species presently assigned to *Caspiohydrobia* Starobogatov, 1970, including its type species, *Pyrgohydrobia eichwaldiana* Golikov & Starobogatov, 1966, range within the morphological variability of this species. Previous examination of both reproductive systems (Sitnikova et al. 1992) and juvenile shells (Filippov and Riedel 2009) did not yield criteria supporting interspecific differentiation. Very likely all of the thirty *Caspiohydrobia* species listed by Kantor and Sysoev (2006) are morphotypes of a single species, probably *E. grimmi*. Given the problems of using shell morphology to identify *Ecrobia*, taxonomic conclusions on the synonymy of the *Caspiohydrobia* species require molecular data.

Note on species authority. W. Dybowski (1887: 7) noted that all diagnoses were drafted by Clessin and himself and most new species were therefore marked with “nob.” (Lat. *nobis*, “us”). However, W. Dybowski obviously made exceptions. In case of the new genus *Clessinia*, he marked the authority with “m.” (Lat. *meus*, “mine”). For *Hydrobia grimmi*, the authority is clearly indicated with “Cless.”, making Clessin the sole author of the species (unlike indicated by several authors).

Distribution. Caspian Sea; Lake Sawa, Iraq (Haase et al. 2010); salt lakes near Chelyabinsk, Russia (Shishkoedova 2010). Subfossil records derive from Holocene deposits of the Aral Sea (Filippov and Riedel 2009).

Subfamily Pyrgulinae Brusina, 1882

1882 Pyrgulinae Brusina: 230.

1914 Micromelaniidae B. Dybowski & Grochmalicki: 276.

1915 Turricaspiinae B. Dybowski & Grochmalicki: 103.

2017 Pyrgulinae Brusina, 1882. – Bouchet et al.: 212, 346 [cum syn.].

Discussion. The Caspian Pyrgulinae (sensu lato) encompasses 64 species that are considered accepted in the current literature (Vinarski and Kantor 2016). However, most of them are poorly known, documented by insufficient descriptions and drawings; for many, the type material has not been found (Kantor and Sysoev 2006, Vinarski and Kantor 2016). The extreme morphological variability of several representatives, such as those detected in the material from Selitrennoye, led previous authors to introduce numerous species based on shells with only minor deviations in shape, size or whorl outline. The Caspian Pyrgulinae therefore requires careful revision using molecular and anatomical data as far as available.

In addition to the problems associated with distinguishing species, genus-level classification is poorly resolved as well. Several attempts have been made to categorize this vast variability, and genus concepts have changed tremendously (e.g., B. Dybowski and Grochmalicki 1915, 1917, Zhadin 1952, Logvinenko and Starobogatov 1969, Kantor and Sysoev 2006, Vinarski and Kantor 2016). Twelve genus names have been described for members of the Caspian Pyrgulinae, based on quite different concepts of traits considered diagnostic. Currently, all species are classified within *Caspia* Clessin & W. Dybowski, 1887, *Pyrgula* De Cristofori & Jan, 1832 and *Turricaspia* B. Dybowski & Grochmalicki, 1915 (Kantor and Sysoev 2006, Vinarski and Kantor 2016). This scheme unites quite a variety of different morphologies under the same genus names, while at the same time similar species are assigned to different genera (e.g., Kantor and Sysoev 2006). Unfortunately, hardly any previous study provided explanations for their genus classifications or systematic concepts in general.

A thorough revision of all Caspian Pyrgulinae is beyond the scope of this study, but we discuss and revise the concepts that have been applied to the species studied herein.

Vinarski and Kantor (2016) listed 38 species of the genus *Pyrgula* for the Caspian Sea. The type species of *Pyrgula* De Cristofori & Jan, 1832, *P. annulata* (Linnaeus, 1758), lives in freshwater lakes and springs in Italy and Dalmatia (Welter-Schultes 2012). Shell morphology, anatomy and protoconch characteristics are very similar to Pontocaspian Pyrgulinae, e.g., some species of *Turricaspia* (compare also discussion in Riedel et al. 2001). However, molecular evidence suggests that *Pyrgula annulata* is only distantly related to the Pontocaspian species flock within the Pyrgulinae, with the last common ancestor dating back to the late Miocene (Wilke et al. 2007). Therefore, Pontocaspian species should not be attributed to *Pyrgula*, despite apparent morphological congruence, especially of some of the keeled Pontocaspian Pyrgulinae. A separation on subfamily level as proposed by B. Dybowski and Grochmalicki (1915) is opposed by the latest phylogeny of rissooidean gastropods, which suggests a rather close relationship (Wilke et al. 2013).

Turricaspia B. Dybowski & Grochmalicki, 1915 (type species: *Micromelania turricula* B. Dybowski & Grochmalicki, 1915) was introduced for species with turritiform, elongate shells with numerous whorls. Presently, the genus includes 22 Caspian species, encompassing elongate and broad, conical and ovoid, and sculptured and smooth species (Kantor and Sysoev 2006, Vinarski and Kantor 2016). Many species assigned to *Pyrgula* by Kantor and Sysoev (2006) and Vinarski and Kantor (2016) actually re-

semble *Turricaspia turricula* with respect to the turritiform, conical shell. This similarity also regards the type species of the genera *Caspiopyrgula* Logvinenko & Starobogatov, 1969 (type species: *Turricaspia nossovi* Kolesnikov, 1947), *Eurycaspia* Logvinenko & Starobogatov, 1969 (*Micromelania pseudodimidiata* B. Dybowski & Grochmalicki, 1917), *Oxypyrgula* Logvinenko & Starobogatov, 1969 (*Pyrgula pseudospica* Logvinenko & Starobogatov, 1969), and *Trachycaspia* B. Dybowski & Grochmalicki, 1917 (*Rissoa dimidiata* Eichwald, 1838). After examination of descriptions and illustrations of the type species (e.g., Kantor and Sysoev 2006), we conclude that these genera should be considered as junior synonyms of *Turricaspia*.

Some of the species classified as *Turricaspia* by Kantor and Sysoev (2006) and Vinnarski and Kantor (2016) differ considerably from *Turricaspia* s.s. in shell shape. This contains the type species of the genera *Caspiella* Thiele, 1928 (*Rissoa conus* Eichwald, 1838), *Clessiniola* Lindholm, 1924 (*Paludina variabilis* Eichwald, 1838), and *Laevicaspia* B. Dybowski & Grochmalicki, 1917 (*Rissoa caspia* Eichwald, 1838). In turn, some species presently attributed to the genus *Euxinipyrgula* Sitnikova & Starobogatov, 1999 (type species: *Pyrgula milachevitchi* Golikov & Starobogatov, 1966) closely resemble species of the *Laevicaspia*–*Caspiella* group (compare Anistratenko et al. 2011).

Based on a review of the Pontocaspian species formerly attributed to these genera and illustrated in the literature (Golikov and Starobogatov 1966, Logvinenko and Starobogatov 1969, Alexenko and Starobogatov 1987, Kantor and Sysoev 2006, Anistratenko 2008), we propose to distinguish the genera *Clessiniola* and *Laevicaspia* from *Turricaspia*, and to treat *Caspiella* and *Euxinipyrgula* as junior synonyms of *Laevicaspia*.

Clessiniola species can be easily distinguished from species attributed to other genera based on their broad shells with a large body whorl and aperture. The situation for the *Laevicaspia*–*Caspiella*–*Euxinipyrgula* is more difficult. The three type species (see above) share the ovoid shape with cyrticonoid spire, the high whorl accretion rate, the shape, inclination, lateral sinuation and thickening of the aperture, and the extent and sculpture of the protoconch (e.g., Kantor and Sysoev 2006, Anistratenko 2008, and this study). The only differences are shell size and whorl convexity, which we do not consider sufficient to distinguish genera. The adapical thickening of the aperture resulting from downward growing of the shell in late ontogeny as stated in the diagnosis of the genus *Euxinipyrgula* by Sitnikova and Starobogatov (1999) is also shown for species that have been attributed to *Caspiella* (see below). The features of the soft-part anatomy considered diagnostic by these authors need to be rechecked and compared to live material from the Caspian Sea to reevaluate the position of *Euxinipyrgula*. Sitnikova and Starobogatov (1999) also discussed the similarities between *Caspiella* and *Euxinipyrgula*, concluding that *Caspiella* should perhaps be included in the genus *Euxinipyrgula*, possibly as a separate subgenus (which would be nomenclaturally invalid however).

The ovoid shape, lateral sinuation and thickening of the aperture typical for the *Laevicaspia*–*Caspiella*–*Euxinipyrgula* group are also found among species of the genus *Prososthenia* Neumayr, 1969 from the middle Miocene of the Dinaride Lake System (e.g., Neubauer et al. 2016b). These species, however, differ in the granulate protoconch making up less than one whorl.

Species of *Turricaspia* differ from *Laevicaspia* in the slower, regular whorl accretion, producing a conical spire and a higher number of whorls at the same size. In addition, *Turricaspia* species have usually more fragile shells, thinner peristomes and often more strongly sinuate growth lines.

The genus *Caspia* is listed among Pyrgulinae in latest catalogues (Kantor and Sysoev 2006, Vinarski and Kantor 2016), but it has been shown to be unrelated to that subfamily (Anistratenko 2013, Bouchet et al. 2017; see discussion of the Caspiinae above).

Finally, several Pontocaspian Pyrgulinae have been previously assigned to the genus *Micromelania* Brusina, 1874 (e.g., W. Dybowski 1887, B. Dybowski and Grochmalicki 1917). Its type species, *Micromelania cerithiopsis* Brusina, 1874 (subsequent designation by Dollfus 1912), derives from late Miocene deposits of Lake Pannon. It differs considerably from Pontocaspian Pyrgulinae regarding the presence of 2–4 noded keels and the small size (4.5 × 1.33 mm after Brusina 1874) compared to the rather high number of eight whorls.

Genus *Clessiniola* Lindholm, 1924

1887 *Clessinia* W. Dybowski: 41 [non Doering, 1875].

1924 *Clessiniola* Lindholm: 32–33, 34.

1928 *Clessinola* Strand: 68 [junior objective synonym of *Clessiniola*].

Type species. *Paludina variabilis* Eichwald, 1838; by typification of replaced name (*Clessinia* W. Dybowski, 1887). Volga delta and Caspian Sea, Quaternary to Recent.

Clessiniola variabilis (Eichwald, 1838)

Fig. 7A–I

*1838 *Paludina variabilis* m.; Eichwald: 151–152.

1841 *Paludina variabilis* m. – Eichwald: 253–254, pl. 38, figs 6–7.

1853 *Pal[udina] variabilis* m. – Eichwald: 285.

1887 *Clessinia variabilis* Eichw. sp. – W. Dybowski: 41–42.

1888 [*Clessinia*] *variabilis* Eichw. sp. – W. Dybowski: 79, pl. 2, fig. 6.

1952 *Clessiniola variabilis* (Eichwald, 1841). – Zhadin: 255, fig. 199.

1966 *P[yrghula] (Clessiniola) variabilis*. – Golikov & Starobogatov: 356, fig. 2 (2).

1969 *Pyrgula [(Clessiniola)] variabilis* (Eichw.) – Logvinenko & Starobogatov: 377, fig. 367 (1).

1987 *T[urricaspia] variabilis* (Eichw.). – Alexenko & Starobogatov: 34, fig. 5.

2006 *Turricaspia variabilis* (Eichwald, 1838). – Kantor & Sysoev: 111, pl. 49, fig. J.

2011 *Turricaspia variabilis* (Eichwald, 1838). – Anistratenko et al.: 85, fig. 3 (15).

2014 *Turricaspia variabilis*. – Taviani et al.: 4, fig. 3b.

2016 *Turricaspia variabilis* (Eichwald, 1838). – Vinarski & Kantor: 251.

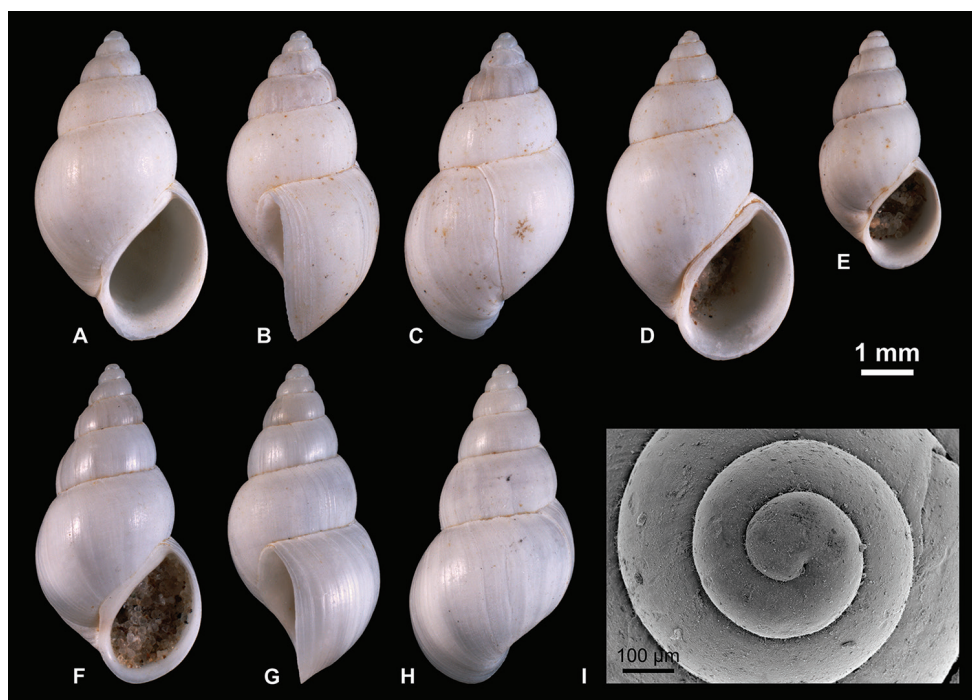


Figure 7. Pyrgulinae. **A–C** *Clessiniola variabilis* (Eichwald, 1838), LV 201507, broad morphotype **D** *C. variabilis*, RGM 1310246, broad morphotype **E** *C. variabilis*, RGM 1310245, slender morphotype **F–H** *C. variabilis*, RGM 1310243, slender morphotype **I** *C. variabilis*, RGM 1309827.

Material. 4867 specimens (RGM 1309815, RGM 1309826, RGM 1309827, RGM 1309831, RGM 1310243–1310247, LV 201507).

Type material. Not traced.

Type locality. “In Volgae ostio prope Astrachanum, et versus mare Caspium; etiam fossili in calcatio lapide conglutinato recentissimo Dagesthanici littoris” (at the Volga river mouth near Astrakhan, and towards the Caspian Sea; also in recently lithified fossil limestone at the shores of Dagestan).

Dimensions. 5.91×3.31 mm (LV 201507, Fig. 7A–C); 6.31×3.59 mm (RGM 1310246, Fig. 7D); 4.60×2.35 mm (RGM 1310245, Fig. 7E); 6.08×3.18 mm (RGM 1310243, Fig. 7F–H); 6.85×3.89 mm (RGM 1310244).

Description. Broadly drop-shaped to rarely conical shell of up to six whorls. Protoconch insufficiently preserved to specify extent and surface sculpture; P/T transition indistinct; first whorl measures ca. $340 \mu\text{m}$ in diameter. Teleoconch whorls moderately and regularly convex; sometimes, spire is very faintly stepped; suture narrow. In many specimens, shells starts to grow stronger in abapical direction in course of last (two) whorl(s), producing non-parallel suture and relatively higher penultimate whorl. Rarely, forms with comparatively slender shape and regularly increasing whorls (and thus relatively smaller last and penultimate whorls) occur. Both types are linked via intermediates. Aperture regularly ovoid, inclined; inner lip glossy, weakly to sometimes more

prominently thickened; strongly adnate, sheet-like expanded over base of penultimate whorl and columella, rarely leaving very narrow umbilicus; broad, shallow spout occurs at transition between columella and base; outer lip mainly thin, sometimes weakly thickened at anterior notch. Growth lines very faint, with prosocline upper third and near orthocline lower two-thirds.

Discussion. This species displays a large morphological variability within our ample material. Shell shape ranges between slender conical to broadly ovoid, sometimes with weakly irregular growth. Likewise, shell size, whorl convexity, and number of whorls vary considerably. Yet, these features intergrade without clear boundary, rendering a distinction of species unreasonable.

The morphological variability is not restricted to our material but a general feature of *Clessiniola*. It was documented by several previous authors, partly for specimens from the same localities (e.g., Eichwald 1838, Issel 1865, W. Dybowski 1887–1888, Golikov and Starobogatov 1966, Logvinenko and Starobogatov 1969, Alexenko and Starobogatov 1987, Anistratenko et al. 2011). The species concepts applied by the different authors, however, varied greatly. The present material includes shells that have been variably attributed to the species *C. variabilis* (Eichwald, 1838), *C. triton* (Eichwald, 1838) and *C. martensii* (Clessin & W. Dybowski in W. Dybowski, 1887). The *triton*-morphotype sensu Eichwald characterizes broad specimens with slightly detached aperture (see also Kantor and Sysoev 2006); these forms are rarely represented in our material. Eichwald (1838, 1841) himself confirmed the rarity of the form, also stating that he did not find a living representative (in contrast to *C. variabilis*). The *martensii*-morphotype was introduced for similarly broad morphologies. (Note that Clessin and W. Dybowski used a different concept of *C. triton*, there having a rather elongate conical shell.)

Because of the fluent morphological transition between forms traditionally referred to as *C. variabilis*, *C. triton* and *C. martensii*, as well as their joint occurrence in several localities in the Pontocaspian region, one might consider all of them synonymous. Personal observations on Holocene material from Dagestan area, however, indicate indeed distinguishable morphotypes without intermediates. Moreover, frequent shell repair found in most of the Selitrennoye specimens additionally complicates an unbiased view on morphological diversity. A more in-depth investigation comparing undamaged material from different sites is thus required.

Given the large variability, the Caspian species *Clessiniola ovum* (Logvinenko & Starobogatov, 1969) and *C. trivialis* (Logvinenko & Starobogatov, 1969), as well as *C. pseudotriton* (Golikov & Starobogatov, 1966) from the Dniester River mouth (compare Kantor and Sysoev 2006), might too be considered as synonyms of *C. variabilis*. However, the original descriptions and drawings provided impede clarification of their statuses.

Clessinia ahngeri Westerlund, 1902 is often listed as junior synonym of *C. variabilis*, but without discussion (e.g., Logvinenko and Starobogatov 1969, Vinarski and Kantor 2016). The original description of *C. ahngeri* suggests close similarities indeed between both species claiming, however, that it differs from other congeners in the much larger spire (11 × 5 mm) and the slightly sinuate outer lip. Examination of Westerlund's (1902b) material is required to ascertain the alleged synonymy.

The record of “*Paludina Eichwaldi* Kryn.” Eichwald (1841) listed in synonymy of *C. variabilis* refers to a nomen nudum mentioned in a species list by Krynicki (1837).

Distribution. Endemic to the Pontocaspian region. Found in the Caspian Sea and the lower courses of rivers and freshwater parts of the Azov and Black seas (Anis-tratenko et al. 2011, Vinarski and Kantor 2016). Also reported from Neoeuxinian (late Pleistocene) deposits of the Marmara Sea (Taviani et al. 2014).

Genus *Laevicaspia* B. Dybowski & Grochmalicki, 1917

? 1902a *Thaumasia* Westerlund: 104 [non Perty, 1833; non Albers, 1850].

1917 *Laevicaspia* B. Dybowski & Grochmalicki: 5.

