The Late Pleistocene mollusk fauna of Selitrennoye (Astrakhan province, Russia): A natural baseline for endemic Caspian Sea faunas

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ABSTRACT

The native Caspian Sea fauna underwent severe changes since the early 20th century, mostly due to anthropogenic activities. However, the nature, magnitude and rate of biodiversity change can only be assessed by comparison with natural baseline settings. A mostly in-situ mollusk fauna retrieved from Late Pleistocene (Hyrcanian, 107 ± 7 ka) deposits at Selitrennoye (Astrakhan province, Russia) provides a snapshot of a natural Caspian assemblage. In total, 24 gastropod and 13 bivalve species were identified. The fauna is predominantly endemic/native (94% in species numbers and 99% in abundance) and is dominated by three families (Cardiidae, Dreissenidae and Hydrobiidae). The Selitrennoye assemblage is a natural baseline of a pre-invasive Caspian Sea fauna living in a shallow (15–25 m), lower mesohaline (5–8 psu) open lake environment. The species-rich Selitrennoye fauna contrasts with the largely depleted and invasive-dominated fauna that currently occupies similar habitats in the Caspian Sea and underlines the magnitude of the current biodiversity crisis.

Introduction

The Caspian Sea (CS) is the Earth's largest inland water body. During the Quaternary, it has had a dynamic history of transgression and regression events (Forte and Cowgill, 2013; Krijgsman et al., 2019 and references therein; Yanina, 2014). While during large parts of the Quaternary it was an isolated sea, such as today, it had episodic connections to the Black Sea. During such highstands, it was considerably larger than today and extended to the North and occasionally to the Aral Sea. In contrast, the CS was a restricted and partly much smaller water body during lowstands (Krijgsman et al., 2019). In response to the dynamic history of the basin, the CS fauna has a long record of diversification and turnover events. Throughout the Quaternary, the fauna was subjected to a constant variation in salinity regimes (Kosarev and Yablonskaya, 1994) and is now characterized by a high degree of endemism (Kostianoy et al., 2010). The estimated number of accepted non-invasive mollusk species living in the CS today stands at 56, of which 49 are endemic (Wesselingh et al., 2019).

Since the early 20th century, native Caspian faunas have undergone dramatic turnover (Karpinsky, 2010a, 2010b; Kosarev and Yablonskaya, 1994; Latypov, 2015). Specifically endemic species were marginalized mostly by human activities, such as the introduction of invasive species, chemical and agricultural pollution and poaching (Dumont, 1995;

Grigorovich et al., 2003; Kosarev and Yablonskaya, 1994; Kostianoy et al., 2010; Rekacewicz and Dejouhanet, 2002; Rodionov, 1994; Stolberg et al., 2013). In many areas, the benthic communities have been almost completely replaced by communities dominated by invasives (Grigorovich et al., 2003; Karpinsky, 2010a; Kosarev and Yablonskaya, 1994; Latypov, 2015; Leroy et al., 2018; Orlova et al., 2005; Rekacewicz and Dejouhanet, 2002; Stolberg et al., 2013; Therriault et al., 2004). Some species were deliberately introduced, such as *Abra segmentum*; others, such as *Mytilaster minimus* and *Mytilopsis leucophaeata*, were accidentally introduced and caused widespread changes in benthic communities (Chepalyga and Tarasov, 1997; Grigorovich et al., 2003; Kosarev and Yablonskaya, 1994; Latypov, 2015). These invasives triggered the demise and, in some cases, the extinction of endemic species (Wesselingh et al., 2019 and references therein).

Understanding the nature and severity of the modern CS biodiversity crisis is hampered by a lack of comparison with natural baseline data (Kostianoy et al., 2010; Rekacewicz and Dejouhanet, 2002), as well as a poorly resolved taxonomy (Wesselingh et al., 2019). A baseline dataset ideally contains a well preserved in situ fauna together with a characterization of the habitat in order to allow comparison with faunas from similar habitats of today. However, no long-term (pre-impact) standardized data sets exist for the CS that allow us to document the nature and severity of biodiversity change of today. Hence, we need alternative approaches to establish a biodiversity baseline for the anthropogenic biodiversity crisis.

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A very well-preserved Late Pleistocene mollusk fauna found along a tributary of the lower Volga River in Astrakhan province (Russia) provides the opportunity to establish a natural baseline for 20th century biodiversity change. The fauna derives from an outcrop below the village of Selitrennoye from an interval attributed to the regional Late Khazarian epoch (Neubauer et al., 2018; Sedaikin, 1988; Svitoch and Yanina, 1997). In the present study, we specify the stage as Hyrcanian. According to the most recent dates based on optically stimulated luminescence, the age of the Hyrcanian transgression is estimated at 107 ± 7 ky (Kurbanov et al., 2018), corresponding to the early Late Pleistocene. The presence of paired bivalves and the excellent preservation imply a largely in-situ fauna. The fauna and sediment characteristics constrain paleoecological properties. The gastropod taxonomy was addressed by the revision of the fauna by Neubauer et al. (2018); here, we investigate the bivalve fauna.

In this paper, we (1) document mollusk species composition and richness of the Selitrennoye fauna along with taxonomic remarks, (2) assess the taphonomic fidelity of the fauna, and (3) characterize the paleoenvironment of the fauna. The established baseline enables comparison with anthropogenically affected CS faunas living in similar environments today, a prerequisite to investigate past and present biodiversity change.

Environmental setting

Today, the Caspian Sea is an isolated, endorheic anomalohaline lake (Fig. 1a). Its lake level (currently at around 27 m below oceanic level) reflects a balance between runoff, precipitation and evaporation (Arpe et al., 2018; Krijgsman et al., 2019). The CS is subdivided into three subbasins. The North Caspian Basin is a shallow shelf area where major rivers such as Volga and Ural strongly determine water properties. Salinities range from 0 psu (practical salinity unit) at river mouths to approximately 10 psu at the transition to the Middle Caspian Basin (Kosarev and Yablonskaya, 1994; Kostianoy et al., 2010). The Middle and South Caspian basins are deep, and salinities range from about 10 to 13 psu (Kostianoy et al., 2010). The CS benthic community is dominated by bivalve mollusks and crustaceans (Kostianoy et al., 2010). Although bivalves have fewer species numbers, they represent >90% of the total benthic biomass (Kosarev and Yablonskaya, 1994; Kostianoy et al., 2010).

During the previous interglacial (MIS5), CS lake levels fluctuated between −50 and +30 m (Krijgsman et al., 2019) and episodically spilled over into the Black Sea (Krijgsman et al., 2019; Svitoch, 2012; Yanina, 2012, 2017). During highstands, the northern Caspian Sea was much larger and the average salinity in the CS was slightly lower, because of the influence of fresh water from the Volga, Terek and other smaller rivers (Yanina, 2012). The Late Khazarian epoch (MIS5) can be subdivided into the late Khazarian stage and the Hyrcanian (or Girkanian) stage. The latter marked the end of two transgressions that occurred during the last interglacial. At the onset of the Hyrcanian, CS water level was above the threshold (around 26 m above sea level) of the Manych-Kerch spillway north of the Caucasus (Fig. 1b), and water flooded from the CS into the Black Sea. The Hyrcanian ended with the MIS4 Atelian regression when CS lake level dropped to about 130 m below oceanic levels (Krijgsman et al., 2019). Although the late Khazarian and the Hyrcanian were two warm-water transgressive basins, climate was already cooling down at the end of the Hyrcanian (Yanina, 2012). Conditions were cooler than today, with smaller seasonal contrasts (Kurbanov et al., 2018).

Methods

Study site and geological context

The study site Selitrennoye (47°10′21.19″ N, 47°26′25.41″ E) is located at the eastern margin of the lower Volga valley (Fig. 1a). The 14 m thick cliff section (Fig. 2) is located next to the Akhtuba River, the eastern branch of the Volga River. During summer, low water levels expose the full outcrop, which consists of a succession of fine sand, silt and clay intervals with variable fossil content. The Hyrcanian level that yielded the mollusk fauna studied herein is located within the basal unit of the outcrop. This 2.5 m thick interval is composed of mostly well sorted, fine-grained sands with dispersed shells and lenses of shells. The presence of wavy bedding and some fine-scale cross-stratification indicates deposition above storm wave base, yet the presence of paired bivalves implies relatively low-energy conditions.

