


A review of the Ponto-Caspian genus *Caspiohydrobia* (Mollusca: Gastropoda: Hydrobiidae)

Обзор видов понто-каспийского рода *Caspiohydrobia* (Mollusca: Gastropoda: Hydrobiidae)


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Abstract. The paper reviews all available information on the species content, distribution and ecology of brackishwater hydrobiid snails belonging to the genus *Caspiohydrobia* Starobogatov, 1970. The annotated list of nominal species with remarks on their taxonomy, nomenclature and distribution is provided as well as photographic images of some type specimens and/or topotypes. In total, the genus includes 31 nominal species distributed almost exclusively within the former Paratethys basin. The lectotype for the species *C. cylindrica* Logvinenko et Starobogatov, 1969 is designated. A short overview of the known habitat preferences of various *Caspiohydrobia* species is provided. We consider *Caspiohydrobia* a genus of Ponto-Caspian origin, whose range extends southwards to Iraq, Iran and Tajikistan and northwards to West Siberia. The actual species content of the genus as well as its generic independence require a further integrative revision, since most of the nominal species of *Caspiohydrobia* are still known from dried shells only and may actually be synonyms of a few (or even a single) species.

Резюме. В статье обобщены все имеющиеся сведения о видовом составе, распространении и экологии солоноватоводных моллюсков рода *Caspiohydrobia* Starobogatov, 1970 (Hydrobiidae). Приведен аннотированный список номинальных видов с замечаниями по их таксономии, номенклатуре и распространению, а также фотографии некоторых типовых экземпляров и/или топотипов. В состав рода входит 31 номинальный вид; распространены они почти исключительно в пределах бывшего бассейна Паратетис. Обозначается лектотип вида *C. cylindrica* Logvinenko et Starobogatov, 1969. Дан краткий обзор известных ареалов различных видов рода *Caspiohydrobia* рассматривается как группа понто-каспийского происхождения, ареал которой простирается на юг до Ирака, Ирана и Таджикистана и на север до Западной Сибири. Фактический видовой состав таксона, а также его родовая самостоятельность требуют интегративно-таксономической ревизии, поскольку большинство номинальных видов *Caspiohydrobia* до сих пор известны только по сухим раковинам и могут фактически быть синонимами нескольких видов (или даже одного).

Key words: brakishwater Gastropoda, taxonomic catalogue, nomenclature, distribution, Ponto-Caspian fauna

Ключевые слова: солоноватоводные Gastropoda, таксономический каталог, номенклатура, распространение, Понто-Каспийская фауна

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Introduction

The Ponto-Caspian Region hosts a unique malacofauna characterised by a high level of endemism and a relatively old age, with many relic genera and species of the Ponto-Caspian gastropods and bivalves being direct descendants of the malacofauna of the Paratethys, a large sea that once spread over a large area from Central Europe to Western Asia. A series of works aimed at reviewing the taxonomic content and biogeographical features of the recent Ponto-Caspian malacofauna (Golikov & Starobogatov, 1966, 1972; Logvinenko & Starobogatov, 1969; Starobogatov, 1970, 1974; Sitnikova & Starobogatov, 1998, 1999; Andreeva & Andreev, 2003; Anistratenko et al., 2011, 2018, 2019, 2020, 2021a; Kijashko, 2013; Wesselingh et al., 2019; Aladin et al., 2022). Currently, this unique endemic malacofauna is under threat of total disappearance, with human activity and biological invasions being the most important driving causes of its ongoing extinction (Lattuada et al., 2019, 2020; Wesselingh et al., 2019; Gogaladze et al., 2021). The conservation efforts, however, are constrained by many factors, including the so-called ‘taxonomic impediment’. The vast majority of the Ponto-Caspian mollusc species were established during the first, purely conchological, period of malacological systematics, when shell features alone served as the basis for species delineation. What is worse, a significant portion of the Ponto-Caspian endemic species have never been found alive, and there are some doubts about their belonging to the recent fauna; it is likely that some of the species are in fact (sub)fossils washed out from Pleistocene or Early Holocene sediments (Anistratenko et al., 2021a, 2022). Another cause of the taxonomic impediment is the lack of knowledge on the identity, variability and distribution of many dozens of nominal species of Ponto-Caspian gastropods and bivalves described in the 19th and first half of the 20th century. In many cases, these species

have not been revised since their description, chiefly due to a lack of anatomical and/or molecular information.

During the last several years, considerable efforts were made to resolve and clarify the problems of taxonomy of the Ponto-Caspian molluscs. Annotated check-lists and catalogues were published (Kijashko, 2013; Vinarski & Kantor, 2016; Wesselingh et al., 2019) alongside with papers focused on systematics of particular taxa (e.g., Neubauer et al., 2018, 2021; Sands et al., 2019; Anistratenko et al., 2021a) and publications on type materials of species endemic to the region (Anistratenko et al., 2018, 2019, 2020, 2021b).

This paper is a direct continuation of this series of publications. The aim of our work is to review and illustrate the nominal species of the Ponto-Caspian genus *Caspiohydrobia* Starobogatov, 1970 of the caenogastropod family Hydrobiidae Stimpson, 1865. This genus has, probably, the broadest native area among the Ponto-Caspian genera of Gastropoda; its representatives are distributed over an area stretching from the Black Sea in the west to Tajikistan in the east (Starobogatov, 1970; Vinarski & Kantor, 2016). In the malacofauna of the former USSR, 30 nominal species have been included to this genus (Vinarski & Kantor, 2016).

The taxonomic status of the genus *Caspiohydrobia* is disputable. In the Russian literature, it has been accepted as a distinct taxon at the rank of genus, classified within the (sub)family Pyrgulinae Brusina, 1882 or, sometimes, Caspiinae B. Dybowski, 1913 of the family Hydrobiidae (Starobogatov, 1970, 1974; Golikov & Starobogatov, 1972; Andreeva, 1987; Sitnikova et al., 1992; Anistratenko & Stadnichenko, 1995; Vinarski & Kantor, 2016). Wesselingh et al. (2019), in their recent revision of the Caspian gastropods, consider *Caspiohydrobia* a junior synonym of the genus *Ecrobia* Stimpson, 1865. The authors suggested even that all thirty nominal species included in *Caspiohydrobia* may represent only intraspecific

forms of the very variable and broadly distributed species *Ecrobia grimmeri* (Clessin in Dybowski, 1887). Vandendorpe et al. (2019) hold the same point of view. However, as Wesselingh et al. (2019: 74) acknowledge, “no molecular data are known to confirm the identity of the Central Asian snails” of this genus. Many nominal species of *Caspiohydrobia*, introduced between 1974 and 1989, with type localities situated in Tajikistan, Kazakhstan and the Aral Sea, wait for their reassessment. Some of them may represent distinct taxa, not identical with *E. grimmeri*. Unfortunately, anatomical information, let alone molecular one, is available for only a few species (e.g., Sitnikova et al., 1992).

The most important taxonomic works on the genus *Caspiohydrobia* are those by Starobogatov & Izzatullaev (1974), Starobogatov & Andreeva (1981), Sitnikova et al. (1992), and Anistratenko & Stadnichenko (1995). Tadjalli-Pour (1980) listed and illustrated the species of this genus (he used the generic name *Pyrgohydrobia* Radoman, 1983) of the Iranian part of the Caspian Sea. Andreeva & Andreev (2003) summarised the available information on *Caspiohydrobia* of the Aral Sea. Kantor & Sysoev (2006) and Vinarski & Kantor (2016) have provided catalogues of the living representatives of this genus, with the former of these two also providing illustrations. Shirokaya et al. (2019) published an illustrated review of gastropod taxa described by the Tajik-Uzbek malacologist Zuvaidullo Izzatullaev, including six species of *Caspiohydrobia* discovered by him in Tajikistan. Izzatullaev (2018) in his monograph presented some data on the distribution and ecology of *Caspiohydrobia* species known from the Central Asian part of the former USSR (with the exception for the Caspian Sea). Izzatullaev (2019) published an annotated list of these species, accompanied by an identification key. Vandendorpe et al. (2019) published some molecular data on *Caspiohydrobia* (= *Ecrobia grimmeri* s. l.) collected from three localities in southern Kazakhstan and Russia. A paper by Andreeva et al. (2020) provides new information on the distribution of *Caspiohydrobia* species in the Caspian Lowland.

The distribution of the recent *Caspiohydrobia* is patchy; the range of the genus is divided in a series of isolated or semi-isolated areas, some of them (Tajikistan, Southern Urals and Transuralia) lie

beyond the former Paratethys, which probably reflect the ways of snail dispersal in the geological past. Table 1 summarises the data on distribution of the recent *Caspiohydrobia*. A few fossil species assigned to this genus were described from the Black Sea (Ilyina et al., 1976; Badzoshvili, 1979) and the Mediterranean (Rust, 1997) regions. They are neither discussed nor illustrated in our paper. Probably, none of these species is closely related with extant *Caspiohydrobia* species from the Ponto-Caspian basin. An in-depth revision of the fossil representatives is required to clarify their current genus allocation (T.A. Neubauer, pers. comm., 21.XI.2022).

The former range of the genus included also the southern part of West Siberia, where subfossil shells of *Caspiohydrobia* were found in lacustrine sediments of the Early Holocene age (Gusakov et al., 2008). Alongside with findings of some Foraminifera and Ostracoda species in the same sediments, these records indicate the former connection between the West Siberian Plain and the Aral Sea, that took place about 6.7 kyr (Gusakov et al., 2011; Riedel et al., 2011).

In this publication, we present an illustrated and annotated review of all recent species of *Caspiohydrobia*, with data on their nomenclature, distribution and type series (where available). We tried to illustrate all extant holotype specimens of *Caspiohydrobia*, except for those described by Starobogatov & Izzatullaev (1974) from Tajikistan. These holotypes were recently illustrated by Shirokaya et al. (2019).

We did not aim to redescribe any nominal species of *Caspiohydrobia*, though at least those described by Kolesnikov (1947) are worthy of such a redescription. Kolesnikov's paper is essentially an identification key, and he did not publish extended descriptions of the new species, which provides only limited morphological information on the new taxa, just enough to make them nomenclaturally available. Kolesnikov (1947) promised to publish the full descriptions of the species established by him in a special monograph on the Caspian Mollusca, but his death in 1948 prevented him from realising this project. Our intention was to summarise the accumulated information about this snail genus and to illustrate all nominal extant species, whereas

Table 1. Distribution of the recent *Caspiohydrobia* species.