1928 *Caspiella* Thiele: 353, 381.

1999 *Euxinipyrigula* Sitnikova & Starobogatov: 158, 162.

Type species. *Rissoa caspia* Eichwald, 1838; by subsequent designation by Logvinenko and Starobogatov (1969). Caspian Sea, Pleistocene.

Discussion. Lindholm (1922) studied the type material of *Buliminus goebeli* Westerlund, 1896 from Mangyschlak (Mangystau Peninsula, Kazakhstan) and concluded that is a junior synonym of “*Micromelania*” *caspia* (Eichwald, 1838). Westerlund (1902a), considering *Buliminus goebeli* as a member of terrestrial “Bulimoidea” (= Enidae), introduced the new genus *Thaumasia*, which would take precedence over *Laevicaspia* B. Dybowski & Grochmalicki, 1917. However, *Thaumasia* Westerlund, 1902 is invalid as a junior homonym of *Thaumasia* Perty, 1833 (Arachnida) and *Thaumasia* Albers, 1850 (Gastropoda, Subulinidae) (see also Lindholm 1925).

Laevicaspia caspia (Eichwald, 1838)

Fig. 8A–K

*1838 *Rissoa caspia* m.; Eichwald: 154–155.

1841 *Rissoa caspia* – Eichwald: 256–257, pl. 38, figs 14–15.

1853 *Riss.[oa] caspia* m. – Eichwald: 273.

non 1876 *Hydrobia caspia*, Eichw. – Grimm: 150–153, pl. 6, fig. 15.

non 1877 *Hydrobia caspia*, Eichw. – Grimm: 79–80, pl. 7, figs 3a–d.

non 1887 *Micromelania caspia* Eichw. sp. – W. Dybowski: 21.

non 1888 *Micr.[omelania] caspia* Eichw. sp. – W. Dybowski: 78, pl. 1, fig. 1.

? 1896 *B.[uliminus] (Napaeus?) goebeli* Westerlund: 188.

1914 *Micromelania* (?) *curta* Nalivkin: 21–22, 31, pl. 6, figs 1–2 [partim; non figs 3–4, 7, 9–14].

1914 [*Micromelania* (?) *curta*] var. *plano-convexa* Nalivkin: 22, 31, pl. 6, figs 15–18.

non 1914 *Micromelania caspia* Eichw. – Nalivkin: 22, 31, pl. 6, figs 5–6 [partim; non fig. 8].

- non 1917 *Micromelania* (*Turricaspia*, *Laevicaspia*) *caspia* Eichw. – B. Dybowski & Grochmalicki: 5–8, 36–38, pl. 1, figs 1–3.
- non 1969 *Pyrgula caspia* (Eichw.). – Logvinenko & Starobogatov: 369–370, fig. 364 (1).
- 1987 *T.[urricaspia] caspia* (Eichw.). – Alexenko & Starobogatov: 33, fig. 2.
- 2006 *Turricaspia caspia* (Eichwald, 1838). – Kantor & Sysoev: 106, pl. 49, fig. M.
- 2014 *Euxinipyrgula lincta*. – Taviani et al.: 4, fig. 3c [non *Micromelania lincta* Milashevich, 1908].
- 2016 *Turricaspia caspia* (Eichwald, 1838). – Vinarski & Kantor: 246.

Material. 300 specimens (RGM 1309788, RGM 1309789, 1309797, RGM 1309798, RGM 1310196, RGM 1310257, RGM 1310258, LV 201511).

Type material. Lectotype: ZIN (No. 1 in systematic catalogue), designated by Alexenko and Starobogatov (1987).

Type locality. “In eodem lapide calcario Dagesthanico, fossilis” (in the same limestone of Dagestan [referring to the previous species, also found in Dagestan], fossil).

Dimensions. 9.01 × 3.31 mm (RGM 1310257, Fig. 8A–C); 7.88 × 3.31 mm (RGM 1310258, Fig. 8D–F); 10.33 × 3.92 mm (LV 201511, Fig. 8I–K); 9.92 × 3.83 mm; 10.21 × 3.88 mm; 9.52 × 3.54 mm; 9.69 × 3.61 mm.

Description. Large, slender ovoid shell comprising up to 8.3 whorls. Protoconch large, measuring 535–600 µm at 1.15–1.2 whorls, with initial part inflated; nucleus almost immersed, 190–230 µm wide; nucleus and early protoconch bear intentions of malleate sculpture, which passes into granular surface after half a whorl accompanied by onset of spiral striae; P/T boundary indistinct. Whorl convexity decreasing rapidly: first teleoconch whorl moderately convex, second to last whorl low convex, sometimes almost straight-sided; maximum convexity is in lower half; whorls closely attached, suture narrow; a very small but marked convexity appears at upper suture, producing a faintly stepped spire; occasionally, it is accompanied by shallow abapical concavity. Last whorl makes up 46–50% of shell height, passing over regular but weakly convex to near straight-sided to slightly concave base. Aperture slender ovoid, inclined, closely attached to preceding whorl; in latest ontogeny, shell growth is more abapically directed, resulting in marked thickening at adapical tip. Peristome simple, thin, slightly expanded and indented at base; distinctly and regularly sigmoidal in lateral view, with upper half broadly indented and lower half broadly protruding; inner lip protrudes in lateral view, extending sheet-like over base of penultimate whorl; umbilicus mostly closed, rarely very narrow, slit-like. Growth lines weakly sigmoidal: strongly prosocline in upper half, weakly opisthocline in lower half. Several specimens show faint spiral threads on last and penultimate whorls.

Discussion. Different concepts of this species previously applied have led to considerable confusion about its real identity. This is partly rooted in the description and illustration provided by Eichwald (1838, 1841) that were insufficient to allow safe discrimination from similar species. For instance, *Micromelania caspia* sensu Grimm (1876, 1877), W. Dybowski (1887–1888) and B. Dybowski and Grochmalicki (1917) differs from the present species in the acute apex, the moderately convex whorls, the

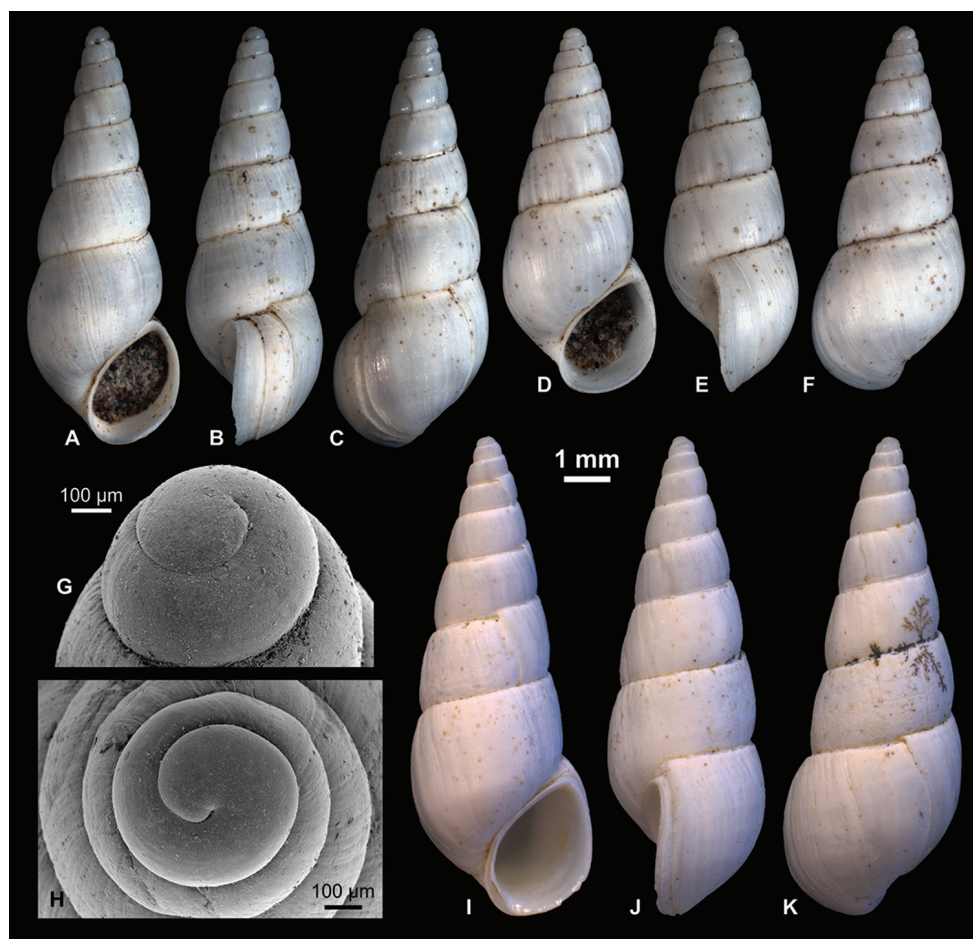


Figure 8. Pyrgulinae. **A–C** *Laevicaspia caspia* (Eichwald, 1838), RGM 1310257 **D–F** *L. caspia*, RGM 1310258 **G** *L. caspia*, RGM 1310197 **H** *L. caspia*, RGM 1310198 **I–K** *L. caspia*, LV 201511.

deep suture and the thin peristome. As already noted by Alexenko and Starobogatov (1987), it represents a different species, i.e., *Laevicaspia lincta* (Milashevich, 1908). That species was described from Lake Katlabukh near the Danube delta in Ukraine (lectotype, which matches Milashevich's description, is illustrated in Kantor and Sysoev 2006: 95, pl. 45, fig. D; as *Euxinipyrgula lincta*). Specimens from the Neoeuxinian (late Pleistocene) of the Marmara Sea identified as *E. cf. lincta* by Taviani et al. (2014) differ from that species in the near straight-sided whorls and thickened peristome; in fact, the material corresponds well to *L. caspia*.

Micromelania caspia sensu Nalivkin (1914) comprises at least two species, both being more elongate, having more whorls and relatively smaller last whorls than *L. caspia*. In turn, some of the illustrated syntypes of "*Micromelania*" *curta* Nalivkin, 1914 and the variety "*Micromelania*" *curta* var. *planoconvexa* Nalivkin, 1914 from Bakunian deposits of Shikhovo, Apsheron Peninsula, Azerbaijan, closely resemble the present spe-

cies and are thus (partly) considered synonymous. “*Micromelania*” *curta* encompasses a great variability of shapes, ranging from slender, elongate (*caspia*-type) to broad, conical shells. Since no holotype or lectotype have been designated, the status of this species is unresolved at present. Note that *Pyrgula curta* sensu Logvinenko and Starobogatov (1969) and Kantor and Sysoev (2006) does not correspond to Nalivkin’s species but rather to the specimens Nalivkin (1914) misidentified as *Micromelania caspia*.

Similarly, *Pyrgula caspia* sensu Logvinenko and Starobogatov (1969) is a quite different species, showing highly convex whorls and an inflated last whorl. It rather ranges within the morphological variability of *Turricaspia meneghiniana* (see below).

Alexenko and Starobogatov (1987) finally brought stability to the identity of *L. caspia* by designating a lectotype (see Kantor and Sysoev 2006: 106, pl. 49, fig. A; as *Turricaspia caspia*), which matches well our specimens. The label accompanying their specimen reads “Kaspiyskoye more” (“Caspian Sea”), which differs from the information provided by Eichwald (Dagestan) (see also discussion in Vinarski and Kantor 2016: 246). Inspection of the catalogue of the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN), however, confirmed that the lectotype is based on Eichwald’s original material.

The similar *Laevicaspia iljinae* (Golikov & Starobogatov, 1966) from Holocene deposits of the Crimean Peninsula can be distinguished in its more slender shape and the spruce-like whorl outline (i.e., steep, straight-sided upper two-thirds passing over convexity into flatter, convex lower third; see also Kantor and Sysoev 2006: 108, pl. 49, fig. D).

Distribution. Endemic to the Caspian Sea (Logvinenko and Starobogatov 1969 stated that the species occurs at a depth of 30–150 m in the middle and southern Caspian Sea, but these data have to be revised given their incorrect concept of *L. caspia*).

Laevicaspia cincta (Abich, 1859) comb. n.

Fig. 9A–H

*1859 *Rissoa cincta*; Abich: 57, pl. 2, fig. 6.

?1887 *Caspia Orthii* Clessin & W. Dybowski in W. Dybowski: 40.

?1888 [*Caspia*] *Orthii* n. sp. – W. Dybowski: 79, pl. 3, fig. 6.

1969 *Pyrgula* [(*Caspiella*)] *cincta* (Abich). – Logvinenko & Starobogatov: 372, fig. 366 (4).

2006 *Pyrgula cincta* (Abich, 1859). – Kantor & Sysoev: 98, pl. 47, fig. L.

2016 *Pyrgula cincta* (Abich, 1859). – Vinarski & Kantor: 236.

Material. 174 specimens (RGM 1309806, RGM 1309807, RGM 1310200, LV 201514).

Type material. Not traced.

Type locality. Abich (1859) specified the type locality on p. 12–13 as “Gulf of Baku”.

Dimensions. 3.83 × 1.93 mm (LV 201514, Fig. 9A, B); 4.05 × 1.89 mm (RGM 1309807, Fig. 9C–E); 4.41 × 2.10 mm (RGM 1309806, Fig. 9F–H); 4.73 × 2.11 mm; 4.59 × 2.10 mm; 4.58 × 2.17 mm.

Description. Slender ovoid shell with up to 6.5 whorls. Protoconch broad, low dome-shaped, consists of 1.2 whorls that measure 415 µm in diameter, with slightly

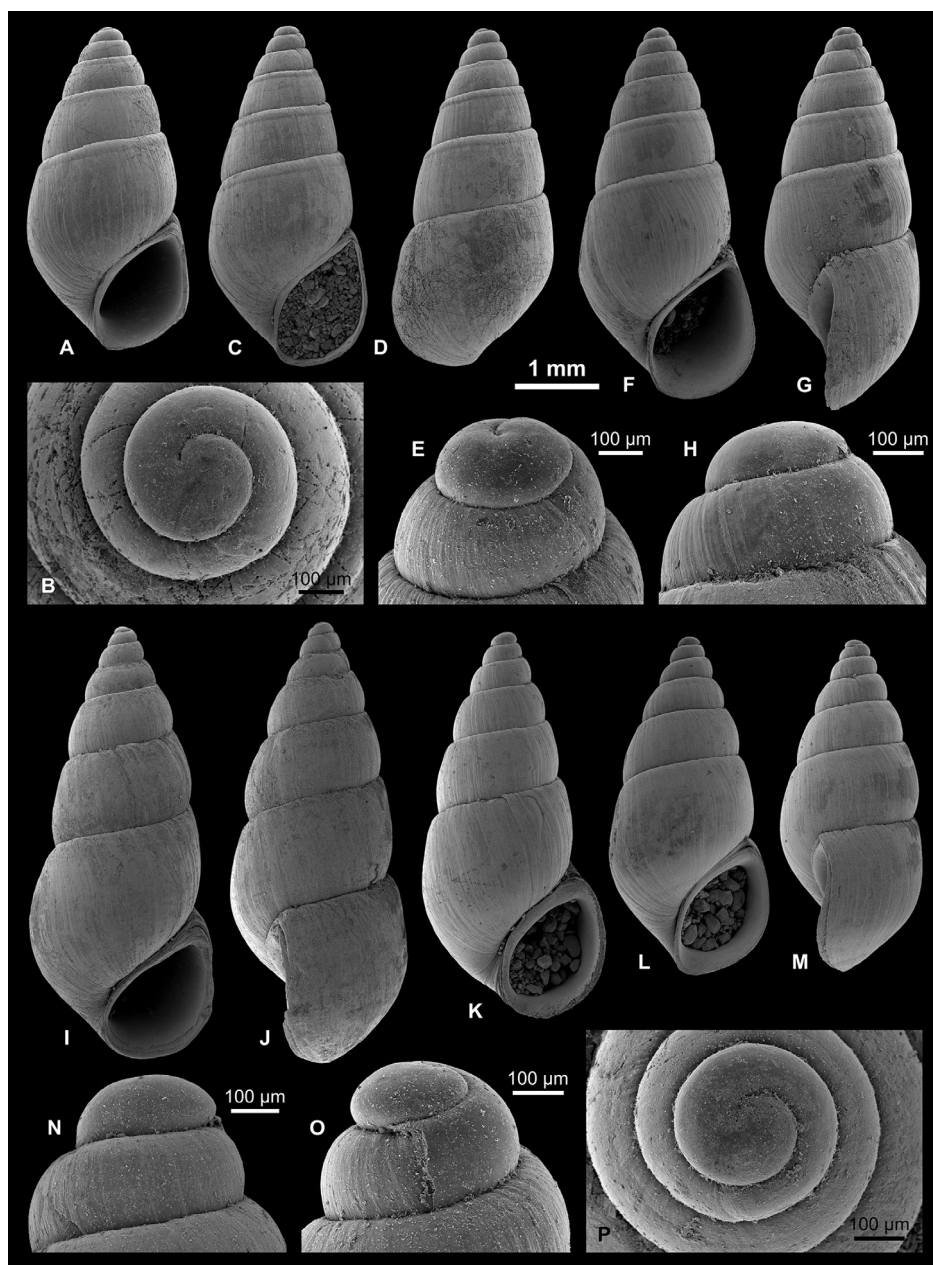


Figure 9. Pyrgulinae. **A, B** *Laevicaspia cincta* (Abich, 1859), LV 201514 **C–E** *L. cincta*, RGM 1309807 **F–H** *L. cincta*, RGM 1309806 **I, J** *L. cincta*, RGM 1309830 **K** *Laevicaspia conus* (Eichwald, 1838), LV 201515 **L–O** *L. conus*, RGM 1309829 **P** *L. conus*, RGM 1309828.

inflated initial part; nucleus 150 µm wide; protoconch surface weakly granulate, with intentions of striae on second half; P/T transition distinct, formed by sharp, thin axial line. Whorl convexity decreases steadily during ontogeny, with early teleoconch

whorls being moderately convex and penultimate and last whorl low convex to almost straight-sided. On third teleoconch whorl, weak subsutural band emerges that slightly enhances during ontogeny; band forms weak bulge throughout, with maximum convexity in its lower half and steep, almost straight-sided ramp in upper half; abapical demarcation clear, sometimes accompanied by thin groove. Last whorl attains 54–65% of shell height, passing from flattened whorl flank over marked convexity into steep, straight-sided base. Aperture near drop-shaped, inclined, with acute adapical angle, straight parietal margin, obtuse angle between parietal and columellar margins, sometimes slightly expanded palatal margin. Peristome not thickened, weakly expanded at columella and base; regularly sinuate in lateral view, with broad adapical indentation and about equally broad and high abapical protrusion. Umbilicus closed or very narrow. Growth lines weakly prosocline in upper half, near orthocline in lower half.

Discussion. The *Selitrennoye* specimens match with the original description in terms of size (shell height: 3–4 mm), the ovoid shell shape, the number of whorls, the rounded last whorl and the simple peristome margin; they differ in the expression of the subsutural band, which Abich indicated to be “weakly keeled”. We consider these differences to range within the intraspecific variability of this species.

Laevicaspia cincta can be readily distinguished from other Pontocaspian Pyrgulinae by its ovoid, slightly stepped shell with broad, blunt apex, subsutural band and flattened whorls in later ontogeny. *Laevicaspia abichi* (Logvinenko & Starobogatov, 1969) from the middle Caspian Sea, differs in the much larger size (6.8×3 mm), the conical shape, the narrower subsutural band and the larger aperture. The Caspian endemic species *Laevicaspia kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1887) resembles *L. cincta* very closely in terms of the slender ovoid shape with near straight-sided whorls, the closely attached aperture with thin peristome, and the lacking umbilicus; it differs in the lack of a subsutural band and the more elongate shape.