Taphonomy

We washed approximately 5 kg of sediment over a sieve with a mesh size of 0.5 mm. The residue was checked for five different taphonomic criteria: color mixing, fragmentation, dissolution, abrasion, and predation/bio-erosion intensity. Color mixing measures the percentage of shells with colors other than the dominant color. Fragmentation describes the percentage of fragments and broken shells. Dissolution
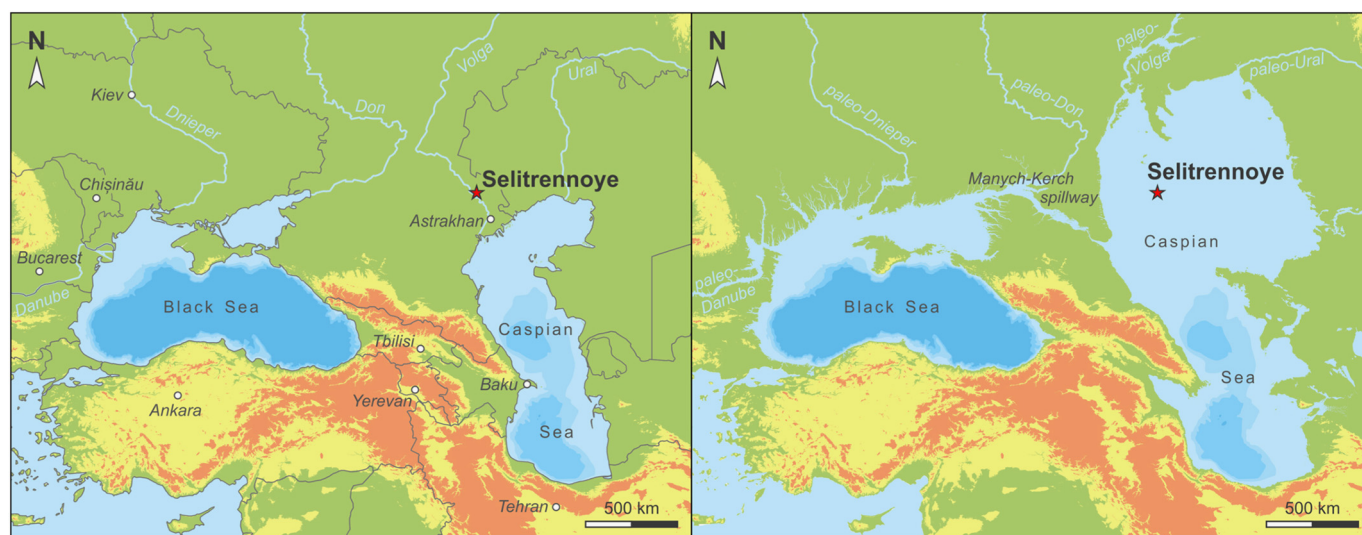

Fig. 1. Caspian Sea today (left panel) and during the Late Pleistocene Hyrcanian regional stage (right panel) (modified after Neubauer et al., 2018). The study site of Selitrennoye is indicated with a red star. Hyrcanian lake level was modeled in ESRI ArcGIS 10.4 based on Krijgsman et al. (2019), who suggested an absolute lake level of 30 m above sea level. (i.e., 57 m higher than today) at that time following Popov (1983). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. Location and section of the Selitrennoye outcrop next to Akhtuba river. Updated from Neubauer et al. (2018) to show new allocation of stratigraphic units.

concerns the shells' majority state of dissolution, including pits or shell layers that have become softened. Abrasion relates to the total percentage of fine details preserved. Predation and bioerosion involves the percentages affected by encrustation (the formation of a crust/hard-coating) or (predatory) borings. The taphonomic signatures were used to assess the fidelity of the Selitrennoye sample, and percentages always concern the whole assemblage. The presence of paired bivalves and the occurrence of juveniles were specifically noted.

Mollusk community

Mollusks were identified to the species level and the amount of individuals per species was counted. The gastropod fauna was already treated by Neubauer et al. (2018), here we provide details on the bivalves. We discuss morphological variation, taxonomic issues and available ecological data for each species identified. All valves and fragments containing more than half the hinge were counted. Each valve accounted for a half individual and numbers were rounded up to the next integer. Selected specimens were photographed with a Zeiss SteREO Discovery.V20 inverted Axiomat microscope using the stacking function for thoroughly focused images. Mollusks that were too big to fit the microscope vision were photographed with a Nikon D70. Shell measurements and abbreviations included: H – maximum height in mm (measured from dorsal margin to ventral margin), L – maximum length in mm (from posterior to anterior margin), LV – left valve, and RV – right valve.

The systematic classification of *Didacna* species follows mostly Nevesskaja (2007); for other bivalve species, we used Bogutskaya et al. (2013), Wesselingh et al. (2019). Synonymy lists provide first descriptions and records with illustrations (Bogutskaya et al., 2013; Kantor and Sysoev, 2006; Nevesskaja, 2007; Wesselingh et al., 2019); further synonymy can be found in Vinarski and Kantor (2016) and Wesselingh et al. (2019).

For the analysis of the mollusk community structure, we combined the data of gastropods (Neubauer et al., 2018) and bivalves. We used R version 3.5.2 (R Core Team, 2018) and the package 'iNext' 2.0.19 (Chao et al., 2014; Hsieh et al., 2016) to perform a rarefaction analysis to estimate the representativeness of the sample (Raup, 1975).

Paleoecology

We used published data on salinity, depth ranges, and habitat substrate available to reconstruct the paleoenvironment (Andreev and Andreeva, 2003; Bogutskaya et al., 2013; Chukhchin, 1984; Glöer, 2002; Grigorovich et al., 2003; Logvinenko and Starobogatov, 1969; Mirzoev and Alekperov, 2017; Mordukhay-Boltovskoy, 1974; Neubauer et al., 2018; Nevesskaja, 2007; Parr et al., 2007; Starobogatov, 1994, 2000; Yanina, 1981). Published information was supplemented with personal observations. For the extinct *Didacna* species, salinity estimates could only be inferred. Today, the salinity range for *Didacna* species is 3–14 psu (Bogutskaya et al., 2013); hence, we estimated salinity ranges for all extinct species accordingly. The depth range of most currently living *Didacna* species is established from 0 to 50 m. Because only few exceptions are known of species living deeper than 70 m (Bogutskaya et al., 2013), we estimated depth ranges for extinct *Didacna* between 0 and 50 m. The estimated maximum salinity for species nowadays living in the Middle and Southern CS basins is 12–13 psu, which relates to the current average salinity in those basins (Kosarev and Yablonskaya, 1994).

Results

Taphonomy

The Selitrennoye mollusk fauna is exceptionally well preserved. The dominating shell color is white, with little admixture of other colors

(5%). The fragmentation rate is low (20%). Individual species with a fragile shell such *Adacna* spp. are mostly broken, but breakage appears to be the result of sample processing. Within the outcrop, these shells were found often complete but with cracks. Overall dissolution density is as low as 5%, with no pits visible, but some of the shells have a rough outer surface that either may result from dissolution, abrasion or both. However, visible abrasion was encountered in <1% of the specimens only. Few individuals with signs of predation or bio-erosion were found (<5%). Of the bivalve species 50% contained paired individuals, which indicates an in-situ fauna. Gastropods altered by taphonomy were very rarely encountered. The preservation of the six non-endemic species (*Esperiana esperi*, *Bithynia* sp., *Lithoglyphus naticoides*, *Valvata piscinalis*, *Anisus* cf. *spirorbis*, *Planorbis* cf. *planorbis*) differs from the endemic Caspian species (Neubauer et al., 2018). They are typical Palearctic fresh water species and were excluded from further analyses (Neubauer et al., 2018).

Fauna composition

We encountered 13 bivalve and 24 gastropod species in the 20,569 counted specimens (Table 1). Both adult and juvenile shells are preserved. The mollusk assemblage is almost fully endemic Pontocaspian (>99% of individuals; Table 1). The majority of the species (90%) are represented by three families: Dreissenidae (3 species), Cardiidae (10 species), and the Hydrobiidae (17 species: see Neubauer et al., 2018). The most abundant bivalve species is *Adacna minima* (4678 individuals) and the most abundant gastropod is *Clessiniola variabilis* (4867 individuals). Twenty-nine of the 37 species are Pontocaspian endemics (sensu Wesselingh et al., 2019), the others are native to the region. Nine species in the sample are represented by less than ten individuals. The rarefaction curve is nearly saturated, suggesting that our sample represents an appropriate estimate of the true richness (Fig. 3).

Paleoenvironment

The fauna from Selitrennoye lived in the open northern CS (Fig. 1b). Autecological data for the mollusk species are listed in Table 2. The gastropod fauna reflects mesohaline (5–13 psu) conditions. Although the majority of bivalves give a similar signal (5–13 psu), a few species show restrictions for their optimal living conditions. *Monodacna caspia* has a maximum salinity preference of 8 psu. Based on current living *Didacna* species a paleosalinity around 8–13 psu is estimated for all *Didacna* species. Though, it is known that in general trigonoid *Didacna* species prefer somewhat less saline waters (Yanina, 2012). Also *D. subcatillus* is reported to have lived in lower saline conditions than most *Didacna* species (Nevesskaja, 1958; Yanina, 2012). Although the preferred salinity ranges of the 31 analyzed in-situ species overlap between 5 and 13 psu, we estimate paleosalinity around 5–8 psu, limited by the salinity preferences of *Monodacna* and *Didacna*. All other species are able to survive under those conditions as well.