Region / basin	Species of <i>Caspiohydrobia</i>	Source
Aral Sea	<u><i>Caspiohydrobia aralensis</i></u> , <u><i>C. behningi</i></u> , <u><i>C. bergi</i></u> , <u><i>C. chrysopsis</i></u> , <u><i>C. conica</i></u> , <u><i>C. convexa</i></u> , <u><i>C. curta</i></u> , <u><i>C. cylindrica</i></u> , <u><i>C. dubia</i></u> , <u><i>C. gemmata</i></u> , <u><i>C. grimmi</i></u> , <u><i>C. husainovae</i></u> , <u><i>C. kazakhstanica</i></u> , <u><i>C. nikitinskii</i></u> , <u><i>C. nikolskii</i></u> , <u><i>C. obrutchevi</i></u> , <u><i>C. oviformis</i></u> , <u><i>C. parva</i></u> , <u><i>C. pavlovskii</i></u> , <u><i>C. sidorovi</i></u> , <u><i>C. sogdiana</i></u> , <u><i>C. subconvexa</i></u> , <u><i>C. tahzhikistanica</i></u>	Andreeva, 1987
Azov and Black Sea (in limans)	<i>Caspiohydrobia convexa</i> , <u><i>C. eichwaldiana</i></u>	Golikov & Starobogatov, 1972; Anistratenko & Stadnichenko, 1995; Anistratenko et al., 2011
Caspian Lowland	<i>Caspiohydrobia aralensis</i> , <i>C. behningi</i> , <i>C. chrysopsis</i> , <i>C. conica</i> , <i>C. convexa</i> , <i>C. cylindrica</i> , <i>C. johanseni</i> , <i>C. oviformis</i> , <i>C. parva</i> , <i>C. sidorovi</i>	Andreeva et al., 2020
Caspian Sea	<u><i>Caspiohydrobia chrysopsis</i></u> , <u><i>C. conica</i></u> , <u><i>C. convexa</i></u> , <u><i>C. curta</i></u> , <u><i>C. cylindrica</i></u> , <u><i>C. dubia</i></u> , <u><i>C. eichwaldiana</i></u> , <u><i>C. gemmata</i></u> , <u><i>C. grimmi</i></u> , <u><i>C. oviformis</i></u> , <u><i>C. parva</i></u> , <u><i>C. subconvexa</i></u> , <u><i>C. turrita</i></u>	Logvinenko & Starobogatov, 1969; Andreeva, 1987; Vinarski & Kantor, 2016
Iraq	<i>“Caspiohydrobia” elata*</i>	Starobogatov, 1970
Northern Kazakhshtan	<i>Caspiohydrobia aralensis</i> , <i>C. behningi</i> , <i>C. bergi</i> , <u><i>C. borealis</i></u> , <u><i>C. husainovae</i></u> , <u><i>C. johanseni</i></u> , <u><i>C. kazakhstanica</i></u> , <u><i>C. nikitinskii</i></u> , <u><i>C. sidorovi</i></u> , <u><i>C. sogdiana</i></u>	Andreeva, 1987
Southern Kazakhstan	<i>Caspiohydrobia aralensis</i> , <i>C. husainovae</i>	Andreeva, 1987
Southern Urals and southern Transuralia	<i>Caspiohydrobia aralensis</i> , <i>C. borealis</i> , <i>C. chrysopsis</i> , <i>C. conica</i> , <i>C. coniformis</i> , <i>C. convexa</i> , <i>C. grimmi</i> , <i>C. husainovae</i> , <i>C. johanseni</i> , <i>C. kazakhstanica</i> , <i>C. nikolskii</i> , <i>C. oviformis</i> , <i>C. sidorovi</i> , <i>C. sogdiana</i>	Shishkoedova, 2011; own data
Southern part of West Siberia (Holocene)	<i>Caspiohydrobia bergi</i> , <i>C. borealis</i> , <i>C. coniformis</i> , <i>C. elongata</i> , <i>C. johanseni</i> , <i>C. kazakhstanica</i> , <i>C. ljaurica</i>	Gusskov et al., 2008
Tajikistan	<u><i>Caspiohydrobia coniformis</i></u> , <u><i>C. elongata</i></u> , <u><i>C. ljaurica</i></u> , <u><i>C. pavlovskii</i></u> , <u><i>C. sogdiana</i></u>	Starobogatov & Izzatullaev, 1974; Shirokaya et al., 2019

Note. Names of species whose type localities are situated in this region/basin are underlined. * Starobogatov (1970) included to the genus *Caspiohydrobia* the species *Paludina elata* Küster, 1852 described from Iraq (Küster, 1852). Its taxonomic identity is unclear; possibly, this species is a synonym of *Ecrobia grimmi*, which is also known from Iraq (Haase et al., 2010) and Iran (Glöer, Pešič, 2012).

the proper taxonomic work, which would result in opinions on the status of particular species, would require a special study based on numerous samples of fixed specimens suitable for molecular and anatomical studies.

The order of species appearance in the annotated catalogue below is geographical, not alphabetical. At first the species with type localities situated in the Black and Caspian seas are characterised. And then the species described from the Aral Sea and other parts of Central Asia are listed. The only nominal species of *Caspiohydrobia* not recorded from the former USSR (*C. elata*) is placed at the end of our catalogue.

Material and methods

The field works for this study were carried out by the senior author, Svetlana Andreeva, in 1978–1992 in the Aral Sea and various areas of northern and central Kazakhstan, where a vast collection of *Caspiohydrobia* spp. and the data on their distribution and ecology were gathered. Another author, Maxim Vinarski, collected *Caspiohydrobia* in the Kushmurun Lake of northern Kazakhstan in October 2002 and in the Enalych Lake, Kurgan Region of Russia in July 2022.

We studied numerous samples of *Caspiohydrobia* kept in the collection of the Zoological Institute

of the Russian Academy of Sciences in St Petersburg, Russia (ZIN, hereafter). This collection contains both type and non-type specimens of virtually all nominal species of this genus, except the extinct ones. Among other, this includes the type series of *Caspiohydrobia* species described by Starobogatov & Izzatullaev (1974), Starobogatov & Andreeva (1981), and Andreeva & Frolova (1989). Unfortunately, Logvinenko & Starobogatov (1969), who described nine nominal species of *Caspiohydrobia* from the Caspian Sea, neither formed type series nor designated holotypes nor indicated the place where the type material is deposited. Thus, the current whereabouts of the type specimens of many of these species remains unknown (Vinarski & Kantor, 2016). The same is true for the type series of species described by Kolesnikov (1947). Nonetheless, during the preparation of this work, we managed to find and study a few previously unknown type specimens of *Caspiohydrobia* species.

Some of the specimens studied during this work origin from the private collections of Svetlana Andreeva and Maxim Vinarski; now these materials are kept in the Laboratory of Macroecology & Biogeography of Invertebrates, St Petersburg State University (LMBI hereafter).

The measurements of shells were made with accuracy to the nearest 0.1 mm according to the standard scheme (Fig. 1R), with six dimensions taken: shell height (SH), shell width (SW), spire height (SpH), body whorl height (BWH), aperture height (AH), and aperture width (AW).

Scanning electron microscopy (SEM) photos of the shells were taken at the Limnological Institute of RAS by means of a Quanta 200 microscope (USA). The macrophotographs were taken at ZIN (the Core Facilities Centre "Taxon") by means of a Nikon SMZ 25 stereomicroscope with a mounted Nikon DS-Ri2 digital camera.

Systematics

Class **Gastropoda**

Family **Hydrobiidae** Stimpson, 1865

Genus ***Caspiohydrobia*** Starobogatov, 1970

Caspiohydrobia Starobogatov, 1970: 31, 279.

Type species: *Pyrgohydrobia eichwaldiana* Golikov et Starobogatov, 1966 (by original designation).

1. ***Caspiohydrobia eichwaldiana*** (Golikov et Starobogatov, 1966) (Figs 1A, B)

Pyrgohydrobia eichwaldiana Golikov & Starobogatov, 1966: 353, fig. 1(4); Tajalli-Pour, 1980: pl. 17, figs 3, 4.

Caspiohydrobia eichwaldiana Golikov & Starobogatov, 1972: 98, pl. 2, fig. 13; Anistratenko & Stadnichenko, 1995: 109, fig. 87; Kantor & Sysoev, 2006: 91, pl. 43J; Anistratenko et al., 2011: 82, fig. III, 10; Vinarski & Kantor, 2016: 225.

Hydrobia ventrosa var. *evanescens* Kolesnikov, 1947: 106, fig. 5 (non *Hydrobia evanescens* De Guerne, 1880).

Paludina pusilla Eichwald, 1838: 219 (non Brongniart, 1810 nec Basterot, 1825).

Litorinella acuta sensu Eichwald, 1855: 303 (non *Cylostoma acutum* Draparnaud, 1801).

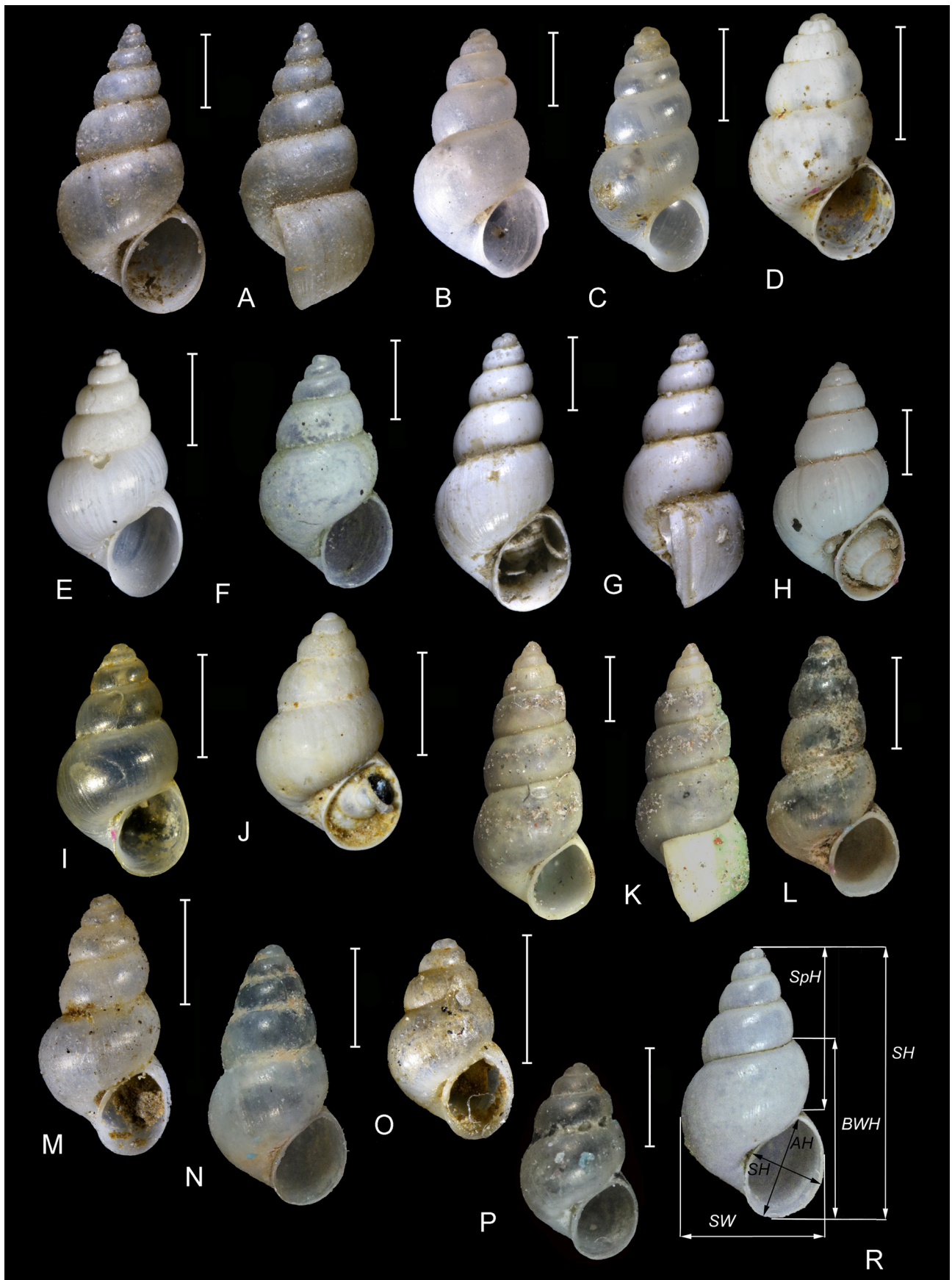
Type locality: Ukraine, Kuyalnik liman near Odessa (ca 46°34'30"N 30°44'30"E).