Caspia orthii Clessin & W. Dybowski in W. Dybowski, 1887 was synonymized with the present species by previous authors (e.g., Logvinenko and Starobogatov 1969, Kantor and Sysoev 2006, Vinarski and Kantor 2016). The original description matches well our specimens in terms of size (4.8×1.9 mm), number of whorls, expression of the subsutural band and shape of the aperture; the only difference is the “elongated-conical” shape compared to the ovoid shells of *L. cincta* described by Abich (1859) and represent by our material. Although not having seen W. Dybowski’s type material, we tentatively follow the previous assessment and consider *Caspia orthii* a junior synonym of *Laevicaspia cincta*.

Note that *Rissoa cincta* Deshayes, 1861 (p. 404, pl. 24, figs 4–6), described from the Eocene (Bartonian) of the Paris Basin, is a junior primary homonym of this species and thus invalid. At present, this species is classified in the genus *Pseudotaphrus* Cossman, 1888 (Ponder 1984: 96).

Distribution. Endemic to the Caspian Sea, in the southern part at a depth of >250 m (Parr et al. 2007).

***Laevicaspia conus* (Eichwald, 1838) comb. n.**

Fig. 9I–P

*1838 *Rissoa Conus* m.; Eichwald: 155.1841 *Rissoa Conus* m. – Eichwald: 257, pl. 38, figs 16a–b [wrongly given as “figs 16–17” on p. 257; see also corrigendum at the end of Eichwald’s work].1853 *Riss.[oa] conus* m. – Eichwald: 273.non 1876 *Eulima conus*, Eichw?. – Grimm: 154–156, pl. 6, fig. 14.1887 *Nematurella conus* Eichw. sp. (non Grimm). – W. Dybowski: 45.1888 [*Nematurella*] *conus* Eichw. sp. – W. Dybowski: 78, pl. 2, fig. 3.? 1896 *Prosostenia* [sic] *conus* Eichw. – Sinzov: 49–50, pl. 1, figs 30–33.1926 ?*Nematurella conus* (Eichwald). – Wenz: 2007.1952 *Caspiella conus* (Eichwald, 1841). – Zhadin: 259, fig. 211.1969 *Pyrgula* [(*Caspiella*)] *conus* (Eichw.). – Logvinenko & Starobogatov: 374, fig. 366 (5–6).non 2006 *Turricaspia conus conus* (Eichwald, 1838). – Kantor & Sysoev: 106, pl. 48, fig. J.2016 *Turricaspia conus conus* (Eichwald, 1838). – Vinarski & Kantor: 246–247.**Material.** 1135 specimens (RGM 1309828, RGM 1309829, RGM 1309830, RGM 1310199, RGM 1310226–1310228, LV 201515).**Type material.** Not traced.**Type locality.** “In eodem lapide calcareo, fossilis” (in the same limestone [referring to previous species, found in Dagestan], fossil).**Dimensions.** 5.14 × 2.19 mm (RGM 1309830, Fig. 9I, J); 4.60 × 2.18 mm (LV 201515, Fig. 9K); 4.02 × 1.91 mm (RGM 1309829, Fig. 9L–O); 3.87 × 1.87 mm (RGM 1309828, Fig. 9P); 4.60 × 2.23 mm (RGM 1310226); 5.12 × 2.37 mm (RGM 1310227); 4.17 × 2.14 mm (RGM 1310228).**Description.** Ovoid, glossy shell with up to 6.8 whorls. Shell outline variable, depending on growth stage: shells with up to 5 whorls are rather broad, nearly conical; in late ontogeny, shell growth is directed adapically, producing more elongate shapes with narrow, high last whorl; sometimes, these slender elongate morphotypes have slightly irregular shape. Protoconch consists of 1.2 whorls with 355 µm in diameter; nucleus almost immersed, 125 µm wide; surface faintly malleate or granulate, with intentions of spiral sculpture detected in some specimens; P/T boundary very distinct, marked by sharp, thin axial line. Teleoconch whorls weakly to moderately convex, sometimes adapically flattened. Last whorl attains between 55–63% of total height, grades into straight-sided or weakly convex base. Aperture drop-shaped, inclined, closely attached to base of preceding whorl, usually covering or rarely leaving slit-like umbilicus. Peristome slightly expanded, thin or thickened all around, especially at adapical tip; regularly sinuate in lateral view, with broad adapical indentation and about equally broad and high abapical protrusion. Growth lines weak, prosocline in upper half, orthocline in lower half.

Discussion. Logvinenko and Starobogatov (1969) listed “*Rissoa conus* Eichwald, 1841, partim” in synonymy of *Pyrgula kolesnikoviana* Logvinenko & Starobogatov in Golikov & Starobogatov, 1966 (now classified in *Laevicaspia*; see below), but without any explanation. The synonymy list was expanded as “*Rissoa conus* sensu Eichwald, 1841, partim, non Eichwald, 1838” by Kantor and Sysoev (2006) and Vinarski and Kantor (2016), yet again without discussion. The synonymy is not mentioned in the original description of *Laevicaspia kolesnikoviana* in Golikov and Starobogatov (1966). Very likely, the synonymy roots in the ambiguous description of Eichwald (1838, 1841), summarizing two different morphologies. Eichwald referred to the typical form as having a conical shell with seven, gently increasing whorls, whereas the last two are much broader; the size was indicated as 2×1 lin., which corresponds to 4.2×2.1 mm (given Eichwald used the Russian *liniya*). In addition, he mentioned rarer, slightly longer (3 lin.) specimens, with deeper suture and straight-sided whorls. In 1841, Eichwald illustrated one of these rare specimens. The description in the 1841-work, however, is almost identical to the original description. In this light, it remains unclear why Kantor and Sysoev (2006) and Vinarski and Kantor (2016) referred to as “*Rissoa conus* sensu Eichwald, 1841, partim, non Eichwald, 1838” in their synonymy lists of *L. kolesnikoviana*. To complete confusion, the specimen illustrated in Kantor and Sysoev (2006) is not *L. conus*, differing in the broad, blunt apex and the near straight-sided whorls; it rather resembles *L. kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1887).

The holotype of *L. kolesnikoviana* illustrated by Kantor and Sysoev (2006, pl. 47, fig. N) corresponds to the description and illustration of the rare, slender morphology of *Laevicaspia conus* sensu Eichwald in terms of the number of whorls and the near straight-sided whorls; it differs only in the considerably smaller size (3.7 mm vs. 6.3 mm). Yet, Golikov and Starobogatov (1966) and Logvinenko and Starobogatov (1969) indicate larger sizes for *L. kolesnikoviana* (5.5 mm and 6.5 mm, respectively), suggesting a great variability in size. On the other hand, the two morphologies delineated by Eichwald also match our own observations on *L. conus*. In late ontogeny, growth is directed almost entirely abapically, resulting in more elongate shells with an additional whorl. These larger morphologies correspond completely to the smaller, relatively bulkier shells in all other aspects, which is why we consider them as morphotypes rather than species-group taxa. Without Eichwald’s material at hand it is difficult to arrive at a conclusion on this matter.

The species has affinities with several representatives of the Azov and Black seas. *Pyrgula (Caspiella) lindholmiana* Golikov & Starobogatov, 1966, today considered as a subspecies of *L. conus* (e.g., Vinarski and Kantor 2016), has a larger and broader shell. Similarly, *Laevicaspia milachevitchi* (Golikov & Starobogatov, 1966) and *Laevicaspia boltovskoji* (Golikov & Starobogatov, 1966) are broader than *L. conus*, while *Laevicaspia lincta* (Milashevich, 1908) and *Laevicaspia limanica* (Golikov & Starobogatov, 1966) are more slender and larger.

“*Eulima conus* Eichwald” as described and illustrated by Grimm (1876, 1877) has little resemblance to actual *L. conus*. He illustrated a very elongate, conical shell with many more and almost perfectly straight-sided whorls. This fact was already noticed by

Clessin and W. Dybowski a few years later, and they introduced *Micromelania grimmi* Clessin & W. Dybowski in W. Dybowski, 1887 for the misidentified species.

The illustrations of specimens from the Kuyalnikian (late Pliocene to early Pleistocene) of the Odessa region identified as *Prososthenia conus* by Sinzov (1896) show shells with similar shape, proportions and whorl convexity. A more detailed examination of material from the region is required to assess whether it is indeed conspecific with *L. conus*.

Distribution. Endemic to the Caspian Sea, reported from depths between 0 and 120 m (Logvinenko and Starobogatov 1969).

***Laevicaspia kolesnikoviana* (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966) comb. n.**

Fig. 10A–E, K, N

*1966 *P[yrghula]* (*Caspiella*) *kolesnikoviana* Logvinenko et Starobogatov; Golikov & Starobogatov: 357, fig. 2 (8–9).

1969 *Pyrgula* [(*Caspiella*)] *kolesnikoviana* Logv. et Star. – Logvinenko & Starobogatov: 372, fig. 366 (1).

2006 *Pyrgula kolesnikoviana* Logvinenko et Starobogatov in Golikov et Starobogatov, 1966. – Kantor & Sysoev: 100, pl. 47, fig. N.

2016 *Pyrgula kolesnikoviana* Logvinenko et Starobogatov in Golikov et Starobogatov, 1966. – Vinarski & Kantor: 239.

Material. 514 specimens (RGM 1309816, RGM 1309818, RGM 1309819, RGM 1310212, RGM 1310221–1310225, LV 201516).

Type material. Holotype: ZIN 4462/1.

Type locality. Caspian Sea, N of Apsheron peninsula, NW from Kamni Dva Brata Island, 40°47'N, 49°42'E, 30 m (Vinarski and Kantor 2016).

Dimensions. 3.55 × 1.63 mm (RGM 1309816, Fig. 10A–C, K); 3.59 × 1.67 mm (LV 201516, Fig. 10D); 3.95 × 1.82 mm (RGM 1309819, Fig. 10E, N); 3.90 × 1.77 mm (RGM 1309818); 4.04 × 1.96 mm (RGM 1310222); 4.49 × 1.99 mm (RGM 1310223); 3.54 × 1.72 mm (RGM 1310224).

Description. Small, slender ovoid, shiny shell with up to 6.9 whorls. Protoconch consists of 1.2 whorls, measuring 355 µm in diameter; nucleus rather long, ca. 130 µm wide; surface finely granulate (maybe due to preservation; traces of finely malleate to irregularly striate pattern occurs on margins of nucleus and initial part); faint striae on last third; P/T boundary distinct. Whorl convexity of teleoconch whorls decreasing: first to second whorl moderately to highly convex, last whorl low to moderately convex. Faint subsutural band appears on later teleoconch whorls in some specimens, sometimes accompanied by weak concavity below. Last whorl attains 50–57% of shell height, passing via broad, regular convexity in to weakly convex base. Aperture ovoid, inclined, closely attached to preceding whorl; in latest ontogeny, shell growth is more abapically directed, resulting in marked thickening at adapical angle. Peristome thin

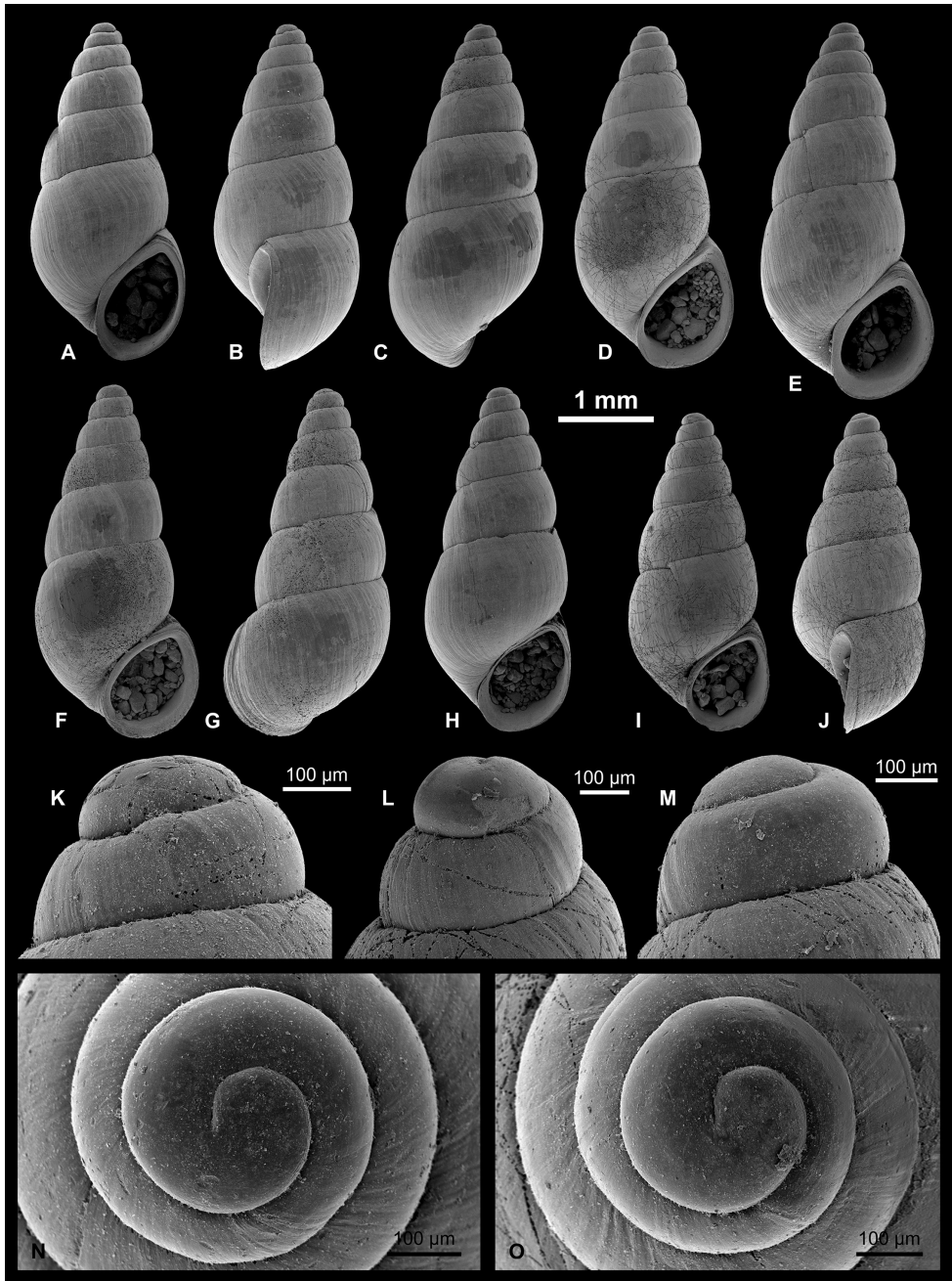


Figure 10. Pyrgulinae. **A–C, K** *Laevicaspia kolesnikoviana* (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966), RGM 1309816 **D** *L. kolesnikoviana*, LV 201516 **E, N** *L. kolesnikoviana*, RGM 1309819 **F, G** *Laevicaspia vinarskii* sp. n., holotype, LV 201517 **H, O** *L. vinarskii* sp. n., RGM paratype, 1309805 **I, J, L, M** *L. vinarskii* sp. n., paratype, RGM 1309821.

or thickened all around, with parietal margin sometimes slightly expanded; weakly but regularly sinuate in lateral view, with broad adapical indentation and about equally broad and high abapical protrusion. Umbilicus usually closed or very narrow, slit-like. Growth lines weak, prosocline in upper half, orthocline in lower half. In addition, faint spiral furrows appear in some specimens.

Discussion. Co-occurring *Laevicaspia vinarskii* sp. n. differs in the consistently lower whorl expansion rate at the same size and the smaller aperture. *Laevicaspia kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1887) can be distinguished by its broader and larger shell.

Distribution. Endemic to the Caspian Sea, reported from depths between 25 and 180 m (Kolesnikov 1947, Logvinenko and Starobogatov 1969).

***Laevicaspia vinarskii* sp. n.**

<http://zoobank.org/8399A902-945D-444A-A8AD-136592F8E527>

Fig. 10F–J, L–M, O

Type material. Holotype: LV 201517; 3.70 × 1.72 mm (Fig. 10F–G). Paratypes: RGM 1309821; 3.34 × 1.48 mm (Fig. 10I, J, L, M). RGM 1309805; 3.61 × 1.54 mm (Fig. 10H, O). LV 201731; 4.14 × 1.93 mm.

Additional material. 5 specimens (RGM 1309793, LV 201732).

Type locality. Selitrennoye, Astrakhan, Russia; northern Caspian Basin; GPS coordinates: 47°10'21.19"N, 47°26'25.41"E (WGS84).

Age. Early Late Pleistocene (late Khazarian, MIS 5).

Etymology. In honor of Maxim Vinarski (Saint Petersburg State University) for his contributions to Malacology.

Diagnosis. Slender ovoid, imperforate shell with up to 6.5 moderately convex whorls, narrow suture, granulate–striate protoconch, high whorl expansion rate and small, adnate, inclined aperture.

Description. Slender ovoid shell with up to 6.5 whorls. Protoconch consists of 1.2 whorls measuring 375 µm; nucleus is 140 µm wide; surface strongly granulate on nucleus, less so on remaining protoconch, striae appear on last 0.25 whorls; P/T transition marked by distinct growth rim. Teleoconch whorls moderately convex, separated by narrow suture; whorls increase slowly in height, with the last attaining 53–57% of shell height, passing into weakly convex base. Weak subsutural band is observed in one specimen. Aperture small, inclined, closely attached to base of preceding whorl, leaving no or slit-like umbilicus. Peristome slightly thickened, especially at adapical tip; regularly sinuate in lateral view, with broad adapical indentation and about equally broad and high abapical protrusion. Distinct spiral furrows occur in well preserved specimens. Growth lines weak, prosocline in upper half, orthocline in lower half.

Discussion. The new species differs from co-occurring *Laevicaspia kolesnikoviana* in the higher whorl expansion rate at about the same size and the larger aperture. *Laevicaspia? ismailensis* (Golikov & Starobogatov, 1966) from lakes Yalpug and Kugur-

lu in the Danube river delta is more slender and larger (5.6 mm) at the same number of whorls and has a less inclined, rounder aperture (see holotype illustrated by Kantor and Sysoev 2006: pl. 50, fig. A).

Distribution. Endemic to the Caspian Sea Pleistocene, so far only known from Selitrennoye.

Genus *Turricaspia* B. Dybowski & Grochmalicki, 1915

1915 *Turricaspia* B. Dybowski & Grochmalicki: 105.

1917 *Trachycaspia* B. Dybowski & Grochmalicki: 22.

1969 *Pyrgula* (*Caspiopyrgula*) Logvinenko & Starobogatov: 366.

1969 *Pyrgula* (*Eurycaspia*) Logvinenko & Starobogatov: 357.

1969 *Pyrgula* (*Oxypyrghula*) Logvinenko & Starobogatov: 366.

Type species. *Micromelania turricula* B. Dybowski & Grochmalicki, 1915; by subsequent designation by Wenz (1939). Caspian Sea, Recent.

Turricaspia andrussowi (B. Dybowski & Grochmalicki, 1915)

Fig. 11A, B

*1915 *Micromelania* (*Turricaspia*) *Andrussowi* nov. sp.; B. Dybowski & Grochmalicki: 125–126, pl. 3, figs 31a–b.