In general, the fauna lived on a sandy lake floor. The depth ranges of the most common species overlap between 0 and 45 m. The abundance of the grazing snail *Theodoxus* indicates photic conditions, and sedimentological features indicate current flows and possible winnowing, which suggests a location just above the storm wave base. By taking approximately half the wave length, the storm wave base can be calculated (Stoker, 1947). Currently the wave lengths in the CS fluctuate between 14 m and 50 m, with an average value of 32 m (Hartgerink, 2005). We therefore estimate storm wave base at 16 m. The reported minimum depths for the gastropod species are between 15 m (*Turricaspia pulla*) and 25 m (*Laevicaspia kolesnikoviana*, *Turricaspia andrussowi* and *T. lyrata*). We therefore estimate paleo-water depths at Selitrennoye to be around 15–25 m.

Table 1

Mollusks species list of Selitrennoye, status and number of specimens. Gastropod data from Neubauer et al. (2018). Asterisks mark ex situ species that have been admixed to the fauna.

Species	Family	Status	Number
Adacna laeviuscula (Eichwald, 1829)	Cardiidae	Endemic	30
Adacna minima Ostroumov, 1907	Cardiidae	Endemic	4678
Didacna cristata Bogachev, 1932	Cardiidae	Endemic	14
Didacna ebersini Fedorov, 1953	Cardiidae	Endemic	27
Didacna emendata Popov, 1983	Cardiidae	Endemic	37
Didacna subcatillus Andrussov, 1910	Cardiidae	Endemic	1888
Didacna subcrassa Pravoslavlev, 1939	Cardiidae	Endemic	34
Didacna subpyramidata Pravoslavlev, 1939	Cardiidae	Endemic	10
Hypanis plicata (Eichwald, 1829)	Cardiidae	Endemic	37
Monodacna caspia (Eichwald, 1829) s.l.	Cardiidae	Endemic	867
Monodacna semipellucida (Logvinenko and Starobogatov, 1967)	Cardiidae	Endemic	1
Dreissena caspia Eichwald, 1855	Dreissenidae	Endemic	1620
Dreissena elata Andrusov, 1897	Dreissenidae	Endemic	588
Dreissena grimmi Andrusov, 1890	Dreissenidae	Endemic	105
Theodoxus pallasi Lindholm, 1924	Neritidae	Native	294
Abeskunus brusinianus (Clessin and Dybowski in Dybowski, 1887)	Hydrobiidae	Endemic	489
Andrusovia brusinai Starobogatov, 2000	Hydrobiidae	Endemic	39
Clessiniola variabilis (Eichwald, 1838)	Hydrobiidae	Endemic	4867
Ecrobia cf. *grimmi* (Clessin in Dybowski, 1887)	Hydrobiidae	Endemic	345
Ulskia ulskii (Clessin and Dybowski in Dybowski, 1887)	Hydrobiidae	Endemic	19
Laevicaspia caspia (Eichwald, 1838)	Hydrobiidae	Endemic	300
Laevicaspia cincta (Abich, 1859)	Hydrobiidae	Endemic	174
Laevicaspia conus (Eichwald, 1838)	Hydrobiidae	Endemic	1135
Laevicaspia kolesnikoviana (Logvinenko and Starobogatov in Golikov and Starobogatov, 1966)	Hydrobiidae	Endemic	514
Laevicaspia vinarskii Neubauer et al., 2018	Hydrobiidae	Endemic	9
Turricaspia andrussowi (Dybowski and Grochmalicki, 1915)	Hydrobiidae	Endemic	3
Turricaspia? dimidiata (Eichwald, 1838)	Hydrobiidae	Endemic	1
Turricaspia lyrata (Dybowski and Grochmalicki, 1915)	Hydrobiidae	Endemic	562
Turricaspia meneghiniana (Issel, 1865)	Hydrobiidae	Endemic	248
Turricaspia pulla (Dybowski and Grochmalicki, 1915)	Hydrobiidae	Endemic	186
Turricaspia pullula (Dybowski and Grochmalicki, 1915)	Hydrobiidae	Endemic	1
Turricaspia? spica (Eichwald, 1855)	Hydrobiidae	Endemic	1420
Bithynia sp.	Bithyniidae	*	4
Lithoglyphus naticoides (Pfeiffer, 1828)	Lithoglyphidae	*	1
Esperiana esperi (Férussac, 1823)	Melanopsidae	*	1
Anisus cf. *spirorbis* (Linnaeus, 1758)	Planorbidae	*	13
Planorbis cf. *planorbis* (Linnaeus, 1758)	Planorbidae	*	3
Valvata piscinalis (Müller, 1774)	Valvatidae	*	8

Systematic paleontology

This section provides information on bivalves only; see Neubauer et al. (2018) for notes on the gastropods.

Family Cardiidae

Adacna laeviuscula (Eichwald, 1829) (Fig. 4: 1).

*1829 G.[lycymeris] laeviuscula Eichwald: 279, pl. 5, fig. 1.

1986 *Adacna* (*Adacna*) *laeviuscula* (Eichwald, 1831). – Yakhimovich et al.: 85, pl. 11, fig. 8.

2013 *Adacna laeviuscula* (Eichwald, 1829). – Bogutskaya et al.: 377, fig. 154, photo 48.

Dimensions – max. L 32 mm, H 21 mm.

Characterization – Large, subquadrate to subtrigonal thin-shelled flat cardiid with strong posterior and slight anterior gape; dorsal margins relatively straight; relatively few ribs that are thin in juvenile stages and become very flat and separated by barely perceptible grooves in adult stages; hinge is a mostly edentulous, straight and flat ridge; in juvenile specimens a small cardinal tooth may be present that disappears in adult stages.
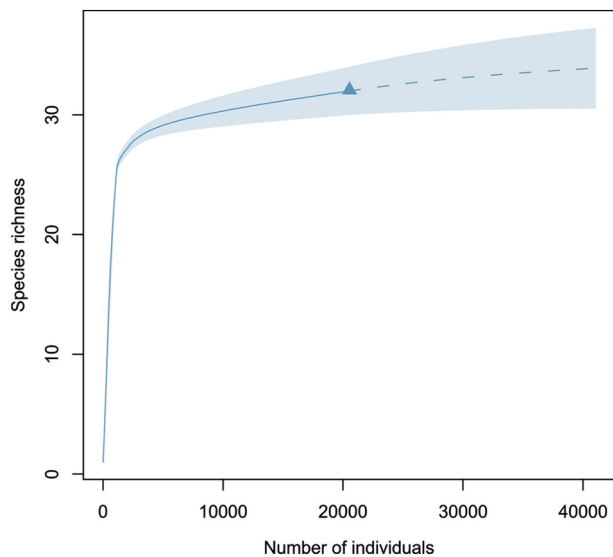
Fig. 3. Rarefaction curve of Selitrennoye diversity with 95% confidence interval and extrapolated richness. The triangle indicates the observed richness.

Ecology – This species has been listed from the entire CS from water depths between 35 and 100 m in salinities of at least 4 psu (Bogutskaya et al., 2013; Logvinenko and Starobogatov, 1969). The common occurrence of fresh, paired specimens on exposed beaches of the middle Caspian (Turali, Russia; Sirvan, Azerbaijan: pers. observ. FW) demonstrates that *A. laeviuscula* has viable populations in foreshore settings above storm wave base indicating shallower habitats than previously reported.

Adacna minima Ostroumov, 1907 (Fig. 4: 2).

*1907 *Adacna minima* Ostroumov: 23, pl. 4, figs. 1–5.

1969 *Adacna minima ostroumovi* Logvinenko and Starobogatov: 338, fig. 354, 3.

2013 *Adacna minima ostroumovi* Logvinenko and Starobogatov, 1969 – Bogutskaya et al.: 378, fig. 146.

Dimensions – max. L 16.5 mm, H 12.7 mm.

Characterization – Relatively small subtriangular to subrounded *Adacna*; shell thin, slightly more convex than other *Adacna* species and in outline resembling some *Monodacna* species, but hinge plate very thin, edentulous with the exception of juvenile stages where a small cardinal tooth in LV can be present that disappears in adult stages; dorsal margins usually more or less straight; ribs low, flat regularly spaced and fading towards anterior and posterior margins; in our material specimens with relatively well developed low ribs to almost smooth specimens and intermediates occur; well-developed growth bands in our material.

Ecology – Species occurs mainly in the middle and south-east of the CS, less often in the north CS (Logvinenko and Starobogatov, 1969). Endemic species living in water with a salinity of at least 5–8 psu, preferably muddy, sandy-muddy and, rarely, sandy bottoms, mainly in the middle and south CS at depths of <40 m (Bogutskaya et al., 2013).

Didacna cristata Bogachev, 1932 (Fig. 5: 6).