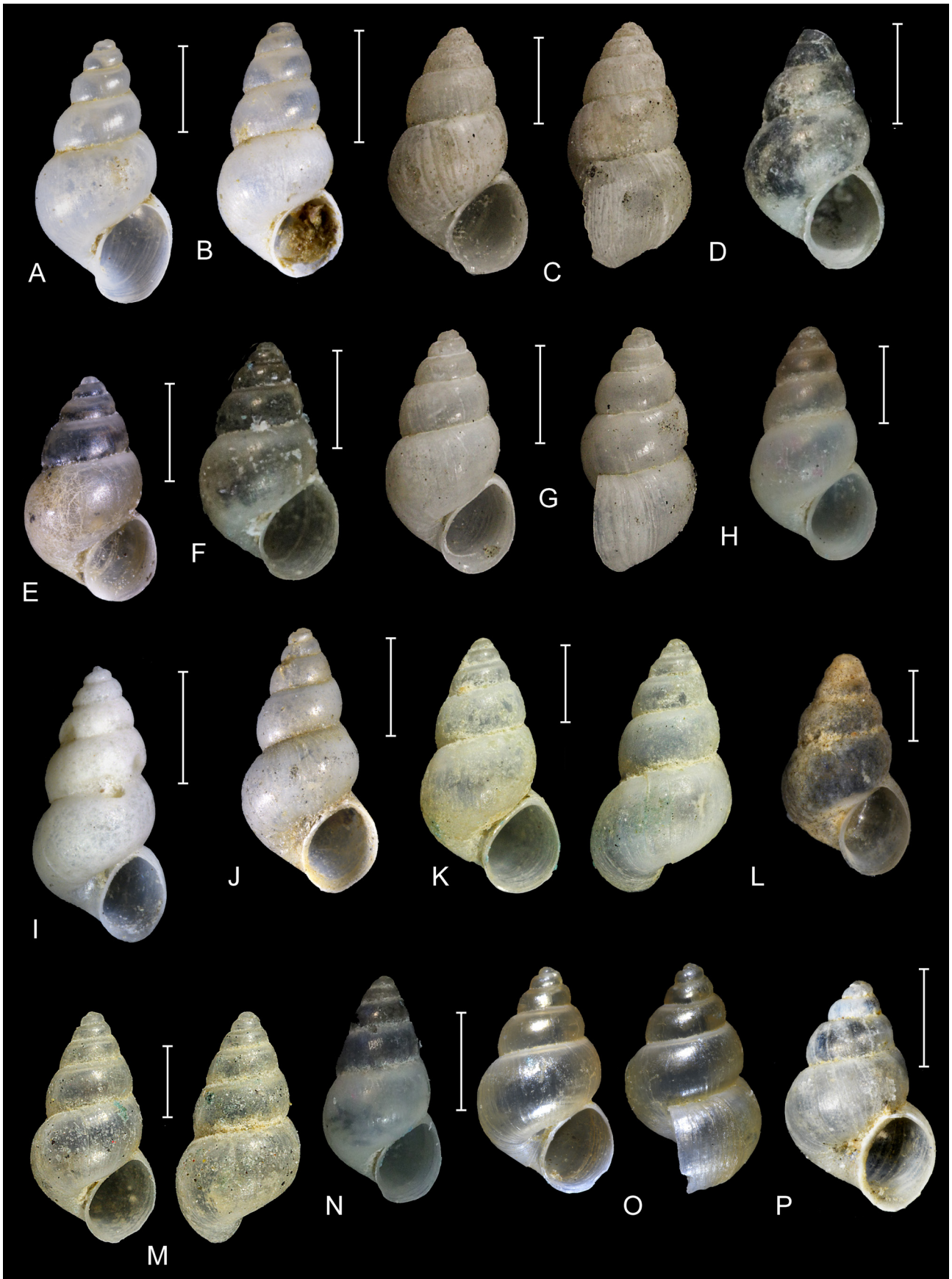
Types: ZIN, No. 4327/1 (holotype), 4328/2, 4329/3 (31 paratypes).

Dimensions of the holotype (mm): SW 4.1; SH 2.1; SpH 2.8; BWH 2.2; AH 1.4; AW 1.2.

Distribution: southern Caspian Sea, limans of the Black and Azov seas.

Fig. 1. Shells of *Caspiohydrobia* species. **A**, *C. eichwaldiana*, ZIN, holotype; **B**, *C. eichwaldiana*, ZIN No. 4332/6, Caspian Sea, without a precise locality; **C**, *C. chrysopsis*, ZIN No. 4308/1, "Transcaspian Area, Uz. Ada" (unknown locality); **D**, *C. chrysopsis*, LMBI, northern Kazakhstan, Kushmurun Lake; **E**, *C. conica*, ZIN No. 4315/6, Caspian Sea, Balkhan Bay (probable syntype); **F**, *C. conica*, ZIN, uncatalogised, Caspian Sea, station 37/57; **G**, *C. convexa*, ZIN, holotype; **H**, *C. convexa*, LMBI, central Kazakhstan, Korgalzhyn Lake; **I**, *C. curta*, LMBI, Aral Sea, nr. Lazarev I.; **J**, *C. curta*, LMBI, central Kazakhstan, Korgalzhyn Lake; **K**, *C. cylindrica*, ZIN, lectotype; **L**, *C. cylindrica*, LMBI, Aral Sea, station 11; **M**, *C. dubia*, ZIN, uncatalogised, Caspian Sea, station 29/57; **N**, *C. dubia*, LMBI, Aral Sea, station 7a; **O**, *C. gemmata*, ZIN, uncatalogised, Caspian Sea, station 151/60; **P**, *C. gemmata*, LMBI, Aral Sea, Lazarev I.; **R**, scheme of shell measurements used in this study. Scale bars: 1 mm. Shells from the Black and Caspian Seas were identified by Ya.I. Starobogatov, those from the other regions, by S.I. Andreeva.





2. *Caspiohydrobia chrysopsis*

(Kolesnikov, 1947)

(Figs 1C, D, 5A)

Hydrobia chrysopsis Kolesnikov, 1947: 106, 110.

Pyrgohydrobia chrysopsis Logvinenko & Starobogatov, 1969: 349, fig. 358 (12); Tajalli-Pour, 1980: pl. 18, fig. 11.

Caspiohydrobia chrysopsis Kantor & Sysoev, 2006: 89, pl. 42B; Vinarski & Kantor, 2016: 227; Izzatullaev, 2019: 179, fig. 78.10.

Type locality: not specified (the Caspian Sea – from the title of Kolesnikov’s publication).

Types: unknown (not traced).

Distribution: southern Caspian Sea, Caspian Lowland, Aral Sea, Southern Urals, and probably southern Transuralia.

3. *Caspiohydrobia conica*

(Logvinenko et Starobogatov, 1969)

(Figs 1E, F, 5D, E)

Pyrgohydrobia conica Logvinenko & Starobogatov, 1969: 346, fig. 358 (3); Tajalli-Pour, 1980: pl. 17, figs 5, 6.

Caspiohydrobia conica Starobogatov, 1974: 257, fig. 226; Kantor & Sysoev, 2006: 89, pl. 42D; Vinarski & Kantor, 2016: 227; Izzatullaev, 2019: 171, fig. 76.2.

Type locality: the original description states that the species is distributed in the northern, middle, and southern Caspian Sea, however, the holotype was not designated, and the concrete type locality is thus not specified.

Types: Logvinenko & Starobogatov (1969) did not specify the type series of this species. Possibly, three shells collected by Grimm in 1874 and kept under accession numbers 4314/5 and 4315/6 in ZIN are the syntypes of *C. conica*. Both lots were collected in the Caspian Sea, 4315/6 from the Balkhan Bay, and the other from an unknown locality. There are more lots, identified by Staro-

bogatov as *C. conica*, in the uncatalogised part of Logvinenko’s Caspian material that is also kept in ZIN. Among these possible syntypes, there are lots sampled from stations 29/1957 (n = 4), 37/1957 (n = 2), 41/1957 (n = 3), and 151/1960 (n = 2). Since we are not aware which precisely specimens served Logvinenko & Starobogatov (1969) to describe a new species, we refrain here from the designation of the lectotype of *C. conica*.

Distribution: southern Caspian Sea, Aral Sea; Southern Urals.

4. *Caspiohydrobia convexa* (Logvinenko et Starobogatov in Golikov et Starobogatov, 1966) (Figs 1G, H, 5B)

Pyrgohydrobia convexa Golikov & Starobogatov, 1966: 353, fig. 1 (2, 3); Logvinenko & Starobogatov, 1969: 346, fig. 358 (1); Tajalli-Pour, 1980: pl. 17, figs 1, 2.

Caspiohydrobia convexa Golikov & Starobogatov, 1972: 98, pl. II, fig. 14; Anistratenko & Stadnichenko, 1995: 110, fig. 88; Kantor & Sysoev, 2006: 90, pl. 42B; Anistratenko et al., 2011: 81, fig. III, 9; Vinarski & Kantor, 2016: 227–228; Izzatullaev, 2019: 172, fig. 76.1.

Type locality: The Caspian Sea, Bol’shoy Kirovskiy Bay (nowadays Kyzylagach Bay).

Types: ZIN, No. 4320/1 (holotype), 4321/2 (4 paratypes).

Dimensions of the holotype (mm): SW 3.8; SH 1.6; SpH 2.4; BWH 2.3; AH 1.4; AW 1.0.

Distribution: southern Caspian Sea, Caspian Lowland, Aral Sea, and Southern Urals.

5. *Caspiohydrobia curta*

(Logvinenko et Starobogatov, 1969)

(Figs 1I, J, 5C)

Pyrgohydrobia curta Logvinenko & Starobogatov, 1969: 348, fig. 358 (7); Tajalli-Pour, 1980: pl. 18, figs 1, 2.

←
Fig. 2. Shells of *Caspiohydrobia* species (continuation). **A**, *C. grimmi*, ZIN, uncatalogised, Caspian Sea, station 43/57; **B**, *C. grimmi*, ZIN, uncatalogised, Caspian Sea, station 46/57; **C**, *C. oviformis*, holotype; **D**, *C. oviformis*, LMBI, Chelyabinsk Prov., Lake Salamatka; **E**, *C. parva*, ZIN No. 4346/1, “Transcaspian Area, Uz. Ada” (unknown locality); **F**, *C. parva*, LMBI, Aral Sea, Kurzhatpes; **G**, *C. subconvexa*, ZIN, probable holotype; **H**, *C. subconvexa*, LMBI, Aral Sea, station 35; **I**, *C. turrita*, ZIN No. 4353/1, Caspian Sea, Balkhan Bay; **J**, *C. turrita*, ZIN, uncatalogised, Caspian Sea, station 30/57; **K**, *C. aralensis*, ZIN, holotype; **L**, *C. aralensis*, LMBI, Kurgan Prov., Elanach Lake; **M**, *C. behningi*, ZIN, holotype; **N**, *C. behningi*, LMBI, Aral Sea, station 74; **O**, *C. bergi*, ZIN, holotype; **P**, *C. bergi*, LMBI, central Kazakhstan, Korgalzhyn Lake. Scale bars: 1 mm. Shells from the Caspian Sea were identified by Ya.I. Starobogatov, those from the other regions, by S.I. Andreeva.