1917 *Micromelania* (*Turricaspia*, *Trachycaspia*) *Andrussowi* nov. sp. – B. Dybowski & Grochmalicki: 26–27, pl. 4, fig. 39.

1969 *Pyrgula* [(*Turricaspia*)] *andrusovi* [sic] (Dyb. et Gr.). – Logvinenko & Starobogatov: 365–366, fig. 362 (4) [partim].

2006 *Turricaspia andrussowi* (B. Dybowski et Grochmalicki, 1915). – Kantor & Sysoev: 104–105, pl. 48, fig. A [partim].

2016 *Turricaspia andrussowi* (B. Dybowski et Grochmalicki, 1915). – Vinarski & Kantor: 245 [partim].

Material. 3 spire fragments (RGM 1309814, RGM 1310205).

Type material. Lectotype: ZIN 4355/1 (specimen illustrated by B. Dybowski and Grochmalicki 1915, 1917), designated by Logvinenko and Starobogatov (1969), illustrated by Kantor and Sysoev (2006: pl. 48, fig. A).

Type locality. Caspian Sea (no locality specified).

Description. Available fragments indicate very slender, conical shell. Apex broad, blunt, bulbous. Whorl profile flattened, very weakly spruce-like, with straight-sided upper two-thirds passing over convexity into weakly convex lower third; in addition, broad, flat subsutural band appears, sometimes accompanied by very narrow concavity below. Umbilicus seems fully closed. Aperture not preserved in any specimen.

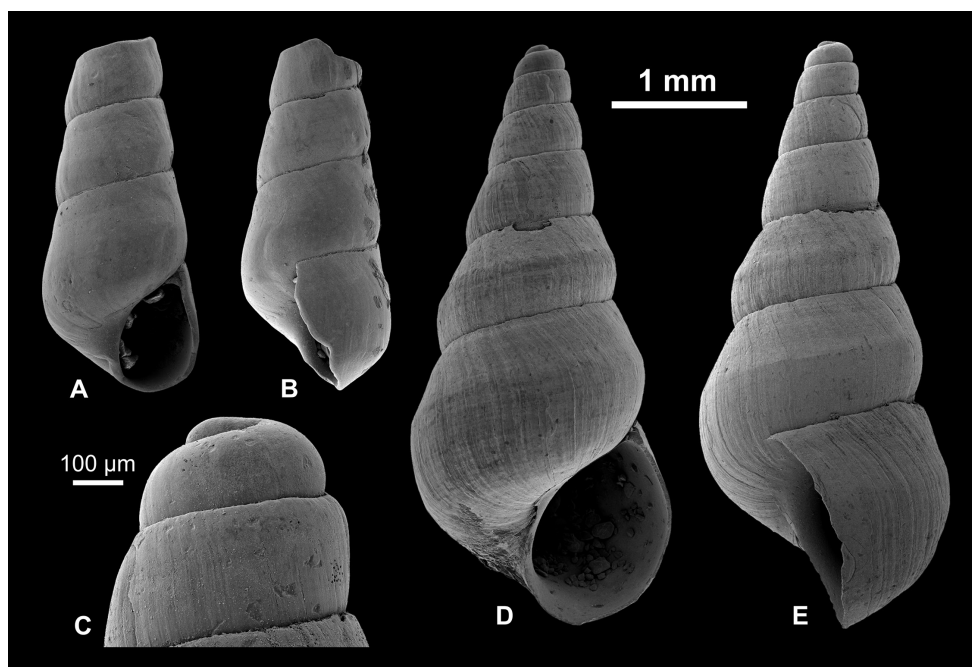


Figure 11. Pyrgulinae. **A–C** *Turricaspia* ? *dimidiata* (Eichwald, 1838), RGM 1309787 **D, E** *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915), RGM 1309814.

Discussion. The identification of the three spire fragments rests upon the strongly adpressed whorls with very narrow suture and the flattened, spruce-like whorl profile, and the large, bulbous protoconch. *Turricaspia eulimellula* (B. Dybowski & Grochmalicki, 1915) has a similarly slender spire with adpressed whorls, but it bears a basal keel and the maximum whorl convexity is around mid-height instead of in the lower third. *Turricaspia grimmi* (Clessin & W. Dybowski in W. Dybowski, 1887) differs in its perfectly straight-sided, rectangular, very weakly stepped whorl profile (see also B. Dybowski and Grochmalicki 1917, pl. 3, figs 34–35; Kantor and Sysoev 2006, pl. 46, fig. L).

A very similar species is *Pyrgula dubia* Logvinenko & Starobogatov, 1969 from the middle Caspian Sea, matching the present one in the weakly spruce-like whorl profile; in fact, it might just be a juvenile specimen of *T. andrussowi*. Similarly, *Pyrgula turkmenica* Logvinenko & Starobogatov, 1969, from the eastern part of southern Caspian Sea, corresponds to *T. andrussowi* in the weak subsutural band accompanied by an abapical concavity; it might as well be a juvenile representative of *T. andrussowi*.

Logvinenko and Starobogatov (1969) synonymized without discussion *Hydrobia spica* sensu Grimm, 1876, *Turricaspia elegantula* sensu B. Dybowski & Grochmalicki, 1915, *T. brusinae* (B. Dybowski & Grochmalicki, 1915), as well as several varieties of *T. spica* and *T. turricula* described by B. Dybowski & Grochmalicki (1915), with *T. andrussowi* (see also Kantor and Sysoev 2006, Vinarski and Kantor 2016). However, none of these taxa actually resembles *T. andrussowi*. This species can be well delim-

ited from these alleged synonyms in its bulbous protoconch and the characteristic, weakly spruce-like whorl profile. (Note that the drawing provided by Logvinenko and Starobogatov 1969 shows a rather broad shell with acute apex; it has little in common with the lectotype designated by them).

Distribution. Endemic to the Caspian Sea (Logvinenko and Starobogatov 1969 indicated occurrences for the middle and southern Caspian Sea at depths of 25–80 m, but based on a much wider concept of the species).

Turricaspia ? dimidiata (Eichwald, 1838)

Fig. 11C–E

?*1838 *Rissoa dimidiata* m.; Eichwald: 156.

? 1841 *Rissoa dimidiata* m. – Eichwald: 258, pl. 38, figs 17a–b [wrongly given as “figs 16–17” on p. 258; see also corrigendum at the end of Eichwald’s work].

? 1853 *Pal[udina] dimidiata* m. – Eichwald: 285–286.

? 1887 *Micromelania dimidiata* Eichw. sp. – W. Dybowski: 31 [partim].

? 1888 *Micromelania dimidiata* Eichw. sp. – W. Dybowski: 78, pl. 1, figs 4a–f, 5 [partim].

? 1917 *Micromelania (Turricaspia) dimidiata* Eichw. – B. Dybowski & Grochmalicki: 32–33, pl. 4, figs 44–47 [partim].

? 1969 *Pyrgula dimidiata* (Eichw.). – Logvinenko & Starobogatov: 358–359, fig. 359 (1).

? 2006 *Pyrgula dimidiata* (Eichwald, 1838). – Kantor & Sysoev: 99, pl. 46, fig. K.

? 2016 *Pyrgula dimidiata* (Eichwald, 1838). – Vinarski & Kantor: 238.

Material. 1 subadult specimen (RGM 1309787).

Type material. Not traced.

Type locality. “In eodem lapide calcareo, fossilis” (in the same limestone [referring to the previous species, found in Dagestan], fossil).

Dimensions. 4.29 × 1.93 mm.

Description. Slender elongate shell with ca. 6.5 whorls preserved. Protoconch granulate, originally perhaps densely malleate. First teleoconch whorl straight-sided in profile, passing into weakly convex outline on 2nd–3rd whorl. Between 3rd and 4th whorl, broad, blunt central swelling emerges, grading into thin angulation on 5th whorl; no keel is developed. Whorl portion above swelling/angulation straight-sided, below weakly convex; directly above it, weak concavity is formed locally. Aperture ovoid, strongly adnate, leaving no umbilicus, with thin peristome. Growth lines rather distinct, with prosocline upper half and near orthocline lower half.

Discussion. A single subadult shell containing ca. 6.5 whorls (including the protoconch) is available. Size and number of whorls as well as the centrally placed angulation correspond well to Eichwald’s (1838, 1841) description and illustration of *T. dimidiata*. However, the central keel is very weakly expressed in our specimen and it starts not before the fourth whorl, which is why we only tentatively attribute it to this species.

Kantor and Sysoev (2006) illustrate a much more elongate specimen with cyrt-conoid spire and more abapically placed keel; it might represent a different species. *Turricaspia bakuana* (Kolesnikov, 1947), likewise described from Caspian Sea, too has a central keel, but differs in the much more slender shell and consistently strong keel from the second teleoconch whorl onwards (cf. Kantor and Sysoev 2006). *Turricaspia basalis* (B. Dybowski & Grochmalicki, 1915) has a broader conical habitus and the keel is placed near the lower suture. The subspecies *T. b. laticarinata* (Logvinenko & Starobogatov, 1969) only differs from *T. basalis* in the thickness of the keel and is herein considered a junior synonym of the nominal species.

Distribution. Endemic to the Caspian Sea, reported from middle and south Caspian Sea at depths between 35 and 200 m (Logvinenko and Starobogatov 1969).

Turricaspia lyrata (B. Dybowski & Grochmalicki, 1915)

Fig. 12A–K

- *1915 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *lyrata* nov. var.; B. Dybowski & Grochmalicki: 117, pl. 2, fig. 18.
- 1915 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *incisata* nov. var.; B. Dybowski & Grochmalicki: 117, pl. 2, fig. 19.
- 1915 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *striata* nov. var.; B. Dybowski & Grochmalicki: 117, pl. 2, fig. 20.
- 1917 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *lyrata* nov. var. – B. Dybowski & Grochmalicki: 17, pl. 3, fig. 25.
- 1917 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *incisata* nov. var. – B. Dybowski & Grochmalicki: 18, pl. 3, fig. 26.
- 1917 *Micromelania* (*Turricaspia*) *spica* Eichw. var. *striata* nov. var. – B. Dybowski & Grochmalicki: 18, pl. 3, fig. 27.
- 1969 *Pyrgula* [(*Turricaspia*)] *lirata* [sic] (Dyb. et Gr.). – Logvinenko & Starobogatov: 365, fig. 362 (2).
- 2006 *Pyrgula lirata* [sic] (B. Dybowski et Grochmalicki, 1915). – Kantor & Sysoev: 101, pl. 46, fig. E.
- 2016 *Pyrgula lirata* [sic] (B. Dybowski et Grochmalicki, 1915). – Vinarski & Kantor: 240.

Material. 562 specimens (RGM 1309802, RGM 1309825, RGM 1310209, RGM 1310213, RGM 1310214, RGM 1310216, RGM 1310218–1310220, LV 201512, LV 201513).

Type material. Lectotype: ZIN 4552/1 (specimen illustrated by B. Dybowski and Grochmalicki 1915, 1917), designated by Logvinenko and Starobogatov (1969), illustrated by Kantor and Sysoev (2006: pl. 46, fig. E).

Type locality. Caspian Sea (no locality specified).

Dimensions. 7.68 × 2.59 mm (RGM 1310213, Fig. 12A–C); 7.99 × 2.42 mm (RGM 1310220, Fig. 12D); 7.34 × 2.28 mm (RGM 1310214, Fig. 12E); 7.54 ×

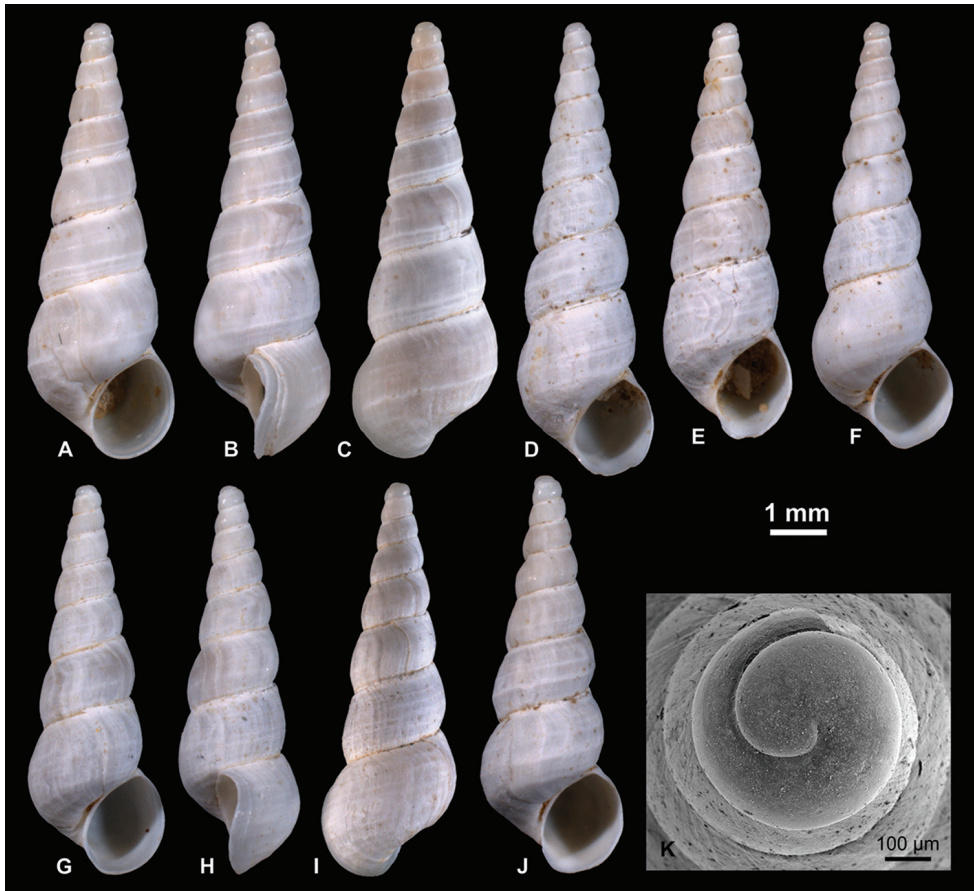


Figure 12. Pyrgulinae. **A–C** *Turricaspia lyrata* (B. Dybowski & Grochmalicki, 1915), RGM 1310213 **D** *T. lyrata*, RGM 1310220 **E** *T. lyrata*, RGM 1310214 **F** *T. lyrata*, LV 201512 **G–I** *T. lyrata*, LV 201513 **J** *T. lyrata*, RGM 1310218 **K** *T. lyrata*, RGM 1309802.

2.50 mm (LV 201512, Fig. 12F); 6.87×2.43 mm (LV 201513, Fig. 12G–I); 7×2.52 mm (RGM 1310218, Fig. 12J).

Description. Slender elongate shell of up to 9 whorls. Protoconch large, measuring about $485 \mu\text{m}$ in diameter; it forms bulbous cap on top of shell and comprises 1.25 whorls; surface weakly granulate, with striae on last 0.25 whorls; nucleus low, broad, ca. $170 \mu\text{m}$ in diameter; P/T transition very distinct, marked by sharp growth cessation. Teleoconch whorls low to moderately convex, often flattened or with straight-sided upper half, which creates spruce-like morphology. Sometimes, very weak and thin bulge appears below suture, producing faintly stepped spire. Most shells bear very low and somewhat irregular spirals, but expression varies considerably concerning its onset (mainly starts on lower whorls), strength (faint traces to distinct but blunt keels) and number of elements (one keel near base to several keels spread across whorl profile). Expression of sculpture varies in most specimens throughout ontogeny, which cre-

ates uneven, rugged appearance. Aperture comparatively small, in most cases regularly ovoid and weakly inclined, covering up umbilicus entirely or leaving very thin opening; peristome simple. Growth lines strongly sigmoidal, with prosocline upper third and opisthocline lower two-thirds.

Discussion. This species can be distinguished from its congeners in its large, bulbous protoconch and the typical, somewhat irregular sculpture. It is consistently larger, more massive and on average bears much stronger sculpture than co-occurring *T. ? spica*. The varieties “*Micromelania (Turricaspia) spica* var. *incisata*” and “*M. (T.) spica* var. *striata*” introduced by B. Dybowski and Grochmalicki (1915) only differ in the depth of the suture and the expression of the teleoconch sculpture, respectively. Given the variability of these features, we consider both of them synonymous with *T. lyrata*. Already Logvinenko and Starobogatov (1969) considered *incisata* and *lyrata* synonymous and, as first revisers, chose *lyrata* as the valid name of the species. The variety “*M. (T.) spica* var. *lordosa*” B. Dybowski & Grochmalicki, 1915 might also be a synonym of this species. However, the apex of the specimen illustrated in B. Dybowski and Grochmalicki (1915, 1917), which contains diagnostic characters, is not preserved. Nevertheless, *striata* and *lordosa* are certainly not synonymous with *T. andrussowi* as suggested by Logvinenko and Starobogatov (1969). That species differs from *T. lyrata* in the much slender whorls with spruce-like, near straight-sided profile.

Distribution. Endemic to the Caspian Sea (after Logvinenko and Starobogatov 1969, it occurs in the western part of the middle and southern Caspian Sea at a depth of 25–50 m; mind however that these authors used a slightly different concept of the species).

***Turricaspia meneghiniana* (Issel, 1865)**

Fig. 13A–K

*1865 *Bythinia Meneghiniana*, Issel; Issel: 21, pl. 1, figs 12–13.

1866 *Bythinia Meneghiniana*, Issel. – Issel: 405, pl. 1, figs 12–13.

1917 *Micromelania (Turricaspia) caspia* Eichw. var. *inflata* nov. var. – B. Dybowski & Grochmalicki: 9, pl. 1, fig. 5.

? 1969 *Pyrgula caspia* (Eichw). – Logvinenko & Starobogatov: 369–370, fig. 364 (1).

? 1969 *Pyrgula meneghiniana* (Issel). – Logvinenko & Starobogatov: 370, fig. 365 (2).

non 1987 *T[urricaspia] meneghiniana meneghiniana* (Iss.). – Alexenko & Starobogatov: 35, fig. 8.

2006 *Turricaspia meneghiniana* (Issel, 1865). – Kantor & Sysoev: 109, pl. 49, fig. E.

2016 *Turricaspia meneghiniana* (Issel, 1865). – Vinarski & Kantor: 248.

Material. 248 specimens (RGM 1309799, RGM 1309800, RGM 1310197, RGM 1310198, RGM 1310256, LV 201518).

Type material. Not traced.

Type locality. “Nei giacimenti fossiliferi di Baku” (from fossil deposits in Baku).