*1932 *Didacna praetrigonoides* var. *cristata* Bogachev: 44, pl. 4, figs. 9–14.

1948 *Didacna cristata* Bogachev – Fedorov: 19, pl. 1, figs. 4–6, pl. 2, figs. 4–8.

1953 *Didacna cristata* Bogachev – Fedorov: 127, pl. 16, figs. 1–11.

1983 *Didacna cristata* Bogachev, 1932 – Popov: 201, pl. 12, figs. 9–22.

Dimensions – max. L 19.8 mm, H 16.3 mm.

Characterization – Medium-sized, relatively high, subtrigonate to subovate convex and robust *Didacna*. Beak clearly defined. Posterodorsal margin steep, thin, well delimited. Semidiameter located on posterior ridge that is well developed and sharp. In about half of the specimens two elevated ribs form the posterior ridge. Posterior margin

Table 2

Selitrennoye species list and paleoecological indications as derived from the literature.

References: a Andreev and Andreeva (2003); b Bogutskaya et al. (2013); e Logvinenko and Starobogatov (1969); f Mirzoev and Alekperov (2017); g Nevesskaja (2007); h Neubauer et al. (2018); i Parr et al. (2007); j Mordukhay-Boltovskoy (1974); k Starobogatov (1994); l Starobogatov (2000); n Wesselingh et al. (2019); o Chukhchin (1984).

| Species	Natural salinity ranges (psu)	Environment	Depth (m)
Adacna laeviuscula	min. 5–8[b], 4–14[b], min. 4[e]	Caspian Sea.[b] Muddy, sandy- mud and, rarely, sandy bottoms.[b]	30–100[b,e]
Adacna minima	min. 5–8[b], 14–26[a]	Middle and South Caspian Sea.[b] Muddy and sandy bottoms.[a]	0–35[b]
Didacna cristata	min. 3, max. 14	Caspian Sea[g]	0–50?
Didacna ebersini	min. 3, max. 14	Caspian Sea[g]	0–50?
Didacna emendata	min. 3, max. 14	Caspian Sea[g]	0–50?
Didacna subcatillus	min. 3, max. 14	Caspian Sea[g]	0–50?
Didacna subcrassa	min. 3, max. 14	Caspian Sea[g]	0–50?
Didacna subpyramidata	min. 3, max. 14	Caspian Sea[g]	0–50?
Hypanis plicata	4–8[b,e], max 12–13	Caspian Sea.[b] Silty-sandy, clayey soils, hard aleurites with shell rock.[b]	0–40[b]
Monodacna caspia	min. 2[b], max. 8[b]	Northern Caspian Sea.[b] Muddy and sandy-mud substrates.[b]	0–200[b,e]
Monodacna semipellucida	min. 5–8[b], max. 12–13	Middle Caspian Sea[n]	0–40[b,e]
Dreissena caspia	Optimum 2–8[b], max. 12–13	Caspian Sea.[b,e]	0–40[b,e]
Dreissena elata	Optimum 2–8[b], max. 12–13	Middle and Southern Caspian Sea.[b]	0–40[b,e,n]
Dreissena grimmi	Optimum 2–8[b], max. 12–13	Middle Caspian Sea.[b,k]	35–100[b,k]
Theodoxus pallasi	Optimum 0–8[b], max. 12–13	Caspian Sea.[b] Low salinity seas and large lakes, limans and estuaries.[e,j]	0–40[b,e,j]
Abeskunus brusinianus	min. 5–8[b], max. 12–13	Middle and South Caspian Sea.[b]	0–250[b,e]
Andrusovia brusinai	min. 5–8[b], max. 12–13	Middle and South Caspian Sea.[b,l]	45–311[b,l]
Clessiniola variabilis	Optimum 0–8[b], 5–7[o], max. 12–13	Caspian Sea.[b,f]	0–300[b,e,f]
Ecrobia cf. *grimmi*	min 2–8[b], max. 12–13	Southern Caspian Sea.[b,f]	25–40[b,e]
Laevicaspia caspia	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b]	30–500[b,e,f]
Laevicaspia cincta	min. 5–8[b], max. 12–13	Southern Caspian Sea.[b]	20–>250[b,i]
Laevicaspia conus	min. 5–8[b], max. 12–13	Caspian Sea.[b,f]	0–300[b,e,f]
Laevicaspia kolesnikoviana	min. 5–8[b], max. 12–13	Southern Caspian Sea.[b]	25–400[b,e,f]
Laevicaspia vinarskii	Unknown	Northern Caspian Sea.[h]	Unknown[c,d,m]
Turricaspia andrussowi	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b,f]	25–500[b,e,f]
Turricaspia? dimidiata	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b,f]	35–500[b,e,f]
Turricaspia lyrata	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b,f]	25–50[b,e]
Turricaspia meneghiniana	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b]	0–40[b,e]
Turricaspia pulla	min. 5–8[b], max. 12–13	Middle and Southern Caspian Sea.[b]	15–300[b,e,f]
Turricaspia pullula	min. 5–8[b], max. 12–13	Middle Caspian Sea.[b]	35–100[b,e]
Turricaspia? spica	min. 5–8[b], max. 12–13	Northern and Middle Caspian Sea.[b]	0–40[b,e]
Ulskia ulskii	min. 5–8[b], max. 12–13	Southern Caspian Sea.[b]	35–300[b,e,f]
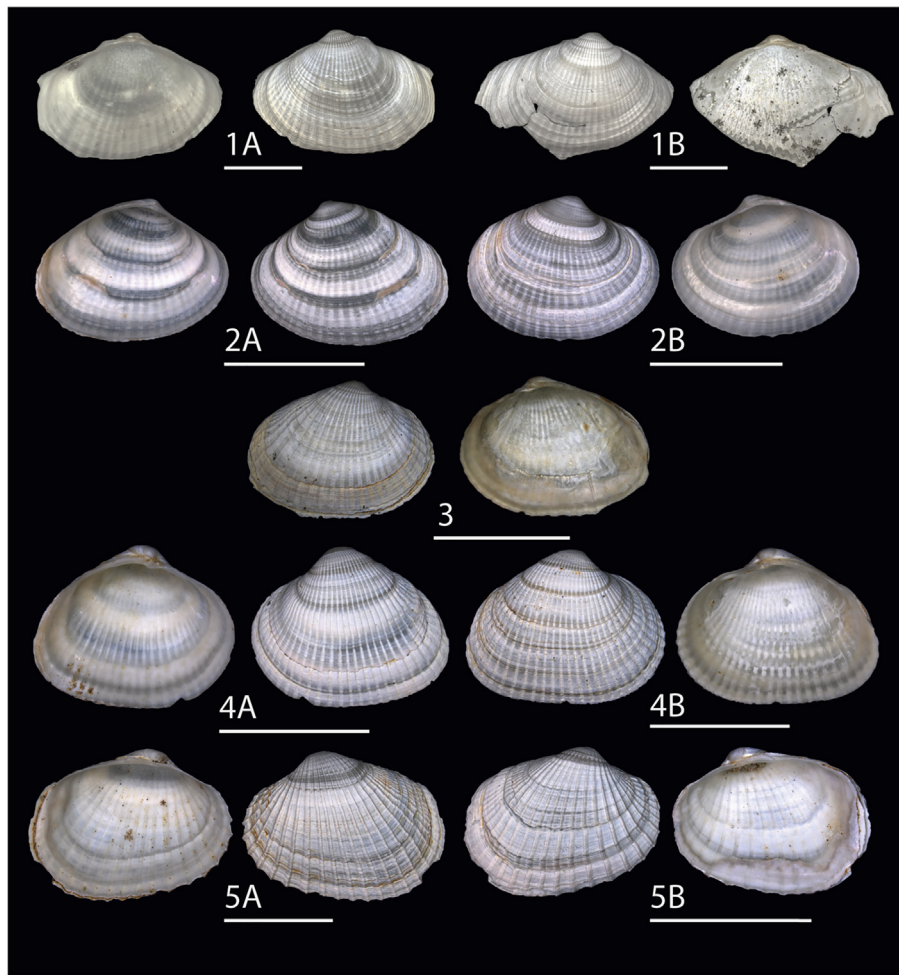
Fig. 4. Cardiidae. (1) *Adacna laeviuscula*; (a) RGM.1309812 LV; (b) RGM.1309813 RV. (2) *Adacna minima*; (A) RGM.1309811 LV; (b) RGM.1309810 RV. (3) *Monodacna semipellucida*, RGM.1309802 RV; (4) *Monodacna caspia* s.l. (a) RGM.1309803 LV; (b) RGM.1309804 RV. (5) *Hypanis plicata*; (a) RGM.1309808 LV (b) RGM.1309809 RV. Scale bars = 1 cm.

rounded angular. Between 15 and 21 posterior ribs that are wide and flat and about three times as wide as the interspaces. Juveniles have a wide trapezoid outline with a rounded lower margin and a subtruncate posterior margin. The hinge plate and cardinal teeth are robust.