Caspiohydrobia curta Kantor & Sysoev, 2006: 90, pl. 42, E; Vinarski & Kantor, 2016: 228; Izzatullaev, 2019: 171, fig. 76.5.

Type locality: unknown, since the exact region of the Caspian Sea where the holotype was collected is not indicated in the original description.

Types: the holotype specimen is illustrated by Logvinenko & Starobogatov (1969, fig. 358, 7), but its current whereabouts is unknown (it is absent from the catalogised part of ZIN collection).

Distribution: middle and southern Caspian Sea, Caspian Lowland, Aral Sea, and Southern Urals.

6. *Caspiohydrobia cylindrica*

(Logvinenko et Starobogatov, 1969)
(Figs 1K, L, 5D)

Pyrgohydrobia cylindrica Logvinenko & Starobogatov, 1969: 350, fig. 358 (13); Tajalli-Pour, 1980: pl. 19, figs 1, 2.

Caspiohydrobia cylindrica Kantor & Sysoev, 2006: 90, pl. 42K; Vinarski & Kantor, 2016: 228; Izzatullaev, 2019: 172, fig. 76.11.

Type locality: Caspian Sea, Bol'shoy Kirovskiy Bay (nowadays Kyzylagach Bay).

Types: the type series of *C. cylindrica* was found during this study in the uncatalogised part of the ZIN collection. It contains three shells collected in 1968 from the Bol'shoy Kirovskiy Bay (Kyzylagach Bay at present) of the Caspian Sea and four other specimens collected from a station 41/1957 (its precise locality remains unknown). None of the specimens bears inscription "holotype" on its label. One of shells from the Bol'shoy Kirovskiy Bay is designated here as the lectotype (see Fig. 1K) of *C. cylindrica*.

Dimensions of the lectotype (mm): SW 4.4; SH 1.9; SpH 3.2; BWH 2.3; AH 1.3; AW 1.1.

Distribution: middle and southern Caspian Sea, Caspian Lowland, and Aral Sea.

7. *Caspiohydrobia dubia*

(Logvinenko et Starobogatov, 1969)
(Figs 1M, N)

Pyrgohydrobia dubia Logvinenko & Starobogatov, 1969: 348, fig. 358 (6).

Caspiohydrobia dubia Kantor & Sysoev, 2006: 91, pl. 42J; Vinarski & Kantor, 2016: 228; Izzatullaev, 2019: 178, fig. 76.4.

Type locality: the original description states that the species is distributed in the northern, middle and southern Caspian Sea, however, the holotype was not designated, and the concrete type locality is thus not specified.

Types: whereabouts unknown. The type series was not specified in the original description. The catalogue of ZIN collection contains no lot of *C. dubia* from the Caspian Sea, and it is unknown which material was used by Logvinenko & Starobogatov (1969) to describe this species.

Distribution: northern, middle and southern Caspian Sea and Aral Sea.

8. *Caspiohydrobia gemmata* (Kolesnikov, 1947) (Figs 1O, P)

Hydrobia grimmi var. *gemma* Kolesnikov, 1947: 106, 110.

Pyrgohydrobia gemmata Logvinenko & Starobogatov, 1969: 349, fig. 358 (8); Tajalli-Pour, 1980: pl. 18, figs 3, 4.

Caspiohydrobia gemmata Kantor & Sysoev, 2006: 91, pl. 43D; Vinarski & Kantor, 2016: 229; Izzatullaev, 2019: 178, fig. 76.6.

Type locality: not specified (the Caspian Sea – from the title of Kolesnikov's publication).

Types: unknown (not traced).

Distribution: northern, middle and southern Caspian Sea and Aral Sea.

9. *Caspiohydrobia grimmi*

(Clessin in W. Dybowski, 1877)
(Figs 2A, B)

Hydrobia grimmi Dybowski, 1877: 55–56, pl. III, fig. 2 (partim?); Kolesnikov, 1947: 106, 100; Zhadin, 1952: 225, fig. 147.

Pyrgohydrobia grimmi Logvinenko & Starobogatov, 1969: 349, fig. 358 (11); Tajalli-Pour, 1980: pl. 18, figs 9, 10.

Caspiohydrobia grimmi Kantor & Sysoev, 2006: 91–92, pl. 43, E; Filippov & Riedel, 2009: 70–72, 74–76, figs 4a–d; Vinarski & Kantor, 2016: 229; Izzatullaev, 2019: 178, fig. 76.9.

Ecrobia grimmi s. l. Haase et al., 2010: 101; Anistratenko et al., 2019: 53; Vandendorpe et al., 2019: 2, fig. 1; Wesselingh et al., 2019: 74; Aladin et al., 2022: 129.

Type locality: Caspian Sea (without a precise locality).

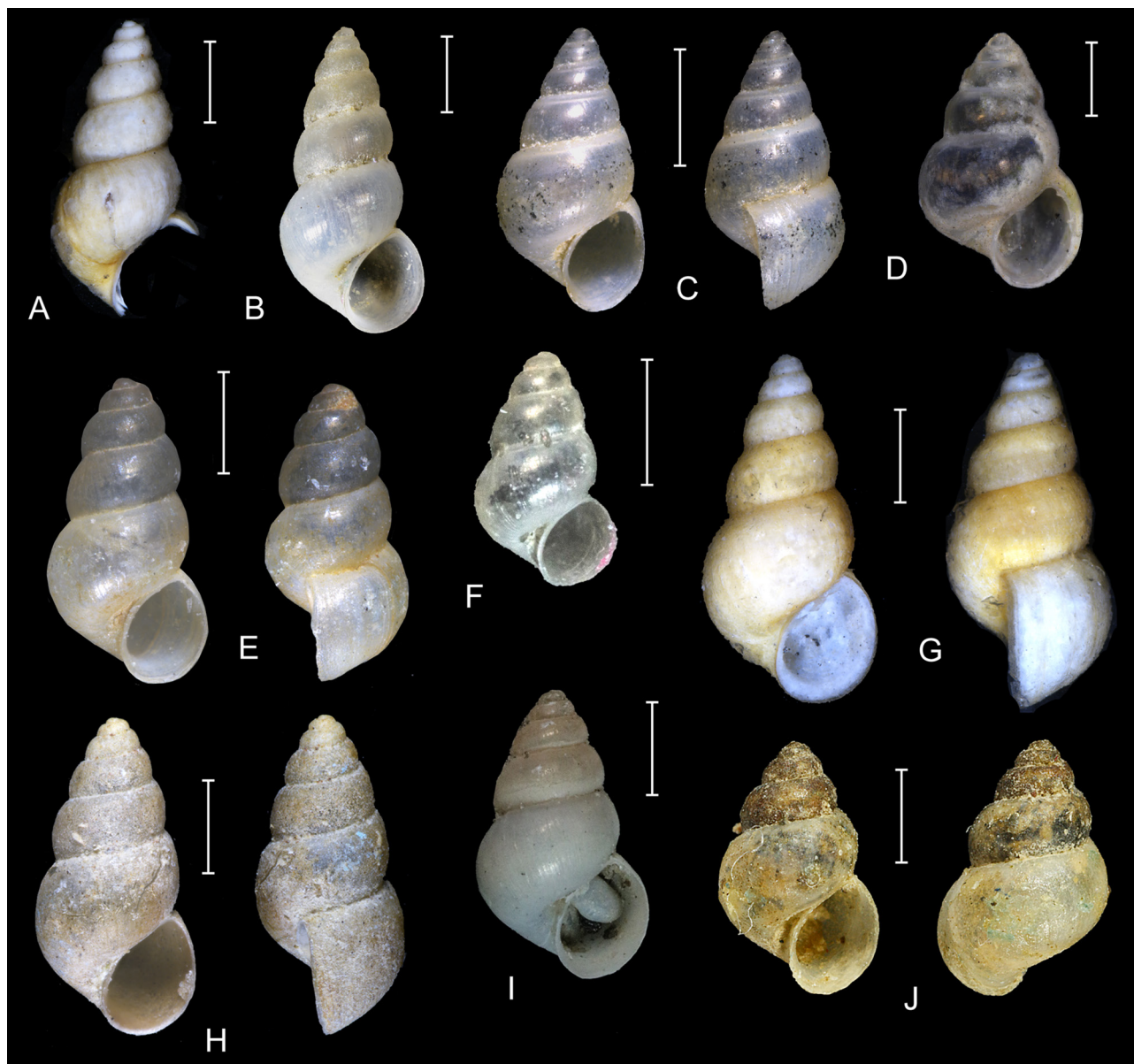


Fig. 3. Shells of *Caspiohydrobia* species (continuation). **A**, *C. husainovae*, ZIN, holotype (damaged); **B**, *C. husainovae*, LMBI, Aral Sea, Bol'shoy Karatyup Cape; **C**, *C. kazakhstanica*, ZIN, holotype; **D**, *C. kazakhstanica*, LMBI, Kurgan Prov., Enalach Lake; **E**, *C. nikolskii*, ZIN, holotype; **F**, *C. nikolskii*, LMBI, Aral Sea, Lazarev I.; **G**, *C. obrutchevi*, ZIN, holotype; **H**, *C. sidorovi*, ZIN, holotype; **I**, *C. sidorovi*, LMBI, northern Kazakhstan, Lake Mnogosopochnoe; **J**, *C. borealis*, ZIN, holotype. Scale bars: 1 mm. All specimens were identified by S.I. Andreeva (except for A, G – identified by Ya.I. Starobogatov).

Types: most probably lost. Clessin's malacological collection, where the types of *Hydrobia grimmi* were kept (Dybowski, 1887; Anistratenko et al., 2019), was totally destroyed during World War II (Dance, 1986).

Distribution: *Caspiohydrobia grimmi* sensu Logvinenko & Starobogatov, 1969 is known from the Aral and Caspian seas as well as from

the Southern Urals. Vandendorpe et al. (2019: 6) using the "wide" concept of this species (i.e., *Ecrobia grimmi* s. l.) describe its range as follows: "[it] is widespread across central Asia, occurring in brackish water bodies from the central Ural Mountains in the north to the Persian Gulf in the south and the Lake Issyk-Kul area in the east".