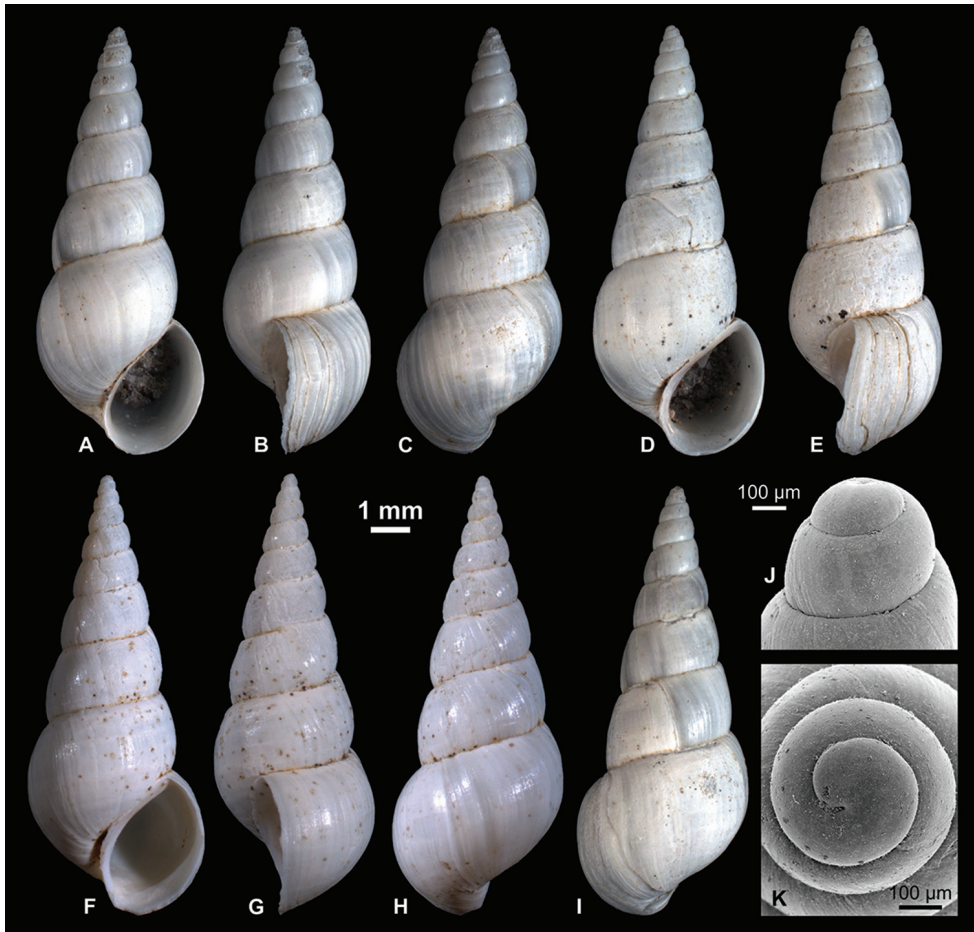


Figure 13. Pyrgulinae. **A–C** *Turricaspi meneghiniana* (Issel, 1865), RGM 1310256 **D, E, I** *T. meneghiniana*, LV 201518 **F–H** *T. meneghiniana*, RGM 1310197 **J, K** *T. meneghiniana*, RGM1309799.

Dimensions. 10.86 × 4.27 mm (RGM 1310256, Fig. 13A–C); 10.91 × 4.36 mm (LV 201518, Fig. 13D, E, I); 11.17 × 4.50 mm (RGM 1310197, Fig. 13F–H); 10.82 × 4.14 mm; 11.23 × 4.40 mm; 11.65 × 4.49 mm.

Description. Conical shell with up to 9.3 whorls. Protoconch comprises 1.3 whorls, measuring 440 µm in diameter, with slightly inflated initial part; nucleus measures 150 µm in diameter; entire protoconch surface weakly granulate; indistinct spiral striae appear on second half; P/T transition distinct, formed by sharp, thin axial line. Teleoconch whorls increase slowly but regularly in height and width; whorls moderately convex, whereas convexity slightly decreases with ontogeny. Last whorl attains 45–48% of shell height, passes over perfect convexity into slightly convex base. Aperture ovoid, inclined, closely attached to base of preceding whorl across almost entire parietal margin. Peristome thin, not thickened, little expanded; weakly sigmoidal in lateral view, with broad, shallow indentation in upper half and broad, weak protre-

sion in lower half; inner lip protrudes in lateral view, extending sheet-like over base of penultimate whorl; umbilicus very narrow, slit-like. Growth lines weakly sigmoidal: strongly prosocline in upper half, weakly opisthocline in lower half. Several specimens show faint spiral threads on last and penultimate whorls.

Discussion. Our material matches well to the description of Issel (1865), corresponding in the conical shell shape, the regularly increasing whorls, the rounded last whorl with faint spiral striae, and the ovate, adapically angulated aperture; only his specimens (13.5 × 5 mm) are larger than ours and consist of more whorls. Compared to his description, Issel's illustration seem to overemphasize the relative height of the last whorl and underrepresent the pronounced whorl convexity. However, variability as to these characteristics is discernible also in our material.

Micromelania subulata Westerlund, 1902 is commonly listed as junior synonym of this species but always without discussion (e.g., Logvinenko and Starobogatov 1969, Kantor and Sysoev 2006, Vinarski and Kantor 2016). Westerlund's (1902b) description refers to a large (15 mm), elongate shell with 9.5–10 whorls and a thickened callus connecting the peristome margins. These features partly oppose Issel's description, which is why we tend to consider both taxa as separate, in contrast to most previous authors. Unfortunately, Westerlund's (1902b) type material of this species could not be traced, neither in the Göteborg Natural History Museum nor the Swedish Museum of Natural History in Stockholm, where the largest part of Westerlund's material is stored (Vinarski et al. 2013).

Another commonly cited synonym is *Micromelania caspia* var. *inflata* B. Dybowski & Grochmalicki, 1915, which indeed matches both Issel's description and our material.

Turricaspia meneghiniana differs from the similarly large *Laevicaspia caspia* (Eichwald, 1838) in its regularly conical profile, the higher number of whorls, and the higher whorl convexity. The drawings of "*Pyrgula meneghiniana* (Issel)" provided by Logvinenko and Starobogatov (1969) indicate a broader shell with low whorl convexity and might represent a different species. In contrast, *Pyrgula caspia* sensu Logvinenko and Starobogatov (1969) (non Eichwald 1838) resembles the present species in terms of the high shell convexity and regular growth rate and might be conspecific. *Turricaspia meneghiniana* sensu Alexenko and Starobogatov (1987), with few, low convex whorls and an angled base, is clearly a different species.

Distribution. Endemic to the Caspian Sea, reported from middle and south Caspian Sea at depths between 0 and 35 m (Logvinenko and Starobogatov 1969).

***Turricaspia pulla* (B. Dybowski & Grochmalicki, 1915)**

Fig. 14A–J

*1915 *Micromelania* (*Turricaspia*) *caspia* Eichw. var. *pulla* nov. var.; B. Dybowski & Grochmalicki: 111, pl. 1, fig. 6a.

1917 *Micromelania* (*Turricaspia*) *caspia* Eichw. var. *pulla* nov. var. – B. Dybowski & Grochmalicki: 10, pl. 1, fig. 7.

1969 *Pyrgula* [(*Turricaspia*)] *pulla* (Dyb. et Gr.). – Logvinenko & Starobogatov: 361–362, fig. 360 (8).

2006 *Pyrgula pulla* (B. Dybowski et Grochmalicki, 1915). – Kantor & Sysoev: 102, pl. 46, fig. C.

2016 *Pyrgula pulla* (B. Dybowski et Grochmalicki, 1915). – Vinarski & Kantor: 242.

Material. 186 specimens (RGM 1309803, RGM 1309804, RGM 1309820, RGM 1310211, RGM 1310253–1310254, LV 201519).

Type material. Lectotype: ZIN 4422/1 (specimen illustrated by B. Dybowski and Grochmalicki 1915, 1917), designated by Logvinenko and Starobogatov (1969), illustrated by Kantor and Sysoev (2006: pl. 46, fig. C).

Type locality. Caspian Sea (no locality specified).

Dimensions. 4.88×2.10 mm (LV 201519, Fig. 14A–C); 5.17×2.11 mm (RGM 1310254, Fig. 14D, I, J); 4.77×1.90 mm (RGM 1310253, Fig. 14E–G); 5.84×2.16 mm (RGM 1309803); 5.54×1.97 mm (RGM 1309804).

Description. Slender conical shell with up to 8 whorls. Protoconch bulbous, weakly granulate, with striae on second half; diameter $410\ \mu\text{m}$, consists of 1.25 whorls; nucleus low, broad, $140\ \mu\text{m}$ wide; transition to teleoconch distinct. Teleoconch whorls weakly convex, with maximum convexity at or slightly below midline of whorl profile; portion above maximum convexity almost straight-sided, portion below weakly convex. Whorls are separated by deep suture. Height of last whorl amounts 45% of total shell. Sometimes intentions of spiral lines appear on lower half of last whorl. Aperture ovoid, oblique, with weakly thickened and slightly expanded peristome; in lateral view, peristome is distinctly sigmoidal, with broad, shallow indentation in upper half and broad, weak protrusion in lower half. Umbilicus very narrow or closed. Growth lines sigmoidal, markedly prosocline in upper half, weakly opisthocline in lower half.

Discussion. The species can be easily distinguished from most other species of *Turricaspia* by its comparably broad conical shape, the low-convex whorls, and its small size. Juvenile specimens of *T. meneghiniana* remind of *T. pulla* but the former have broader shells with more convex whorls. *Turricaspia pullula* is likewise broader and exposes a characteristic tripartite whorl profile (see below).

Distribution. Endemic to the Caspian Sea, reported from middle and south Caspian Sea at depths between 15 and 75 m (Logvinenko and Starobogatov 1969).

Turricaspia pullula (B. Dybowski & Grochmalicki, 1915)

Fig. 14K, L

*1915 *Micromelania* (*Turricaspia*) *caspia* Eichw. var. *pullula* nov. var.; B. Dybowski & Grochmalicki: 111–112, pl. 1, fig. 7.

1917 *Micromelania* (*Turricaspia*) *caspia* Eichw. var. *pullula* nov. var. – B. Dybowski & Grochmalicki: 10–11, pl. 1, fig. 8.

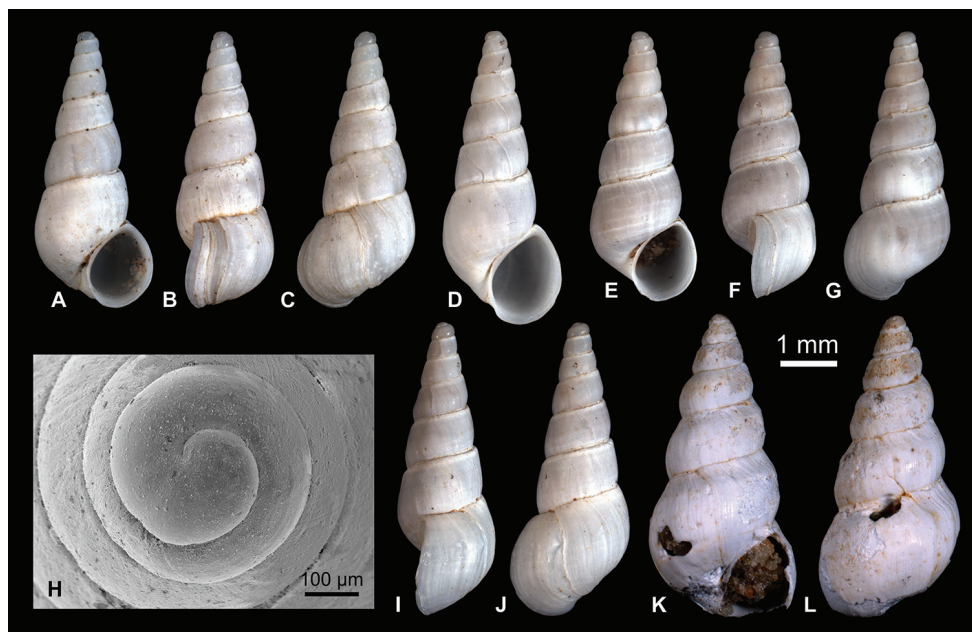


Figure 14. Pyrgulinae. **A–C** *Turricaspia pulla* (B. Dybowski & Grochmalicki, 1915), LV 201519 **D, I, J** *T. pulla*, RGM 1310254 **E–G** *T. pulla*, RGM 1310253 **H** *T. pulla*, RGM 1309820 **K, L** *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915), RGM 1310210.

1969 *Pyrgula* [(*Turricaspia*)] *pullula* (Dyb. et Gr.). – Logvinenko & Starobogatov: 366–367, fig. 363 (3).

2006 *Turricaspia pullula* (B. Dybowski et Grochmalicki, 1915). – Kantor & Sysoev: 109, pl. 50, fig. B.

2016 *Turricaspia pullula* (B. Dybowski et Grochmalicki, 1915). – Vinarski & Kantor: 249.

Material. 1 damaged specimen (RGM 1310210).

Type material. Lectotype: ZIN 4423/1 (specimen illustrated by B. Dybowski and Grochmalicki 1915, 1917), designated by Logvinenko and Starobogatov (1969), illustrated by Kantor and Sysoev (2006: pl. 50, fig. B).

Type locality. Caspian Sea (no locality specified).

Dimensions. 5.36 × 2.62 mm.

Description. A single incomplete specimen of about 6 whorls is preserved. Protoconch is corroded beyond recognition. Early teleoconch whorls are poorly convex to centrally flattened. Convexity strongly increases on about 3rd whorl. From 4th whorl onwards, whorl surface is partitioned into three zones: two lower zones are roughly straight-sided in profile, upper one slightly concave; middle zone slightly wider than other two; zones are separated by blunt angulations, whose expression varies between very faint to distinct (but no keel is formed). Aperture not preserved, but the tight coiling of the last preserved whorl suggests that umbilicus is absent. Growth lines strongly

proscoline in upper third, near orthocline in lower two-thirds; transition coincides with boundary between upper and middle zone.

Discussion. The available specimen corresponds well to the lectotype as illustrated by Kantor and Sysoev (2006). The very characteristic tripartite whorl profile is only discernible on the penultimate whorl of their specimen. Such a pattern is unknown for any other Pontocaspiian Pyrgulinae.

Distribution. Endemic to the Caspian Sea, reported from the western part of the middle Caspian Sea at a depth of 60 m (Logvinenko and Starobogatov 1969).

Turricaspia ? *spica* (Eichwald, 1855)

Fig. 15A–R

- ? *1855 *Paludina spica* m.; Eichwald: 303–304, pl. 10, figs 8–9.
- ? 1887 *Micromelania spica* Eichw. sp. – W. Dybowski: 29–31.
- ? 1888 *Micr.[omelania] spica* Eichw. sp. – W. Dybowski: 78, pl. 1, figs 6a–c, pl. 3, figs 11a–d.
- ? 1917 *Micromelania (Turricaspia) spica* Eichw. – B. Dybowski & Grochmalicki: 16–17, pl. 3, figs 22–27.
- ? 1952 *Micromelania spica* (Eichwald, 1855). – Zhadin: 252–253, fig. 194.
- ? 1992 *Turricaspia spica*. – Anistratenko & Prisyazhniuk: 19, fig. 2d.
- ? 2006 *Turricaspia spica* (Eichwald, 1855). – Kantor & Sysoev: 110, pl. 49, fig. F.
- ? 2009 *Turricaspia* cf. *spica* (Eichwald, 1855). – Filippov & Riedel: 70, 72, 74, 76, figs 4e–f.
- ? 2016 *Turricaspia spica* (Eichwald, 1855). – Vinarski & Kantor: 250.

Material. 1420 specimens (RGM 1309784, RGM 1309785, RGM 1309786, RGM 1309811, RGM 1309812, RGM 1309813, RGM 1310229–1310231, RGM 1310233–1310237, RGM 1310239, RGM 1310240, LV 201501, LV 201502).

Type material. Not traced, most probably in ZIN (Vinarski and Kantor 2016).

Type locality. “Im kapischen Meere, am Ufer der Insel Tschetschnja, vorzüglich nordostwärts von der Insel im Meeresgrunde” (in the Caspian Sea, at the shores of Ostrov Chechen’, especially on the seafloor northeast of the island).

Dimensions. 6.40 × 2.18 mm (RGM 1310237, Fig. 15A–C); 5.93 × 2.27 mm (LV 201501, Fig. 15D–F); 6.13 × 2.19 mm (LV 201502, Fig. 15G–I); 6.36 × 2.21 mm (RGM 1310230, Fig. 15J–L); 6.01 × 1.90 mm (RGM 1310231, Fig. 15M–O); 5.88 × 2.00 mm (RGM 1310233, Fig. 15P); 5.55 × 1.97 mm (RGM 1310236, Fig. 15Q).

Description. Slender elongate shell, with up to nine convex whorls. Protoconch forms small bulbous cap, consisting of 1.3 whorls that measure 365 µm in diameter; surface weakly granulate, spiral striae set in after 0.5 whorls; nucleus is 140 µm wide; P/T boundary marked by thin, sharp axial line. Early teleoconch whorls have low convex profile. Two morphotypes are present: form A is broader, with whorls increasing slightly more in height (thus producing relatively larger last whorl) and little con-

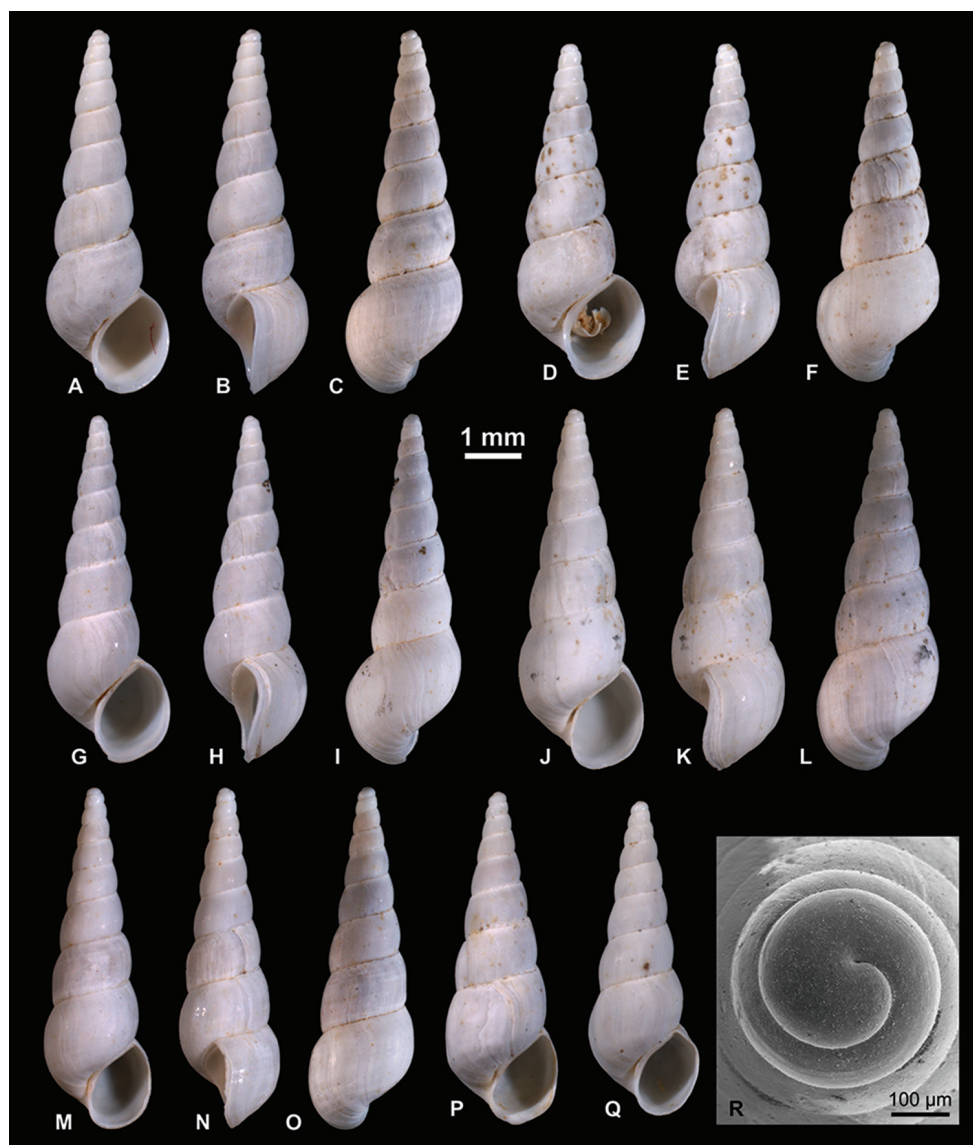


Figure 15. Pyrgulinae. **A–C** *Turricaspia* ? *spica* (Eichwald, 1855), form B, RGM 1310237 **D–F** *T* ? *spica*, transitional form, LV 201501 **G–I** *T* ? *spica*, form B, LV 201502 **J–L** *T* ? *spica*, form A, RGM 1310230 **M–O** *T* ? *spica*, form B, RGM 1310231 **P** *T* ? *spica*, form A, RGM 1310233 **Q** *T* ? *spica*, transitional form, RGM 1310236 **R** *T* ? *spica*, RGM 1309813.

vex whorls; form B is more slender, whorls increase less fast in height in relation to width and whorl profile is stronger and more regularly convex. Both types are linked via intermediates. Generally, whorl profile varies between regularly convex (of varying strength), laterally flattened or bipartite (with near straight-sided upper half and convex lower half; rarely, transition between halves coincides with spiral thread). Suture

is narrow. In some specimens, last whorl is slightly inflated and aperture is expanded. Traces of spiral sculpture, ranging from faint lines to blunt keels of variable number occur on several shells. Aperture expansion and sculpture are found on both morphotypes, as well as in intermediates. Umbilicus mostly covered by inner lip; if open, it is very narrow. Growth lines markedly sigmoidal, with prosocline upper third and opisthocline lower two-thirds.