Taxonomic notes – Bogachev (1932) distinguished the new variety *D. praetrigonoides* var. *cristata* from typical *D. praetrigonoides* by its smaller size, more triangular outline and sharper keel. Fedorov (1953) showed that the variety not only differs in shape and size from *D. praetrigonoides* but also in its stratigraphic position. While *D. praetrigonoides* is character- istic for the upper Khvalynian deposits, *D. praetrigonoides* var. *cristata* is an index fossil of the lower Khvalynian of the east coast of the Caspian Sea. Fedorov (1953) mentioned that the juvenile *D. praetrigonoides* forms are similar to *D. cristata*. Nevesskaja (1958) disagreed with Fedorov while studying a collection of mollusks from the Khvalynian deposits of West Turkmenistan. She stated that the Khvalynian beds of Turkmenistan yielded relatively small shells (up to 50 mm long), with a well- developed plate like a keel and a small number of ribs (23–27). Nevesskaja (1958) concluded that the variety should not be regarded as a distinct taxon because it only shows the plasticity of the species but can- not be well delineated in time or space (see also Nevesskaja, 2007). In contrast, Popov (1983) supported the opinion of Fedorov (1953) based on a comparative statistical analysis of shell dimensions of *D. cristata* and *D. praetrigonoides* (Table 41 in Popov, 1983). He demonstrated that the differences between *D. cristata* and *D. praetrigonides* were bigger than between many others Quaternary *Didacna* species. Here, we follow the view of Fedorov (1953) and Popov (1983).

Ecology – Unknown (extinct). In general trigonoid *Didacna* species prefer low salinities (Yanina, 2012), but since *D. cristata* is extinct the paleosalinities can only be inferred.

Didacna ebersini Fedorov, 1953 (Fig. 5: 5).

*1953 *Didacna ebersini* Fedorov: 125, pl. 14, fig. 2, fig. 5, and fig. 6 (? non figs. 1, 3, 4).

1999 *Didacna ebersini* Fedorov – Fedorov: pl. 12, fig. 1.

1983 *Didacna ebersini* Fedorov – Popov: 203, pl. 16, figs. 1–16.

2007 *Didacna ebersini* Fedorov, 1953 – Nevesskaja: 931, pl. 20, figs. 6–16.

Dimensions – max. L 19.0 mm, H 14.9 mm.

Characterization – Intermediate-sized, flat and thin shelled broad trigonate *Didacna* with flat ribs; posterodorsal margin is low and in adult stages not well delimited. The posterior ridge is low and subangular and fading during growth. The species have 16–22 posterior ribs. Rib width is somewhat irregular but ribs are about as wide as inter- spaces. In cross-section they are markedly low. Juvenile outline is trigonate with a distinct often double keel forming the posterior ridge. The base of the juveniles is flat to somewhat concave just before the posterior ridge.

Ecology – Unknown (extinct).

Didacna emendata Popov, 1983 (Fig. 5: 4).

*1983 *Didacna delenda emendata* Popov: 174, pl. 6, figs. 8–20.

2007 *Didacna emendata* Popov, 1983 – Nevesskaja: 915, pl. 15, figs. 22-23.

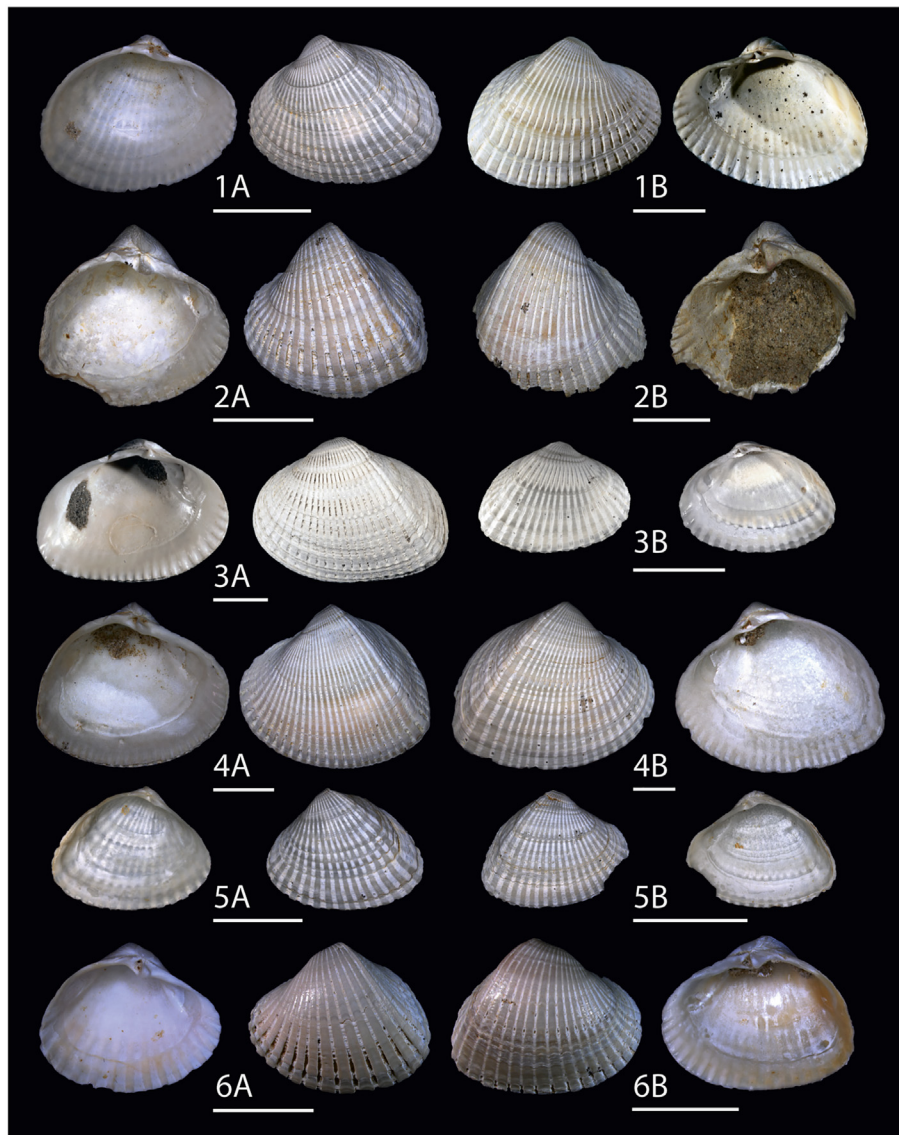*Dimensions* – L 21.2 mm, H 18.3 mm.

Fig. 5. Overview of the Cardiidae. (1) *Didacna subcrassa*; (a) RGM-1309816 LV; (b) RGM-1309815 RV. (2) *Didacna subpyramidata*; (a) RGM-1309797 LV; (b) RGM-1309814 RV. (3) *Didacna subcatillus*; (a) RMG-1309819 LV; (b) RMG-1309820 RV. (4) *Didacna emendata*; (a) RGM-1309799 LV; (b) RGM-1309798 RV. (5) *Didacna ebersini*; A (a) RGM-1309817 LV; (b) RGM-1309818 RV. (6) *Didacna cristata*; (a) RGM.1309800 LV; (b) RGM.1309801 RV. Scale bars = 1 cm.

Characterization – Medium-sized, subrounded-subtrigonate relatively flat to semiconvex, high and thin-shelled *Didacna*. Beak clearly defined but low. Posterodorsal margin steep, broad, well delimited. Semidiameter located on posterior ridge that is well developed and subrounded. Only few of the specimens develop two elevated ribs that form the posterior ridge. Posterior margin subangular to angular. Individuals show 22–28 posterior ribs that are thin and flat and about two times as wide as the interspaces. Juveniles have a high subtrigonate outline with a rounded lower margin and a straight acute posterior ridge resembling the outline of *Parvicardium* species. The hinge plate is narrow, cardinal tooth well developed.

Ecology – Unknown (extinct).

Didacna subcatillus Andrusov, 1910 (Fig. 5: 3, Fig 6: 1-3).

*1910 *Didacna catillus* var. *subcatillus* Andrusov: 78, pl. 9, figs. 22–23.

1953 *Didacna subcatillus* Andrussov – Fedorov: 127, pl. 14, figs. 16–20.

1958 *Didacna subcatillus* Andrussov – Nevesskaja: 24, pl. 3, figs. 1–6.

1986 *Didacna subcatillus* Andrussov, 1910 – Yakhimovich et al.: 84, pl. 4, figs. 3, 4.

2007 *Didacna subcatillus subcatillus* Andrussoff, 1910 – Nevesskaja: 935, pl. 21, figs. 6–14.

Dimensions – max. L 43.4 mm, H 33.8 mm.