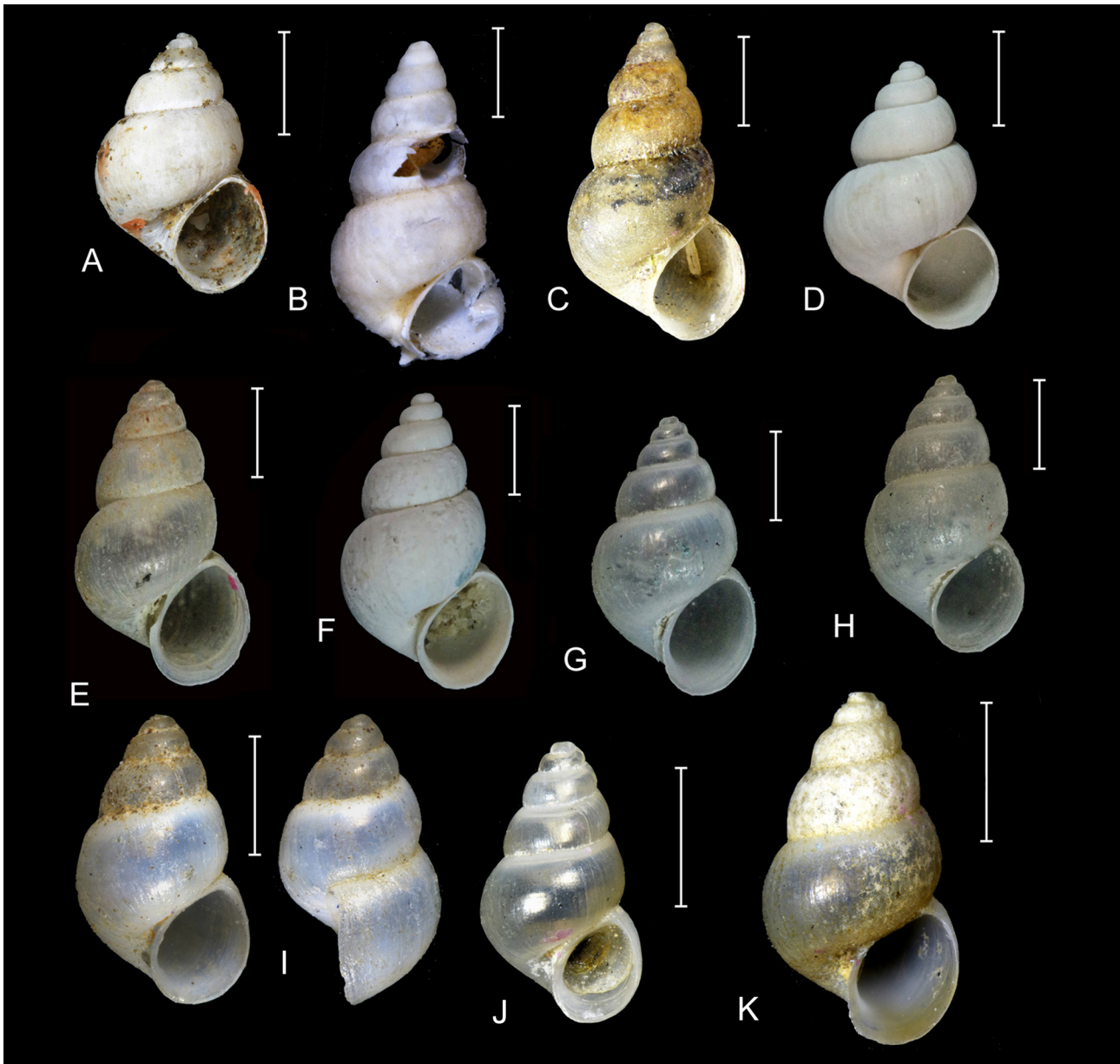


Fig. 4. Shells of *Caspiohydrobia* species (continuation). **A**, *C. borealis*, LMBI, northern Kazakhstan, Lake Kushmurun; **B**, *C. johanseni*, ZIN, lectotype (damaged); **C**, *C. johanseni*, LMBI, Chelyabinsk Prov., Lake Salamatka; **D**, *C. coniformis*, LMBI, Novosibirsk Prov., holocene deposits of Lake Sorgul; **E**, *C. elongata*, LMBI, Aral Sea, station 146/14; **F**, *C. ljaurica*, LMBI, Novosibirsk Prov., holocene deposits of Lake Sorgul; **G**, *C. pavlovskii*, LMBI, Aral Sea, station 1/19; **H**, *C. sogdiana*, LMBI, Aral Sea, Sary-Chaganak Bay; **I**, *C. nikitinskii*, ZIN, holotype; **J**, *C. nikitinskii*, LMBI, Aral Sea, nr. Lazarev I.; **K**, *C. tadjikistanica*, LMBI, Aral Sea, Sary-Chaganak Bay. Scale bars: 1 mm. All specimens were identified by S.I. Andreeva.

Remark. We include this species to *Caspiohydrobia* following the usage accepted in the Russian literature (Logvinenko & Starobogatov, 1969; Vinnarski & Kantor, 2016), however, the most recent authors unanimously place it to the genus *Ecrobia* (see Wesselingh et al., 2019 and references therein).

10. *Caspiohydrobia oviformis*
(Logvinenko et Starobogatov, 1969)
(Figs 2C, D)

Pyrgohydrobia oviformis Logvinenko & Starobogatov, 1969: 349, fig. 358 (9); Tajalli-Pour, 1980: pl. 18, figs 5, 6.

Caspihydrobia oviformis Kantor & Sysoev, 2006: 93, pl. 44, E; Vinarski & Kantor, 2016: 221; Izzatullaev, 2019: 178, fig. 76.7.

Type locality: Caspian Sea, Bol'shoy Kirovskiy Bay (nowadays Kyzylagach Bay).

Types: the holotype shell was illustrated by Logvinenko & Starobogatov (1969; fig. 358, 9), but its current whereabouts has been unknown (Vinarski & Kantor, 2016). During this research, we managed to find this specimen in the uncatalogued part of ZIN collection. Currently, it is catalogued under accession number 1/526-2022. No information about the paratypes is available.

Dimensions of the holotype (mm): SW 2.8; SH 1.6; SpH 1.8; BWH 2.0; AH 1.2; AW 0.9.

Distribution: southern Caspian Sea, Aral Sea, and Caspian Lowland.

11. *Caspihydrobia parva*

(Logvinenko et Starobogatov, 1969)
(Figs 2E, F)

Pyrgohydrobia parva Logvinenko & Starobogatov, 1969: 348, fig. 358 (4); Tajalli-Pour, 1980: pl. 17, figs 7, 8.

Caspihydrobia parva Kantor & Sysoev, 2006: 93, pl. 43F; Vinarski & Kantor, 2016: 231; Izzatullaev, 2019: 178, fig. 76.3.

Type locality: Caspian Sea, Bol'shoy Kirovskiy Bay (nowadays Kyzylagach Bay).

Types: the holotype shell is illustrated by Logvinenko & Starobogatov (1969; fig. 358, 4), but its current whereabouts is unknown. The catalogue of the ZIN collection contains no *C. parva* lots originated from the Caspian Sea. There are three lots of *C. parva* in the uncatalogued part of the collection, which probably constituted the type series of this species. Their sampling sites are as follows: station 37/1957 (n = 2), 38/1957 (n = 3), and 44/1957 (n = 2).

Distribution: northern, middle and southern Caspian Sea, Aral Sea, and Caspian Lowland.

12. *Caspihydrobia subconvexa*

(Logvinenko et Starobogatov, 1969)
(Figs 2G, H, 5A, B)

Pyrgohydrobia subconvexa Logvinenko & Starobogatov, 1969: 349, fig. 358 (10); Tajalli-Pour, 1980: pl. 18, figs 7, 8.

Caspihydrobia subconvexa Kantor & Sysoev, 2006: 94, pl. 44, G; Vinarski & Kantor, 2016: 232; Izzatullaev, 2019: 175, fig. 76.8.

Type locality: Caspian Sea, station 41/1957 (the exact location of this site remains unidentified).

Types: the holotype shell was illustrated by Logvinenko & Starobogatov (1969; fig. 358, 11), but its current whereabouts has been unknown (Vinarski & Kantor, 2016). During this research, we managed to find this specimen in the uncatalogued part of the ZIN collection. Currently, it is catalogued under the accession number 1/527-2022. No information about the paratypes is available.

Dimensions of the holotype (mm): SW 2.6; SH 1.3; SpH 1.6; BWH 1.6; AH 1.0; AW 0.7.

Distribution: northern, middle and southern Caspian Sea and Aral Sea.

13. *Caspihydrobia turrita*

(Logvinenko et Starobogatov, 1969)
(Figs 2I, J)

Pyrgohydrobia turrita Logvinenko & Starobogatov, 1969: 348, fig. 358 (5); Tajalli-Pour, 1980: pl. 17, figs 9, 10.

Caspihydrobia turrita Kantor & Sysoev, 2006: 94, pl. 44B; Vinarski & Kantor, 2016: 232–233.

Type locality: southern part of the Caspian Sea, exact locality is not specified in the original description.

Types: the holotype shell was illustrated by Logvinenko & Starobogatov (1969; fig. 358, 5), but its current whereabouts is unknown. It is absent from the catalogued part of the ZIN collection.

Dimensions of the holotype (mm): SW 2.6; SH 1.3; SpH 1.6; BWH 1.6; AH 1.0; AW 0.7.

Distribution: endemic to the southern Caspian Sea.

14. *Caspihydrobia aralensis*

Starobogatov et Andreeva, 1981
(Figs 2K, L)

Caspihydrobia aralensis Starobogatov & Andreeva, 1981: 31, fig. 5; Kantor & Sysoev, 2006: 88–89, pl. 42F; Vinarski & Kantor, 2016: 226; Izzatullaev, 2019: 178, fig. 79.4.

Type locality: Aral Sea, Sary-Chaganak Bay, 2.5 m.