Discussion. The huge morphological variability with intergrading morphotypes complicates reasonable taxonomic distinctions within this taxon. Moreover, much of the shape variation (especially in later whorls) seems to be a result of shell repair after predator-induced damage.

The variability also hampers linking our material to an existing name. Several species (and varieties) have been introduced for slender elongate, multi-whorled shells from the Caspian Sea. While the sculptured representatives can be fairly well delimited, the smooth-shelled taxa have caused considerable confusion. Particularly challenging are the many small, slender species with pointy apex, moderately to strongly convex whorls and thin peristome. The group includes (aside from *T. spica*): *T. elegantula* (Clessin & W. Dybowski in W. Dybowski, 1887), *T. turricula* (B. Dybowski & Grochmalicki, 1915), *T. nossovi* (Kolesnikov, 1947), *T. concinna* (Logvinenko & Starobogatov, 1969), *T. spasskii* (Logvinenko & Starobogatov, 1969), *T. uralensis* (Logvinenko & Starobogatov, 1969) and *T. astrachanica* (Pirogov, 1971). *Turricaspia lyrata* (B. Dybowski & Grochmalicki, 1915), which was originally introduced as subspecies of *T. spica*, can be well delimited from that group because of its much larger, blunt apex.

A major problem in identifying and discriminating those species is that the concepts applied by later authors occasionally diverge largely from the original perceptions. This especially regards *T. spica* and the species described by B. Dybowski and Grochmalicki (1915). Unfortunately, the types for these species are not known for sure (Kantor and Sysoev 2006, Vinarski and Kantor 2016) and the original descriptions, drawings, and illustrations are mostly insufficient to allow distinction. Beyond that, different traits have been considered as diagnostic by different authors when describing new species, and morphological variability was hardly considered at all.

The identity of *Turricaspia spica* (sensu Eichwald) is dubious. The original description and illustration do not allow distinction from other similar species. The present specimens differ slightly from *T. spica* sensu Kantor & Sysoev, 2006, which is characterized by a faster whorl accretion rate and relatively higher whorls (including the last whorl). In contrast, our material largely fits the concept of *T. spica* as used by B. Dybowski and Grochmalicki (1917). We tentatively classify the Selitrennoye specimens in *Turricaspia spica*, being the oldest available name of the group. Many of the later proposed names might turn out to be junior synonyms. A more in-depth study is required to solve this problematic case.

Distribution. *Turricaspia spica* is endemic to the Caspian Sea. After Logvinenko and Starobogatov (1969), it occurs at a water depth between 0 and 30 m, but those authors applied a different concept of the species.

Hydrobiidae incertae sedis**Genus *Abeskunus* Kolesnikov in Logvinenko & Starobogatov, 1969**

Type species. *Paludina exigua* Eichwald, 1838; by original designation. Caspian Sea, Pleistocene.

Discussion. The genus *Abeskunus* and the species that have been attributed to it have caused considerable confusion. A detailed discussion of the taxonomic and nomenclatural problems associated with *Abeskunus*, considerations on its systematic placement, as well as a description of the type species will be provided in a forthcoming study. Preliminary work confirms classification of the species described below in *Abeskunus*.

***Abeskunus brusinianus* (Clessin & W. Dybowski in W. Dybowski, 1887)**

Fig. 16A–I

*1887 *Zagrabica Brusiniana* nob.; W. Dybowski: 52–53.

1888 *Zagrabica Brusiniana* n. sp. – W. Dybowski: 79, pl. 2, fig. 7.

1952 *Zagrabica brusiniana* W. Dyb., 1888. – Zhadin: 235, fig. 166 [partim].

1969 *Pseudamnicola* [(*Abeskunus*)] *brusiniana* (Cless. et W. Dyb.). – Logvinenko & Starobogatov: 381, fig. 367 (15).

2006 *Pseudamnicola brusiniana* (Clessin et W. Dybowski in W. Dybowski, 1888). – Kantor & Sysoev: 114, pl. 51, fig. J.

2016 *Pseudamnicola brusiniana* (Clessin et W. Dybowski in W. Dybowski, 1888). – Vinarski & Kantor: 222.

Material. 489 specimens (RGM 1309834, RGM 1309842, RGM 1310194, LV 201505).

Type material. Not traced.

Type locality. “Kaspi-See” (Caspian Sea, no further details mentioned).

Dimensions. 4.12 × 3.82 mm (RGM 1309834, Fig. 16A, F); 4.15 × 3.65 mm (LV 201505, Fig. 16B, C, I); 3.00 × 2.74 mm (RGM 1309842, Fig. 16D, E, G, H); 4.14 × 3.42 mm; 4.15 × 3.53 mm; 4.34 × 3.79 mm; 4.39 × 3.87 mm; 4.59 × 3.68 mm.

Description. Shell broadly conical, comprising up to 4.5 whorls. Protoconch broadly domical, with almost immersed initial part; consists of 1.25 whorls, measures 525 µm in diameter; nucleus is ca. 160 µm wide; nucleus surface covered with irregular elongated wrinkles; protoconch surface wrinkled, bearing thin, irregular spiral grooves on first third, passing over irregular pattern of faint spiral grooves and wrinkles into numerous, regularly parallel spiral furrows on last third; P/T transition without growth rim, marked by onset of growth lines. Teleoconch whorls highly convex, with maximum convexity in adapical half, producing slightly stepped spire. Last whorl attains 77–85% of shell height. Aperture drop-shaped, slightly inclined, with marked adapical notch at contact to penultimate whorl. Outer peristome margin not or slightly thickened, columellar and parietal margins weakly thickened; peristome slightly expanded towards columella (pro-

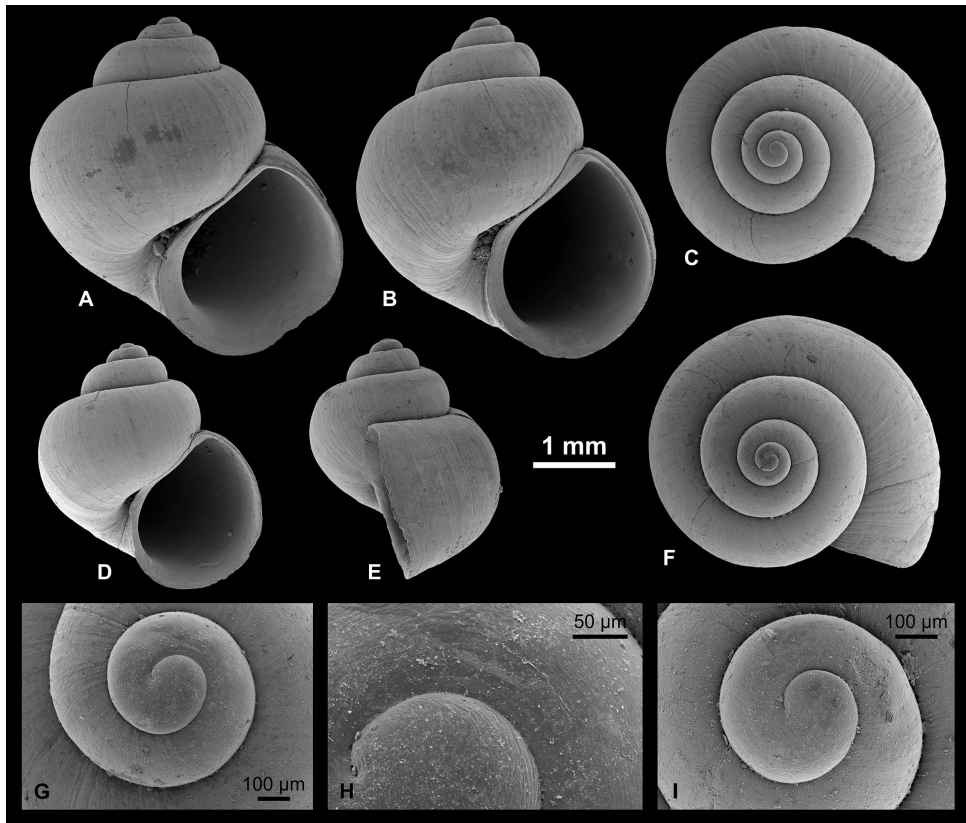


Figure 16. Hydrobiidae incertae sedis. **A, F** *Abeskunus brusinianus* (Clessin & W. Dybowski in W. Dybowski, 1887), RGM 1309834 **B, C, I** *A. brusinianus*, LV 201505 **D, E, G, H** *A. brusinianus*, RGM 1309842.

truding towards umbilicus in lateral view) and strongly towards base; weakly sinuate in lateral view, with broad but weak adapical protrusion and straight-sided abapical part. Umbilicus narrow, slit-like. Prosocline growth lines cover shell surface.

Discussion. The species differs from the type species *A. exiguus* (Eichwald, 1838) in the conical shell, the taller spire, the less inflated last whorl, and the distinct umbilicus. *Abeskunus brusinianus michelae* Tadjalli-Pour, 1977 is much more globular than *A. brusinianus*. The latter species strongly reminds of and might be conspecific with *A. exiguus*. *Pseudamnicola depressispira* Logvinenko & Starobogatov, 1969, which these authors also included in the subgenus *Abeskunus*, differs from the presumed congeners in the valvatoid shape with very wide umbilicus and small but distinct riblets.

Pseudamnicola? brusiniana Pavlović, 1903 is a junior secondary homonym of this species, for which Neubauer et al. (2015b) introduced *Pseudamnicola? babindolensis* as replacement name. Because of the revised classification, *P? brusinianus* [sic] Pavlović is reinstated as valid, with *P? babindolensis* as its junior objective synonym (ICZN 1999, Art. 59.4).

Distribution. Endemic to the Caspian Sea, in the southern and middle part at a depth of >250 m (Logvinenko and Starobogatov 1969, Parr et al. 2007).

Non-indigenous species

In addition to the Pontocaspian elements, six taxa including ubiquitous Palearctic species were identified. They all occur in low numbers and differ from Pontocaspian species in their preservation state. Shells of larger taxa (*Valvata*, *Esperiana*, and *Lithoglyphus*) are eroded and suggest transport. The smaller planorbids are better preserved but differ in their orange color indicating that they were not deposited along with the whitish shells of the Pontocaspian residents. Moreover, all six taxa are typical freshwater dwellers (e.g., Welter-Schultes 2012). They probably derive from rivers flowing into the northern Caspian Sea (Fig. 1).

Anisus cf. *spirorbis* (Linnaeus, 1758) (Fig. 17A–F). – 13 juvenile to semi-adult specimens have been found. They match *A. spirorbis* as depicted by Glöer (2002) and Welter-Schultes (2012) in size, the regularly striated surface, the slightly overlapping whorls, and the weakly asymmetrical lateral profile. However, whorls expand in relative width a bit more rapidly in the Selitrennoye specimens, which is why we only tentatively assign our material to this species.

Planorbis cf. *planorbis* (Linnaeus, 1758) (Fig. 17G–L). – Two juvenile specimens and one semi-adult are available, showing either a distinct or intentions of a keel on the periphery of the apical side, a feature typical of *P. planorbis* (Glöer 2002, Welter-Schultes 2012). In addition, shell size, whorl expansion and lateral profile fit well to this species. Since no adult specimen with fully developed keel have been found, we attribute our specimens to this species provisionally.

Bithynia sp. (Fig. 17M). – Four juvenile specimens are available, consisting of the protoconch and about one teleoconch whorl; the operculum is in-situ preserved in all specimens. The classification is based on the presence and shape of the operculum, the characteristics of the protoconch, as well as the shape of the aperture, all of which are features typical of the genus *Bithynia* (compare Glöer et al. 2005, Neubauer et al. 2016b).

Esperiana esperi (Férussac, 1823) (Fig. 17N). – The single fragmentary specimen matches well the specimens illustrated by Welter-Schultes (2012). The similar and often co-occurring *Microcolpia daudebartii acicularis* (Férussac, 1823) is more elongate and lacks the color pattern (Glöer 2002, Welter-Schultes 2012). In the Russian literature, *E. esperi* is commonly listed as member of the genus *Fagotia* Bourguignat, 1884 (e.g., Starobogatov et al. 2004, Vinarski and Kantor 2016), which is, however, invalid as a junior objective synonym of *Esperiana*. Starobogatov et al. (1992, 2004) listed numerous species of *Fagotia* for extant European water bodies and categorized them into several subgenera. All of them are presently considered junior synonyms of *Esperiana* and *E. esperi*, respectively (for a complete synonymy list, see Vinarski and Kantor, 2016). *Fagotia roseni* Starobogatov in Starobogatov et al., 1992 from Quaternary deposits of Georgia also ranges within the variability of *E. esperi* and is herewith considered synonymous.

Lithoglyphus naticoides (Pfeiffer, 1828) (Fig. 17O). – The shape of the sole specimen ranges well within the large morphological variability of Recent *L. naticoides* (e.g., Glöer 2002). Late Pleistocene *Lithoglyphus jahni* Urbański, 1975 has a relatively taller



Figure 17. Non-indigenous species. **A–D** *Anisus* cf. *spirorbis* (Linnaeus, 1758), LV 201503 **E–F** *A.* cf. *spirorbis*, RGM 1309801 **G–I** *Planorbis* cf. *planorbis* (Linnaeus, 1758), LV 201504 **J–L** *P.* cf. *planorbis*, RGM 1309835 **M** *Bithynia* sp., juvenile, RGM 1309853 **N** *Esperiana esperi* (Férussac, 1823), RGM 1309792 **O** *Lithoglyphus naticoides* (Pfeiffer, 1828), RGM 1309832 **P** *Valvata piscinalis* (Müller, 1774), RGM 1310249. Scale bar equals 1 mm unless indicated otherwise. Note that all Planorbidae are figured at the same scale to facilitate comparison.

conical shell and elevated spire (Kondrashov 2007). Coeval *Lithoglyphus pyramidatus* Möllendorf, 1873 is more elongate and lacks the stepped spire (Glöer 2002).

Valvata piscinalis (Müller, 1774) (Fig. 17P). – The eight, partly fragmented and corroded shells correspond well to Recent representatives of the species (Glöer 2002, Welter-Schultes 2012). Several of the *Valvata* species listed for the Volga delta region by Starobogatov et al. (1994, fig. 2) might be synonymous with this species. A conclusion on that matter requires examination of the material, which is unavailable to us.

Discussion

The current work provides a first insight into the magnitude of endemic Caspian gastropod biodiversity. The gastropod fauna of Selitrennoye is composed of 24 species, 16 of which are Pontocaspian endemic species and 15 exclusively Caspian. Six species are considered to be non-indigenous based on the combination of a truly freshwater autecology, a general wide spread palearctic distribution and a slightly different preservation from the bulk of the well preserved Caspian lacustrine species in the material. The non-Caspian gastropods are low in numbers, and we suspect they may have either floated into the Caspian Sea during periods of high river discharge or, more likely, were mixed in from underlying sediment layers through bioturbation. The Selitrennoye fauna was deposited in open lacustrine settings at a paleosalinity of approximately 10–11 psu as suggested by the general composition of the mollusk fauna (Yanina 2012). The presence of paired bivalves in the same sample indicates the in-situ character of the fauna. The shelly levels are located around 17 m b.s.l., and late Khazarian maximum sea levels are estimated as 10 m b.s.l. The presence of very sandy sediments with lenses suggests deposition above storm wave base. Altogether, this might translate into a sea floor at about 7 m water depth. The settings can be best compared with the present-day southernmost part of the northern Caspian Basin.

The taxonomy and systematics of Caspian gastropods is very much in need of an update. The abundant and well-preserved material presented here has given an indication about the generic placements of species and the magnitude of species richness. When compared to the latest inventory of Caspian gastropods by Vinarski and Kantor (2016), who presented 92 species for the entire Caspian Sea, our numbers (that represent a single locality) are still rather low. The synonymization of species we propose points in general to lower species numbers for Caspian gastropod faunas as reported before. However, the possibility exists that some of the species considered synonyms are sibling species. In order to test for that, we will require extensive new living material to perform combined genetic and morphometric analyses. In recent expeditions in the coastal areas of Azerbaijan and in the Caspian territory of Kazakhstan, we failed to detect living endemic Pyrgulinae gastropod species. All Caspian endemics are suffering badly from invasive species that have caused a total turnover of the fauna during the 20th century (Kosarev and Yablonskaya 1995, Grigorovich et al. 2003, Orlova et al. 2005, Therriault et al. 2004, Riedel et al. 2006, Heiler et al. 2010, Albrecht et

Table 1. List of species recovered from the late Khazarian deposits at Selitrennoye, with indication of their status as endemic to the Caspian Sea and the Pontocaspian region as a whole.