Characterization – *Didacna subcatillus* is a broad trapezoid highly variable species that does harbor several specific forms that we could link through intermediates forms in the studied material (Fig. 6: 1–3). The posterodorsal keel is usually low, the posterior margin is rounded. The posterior ridge is pronounced and mostly angular in juvenile stages and can become more subrounded in adult stages. The posterior ribs range between 18 and 25. Interspaces are narrow (about 40–60% of the width of the ribs). Towards the anterior margin ribs become often less pronounced and the posterior rib width and prominence increases towards the posterodorsal ridge. The rib cross-section is irregular, usually flat or subrounded. The location of the semidiameter is on the posterior ridge in juveniles and close to the center of the shell in adults. The ventral half of the shell is typically straight and dipping. Juvenile shells have already a trapezoid to low trigonate outline with a barely rounded lower margin and a well-developed posterodorsal keel. We found strong variations in shell shapes and sizes and investigated the possible presence of sibling (sub-)species. Some individuals grow as large as 43.4 mm (L) × 33.8 mm (H), while 95% of individuals show maximum dimensions of 15 mm (L) × 12 mm (H). One particular phenotype is
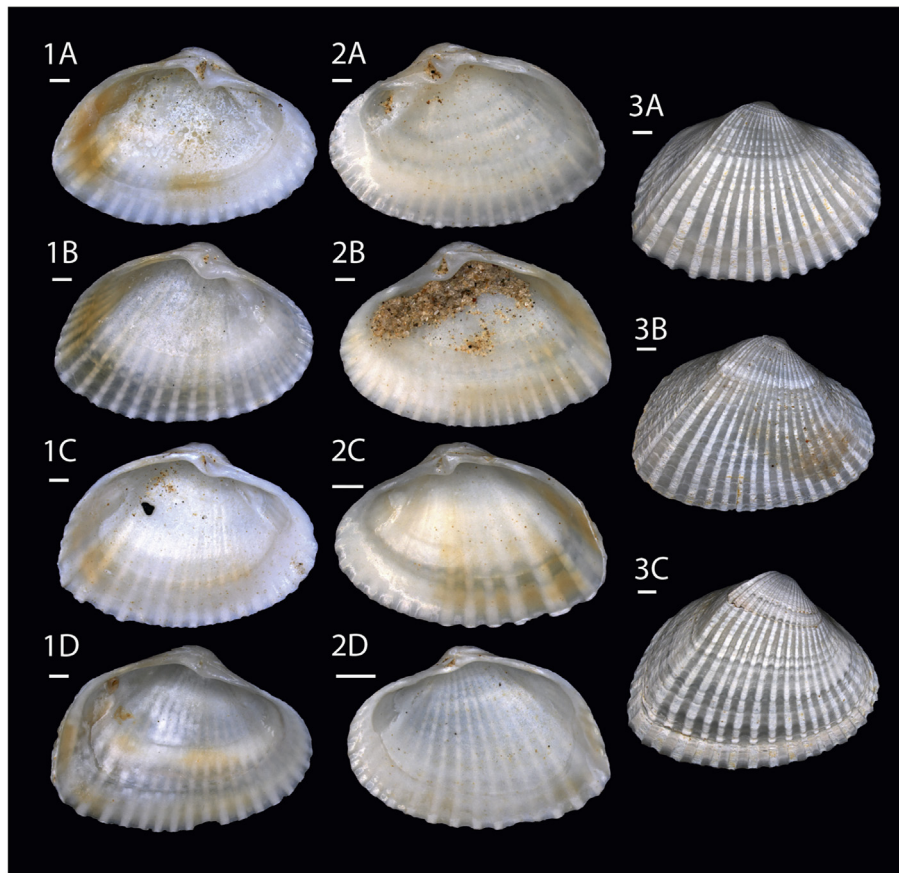
Fig. 6. Shape variation in *Didacna subcatillus* RGM.1310272. (1) Variability of dentition in LV: (a) thick hinge, to (d) thin hinge. (2) Variability of dentition in RV: (a) thick hinge, to (d) thin hinge. (3) Shape variability of LV (a) oval (b) oval/triangular, (c) triangular. Scale bars = 1 mm.

small, has a thick shell that is somewhat convex and has markedly thick hinge plate and teeth and regularly developed ribs that have a more or less rounded cross-section (Fig. 6: 1a, 2a). This form however is connected via intermediates (Fig. 6: 1b, 1c, 2b, 2c) with thin-shelled forms that are less convex and have thinner hinge features (Fig. 6: 1d, 2d).

Taxonomic notes – The various forms of *Didacna subcatillus* have been attributed to a number of species and forms in the past, to which Nevesskaja (2007) attributed biostratigraphic value. However, we were unable to delimit these forms in our variable material (Fig. 8) and consider them synonyms.

Ecology – Unknown (extinct). *Didacna subcatillus* preferred lower saline waters than most *Didacna* species (Nevesskaja, 1958; Yanina, 2012).

Didacna subcrassa Pravoslavlev, 1939 (Fig. 5: 1).
*1939 *Didacna subcrassa* Pravoslavlev: 227, pl. 4, figs. 6–11.
1983 *Didacna subcrassa* Pravoslavlev, 1939 – Popov: 199, pl, 8, figs. 11–16.
2007 *Didacna subcrassa subcrassa* Pravoslavlev, 1939 – Nevesskaja: 920, pl. 16, figs. 14–18.
Dimensions – max. L 32.5 mm, H 25.5 mm.
Characterization – Thin-shelled subtrapezoid to subovate to subtrigonate species, usually flat and trigonoid in juvenile stages. The posterodorsal keel is poorly delimited, the low angle posterior bend is rounded. The posterior ridge is subrounded. It is more pronounced in juvenile stages and fading in adult stages. The species has 19–26 posterior ribs. Interspaces are about half to equal width of the ribs. Anterior ribs are sometimes poorly developed and rib width increases towards the posterior keel. Beak is protruding, the hinge is thin. The location of the semidiameter in juveniles is on the posterior ridge but in adults becomes located towards the center of the shell.

Ecology – Unknown (extinct).
Didacna subpyramidata Pravoslavlev, 1939 (Fig. 5: 2).
*1939 *Didacna subpyramidata* Pravoslavlev: 212, pl. 1, figs. 7–8.
1953 *Didacna subpyramidata* Pravoslavlev, 1939 – Fedorov: 122, pl. 9, figs. 4, 8, pl. 10, figs. 7–10.
1969 *Didacna subpyramidata* Pravoslavlev, 1939 – Vekilov: 83, pl. 14, figs. 1–4.
1983 *Didacna subpyramidata* Pravoslavlev, 1939 – Popov: 198, pl. 7, figs. 1–6.
2007 *Didacna subpyramidata* Pravoslavlev, 1939 – Nevesskaja: 908, pl. 13, figs. 13–18.
Dimensions – max. L 43.8 mm, H 39.5 mm.
Characterization – Large, high, trigonate-convex species with protruding beak; posterodorsal margin very steep and clearly delimited; the posterior ridge is sharp and massive. The species show 17–21 posterior ribs that are typically 2–3 times as wide as the interspaces. The ribs have a subangular to flat-square cross-section. Shells are thick and robust as is the hinge. Outline of juvenile shells is trigonate and very similar as *Didacna emendata* but with fewer ribs.

Ecology – Unknown (extinct).
Hypanis plicata (Eichwald, 1829) (Fig. 4: 5).
*1829 *G.[lycymeris] plicata* Eichwald: 279, pl. 5, fig. 2a–d.
1986 *Adacna* (*Hypanis*) *plicata* (Eichwald, 1829) – Yakhimovich et al.: 85, pl. 7, fig. 2.
2013 *Hypanis plicata* (Eichwald, 1829) – Bogutskaya et al.: 387, fig. 164, photo 56.
Dimensions – Estimated max. L 19.5 mm, H 14 mm (all larger shells in the sample are broken). Logvinenko and Starobogatov (1969) reported L 35 mm and H 26 mm for this species.
Characterization – Thin-shelled, subquadrangular to subelliptical intermediate convex shell with edentulous hinge;

shell flattened; ribs are thin, erect and separated by wide concave interspaces.

Taxonomic notes – In the Northern Caspian, there are sometimes smaller individuals that can resemble somewhat the outline of *Adacna vitrea* forma *glabra*, from which they differ by their well-developed ribs (Logvinenko and Starobogatov, 1969).

Ecology – The species occurs on muddy to sandy-muddy lake floors and shelly firm grounds in the north, middle and south CS (Bogutskaya et al., 2013). Lives down to 30 m water depth in salinities between 4 and 8 psu (Bogutskaya et al., 2013; Logvinenko and Starobogatov, 1969). However, our own observations of *Hypanis* washed ashore along coasts of the Middle and South Caspian basins suggest they may have lived in slightly higher salinities as well.

Monodacna caspia (Eichwald, 1829) s.l. (Fig. 4: 4, Fig. 7: 1).

*1829 C.[orbula] caspia Eichwald: 281, pl. 5, fig. 6.