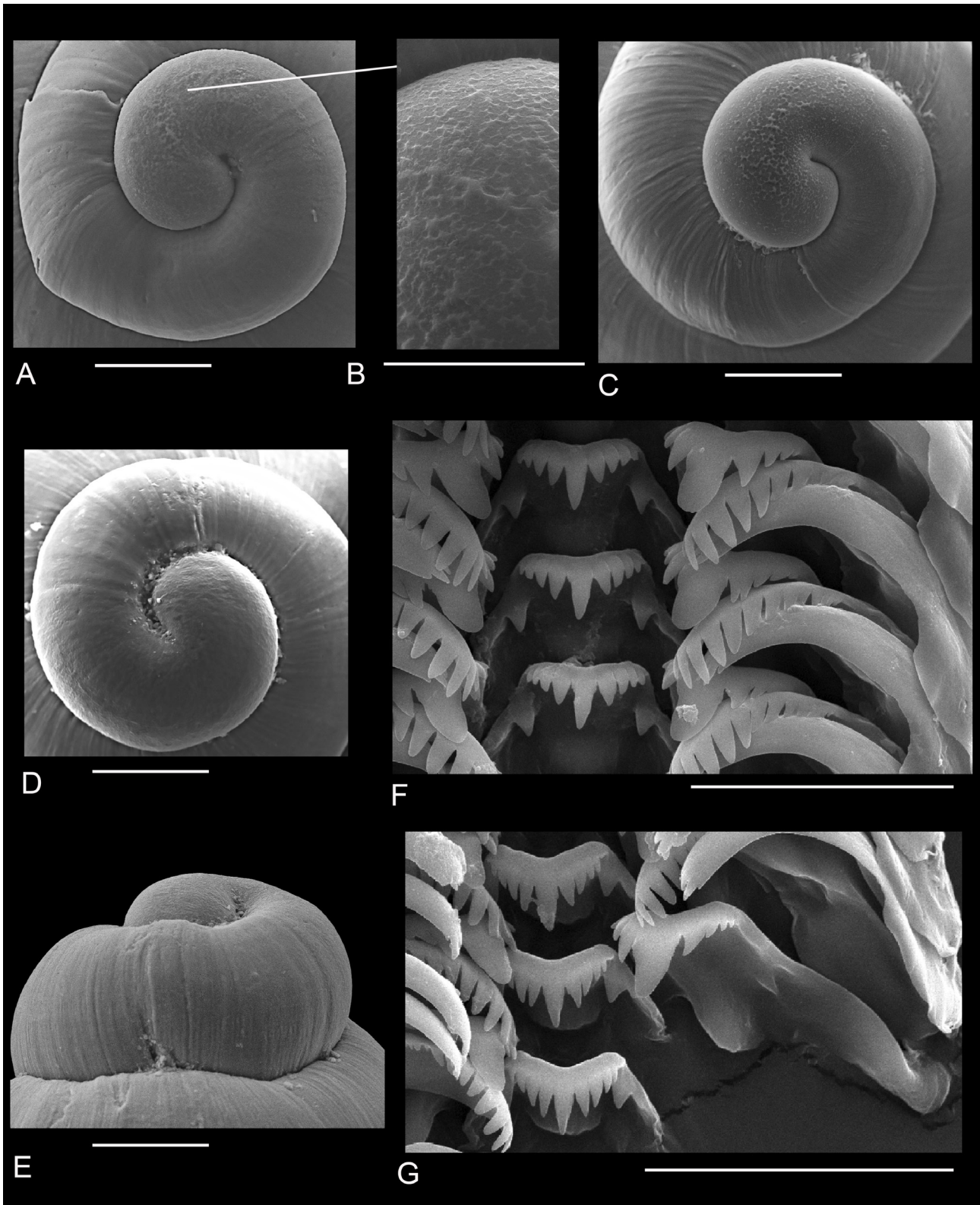


Fig. 5. SEM images of protoconchs and radulae of selected representatives of *Caspiohydrobia*. **A, B, C.** *subconvexa*, Caspian Sea (**B**, increasing non-spiral part); **C.** *pavlovskii*, Aral Sea, Sary-Chaganak; **D, E.** *C. conica*, Caspian Sea; **F, G.** two fragments of radula (*Caspiohydrobia cf. johanseni*, Enalach Lake). Scale bars: 100 μm (**A, C, D, E**), 40 μm (**B, F**), and 50 μm (**G**).

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (10 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 3.2; SH 1.8; SpH 2.1; BWH 2.1; AH 1.2; AW 0.9.

Distribution: Aral Sea, saline lakes of northern and central Kazakhstan, Southern Urals; Caspian Lowland.

15. *Caspihydrobia behningi*

Starobogatov et Andreeva, 1981

(Figs 2M, N)

Caspihydrobia behningi Starobogatov & Andreeva, 1981: 31, fig. 2; Sitnikova et al., 1992: 8, fig. 1 (11); Kantor & Sysoev, 2006: 89, pl. 42I; Vinarski & Kantor, 2016: 226; Izzatullaev, 2019: 177, fig. 79.3.

Type locality: Aral Sea, central part of Bol'shoe More, 21 m.

Types: ZIN, Nos. 1 (holotype) and 2 (7 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 3.3; SH 1.8; SpH 2.1; BWH 2.0; AH 1.2; AW 0.9.

Distribution: Aral Sea, saline lakes of northern and central Kazakhstan; Caspian Lowland.

16. *Caspihydrobia bergi*

Starobogatov et Andreeva, 1981

(Figs 2O, P)

Caspihydrobia bergi Starobogatov & Andreeva, 1981: 34, fig. 9; Sitnikova et al., 1992: 8, fig. 1 (13); Kantor & Sysoev, 2006: 89, pl. 42A; Vinarski & Kantor, 2016: 226; Izzatullaev, 2019: 177, fig. 79.2.

Type locality: Aral Sea, north-east from Vozrozhdenie Island, 8 m.

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (8 paratypes) in the catalogue.

Dimensions of the holotype (mm): SW 2.4; SH 1.4; SpH 1.6; BWH 1.6; AH 0.9; AW 0.7.

Distribution: Aral Sea, saline lakes of northern Kazakhstan; Holocene deposits of West Siberia.

17. *Caspihydrobia borealis*

Andreeva et Frolova, 1989

(Figs 3J, 4A)

Caspihydrobia borealis Andreeva & Frolova, 1989: 134–135, fig. a; Kantor & Sysoev, 2006: 89, pl. 42C; Vinarski & Kantor, 2016: 226–227.

Type locality: Kazakhstan, Kustanay Province, Ubagan River near its exit from Kushmurun Lake.

Types: ZIN, Nos. 1/530-1987 (holotype) and 2/530-1987 (9 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 2.7; SH 1.7; SpH 1.6; BWH 1.9; AH 1.3; AW 0.9.

Distribution: northern and central Kazakhstan; Holocene deposits of West Siberia.

18. *Caspihydrobia coniformis*

Starobogatov et Izzatullaev, 1974

(Fig. 4D)

Caspihydrobia coniformis Starobogatov & Izzatullaev, 1974: 933–934, fig. 1; Kantor & Sysoev, 2006: 90, pl. 42H; Vinarski & Kantor, 2016: 227; Izzatullaev, 2019: 175, fig. 77.2.; Shirokaya et al., 2019: 232, fig. 11D.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (9 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya et al. (2019, fig. 11D). The current whereabouts of the 121 paratypes originally deposited in the collection of the E.N. Pavlovsky Institute of Zoology and Parasitology of the Tajik Academy of Sciences in Dushanbe (IZIP hereafter) is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan (Dzhilantau Mountains), Southern Urals; Holocene deposits of West Siberia.

19. *Caspihydrobia elongata*

Starobogatov et Izzatullaev, 1974

(Fig. 4E)

Caspihydrobia coniformis Starobogatov & Izzatullaev, 1974: 933–934, fig. 2; Kantor & Sysoev, 2006: 91, pl. 43I; Vinarski & Kantor, 2016: 228; Izzatullaev, 2019: 173, fig. 77.11; Shirokaya et al., 2019: 232, fig. 11E.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (10 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya

et al. (2019, fig. 11E). The current whereabouts of the 60 paratypes originally deposited in IZIP is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan, Dzhilantau Mountains; Holocene deposits of West Siberia.

20. *Caspihydrobia husainovae*

Starobogatov, 1974

(Figs 3A, B)

Caspihydrobia husainovae Starobogatov, 1974: 257, fig. 227; Sitnikova et al., 1992: 8, fig. 1 (9, 10, 14); Kantor & Sysoev, 2006: 92, pl. 43K; Vinarski & Kantor, 2016: 229; Izzatullaev, 2019: 175, fig. 79.1.

Type locality: Aral Sea, about 20 m km NW of Obruchev Island, 20 m.

Types: ZIN, Nos. 1/506-1980 (holotype) and 2/506-1980 (a single paratype) in the systematic catalogue.

Dimensions of the holotype (mm): SW 3.7; SH 1.8; AH 1.1; AW 0.8 (Starobogatov, 1974).

Distribution: Aral Sea, saline lakes of northern and southern Kazakhstan, Southern Urals.

21. *Caspihydrobia johanseni*

Frolova, 1984

(Figs 4B, C, 6A–E, K–L)

Caspihydrobia johanseni Frolova, 1984: 46, fig. 1; Andreeva & Frolova, 1989: 135, fig. 6; Kantor & Sysoev, 2006: 92; Vinarski & Kantor, 2016: 229–230.

Type locality: Kazakhstan, Pavlodar Province, lower stream of the Karasu-Shiderty River, 5 km from Zagotskot settlement.

Types: ZIN, Nos. 6/283-1975 (lectotype) and 4/529-1987 (3 paralectotypes) in the systematic catalogue. The lectotype was designated by Andreeva & Frolova (1989).

Distribution: Aral Sea, saline lakes of northern and central Kazakhstan, Caspian Lowland, Southern Urals; known from Holocene deposits in the south of West Siberia.

22. *Caspihydrobia kazakhstanica*

Starobogatov et Andreeva, 1981

(Figs 3C, D; 6F–J)

Caspihydrobia kazakhstanica Starobogatov & Andreeva, 1981: 30, fig. 1; Kantor & Sysoev, 2006: 92, Fig. 43C; Vinarski & Kantor, 2016: 230; Izzatullaev, 2019: 176, fig. 79.2.

Type locality: Aral Sea, Bol'shoye More (the central part), 19 m.

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (10 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 2.9; SH 1.6; SpH 1.9; BWH 1.9; AH 1.2; AW 0.8.

Distribution: Aral Sea, saline lakes of northern Kazakhstan, Southern Urals and Transuralia; known from Holocene deposits in the south of West Siberia.

23. *Caspihydrobia ljaurica*

Starobogatov et Izzatullaev, 1974

(Fig. 4F)

Caspihydrobia ljaurica Starobogatov & Izzatullaev, 1974: 934, fig. 5; Kantor & Sysoev, 2006: 92, pl. 43H; Vinarski & Kantor, 2016: 230; Izzatullaev, 2019: 173, fig. 77.3; Shirokaya et al., 2019: 233, fig. 11F.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (10 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya et al. (2019, fig. 11F). The current whereabouts of the 40 paratypes originally deposited in IZIP is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan, Dzhilantau Mountains; Holocene deposits of West Siberia.

24. *Caspihydrobia nikitinskii*

Starobogatov et Andreeva, 1981

(Figs 4I, J)

Caspihydrobia nikitinskii Starobogatov & Andreeva, 1981: 33, fig. 7; Kantor & Sysoev, 2006: 92, pl. 43G; Vinarski & Kantor, 2016: 230; Izzatullaev, 2019: 179, fig. 79.6.

Type locality: Aral Sea, near Baigubekmuryn Cape, 4.8 m.

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (9 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 2.4; SH 1.4; SpH 1.5; BWH 1.8; AH 1.0; AW 0.8.

Distribution: Aral Sea, saline lakes of northern Kazakhstan.