Species	Family	No. of specimens	Caspian endemic	Pontocaspian endemic
<i>Theodoxus pallasi</i> Lindholm, 1924	Neritidae	294		
<i>Ulskia ulskii</i> (W. Dybowski & Clessin in W. Dybowski, 1888)	Hydrobiidae	19	x	x
<i>Andrusovia brusinai</i> Starobogatov, 2000	Hydrobiidae	39	x	x
<i>Ecrobia</i> cf. <i>grimmeri</i> (Clessin in W. Dybowski, 1888)	Hydrobiidae	345		
<i>Clessiniola variabilis</i> (Eichwald, 1838)	Hydrobiidae	4867		x
<i>Laevicaspia caspia</i> (Eichwald, 1838)	Hydrobiidae	300	x	x
<i>Laevicaspia cincta</i> (Abich, 1859)	Hydrobiidae	174	x	x
<i>Laevicaspia conus</i> (Eichwald, 1838)	Hydrobiidae	1135	x	x
<i>Laevicaspia kolesnikoviana</i> (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966)	Hydrobiidae	514	x	x
<i>Laevicaspia vinarskii</i> sp. n.	Hydrobiidae	9	x	x
<i>Turricaspia andrussowi</i> (B. Dybowski & Grochmalicki, 1915)	Hydrobiidae	3	x	x
<i>Turricaspia</i> ? <i>dimidiata</i> (Eichwald, 1838)	Hydrobiidae	1	x	x
<i>Turricaspia lyrata</i> (B. Dybowski & Grochmalicki, 1915)	Hydrobiidae	562	x	x
<i>Turricaspia meneghiniana</i> (Issel, 1865)	Hydrobiidae	248	x	x
<i>Turricaspia pulla</i> (B. Dybowski & Grochmalicki, 1915)	Hydrobiidae	186	x	x
<i>Turricaspia pullula</i> (B. Dybowski & Grochmalicki, 1915)	Hydrobiidae	1	x	x
<i>Turricaspia</i> ? <i>spica</i> (Eichwald, 1855)	Hydrobiidae	1420	x	x
<i>Abeskunus brusinianus</i> (W. Dybowski & Clessin in W. Dybowski, 1888)	Hydrobiidae	489	x	x
<i>Valvata piscinalis</i> (Müller, 1774)	Valvatidae	8		
<i>Esperiana esperi</i> (Férussac, 1823)	Melanopsidae	1		
<i>Bithynia</i> sp.	Bithyniidae	4		
<i>Lithoglyphus naticoides</i> (Pfeiffer, 1828)	Lithoglyphidae	1		
<i>Anisus</i> cf. <i>spirorbis</i> (Linnaeus, 1758)	Planorbidae	13		
<i>Planorbis</i> cf. <i>planorbis</i> (Linnaeus, 1758)	Planorbidae	3		

al. 2014). This situation appears to complicate or even make it impossible to follow such an integrated approach. Especially for the genera *Clessiniola*, *Laevicaspia*, and *Turricaspia*, we think devoted taxonomic revisions will be required to assess the number of species and potential presence of siblings.

The present revision does elucidate generic concepts. Even though it is open for further improvement, it will provide a basis for the establishment of evolutionary relationships within genera by comparison with older (Bakunian/Apsheronian) and younger Caspian faunas. By understanding species richness and evolutionary relationships of Caspian faunas, we will be able to document the nature and severity of the Anthropocene biodiversity crisis in this long-lived lake.

Author contributions

FPW and TY conducted field work and collected the material; SV and FPW processed the material; TAN, SV, and FPW identified the species; TAN and FPW wrote the manuscript.

Acknowledgements

We are grateful to Vitaliy V. Anistratenko, Maxim Vinarski, Jan Johan ter Poorten, Anita Eschner, and Yuri Kantor for support during literature research. Maxim Vinarski is moreover thanked for inspection of the collection catalogue of the Zoological Institute of the Russian Academy of Sciences in St. Petersburg. We thank Ronald Pouwer and Marjan Helwerda for assistance in sample sorting. Our sincere thanks also go to Dietrich Kadolsky, Mathias Harzhauser, Peter Glöer, Diana Delicado, and Daniela Esu for sharing taxonomic considerations. Tom Wilke shared information on unpublished molecular data of the Caspian hydrobiids. Ted von Proschwitz and Anna Persson are thanked for their effort in trying to locate Westerlund's type material. Thomas Nichterl helped with Latin translations. The careful reviews by Vitaliy V. Anistratenko and Frank Riedel greatly improved the quality of this work. This paper contributes to the PRIDE Project ("Drivers of Pontocaspian Biodiversity Rise & Demise") funded by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 642973. It also contributes to the FreshGEN Project ("Freshwater systems in the Neogene and Quaternary of Europe: Gastropod biodiversity, provinciality, and faunal gradients") funded by the Austrian Science Fund FWF (project no. P25365-B25). T.A.N. was supported by an Alexander-von-Humboldt Scholarship and a Martin Fellowship granted by Naturalis Biodiversity Center. T.Y. was supported by the Russian Science Foundation (grant no. 16-17-10103).

References

After Anistratenko (2013), the publication dates of W. Dybowski's "Die Gastropoden-Fauna des Kaspischen Meeres" is not 1888 as indicated in the respective journal volume. Issue 1 (pp. 1–64, containing all descriptions) was published in 1887; issues 2 (pp. 65–79, summary and plate captions) and 3 (pls. 1–3) appeared in 1888.

B. Dybowski and Grochmalicki (1917) is a slightly altered version of B. Dybowski and Grochmalicki (1915). That work is a preprint initially destined to be published in the "Annuaire du Musée Zoologique de l'Académie impériale des Sciences de St Petersburg", vol. 20, but it was withdrawn from the volume by the editors. It is nonetheless nomenclaturally available. Since the authors thought their work had remained unpublished, they slightly emended it and re-published it in 1917, re-describing most of the

taxa they introduced in 1915 as new and adding new ones. Despite considerable effort, we were unable to obtain a copy of that rare work.

The publication date of Birshtein et al.'s comprehensive systematic account of the Caspian fauna, including the catalogue of Caspian mollusks by Logvinenko and Starobogatov, is usually given as “1968” and so it says in the book itself. According to Sysoev and Kantor (1992), however, the book was published in April 1969.

- Abich H (1859) Vergleichende chemische Untersuchungen der Wasser des Caspischen Meeres, Urmia- und Van-See's. Mémoires de l'Académie impériale des sciences de St.-Petersbourg, 6e série, Sciences mathématiques, physiques et naturelles 7: 1–57. <https://biodiversitylibrary.org/page/46467180>
- Agusa T, Kunito T, Tanabe S, Pourkazemi M, Aubrey DG (2004) Concentrations of trace elements in muscle of sturgeons in the Caspian Sea. Marine Pollution Bulletin 49(9–10): 789–800. <https://doi.org/10.1016/j.marpolbul.2004.06.008>
- Albers JC (1850) Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet. Enslin, Berlin, 262 pp.
- Albrecht C, von Rintelen T, Sereda S, Riedel F (2014) Evolution of ancient lake bivalves: the Lymnocardiiinae (Cardiidae) of the Caspian Sea. Hydrobiologia 739(1): 85–94. <https://doi.org/10.1007/s10750-014-1908-3>
- Alexenko TL, Starobogatov YaI (1987) Vidy *Caspia* i *Turricaspia* (Gastropoda, Pectinibranchia, Pyrgulidae) Azovo-Chernomorskogo basseyna. Vestnik Zoologii 21(3): 32–38.
- Anan Y, Kunito T, Tanabe S, Mitrofanov I, Aubrey DG (2005) Trace element accumulation in fishes collected from coastal waters of the Caspian Sea. Marine Pollution Bulletin 51(8–12): 882–888. <https://doi.org/10.1016/j.marpolbul.2005.06.038>
- Anistratenko VV (2008) Evolutionary trends and relationships in hydrobiids (Mollusca, Caenogastropoda) of the Azov-Black Sea Basin in the light of their comparative morphology and paleozoogeography. Zoosystematics and Evolution 84(2): 129–142. <https://doi.org/10.1002/zoos.200800001>
- Anistratenko VV (2013) On the taxonomic status of the highly endangered Ponto-Caspian gastropod genus *Caspia* (Gastropoda: Hydrobiidae: Caspiinae). Journal of Natural History 47(1–2): 51–64. <https://doi.org/10.1080/00222933.2012.742934>
- Anistratenko VV, Khaliman IA, Anistratenko OY (2011) Mollyuski Azovskogo morya. Naukova dumka, Kiev, 171 pp.
- Anistratenko VV, Prisyazhniuk VA (1992) Novyye dannyye o mollyuskakh golotsenovykh otlozheniy Chernogo morya na Ukraine. Vestnik Zoologii 5: 15–21.
- Anistratenko VV, Zettler ML, Anistratenko OY (2017) On the taxonomic relationship between *Theodoxus pallasii* and *T. astrachanicus* (Gastropoda: Neritidae) from the Ponto-Caspian region. Archiv für Molluskenkunde 146(2): 213–226. <https://doi.org/10.1127/arch.moll/146/213-226>
- Arconada B, Ramos MA (2006) Revision of the Genus *Islamia* Radoman, 1973 (Gastropoda, Caenogastropoda, Hydrobiidae) on the Iberian Peninsula and Description of Two New Genera and Three New Species. Malacologia 48(1/2): 77–132. <https://biodiversitylibrary.org/page/13115520>

- Bank R (2017) Horatiinae D.W. Taylor, 1966 – MolluscaBase. World Register of Marine Species. <http://molluscabase.org/aphia.php?p=taxdetails&id=1000097> [on 2018-02-01]
- Boeters HD, Glöer P, Georgiev D, Dedov I (2015) A new species of *Caspia* Clessin et W. Dybowski, 1887 (Gastropoda: Truncatelloidea: Hydrobiidae) in the Danube of Bulgaria. *Folia Malacologica* 23: 177–186. <https://doi.org/10.12657/folmal.023.014>
- Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61(1–2): 1–526. <https://doi.org/10.4002/040.061.0201>
- Bourguignat JR (1884) Histoire des mélanien du système européen. *Annales de Malacologie* 2: 1–168. <https://biodiversitylibrary.org/page/16301109>
- Bourguignat JR (1887) Étude sur les noms génériques des petites paludinidées a opercule spirescent suivie de la description du nouveau genre *Horatia*. Tremblay, Paris, 56 pp. <https://doi.org/10.5962/bhl.title.10453>
- Brusina S (1874) Fossile Binnen-Mollusken aus Dalmatien, Kroatien und Slavonien nebst einem Anhang. Actienbuchdruckerei, Agram, 138 pp.
- Brusina S (1882) Le Pyrgulinae dell'Europa orientale. *Bollettino della Società Malacologica Italiana* 7(13–19)[1881]: 229–292. <https://biodiversitylibrary.org/page/39283992>
- Büyükeriç Y, Wesselingh FP (2018) New cockles (Bivalvia: Cardiidae: Lymnocardiinae) from Late Pleistocene Lake Karapınar (Turkey): Discovery of a Pontocaspian refuge? *Quaternary International* 465 (A): 37–45. <https://doi.org/10.1016/j.quaint.2016.03.018>
- Clessin S (1886) Binnenmollusken aus Rumänien. *Malakozoologische Blätter (Neue Folge)* 8: 49–56. <https://biodiversitylibrary.org/page/35594868>
- Cox LR (1960) Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239–261.
- Cuvier G (1795) Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* 2: 433–449.
- De Cristofori G, Jan G (1832) *Catalogus in IV. sectiones divisus rerum naturalium in museo exstantium Josephi De Cristofori et Georgii Jan plurium Acad. Scient. et Societ. Nat. Cur. Sodalium complectens adumbrationem oryctognosiae et geognosiae atque prodromum faunae et floriae Italiae Superioris. Sectio II. Conchyliologia. Pars I. Conspectus methodicus molluscorum. Fasc. 1. Testacea terrestria et fluviatilia. Carmignani, Parma, pp. 1–2 [unnumbered] [Dispositio methodica generum], pp. 1–8 [Conchyliia terrestria et fluviatilia], pp. 1–4 [Mantissa in secundam partem catalogi testaceorum exstantium in collectione quam possident], pp. 1–4 [Excerptum e primo nostre programmate], pp. 1–16 [Conchyliia fossilia]* <https://biodiversitylibrary.org/page/39520781>
- Deshayes GP (1861–1864) Description des animaux sans vertèbres découverts dans le bassin de Paris pour servir de supplément a la description des coquilles fossiles des environs de Paris comprenant une revue générale de toutes les espèces actuellement connues. Tome deuxième. – Texte. Mollusques Acéphalés Monomyaire et Brachiopodes. Mollusques céphalés. Première Partie. J.-B. Baillière et Fils, Paris, 968 pp. <https://biodiversitylibrary.org/page/35623270>

- Doering A (1875) Estudios sistemáticos y anatómicos sobre los moluscos pulmoníferos de los países del Plata. *Periódico Zoológico* 1(3): 129–204.
- Dollfus GF (1912) Recherches critiques sur quelques genre et espèces d'*Hydrobia* vivants ou fossiles. *Journal de Conchyliologie* 59(3): 179–270. <https://biodiversitylibrary.org/page/16299461>
- Dumont HJ (1998) The Caspian Lake: History, biota, structure, and function. *Limnology and Oceanography* 43 (1): 44–52. <https://doi.org/10.4319/lo.1998.43.1.0044>
- Dunker W (1861) Beschreibung neuer Mollusken. *Malakozoologische Blätter* 8: 35–45. <https://biodiversitylibrary.org/page/15919848>
- Dybowski B (1913) Ueber Kaspische Schnecken aus der Abteilung Turricaspiinae subfam. nova, zum Vergleich mit den Turribaicaliinae subfam. nova. *Bulletin de l'Académie Impériale des Sciences de St.-Petersbourg, sixième série* 7 (16): 905–906. <https://biodiversitylibrary.org/page/4183344>
- Dybowski B, Grochmalicki J (1914) Beitrage zur Kenntnis der Baikalmollusken, I. Baicaliidae, 1. Turribaicaliinae subfam. nova. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Pétersbourg* 18 (2): 268–316. <https://biodiversitylibrary.org/page/8508337>
- Dybowski B, Grochmalicki J (1915) Ueber kaspische Schnecken aus der Abteilung “Turricaspiinae” subfam. nova zum Vergleich mit den Turribaikalina nobis. *Petrograd*, 34 pp. [numbered 103–136], 3 pls.
- Dybowski B, Grochmalicki J (1917) Studien über die turmförmigen Schnecken des Baikalsees und des Kaspimeeres (Turribaicaliinae – Turricaspiinae). *Abhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 9 (3): 1–55. <https://biodiversitylibrary.org/page/5550074>
- Dybowski W (1887–1888) Die Gasteropoden-Fauna des Kaspischen Meeres. Nach der Sammlung des Akademikers Dr. K. E. v. Baer. *Malakozoologische Blätter (Neue Folge)* 10(1–3): 1–64 [issue 1, 1887], 65–79 [issue 2, 1888], pl. 1–3 [issue 3, 1888]. <https://biodiversitylibrary.org/page/35483241>
- Eichwald E (1838) Faunae Caspii Maris primitiae. *Bulletin de la Société Impériale des Naturalistes de Moscou* 11 (2): 125–174. <https://biodiversitylibrary.org/page/41342125>
- Eichwald E (1841) Fauna Caspio-Caucasica nonnullis observationibus novis illustravit. *Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou* 7: 1–290. <https://biodiversitylibrary.org/page/33163057>
- Eichwald E (1853) *Lethaea Rossica ou Paléontologie de la Russie, décrite et figurée. Troisième volume. Dernière période.* Schweizerbart, Stuttgart, 533 pp. <https://biodiversitylibrary.org/page/36423437> [text], <https://biodiversitylibrary.org/page/39452522> [plates]
- Erőss ZP, Petrő E (2008) A new species of the valvatiform hydrobiid genus *Hauffenia* from Hungary (Mollusca: Caenogastropoda: Hydrobiidae). *Acta Zoologica Academiae Scientiarum Hungaricae* 54 (2): 159–167.
- Férussac AEJPF d'A d (1823) Monographie des espèces vivantes et fossiles du genre mélanopside, *Melanopsis*, et observations géologiques à leur sujet. *Mémoires de la Société d'Histoire Naturelle de Paris* 1(1): 132–164. <https://biodiversitylibrary.org/page/3555191>

- Filippov A, Riedel F (2009) The late Holocene mollusc fauna of the Aral Sea and its biogeographical and ecological interpretation. *Limnologica* 39(1): 67–85. <https://doi.org/10.1016/j.limno.2008.04.003>
- Forte AM, Cowgill E (2013) Late Cenozoic base-level variations of the Caspian Sea: A review of its history and proposed driving mechanisms. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386: 392–407. <https://doi.org/10.1016/j.palaeo.2013.05.035>
- Frýda J (1998) Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. In: Bieler R, Mikkelsen PM (Eds) 13th International Malacological Congress, Abstracts. Washington, DC, 108.
- Glöer P (2002) Die Tierwelt Deutschlands, 73. Teil: Die Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung. ConchBooks, Hackenheim, 327 pp.
- Glöer P, Falniowski A, Szarowska M (2005) *Bithynia leachii* (Sheppard 1823) and *B. troschelii* (Paasch 1842), two distinct species? *Heldia* 6: 49–56.
- Golikov AN, Starobogatov YaI (1966) Ponto-kaspiyskiy bryukhonogiye mollyuski v Azovo-Chernomorskom bassejne. *Zoologicheskii Zhurnal* 45 (3): 352–362.
- Golikov AN, Starobogatov YaI (1975) Systematics of prosobranch gastropods. *Malacologia* 15 (1): 185–232.
- Gorthner A (1994) What is an ancient lake? In: Martens K, Goddeeris B, Coulter G (Eds) Speciation in Ancient Lakes. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie* 44 : 97–100.
- Gray JE (1840) Shells of molluscous animals. In: Synopsis of the contents of the British Museum (42th edn). G. Woodfall, London, 105–152.
- Grigorovich IA, Theriault TW, MacIsaac HJ (2003) History of aquatic invertebrate invasions in the Caspian Sea. *Biological Invasions* 5: 103–115. <https://doi.org/10.1023/A:1024050824073>
- Grimm OA (1876) Kaspiyskoye more i yego fauna. Tetrad' 1. Trudy Aralo-Kaspiyskoy Ekspeditsii 2: 1–168. http://www.cawater-info.net/library/rus/hist/2_grimm.pdf
- Grimm OA (1877) Kaspiyskoye more i yego fauna. Tetrad' 2. Trudy Aralo-Kaspiyskoy Ekspeditsii 2(2): 1–105. http://www.cawater-info.net/library/rus/hist/2_grimm.pdf
- Haase M, Naser MD, Wilke T (2010) *Ecrobia grimmeri* in brackish Lake Sawa, Iraq: indirect evidence for long-distance dispersal of hydrobiid gastropods (Caenogastropoda: Rissooidea) by birds. *Journal of Molluscan Studies* 76: 101–105. <https://doi.org/10.1093/mollus/eyp051>
- Heiler KCM, Nahavandi N, Albrecht C (2010) A New Invasion Into an Ancient Lake – The Invasion History of the Dreissenid Mussel *Mytilopsis leucophaeata* (Conrad, 1831) and Its First Record in the Caspian Sea. *Malacologia* 53 (1): 185–192. <https://doi.org/10.4002/040.053.0112>
- ICZN (1999) International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, London, 306 pp. <http://www.nhm.ac.uk/hosted-sites/iczn/code/index.jsp>
- Issel A (1865) Catalogo dei molluschi raccolti dalla missione italiana in Persia aggiuntavi la descrizione delle specie nuove o poco note. Stamperia Reale, Torino, 55 pp. <http://magtecafi-ese.inera.it/unifi/opac/unifi/scheda.jsp?pid=mag:13023>

- Issel A (1866) Catalogo dei molluschi raccolti dalla missione italiana in Persia aggiuntavi la descrizione delle specie nuove o poco note. Memorie della Reale accademia delle scienze di Torino, 2. serie 23: 387–439. <https://biodiversitylibrary.org/page/31197934>
- Kantor YuI, Sysoev AV (2005) Katalog mollyuskov Rossii i sopredel'nykh stran. KMK Scientific Press, Moscow, 627 pp.
- Kantor YuI, Sysoev AV (2006) Morskiye i solonovatovodnyye bryukhonogiye mollyuski Rossii i sopredel'nykh stran: illyustrirovannyi katalog. KMK Scientific Press, Moscow, 372 pp., 140 pls.
- Kantor YuI, Vinarski MV, Schileyko AA, Sysoev AV (2010) Catalogue of the Continental Mollusks of Russia and Adjacent Territories. Version 2.3.1. http://www.ruthenica.com/documents/Continental_Russian_molluscs_ver2-3-1.pdf
- Kolesnikov VP (1947) Tablitsa dlya opredeleniya kaspiyskikh gastropod. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel Geologicheskiiy 22(1): 105–112.
- Kondrashov PE (2007) New gastropod species from the Pleistocene of the Upper Don basin. Paleontological Journal 41 (5): 513–519. <https://doi.org/10.1134/S0031030107050061>
- Kosarev AN, Yablonskaya EA (1994) The Caspian Sea. SPB Academic Publishing, The Hague, 259 pp.
- Krynicky AJ (1837) Conchyliia tam terrestria, quam fluviatilia et e maribus adjacentibus Imperii Rossici indigena, quae pro mutua offeruntur historiae naturalis cultoribus commutatione. Bulletin de la Société Impériale des Naturalistes de Moscou 10(2): 50–64. <https://biodiversitylibrary.org/page/5521585>
- Lehner B, Döll P (2004) Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology 296(1–4): 1–22. <https://doi.org/10.1016/j.jhydrol.2004.03.028>
- Lindholm VA (1922) Miscellaneous notes on palaearctic land and freshwater Mollusks. Ezhegodnik Zoologicheskogo Muzeya Imperatorskoy Akademii Nauk 23(3–4): 304–320. <https://biodiversitylibrary.org/page/8483531>
- Lindholm VA (1924) K nomenklature nekotorykh kaspiyskikh gastropod. Russkiy Gidrobiologicheskiiy Zhurnal 3 (1–2): 32–34.
- Lindholm VA (1925) Beitrag zur Systematik und Nomenklatur der Familie Enidae (Buliminidae). Archiv für Molluskenkunde 57: 23–41. https://www.zobodat.at/pdf/Archiv-fuer-Molluskenkunde_57_0023-0041.pdf
- Lindholm VA (1930) Drei interessante Wasserschnecken (Gastropoda) aus dem westlichen Turkestan. Doklady Akademii Nauk SSSR 1929: 311–314.
- Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius, Holmiae, 824 pp. <https://biodiversitylibrary.org/page/726886>
- Logvinenko BM, Starobogatov YaI (1969) Mollusca. In: Birshtein YaA, Vinogradov LG, Kondakov NN, Kuhn MS, Astakhova TV, Romanova NN (Eds) Atlas bespozvonochnykh Kaspiyskogo morya. Pishchevaya Promyshlennost (Vsesoyuznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozyaistva i Okeanografii), Moskva, 308–385.
- Milashevich KO (1908) Mollyuski, sobrannyye vo vremya ekskursii S.A. Zernova na minonostse No. 264 na r. Dunay s 28 iyunya po 3 iyulya 1907 goda. Bulletin de l'Académie Impériale des Sciences de St.-Petersbourg, sixième série 2(12): 991–996.