1986 *Monodacna caspia* (Eichwald), 1938 – Yakhimovich et al.: 84, pl. 12, fig. 12.

2013 *Adacna* (*Monodacna*) *caspia caspia* (Eichwald, 1829) – Bogutskaya et al.: 380, fig. 154.

Dimensions – max. L 23.3 mm, H 18.6 mm.

Characterization – The small-sized cardiid shows a variety of shapes and sizes in our Selitrennoye material. The presence of a series of intermediate morphologies (Fig. 7: 1a–d) suggests a single polymorphic species. All specimens have a single cardinal tooth and lack the lateral tooth that typifies *Monodacna*, yet the thickness and expression of the hinge is extremely variable. A common form is thin-shelled, relatively convex with straight posterior margin and relatively well developed, regularly spaced but thin ribs (Fig. 7: 1c). This shape conforms to shells of *M. caspia* illustrated in Bogutskaya et al. (2013). Another form is flatter, in general slightly thicker shelled and has a distinct wedge-shape (Fig. 7: 1a). Its ribs are lower and slightly more irregular than in the previous form. This wedge-shaped form conforms to several modern *Monodacna* species as reported in Bogutskaya et al. (2013) such as *Monodacna albida* (Logvinenko and Starobogatov, 1967) and *M. polymorpha*

(Logvinenko and Starobogatov, 1967) that have been tentatively grouped into one species by Wesselingh et al. (2019).

Taxonomic notes – Our findings of a large morphological variation in *Monodacna*, with typical forms conforming to modern species but also with all kind of intermediates, either shows that (1) we are dealing with an ancestral species of all or most of the present-day Caspian *Monodacna* species or (2) that several of the present-day species should be regarded as a single species. A combined morphological-molecular approach is required to assess the species delimitations within living faunas.

Ecology – Caspian *Monodacna* species occur in a wide range of habitats today, and given the uncertainty of the identity of these species, it is difficult to report the ecological characteristics. Species live mainly in northern CS on muddy and sandy-muddy substrates at a maximum depth of 40 m (Bogutskaya et al., 2013). *Monodacna* species are filter feeders whose salinity preferences range mostly from 2 to 8 psu (Bogutskaya et al., 2013).

Monodacna semipellucida (Logvinenko and Starobogatov, 1967) (Fig. 4: 3).

*1967 *Hypanis semipellucida* Logvinenko and Starobogatov: 232–233.

1973 *Hypanis semipellucida* Logvinenko and Starobogatov, 1967 – Grossu: 144, fig. 27.

2013 *Adacna* (*Monodacna*) *semipellucida* Logvinenko and Starobogatov, 1967 – Kijashko in Bogutskaya et al.: 384, fig. 161, photo 55.

Dimensions – max. L 23 mm, H 16 mm.

Characterization – This species is relatively thin-walled and low, often has an elliptical outline in adult stages with low, broad and smooth ribs and narrow interspaces. The ribs and interspaces are well visible on the shell's interior. The most distinct character is the cardinal tooth that is a very narrow but well delimited knob that is located well towards the base of the hinge platform.

Ecology – *Monodacna semipellucida* lives in the Middle Caspian Sea (Bogutskaya et al., 2013; Logvinenko and Starobogatov, 1969;
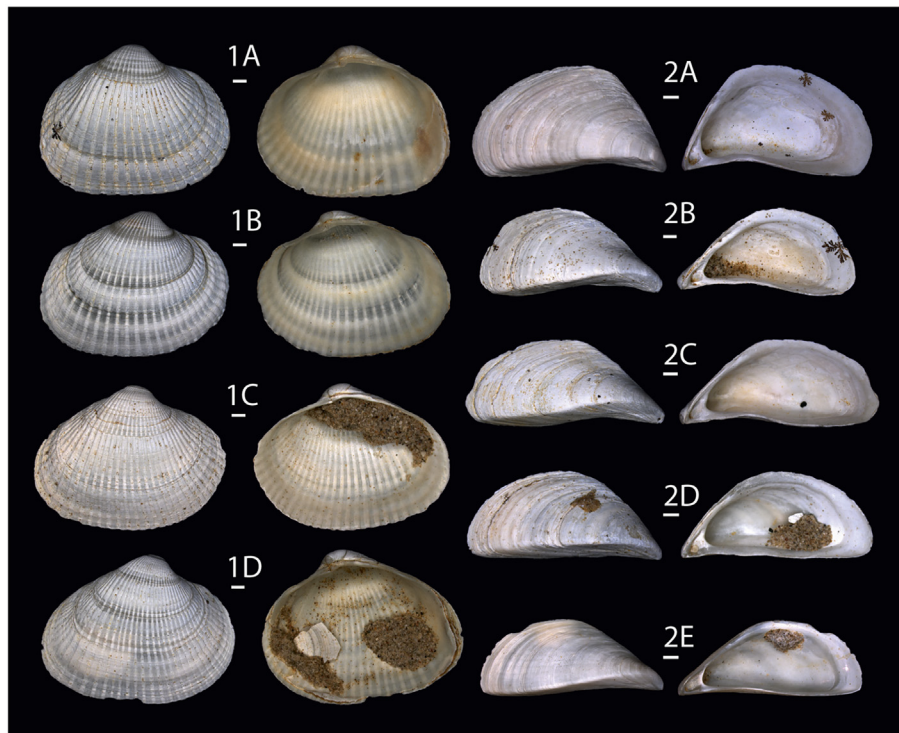

Fig. 7. Plasticity (shape variability) of (1) *Monodacna caspia* RGM.1309807. (a) umbo in the middle, more square (b) umbo not in middle, more round (c) umbo in the middle, oval (d) umbo not in middle, more oval shape. (2) *Dreissena elata*. (a) RGM.1310278 short, curved (b) RGM.1310280 medium, curved (c) RGM.1310280 long, curved (d) RGM.1310280 medium, straight (e) RGM.1310282 long, straight. Scale bars = 1 mm.

Wesselingh et al., 2019), down to 40 m water depth and minimum salinities of 5–8 psu (Bogutskaya et al., 2013; Logvinenko and Starobogatov, 1969).

Family Dreissenidae

Dreissena caspia Eichwald, 1855 (Fig. 8: 1–3).

*1855 *Dreissena caspia* Eichwald: 311–312, pl. 10, figs. 19–21.

2013 *Dreissena caspia* Eichwald, 1855 – Bogutskaya et al.: 321, fig. 109.

Dimensions – max. L 7.4 mm, H 22.7 mm.

Characterization – Elongate, somewhat flat *Dreissena* with rounded margins; keel low or absent resulting in rounded cross-profile. The semidiameter is initially located at the dorsal margin but in sub adult stages crosses to the ventral margin. In adult stages, the semidiameter becomes less pronounced and is located in the middle of the shell. The posterodorsal margin is broadly rounded (and not subangular as in *D. elata*), the posterior margin is rounded and the anterior margin is straight to slightly round. The hinge platform is flat and solid.

Ecology – *Dreissena caspia* is a filter feeder that used to be common all over the CS but is now possibly extinct (Bogutskaya et al., 2013). The species seems to be completely outcompeted by *Mytilaster minimus* (Logvinenko and Starobogatov, 1969). The species was most abundant at depths up to 40 m (Logvinenko and Starobogatov, 1969), and in a salinity range between 2 and 8 psu (Bogutskaya et al., 2013).

Dreissena elata Andrusov, 1897 (Fig. 7: 2, Fig. 8: 4–5).

*1897 *Dreissensia* [sic] *polymorpha* var. *elata* Andrusov: 353, pl. 20, fig. 25.

2013 *Dreissena elata* (Andrusov, 1897) – Bogutskaya et al.: 321, fig. 108.

Dimensions – max. L 9 mm, H 19.4 mm. Logvinenko and Starobogatov (1969) reported H up to 30 mm.