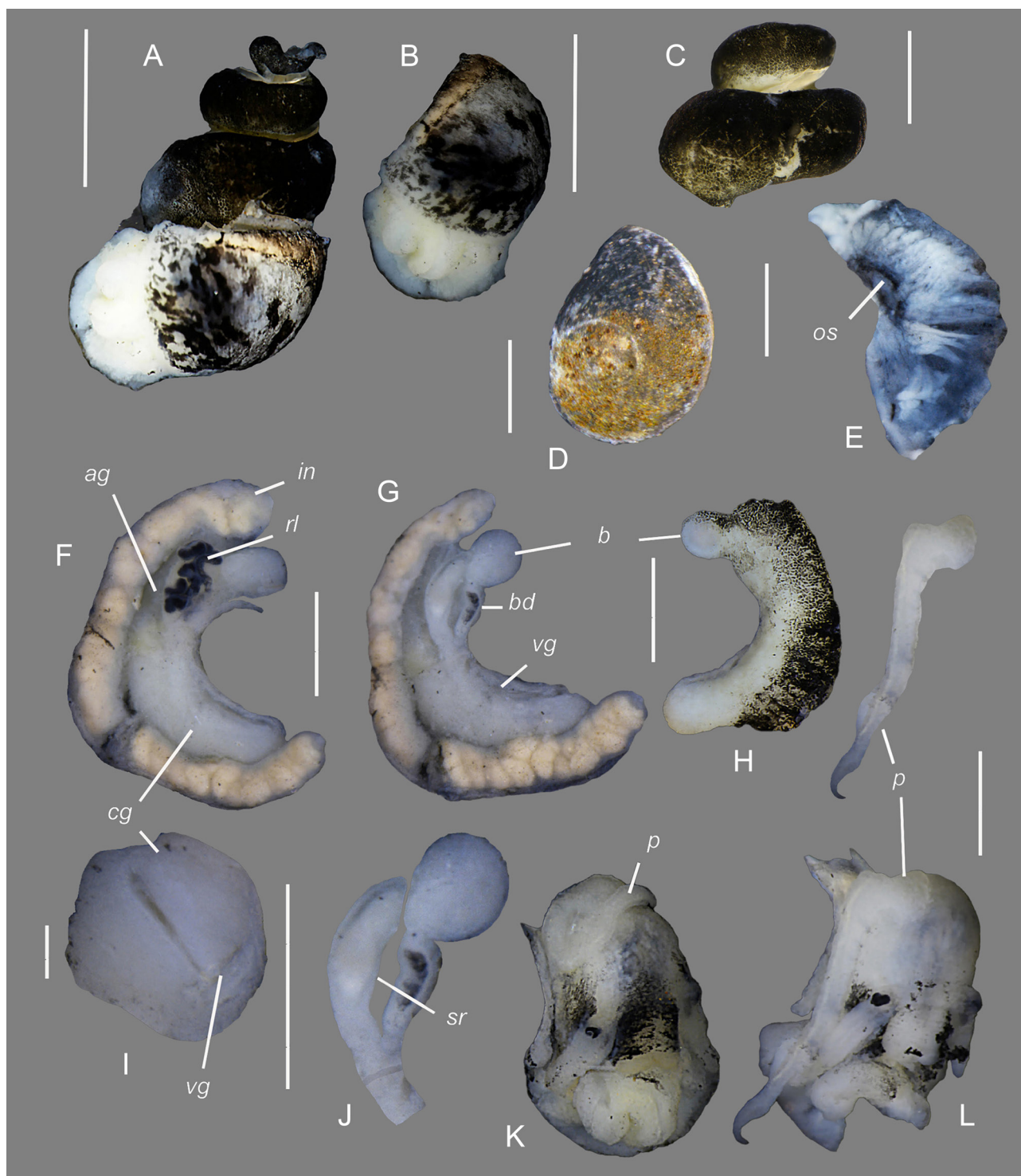


Fig. 6. Soft body anatomy of *Caspihydrobia* as exemplified by *C. johanseni* (A–E, K–L) and *C. kazakhstanica* (F–J) from Lake Elanach. **A**, general appearance of soft body; **B**, external view of last whorl above mantle cavity; **C**, third and fourth whorls of soft body; **D**, operculum; **E**, gill with osphradium; **F**, ventral view of female reproductive system (renal loop is shown); **G**, ventral view of female reproductive system with renal loop removed; **H**, dorsal view of female reproductive system; **I**, cross section through capsulae gland; **J**, increasing renal part of female reproductive duct; **K–L**, view of male reproductive system before (**K**) and after (**L**) copulation. Abbreviations: *ag* – albumen gland; *b* – bursa; *bd* – bursa duct; *cg* – capsulae gland; *in* – intestine; *os* – osphradium; *p* – penis; *rl* – renal loop; *sr* – seminal receptacle; *vg* – ventral groove. Scale bars: 1 mm (A, B), 0.5 mm (C–H, J–L), 0.1 mm (I), and 50 μm (M).

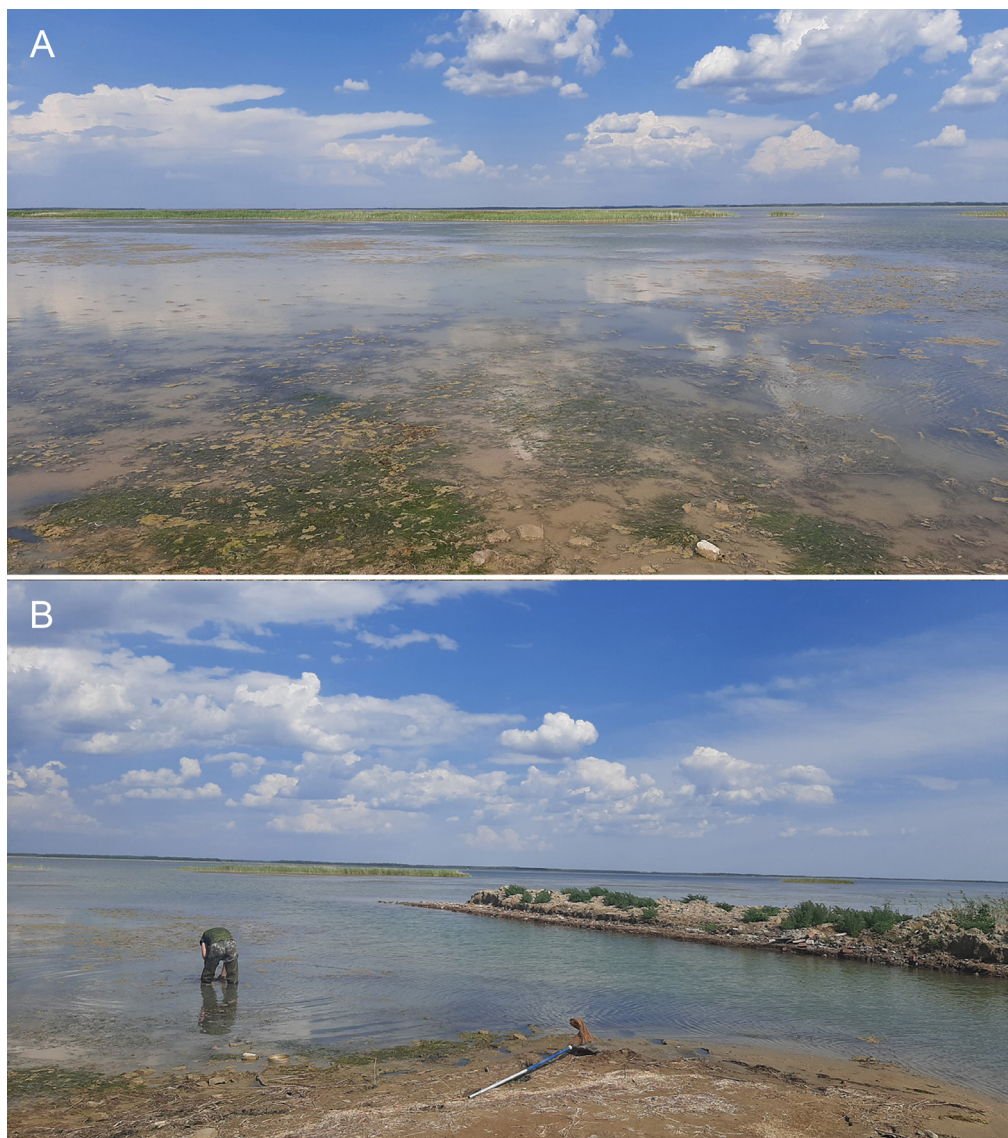


Fig. 7. General view of Lake Elanach, habitat of seven nominal species of *Caspiohydrobia* (A) and process of sampling from shallow zone of the lake, depth < 0.5 m (B).

25. *Caspiohydrobia nikolskii*

Starobogatov et Andreeva, 1981
(Figs 3E, F)

Caspiohydrobia nikolskii Starobogatov & Andreeva, 1981: 33, fig. 8; Kantor & Sysoev, 2006: 92, pl. 43B; Vinarski & Kantor, 2016: 230; Izzatullaev, 2019: 179, fig. 78.1.

Type locality: Aral Sea, Aktumsuk Cape, 10 m.

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (9 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 2.1; SH 1.1; SpH 1.4; BWH 1.2; AH 0.8; AW 0.6.

Distribution: Aral Sea, saline lakes of Southern Urals and southern Transuralia.

26. *Caspiohydrobia obrutchevi*

(Starobogatov et Andreeva, 1981)
(Fig. 4G)

Caspiohydrobia obrutchevi Starobogatov, Andreeva, 1981: 31–32, fig. 4; Kantor & Sysoev, 2006: 93, pl. 43A; Vinarski & Kantor, 2016: 231; Izzatullaev, 2019: 177, fig. 78.3.

Type locality: Aral Sea, southern part of Bol'shoye More, 20 km NW from Obruchev Island, 20 m.

Types: ZIN, Nos. 1/506-1980 (holotype) and 2/506-1980 (6 paratypes) in the systematic catalogue.

Dimensions of the holotype (mm): SW 3.8; SH 1.9; SpH 2.2; BWH 2.6; AH 1.4; AW 1.0.

Distribution: this is one of the rarest species of *Caspihydrobia*, not known outside its type locality. To the best of our knowledge, no findings of *C. obrutchevi* have been reported since its description. The only material on this species available during our study was its type series.

27. *Caspihydrobia pavlovskii*

Starobogatov et Izzatullaev, 1974
(Figs 4G, 5C)

Caspihydrobia pavlovskii Starobogatov & Izzatullaev, 1974: 935, fig. 6; Kantor & Sysoev, 2006: 93, pl. 44C; Vinarski & Kantor, 2016: 231; Izzatullaev, 2019: 174, fig. 78.6.; Shirokaya et al., 2019: 234, fig. 11G.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (10 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya et al. (2019, fig. 11G). The current whereabouts of the 110 paratypes originally deposited in IZIP is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan, Dzhilantau Mountains and Aral Sea.

28. *Caspihydrobia sidorovi*

Starobogatov et Andreeva, 1981
(Figs 3H, I)

Caspihydrobia sidorovi Starobogatov, Andreeva, 1981: 33, fig. 6; Kantor & Sysoev, 2006: 94, pl. 44, fig. A; Vinarski & Kantor, 2016: 231–232; Izzatullaev, 2019: 179, fig. 79.5.

Type locality: Aral Sea, Sary-Chaganak Bay, 2.5 m.

Types: ZIN, Nos. 1/505-1980 (holotype) and 2/505-1980 (10 paratypes) in the catalogue.

Dimensions of the holotype (mm): SW 3.5; SH 1.8; SpH 2.3; BWH 2.1; AH 1.4; AW 1.0.

Distribution: Aral Sea, brackish lakes of northern Kazakhstan and Southern Urals; Caspian Lowland.

29. *Caspihydrobia sogdiana* Starobogatov et

Izzatullaev, 1974
(Fig. 4H)

Caspihydrobia sogdiana Starobogatov & Izzatullaev, 1974: 935, fig. 3; Kantor & Sysoev, 2006: 94, pl. 44,

fig. D; Vinarski & Kantor, 2016: 232; Izzatullaev, 2019: 174, fig. 78.4.; Shirokaya et al., 2019: 234, fig. 11H.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (10 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya et al. (2019, fig. 11H). The current whereabouts of the 42 paratypes originally deposited in IZIP is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan, Dzhilantau Mountains, Aral Sea, brackish lakes of north Kazakhstan and Southern Urals.

30. *Caspihydrobia tadzhikistanica*

Starobogatov et Izzatullaev, 1974
(Fig. 4K)

Caspihydrobia tadzhikistanica Starobogatov & Izzatullaev, 1974: 935, fig. 4; Kantor & Sysoev, 2006: 94, pl. 44, F; Vinarski & Kantor, 2016: 232; Izzatullaev, 2019: 175, fig. 78.5.; Shirokaya et al., 2019: 235, fig. 13A.

Type locality: Tajikistan, Khatlon Province, Danghara District, vicinities of Lyaur village, bank deposits of a brackish water river.

Types: ZIN, Nos. 1/163-1973 (holotype) and 2/163-1973 (10 paratypes) in the systematic catalogue. The holotype is illustrated by Shirokaya et al. (2019, fig. 13A). The current whereabouts of the 112 paratypes originally deposited in IZIP is unknown (Shirokaya et al., 2019).

Distribution: Tajikistan, Dzhilantau Mountains, Aral Sea, brackish lakes of Southern Urals.