- Möllendorff Ov (1873) Beiträge zur Fauna Bosniens. Inauguraldissertation, Görlitz. <https://biodiversitylibrary.org/page/12924443>
- Montfort PDd (1810) Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Tome second. Schoell, Paris, 676 pp. <https://biodiversitylibrary.org/page/11065017>
- Nalivkin DV (1914) Mollyuski gory bakinskogo yarusa. Trudy Geologicheskogo Komiteta, novaya seriya 116: 1–32.
- Neubauer TA, Georgopoulou E, Harzhauser M, Mandic O, Kroh A (2016a) Predictors of shell size in long-lived lake gastropods. Journal of Biogeography 43(10): 2062–2074. <https://doi.org/10.1111/jbi.12777>
- Neubauer TA, Harzhauser M, Georgopoulou E, Kroh A, Mandic O (2015a) Tectonics, climate, and the rise and demise of continental aquatic species richness hotspots. Proceedings of the National Academy of Sciences of the United States of America 112(37): 11478–11483. <https://doi.org/10.1073/pnas.1503992112>
- Neubauer TA, Kroh A, Harzhauser M, Georgopoulou E, Mandic O (2015b) Taxonomic note on problematic Neogene European freshwater Gastropoda. Annalen des Naturhistorischen Museums in Wien, Serie A 117: 95–100. http://verlag.nhm-wien.ac.at/pdfs/117A_095100_Neubauer.pdf
- Neubauer TA, Mandic O, Harzhauser M (2016b) The freshwater mollusk fauna of the Middle Miocene Lake Drniš (Dinaride Lake System, Croatia): a taxonomic and systematic revision. Austrian Journal of Earth Sciences 108(2): 15–67. <https://doi.org/10.17738/ajes.2015.0013>
- Neumayr M (1869) Beiträge zur Kenntniss fossiler Binnenfaunen. Jahrbuch der k. k. geologischen Reichsanstalt 19: 355–382. <https://biodiversitylibrary.org/page/36221771>
- Orlova MI, Muirhead JR, Antonov PI, Shcherbina GKh, Starobogatov YaI, Biochino GI, Theriault TW, MacIsaac HJ (2005) Range expansion of quagga mussels *Dreissena rostriformis bugensis* in the Volga River and Caspian Sea basin. Aquatic Ecology 38(4): 561–573. <https://doi.org/10.1007/s10452-005-0311-6>
- Parr TD, Tait RD, Maxon CL, Newton III FC, Hardin JL (2007) A descriptive account of benthic macrofauna and sediment from an area of planned petroleum exploration in the southern Caspian Sea. Estuarine, Coastal and Shelf Science 71(1–2): 170–180. <https://doi.org/10.1016/j.ecss.2006.07.018>
- Pavlović PS (1903) Građazapoznavanje tercijara u Staroj Srbiji. Annales Géologiques de la Péninsule Balkanique 6(1): 155–189. <https://archive.org/stream/geoloshkianalib00zavogoog#page/n176/mode/2up>
- Perty JAM (1833) Delectus animalium articulorum, quae in itinere per Brasiliam annis MDCCCXVII–MDCCCXX [1817–1820] jussu et auspiciis Maximiliani Josephi I Bavariae Regis augustissimi peracto, collegerunt Dr. J. B. de Spix et Dr. C. F. Ph. de Martius. Vol. 3. Friedrich Fleischer, Monachii, 224 pp., pl. 25–40. <https://biodiversitylibrary.org/page/47586617>

- Pfeiffer C (1828) Naturgeschichte deutscher Land- und Süsswasser-Mollusken. Dritte Abtheilung. Landes-Industrie-Comptoir, Weimar, 84 pp.
- Pirogov VV (1971) O nakhozhdenii novogo vida mollyuska iz roda *Pyrgula* Crist. et Jan. v avandel'tye reki Volgi. Trudy Astrakhanskogo Zapovednika imeni V.I. Lenina 13: 249–253.
- Poey F (1852) Introduccion a los Ciclostomas con generalidades sobre los moluscos gastropodos y particularmente sobre los terrestres operculados. Memorias sobre la historia natural de la isla de Cuba 1(8): 77–96. <https://biodiversitylibrary.org/page/2524896>
- Pollonera C (1898) Intorne ad alcune Conchiglie del Friuli. Bollettino dei Musei di Zoologi ed Anatomia comparata della Università di Torino 13: 1–4.
- Ponder WF (1984) A review of the Genera of the Rissoidae (Gastropoda: Mesogastropoda: Rissoacea). Records of the Australian Museum Supplement 4: 1–221. https://australian-museum.net.au/uploads/journals/16835/100_complete.pdf
- Popov SV, Shcherba IG, Ilyina LB, Nevesskaya LA, Paramonova NP, Khondkarian SO, Magyar I (2006) Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 238(1–4): 91–106. <https://doi.org/10.1016/j.palaeo.2006.03.020>
- Radoman P (1973) New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. Prirodnjacki Muzej u Beogradu, Posebna Izdanja 32: 3–30.
- Rafinesque CS (1815) Analyse de la nature ou tableau de l'univers et des corps organisés. Privately published by author, Palermo, 223 pp. <http://gallica.bnf.fr/ark:/12148/bpt6k98061z>
- Riedel F, Audzijonyte A, Mugue N (2006) Aliens Associating with Caspian Sea Endemic Bivalves. Biological Invasions 8(5): 1067–1071. <https://doi.org/10.1007/s10530-005-5920-4>
- Riedel F, Healy JM, Röpsdorf P, Sitnikova TYa (2001) Ecology, Shell Morphology, Anatomy and Sperm Ultrastructure of Caenogastropod *Pyrgula annulata*, with a Discussion of the Relations between the 'Pyrgulidae' and Caspian and Baikalian Rissoidae. Limnologica 31: 289–302. [https://doi.org/10.1016/S0075-9511\(01\)80031-1](https://doi.org/10.1016/S0075-9511(01)80031-1)
- Schultze FTS (1826) Catalog der Conchylien-Sammlung des verstorbenen Herrn Ober-Einnehmers Freiherrn von der Malsburg, in deren Besitz sich jetzt befindet der Herr Kammerherr Baron v. d. Malsburg zu Escheberg bei Cassel in Cur-Hessen. Berlin, 199 pp.
- Shishkoedova OS (2010) Pervaya nakhodka mollyuskov roda *Caspihydrobia* (Mollusca: Gastropoda) v Chelyabinskoy oblasti. In: Ecology: from the southern mountains to the northern seas. Materials of the young scientists' meeting, 19–23 April, 2010, Yekaterinburg. Goschitsky Publisher, Yekaterinburg, 210–213.
- Shkatova VK (2010) Paleogeography of the Late Pleistocene Caspian Basins: Geochronometry, paleomagnetism, paleotemperature, paleosalinity and oxygen isotopes. Quaternary International 225: 221–229. <https://doi.org/10.1016/j.quaint.2009.05.001>
- Sinzov I (1896) Beschreibung einiger Arten neogener Versteinerungen, welche in den Gouvernements von Cherson und Bessarabien aufgefunden wurden. Zapiski novorossiiskoe obshchestvo estestvoispytatelei 21: 39–88. [In Russian]
- Sitnikova TYa, Starobogatov YaI (1999) Novyye rod semeystva Pyrgulidae (Gastropoda, Pectinibranchia) iz presnykh rod Azovo-Chernomorskogo basseyna (v svyazi s voprosom o Ponto-Kaspiyskikh vidakh v Azovo-Chernomorskogom basseyne). Zoologicheskii Zhurnal 78(2): 158–163.

- Sitnikova TYa, Starobogatov YaI, Anistratenko VV (1992) Anatomiya i sistematicheskoye polozheniye nekotorykh melkikh Pectinibranchia (Mollusca, Gastropoda) fauny Yevropy. Vestnik Zoologii 6: 3–12.
- Starobogatov YaI (1970) Fauna mollyuskov i zoogeographicheskoye rayonirovaniye kontinental'nykh vo do emov zemnogo shara [The mollusk fauna and zoogeographical regionalisation of continental waterbodies of the Earth]. Nauka, Leningrad, 372 pp.
- Starobogatov YaI (2000) Caspian endemic genus *Andrusovia* (Gastropoda Pectinibranchia Horatiidae). Ruthenica 10(1): 37–42.
- Starobogatov YaI, Alexenko TL, Levina OV (1992) Rody *Fagotia* i *Microcolpia* (Gastropoda Pectinibranchia Melanopsidae) i ikh predstaviteli v sovremennoj faune. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel biologicheskoy 97(3): 57–72.
- Starobogatov YaI, Filchakov VA, Antonova LA, Pirogov VV (1994) Novyye dannyye o mollyuskakh i vysshikh rakoobraznykh delty Volgi. Vestnik Zoologii 4–5: 8–12.
- Starobogatov YaI, Prozorova LA, Bogatov VV, Sayenko EM (2004) Mollyuski. In: Tsalolikhin SJ (Ed.) Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territoriy. T. 6. Mollyuski, Polikhety, Nemertiny. Izdatel'stvo "Nauka", St. Petersburg, 9–491.
- Stimpson W (1865) Researches upon the Hydrobiinae and allied forms: chiefly made from materials in the Museum of the Smithsonian Institution. Smithsonian Miscellaneous Collections 7: 1–59.
- Strand E (1928) Miscellanea nomenclatorica zoologica et palaeontologica. I–II. Archiv für Naturgeschichte, Abteilung A 92(8): 30–75.
- Svitoch AA (2008) The Khvalynian Transgression of the Caspian Sea and the New-Euxinian Basin of the Black Sea. Water Resources 35 (2): 165–170. <https://doi.org/10.1134/S0097807808020048>
- Svitoch AA (2012) The Caspian Sea Shelf during the Pleistocene Regressive Epochs. Oceanology 52 (4): 526–539. <https://doi.org/10.1134/S0001437012030113>
- Sysoev AV, Kantor YI (1992) Names of Mollusca introduced by Ya.I. Starobogatov in 1957–1992. Ruthenica 2 (2): 119–159.
- Szarowska M (2006) Molecular phylogeny, systematics and morphological character evolution in the Balkan Rissooidea (Caenogastropoda). Folia Malacologica 14(3): 99–168. <https://doi.org/10.12657/folmal.014.014>
- Szarowska M, Falniowski A (2014) *Horatia* Bourguignat, 1887: is this genus really phylogenetically very close to *Radomaniola* Szarowska, 2006 (Caenogastropoda: Truncatelloidea)? Folia Malacologica 22(1): 31–39. <https://doi.org/10.12657/folmal.022.003>
- Tadjalli-Pour M (1977) Les Mollusques marins des côtes Iraniennes de la Mer Caspienne (Astara-Hachtpar). Journal de Conchyliologie 114(3–4): 87–117.
- Taviani M, Angeletti L, Çagatay MN, Gasperini L, Polonia A, Wesselingh FP (2014) Sedimentary and faunal signatures of the post-glacial marine drowning of the Pontocaspian Gemlik “lake” (Sea of Marmara). Quaternary International 345: 11–17. <https://doi.org/10.1016/j.quaint.2014.05.045>
- Taylor DW (1966) A Remarkable Snail Fauna from Coahuila, México. The Veliger 9(2): 152–228. <https://biodiversitylibrary.org/page/42521795>
- Therriault TW, Docker MF, Orlova MI, Heath DD, MacIsaac HJ (2004) Molecular resolution of the family Dreissenidae (Mollusca: Bivalvia) with emphasis on Ponto-Caspian species,

- including first report of *Mytilopsis leucophaeata* in the Black Sea basin. Molecular Phylogenetics and Evolution 30(3): 479–489. [https://doi.org/10.1016/S1055-7903\(03\)00240-9](https://doi.org/10.1016/S1055-7903(03)00240-9)
- Thiele J (1928) Revision des Systems der Hydrobiiden und Melaniiden. Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere 55: 351–402.
- Totten JG (1834) Description of some new Shells, belonging to the coast of New England. American Journal of Science and Arts 26: 366–369. <https://biodiversitylibrary.org/page/15985663>
- Urbański J (1975) *Lithoglyphus jahni* n. sp. aus den mitteleuropäischen Ablagerungen des Mindel/Riss Interglazials nebst Bemerkungen über den nordbalkanischen *L. fuscus* (C. Pfeiffer 1828) (= *L. pyramidatus* Moellendorf 1873) – (Gastropoda, Prosobranchia, Hydrobiidae). Bulletin de la Société des Amis des Sciences et des Lettres de Poznan 15: 107–111.
- Van Baak CGC, Vasiliev I, Stoica M, Kuiper KF, Forte AM, Aliyeva E, Krijgsman W (2013) A magnetostratigraphic time frame for Plio-Pleistocene transgressions in the South Caspian Basin, Azerbaijan. Global and Planetary Change 103: 119–134. <https://doi.org/10.1016/j.gloplacha.2012.05.004>
- Verduin A (1977) On a remarkable dimorphism of the apices of sympatric closely-related marine gastropod species. Basteria 41(5-6): 91–95.
- Vinarski MV, Kantor Yul (2016) Analytical catalogue of fresh and brackish water molluscs of Russia and adjacent countries. A.N. Severtsov Institute of Ecology and Evolution of RAS, Moscow, 544 pp.
- Vinarski MV, Nekhaev IO, Glöer P, Proschwitz Tv (2013) Type materials of freshwater gastropod species described by C.A. Westerlund and accepted in current malacological taxonomy: a taxonomic and nomenclatorial study. Ruthenica 23(2): 79–108.
- Vinarski MV, Palatov DM, Glöer P (2014) Revision of ‘*Horatia*’ snails (Mollusca: Gastropoda: Hydrobiidae sensu lato) from South Caucasus with description of two new genera. Journal of Natural History 48(37-38): 2237–2253. <https://doi.org/10.1080/00222933.2014.917210>
- Welter-Schultes FW (2012) European non-marine molluscs, a guide for species identification. Planet Poster Editions, Göttingen, 679 pp.
- Wenz W (1926) Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria. W. Junk, Berlin, vol. VII: 1863–2230.
- Wenz W (1938–1944) Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. In: Schindewolf OH (Ed.) Handbuch der Paläozoologie, Band 6. Verlag Gebrüder Bornträger, Berlin, 1639 pp.
- Westerlund CA (1896) Neue centralasiatische Mollusken. Ezhegodnik Zoologicheskogo Muzeya Imperatorskoy Akademii Nauk 1(3): 181–198. <https://biodiversitylibrary.org/page/9006596>
- Westerlund CA (1902a) Methodus dispositionis Conchyliorum extramarinorum in Regione palaeartica viventium, familias, genera, subgenera et stirpes sistens. Rad Jugoslavenske akademije znanosti i umjetnosti 151: 82–139. <http://dizbi.hazu.hr/object/view/km6Jc2154m>
- Westerlund CA (1902b) Malacologische Bemerkungen und Beschreibungen. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 34: 35–47. <https://biodiversitylibrary.org/page/15598774>

- Wilke T, Albrecht C, Anistratenko VV, Sahin SK, Yildirim MZ (2007) Testing biogeographical hypotheses in space and time: faunal relationships of the putative ancient Lake Egirdir in Asia Minor. *Journal of Biogeography* 34: 1807–1821. <https://doi.org/10.1111/j.1365-2699.2007.01727.x>
- Wilke T, Haase M, Hershler R, Liu H-P, Misof B, Ponder W (2013) Pushing short DNA fragments to the limit: Phylogenetic relationships of ‘hydrobioid’ gastropods (Caenogastropoda: Rissooidea). *Molecular Phylogenetics and Evolution* 66: 715–736. <https://doi.org/10.1016/j.ympev.2012.10.025>
- Yanina TA (2013) Biostratigraphy of the Middle and Upper Pleistocene of the Caspian Region. *Quaternary International* 284: 85–97. <https://doi.org/10.1016/j.quaint.2012.02.008>
- Yanina TA (2014) The Ponto-Caspian region: Environmental consequences of climate change during the Late Pleistocene. *Quaternary International* 345: 88–99. <https://doi.org/10.1016/j.quaint.2014.01.045>
- Yanko-Hombach V, Gilbert AS, Panin N, Dolukhanov PM (Eds) (2007) *The Black Sea Flood Question: Changes in Coastline, Climate and Human Settlement*. Springer, Dordrecht, 971 pp. <https://doi.org/10.1007/978-1-4020-5302-3>
- Zettler ML (2007) A redescription of *Theodoxus schultzei* (Grimm, 1877), an endemic neritid gastropod of the Caspian Sea. *Journal of Conchology* 39(3): 245–251.
- Zhadin VI (1952) *Mollyuski presnykh i solonovatykh vod SSSR*. Izdatel'stvo Akademii Nauk SSSR, Moskva, Leningrad, 376 pp.