31. *Caspihydrobia elata* Küster, 1852

Paludina elata Küster, 1852: 59, pl. 11, figs 11, 12.
Caspihydrobia elata Starobogatov, 1970: 144.

Type locality: stated as “the Tigris River near Mossul in Persia”. However, this area belongs to Iraq, not Persia (nowadays Iran).

Types: not traced, possibly lost.

Distribution: Near East (Iraq and Iran).

Remark. Starobogatov (1970) mentioned this species as inhabiting saline waterbodies of the Iranian zoogeographic province. To the best of



Fig. 8. General view of small patch of Aral Sea shore near Aralsk Town. Photo taken in September 1978 by V. Goshkaderya. Numerous empty shells of *Caspiohydrobia* spp. together with shells of *Theodoxus pallasi* (Lindholm, 1924) formed bulk of this thanatocoenosis.

our knowledge, *C. elata* has not been either discussed or even mentioned in the subsequent Russian literature. Possibly, this species is identical to *Ecrobia grimmi* recorded from Lake Sawa in Iraq (Haase et al., 2010). No specimens of this species were available to us during this study.

Discussion

The major part of the current range of *Caspiohydrobia* lies within the territory that once belonged to the Paratethys basin. This genus may be considered a relic of the Paratethys malacofauna, and its occurrence in relatively remote areas (southern part of West Siberia, Iraq, mountain Tajikistan) is usually explained either by former sea incursions or by bird-mediated dispersal (Guskov et al., 2008, 2011; Haase et al., 2010; Vandendorpe et al., 2019). Starobogatov & Andreeva (1981) hypothesised that *Caspiohydrobia* evolved in the arid inner waterbodies of Central Asia and subsequently dispersed to the Azov-Black, Aral and Caspian Sea basins. Most of the nominal species of *Caspiohydrobia* have been recorded from more than one region (see Table 1). This can be explained either by their high dispersal ability or by the former extensive and continuous range of this genus, which nowadays is split into a se-

ries of isolated patches. One of the most striking patterns of *Caspiohydrobia* zoogeography is that this genus is represented in many studied habitats by several species, including even relatively small locations. For example, a sample of *Caspiohydrobia* spp. taken by us on 26 July 2022 from Elanach Lake in Kurgan Region of Russia (55.179015N, 67.348671E) consisted of representatives of seven species (identified by S. Andreeva): *C. aralensis*, *C. borealis*, *C. chrysopsis*, *C. johanseni*, *C. kazakhstanica*, *C. oviformis*, and *C. sidorovi*. According to Shishkoedova (2011), the saline Salamatka Lake in the Southern Urals harbors as many as nine species of the genus: *C. aralensis*, *C. chrysopsis*, *C. convexa*, *C. conica*, *C. grimmi*, *C. husainovae*, *C. kazakhstanica*, *C. sidorovi*, and *C. sogdiana*. A similar case of coexistence of several nominal species of *Caspiohydrobia* in a very restricted area was recently discovered in the Caspian Lowland by Andreeva et al. (2020). In all instances, no ecological segregation between coexisting species has been reported. For example, in Elanach Lake, seven species of *Caspiohydrobia* were collected from a very limited area (bottom and surface of aquatic plants) in the shallow zone of the lake, not exceeding 1 m² (Fig. 7). This pattern, in our opinion, fits the hypothesis that most of the nominal species of *Caspiohydrobia* are in fact conspecific, being intraspecific conchological morphs of a few of even a single, very variable and widely distributed species (see Vandendorpe et al., 2019; Wesselingh et al., 2019). However, it remains unclear whether there are other ‘good’ species in this group besides *Ecrobia grimmi* sensu Vandendorpe et al. (2019).

The available data on the structure of the protoconchs, radula and reproductive anatomy of *Caspiohydrobia* seem to be almost useless for species delineation in this genus. Though the protoconchs of representatives of the studied genus demonstrate certain weak differences from each other (see Fig. 5), these differences, in our opinion, are not considerable and there is no any clear pattern allowing one to delimit species on its basis. Filippov & Riedel (2009), having examined and measured 165 protoconchs of *Caspiohydrobia* from the Aral Sea, did not reveal any distinctions among them. According to the authors, “the distribution of all measured parameters of *Caspiohydrobia* shells does not deviate from a Gaussian distribution” (Filippov & Riedel, 2009: 72).

Table 2. Depth preferences of *Caspihydrobia* spp. from the Caspian Sea.

Group of species	Species content
Shallow zone	<i>C. chrysoptis</i> (0–10), <i>C. convexa</i> (0–10), <i>C. subconvexa</i> (0–10)
Eurybathic	<i>C. conica</i> (0–35), <i>C. cylindrica</i> (0–35), <i>C. dubia</i> (0–40), <i>C. eichwaldiana</i> (0–35)*, <i>C. gemmata</i> (0–50), <i>C. oviformis</i> (0–30), <i>C. turrita</i> (0–40)
Deep living	<i>C. curta</i> (10–40), <i>C. grimmi</i> (25–40), <i>C. parva</i> (5–40)

Note. In brackets, depth ranges reported by Logvinenko & Starobogatov (1969), in meters. * In the Black Sea, this species is not registered at depths larger than 10 m (Golikov & Starobogatov, 1966).

The absence of substantial anatomical differences between some species of *Caspihydrobia* was reported by Sitnikova et al. (1992). Here, we illustrate the external appearance of the soft body and the gross morphology of the reproductive system of this genus by example of specimens identified as “*C. johanseni*” (female) and “*C. kazakhstanica*” (males) from Lake Elanach (see Fig. 6). The examination of the radulae of three females from this lake did not reveal any substantial differences (see Figs 5E, G).

Morphology in general provides almost no support for the systematics of the genus, with 30 nominal species, that has long been accepted by Russian malacologists (see also Filippov & Riedel, 2009; Wesselingh et al., 2019). The differences between these species are relatively weak differences in the proportions of their shells and the geometry of the whorl coiling. On the other hand, it is a well-known fact that morphological differences between genetically well-established species of hydrobiid snails can be virtually absent, and the values of quantitative characters of shell can greatly overlap among them. Besides, a comparative statistical study of the inter- and intraspecific variability in *Caspihydrobia*, based on representative samples, has never been undertaken. The extent of conchological and anatomical variability in these microsnailes remains virtually unknown. The possibility that there are a few phenotypically cryptic species among *Caspihydrobia* cannot be ruled out, especially given the fact that only a small fraction of nominal species of this genus has been studied genetically. We think that an integrative revision of the genus as a whole is required to know how many valid species it includes and what their actual ranges are. This research was not aimed at making any decisions about the taxonomic status of the studied taxa.

The ecological preferences of *Caspihydrobia* are relatively little studied. The most detailed information on the ecology of these species is that concerning the depths of their habitat and their salinity tolerance. In the Caspian Sea, species of *Caspihydrobia* inhabit depths up to 50 metres (Table 2), whereas in relatively small continental lakes they can be found alive in great numbers within the first 20–50 cm of the water column.

Possibly the most complete set of ecological information about *Caspihydrobia* is that accumulated by Svetlana Andreeva and the late Nikolai Andreev in the Aral Sea in the 1970s–1980s (briefly reviewed in Andreeva et al., 2020). Their observations are summarised in Table 3. These data were collected during the last decades of the existence of the Aral Sea as a whole waterbody, i.e., before the drastic salination of this lake and the fragmentation of this aquatory, which resulted in its division into a series of isolated basins of different sizes (Andreeva & Andreev, 2003; Krivonogov et al., 2014; Aladin et al., 2022).

Caspihydrobia spp. can withstand a wide salinity range compared to many other gastropod taxa. In the waterbodies of the Southern Urals, these snails occur under salinity conditions varying from 0.7 to 15.5 g/L (Shishkoedova, 2011). In the open Aral Sea, before the start of its desiccation in the 1960s, *Caspihydrobia* were relatively rare (average salinity 10.2 g/L; min–max 4–36 g/L). The progressive increase of salinity resulted in a drastic increase of abundance and biomass of these molluscs in the sea, whereas the maximum abundances of *Caspihydrobia* were observed under average salinity 20–28 g/L (Andreev & Andreeva, 1990a). Their empty shells dominated the coastal thanatocoenoses (Fig. 8). However, when salinity of the Aral Sea reached 40–45 g/L, all species of *Caspihydrobia* went locally extinct (Andreeva et al., 2020). When reared

Table 3. Some ecological characteristics of *Caspiohydrobia* of the Aral Sea (observed in the 1970 – early 1980s).

Species name	Depth range, m	Salinity range, ‰	Substrate	Biotope
<i>C. aralensis</i>	<27.0	14.0–20.0	AP, GS(P), MS, SB	B, C, O
<i>C. behningi</i>	<24.0	14.0–26.0	AP, BS, SB	B, O
<i>C. bergi</i>	<15.0	14.0–21.0	MS, SB	C, I
<i>C. chrysopsis</i>	<24.0	14.0–21.0	AP, GS(P)	B, C, I
<i>C. convexa</i>	2.5–17.0	14.0–20.0	AP, GS(P)	B, C
<i>C. conica</i>	<20.0	14.0–20.0	AP, PD, SB	C
<i>C. curta</i>	9.0–19.0	14.0–16.0	MS, SB	I
<i>C. cylindrica</i>	<21.0	14.0–25.0	AP	B, C, O
<i>C. dubia</i>	12.0–19.0	14.0–15.0	MS, SB	C, I
<i>C. gemmata</i>	<19.0	14.0–17.0	MS, SB	C
<i>C. grimmi</i>	15–21	14.0–16.0	AP, GS(P)	C, O
<i>C. husainovae</i>	<21.0	14.0–26.0	AP, BS	B, C, O
<i>C. kazakhstanica</i>	<27.0	14.0–25.0	GS, PD, SB	C, O
<i>C. nikitinskii</i>	2.0–21.0	14.0–20.0	MS, SB	C, O
<i>C. nikolskii</i>	8.0–15.0	14.0–16.0	SB, MS	I
<i>C. obrutchevi</i>	13.0–20.0	14.0–16.0	GS, SB	I
<i>C. oviformis</i>	<21.0	14.0–20.0	MS, SB	C, O
<i>C. parva</i>	<20.0	14.0–20.0	MS, SB	B, C, O
<i>C. pavlovskii</i>	<20.0	14.0–20.0	AP, S, SB	B, C, I
<i>C. sidorovi</i>	<21.0	14.0–18.0	AP, BS, SB(P)	C, O
<i>C. sogdiana</i>	<16.0	14.0–16.0	AP, S, SB	C, I
<i>C. subconvexa</i>	<21.0	14.0–16.0	MS, SB	C, I, O
<i>C. tadzhikistanica</i>	12.0–24.0	14.0–20.0	BS, GS(P)	O

Abbreviations: AP – surface of aquatic plants; B – bays; BS – brown silt; C – coastal shallow-water zone; GS(P) – gray silt with plant debris; I – off islands; MS – mud bottom with shell remains; O – open sea; PD – plant debris; S – silt; SB – sandy bottom.

in laboratory, these snails demonstrated the ability to live under salinity ranging from 6 to 42 g/L (Andreev & Andreeva, 1990b). Possibly the high halotolerance of the genus in combination with frequent bird-mediated dispersal helped its representatives to form an extensive range and to live in habitats of different types, from relatively small and shallow watercourses and lakes to the largest continental lakes of the world and sea estuaries.

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