Characterization – Medium- to thick-shelled triangular-shaped *Dreissena* with a wide range of morphologies, ranging from an elongated form (Fig. 8: 4) to a short form (Fig. 8: 5). In general, the valves have a well-developed keel that runs close to the posteroventral margin; the latter is straight or can be concave in its upper half. The initial part of the dorsal margin is flaring and the inflection towards the
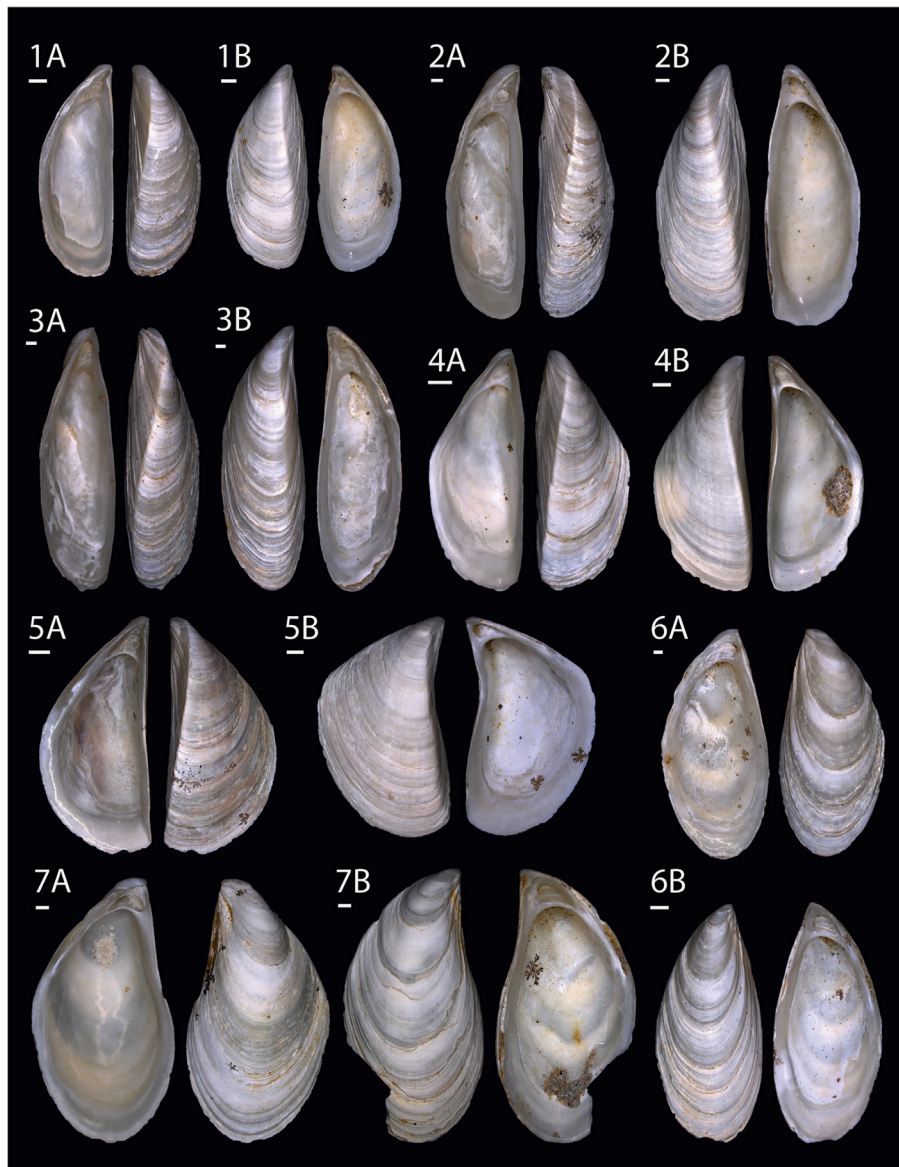

Fig. 8. Dreissenidae. (1–3) *Dreissena caspia* Eichwald, 1855: (1a) RGM.1310289 short type, LV; (1b) RGM.1310288 short type, RV; (2a) RGM.1310286 medium/curved type, LV; (2b) RGM.1310287 medium/curved type, RV; (3a) RGM.1310285 elongated type, LV; (3b) RGM.1310284 elongated type, RV. (4–5) *Dreissena elata* Andrusov, 1897: (4a) RGM.1310283 elongated type, LV; (4b) RGM.1310282 elongated type, RV; (5a) RGM.1310279 short type, LV; (5b) RGM.1310278 short type, RV). (6–7) *Dreissena grimmi* Andrusov, 1890: (6a) RGM.1310276 straight type, LV; (6b) RGM.1310275 straight type, RV; (7a) RGM.1310274 curved type, LV; (7b) RGM.1310273 curved type, RV. Scale bars = 1 mm.

lower dorsal margin is usually well developed. Adult shells can be somewhat flaring. The overall shell is broad and the lower margin is rounded.

Taxonomic notes – The systematics and taxonomy of this species are not resolved. *Dreissena elata* has several characteristics in common with the widespread Eurasian *D. polymorpha* Pallas, 1771 (whose distribution nowadays also includes North America). The Caspian material resembles *D. polymorpha*, especially with regard to shape of the keel, but it is broader, thicker and somewhat flatter. However, also very slender forms exist together with intermediates in the studied material (Fig. 7: 2). Molecular studies would be required to assess whether *D. elata* and *D. polymorpha* are conspecific.

Ecology – Before the introduction of *Mytilaster minimus*, *D. elata* was abundant in the South and Middle Caspian basins at depths of up to 35 m mainly on firm ground and shelly/stony substrate. By now, it is probably extinct (Logvinenko and Starobogatov, 1969). The species occurred in salinities between 2 and 8 psu (Bogutskaya et al., 2013).

Dreissena grimmi Andrusov, 1890 (Fig. 8: 6–7).
*1890 *Dr.*[*eissena*] *Grimmi* Andrusov: 233.
2013 *Dreissena rostriformis* (Deshayes, 1838) – Bogutskaya et al.: 330, fig. 117b.

Dimensions – Max. L 9.9 mm, H 22.5 mm.

Characterization – Relatively flat comma- to tear-shaped *Dreissena* lacking a keel; the ventral margin is somewhat concave in its upper half; often a byssate depression is developed; the line of semidiameter runs in the middle of the shell; the hinge platform is flat, wide and robust.

Taxonomic notes – This species is commonly known as *Dreissena rostriformis* (Deshayes, 1838), a species originally described from Pliocene deposits of Crimea in the Black Sea Basin. Its lectotype (as illustrated in Rosenberg and Ludyanskiy, 1994) shows a different shell shape with almost parallel sides that result in a subquadrangular overall outline. This shape is mirrored by the pallial line on the interior and has not been seen in the drop-shaped outlines of late Quaternary Caspian *Dreissena*. Hence, the name *D. rostriformis* should be abandoned for late Quaternary Caspian material; the next available name is *D. grimmi* (Wesselingh et al., 2019). In addition, the four subspecies described from the CS (Bogutskaya et al., 2013) are likely synonyms as indicated by molecular analyses (Stepien et al., 2013). The latter authors however argue for synonymy with the Black Sea *D. bugensis* Andrusov, 1897. That species has a slight but consistent genetic differentiation but incompatible ecological preferences in the Black Sea Basin compared to the Caspian mussels (e.g. salinity preferences of 0–2 psu versus 7–12 psu; Stepien et al., 2013). The introduction of *D. bugensis* in the Volga catchment in the 1980s has not yet led to reconnection of Caspian population of *D. grimmi* (pers. obs.), hence we consider these species as separate species.

Ecology – *Dreissena grimmi* lives in the Middle and South Caspian Basin at depths between 15 and 300 m water depth and salinities between 7 and 12 psu (Bogutskaya et al., 2013).

Discussion

The taphonomic assessment of the Selitrennoye fauna indicates a very well preserved community that is fit to be used as a natural baseline. The few, rare gastropods that differ in their preservation state represent a different, probably true freshwater habitat and were likely reworked (through bioturbation) from underlying strata or transported to the site by currents. Overall, the taphonomic criteria indicate rapid deposition, little time averaging and little physical disturbance.

The sedimentology, taphonomy and autecology of the fauna allows reconstruction of the paleoenvironments; the studied fauna represents a sandy lake floor assemblage of filter feeders, particle feeders and one herbivore that lived within the photic zone in approximately 15–25 m water depth and lower mesohaline conditions (5–8 psu). During the Hyrcanian stage, the CS level rose, exceeding the CS level of the preceding late Khazarian stage (Kurbanov et al., 2018; Yanina et al., 2017). The

climate was slightly cooler and wetter than during the previous regressive epoch (Yanina et al., 2017). Our salinity approximation matches with the estimated 7–8 psu in the Kerch-Manych strait, where water from the northern CS flowed into the BS (Kurbanov et al., 2018).

Comparison of faunas between Selitrennoye and those of similar environments in the Caspian Sea today give an indication of the magnitude of biodiversity change. Water depths around 15–25 m and salinities around 8 psu occur today at the transition of the North and Middle Caspian Basin, even though the setting is more open towards the deep Middle Caspian basin and wave induced disturbance of the Caspian Sea floor may reach deeper than in Selitrennoye. However, Holocene shelly faunas from these modern environments are different in composition and diversity compared to the Late Pleistocene fauna studied here. A shelly residue from the CS floor on the North-Middle Caspian Basin transition was obtained offshore Kazakhstan during a field campaign 2017 (Fig. 9). The sample is dominated by fresh material of the invasive species *Abra segmentum*, *Cerastoderma glaucum*, and *Mytilaster minimus*, while only very few fresh specimens of very few species of the Pontocaspian endemic complex are present. Similar dominance of Holocene immigrant species and almost entire lack of endemic species has been documented from various localities in the Middle and South Caspian basins (Kosarev and Yablonskaya, 1994; Latypov, 2015; Leroy et al., 2018).

In addition to changing abundances, Late Pleistocene and Holocene Caspian faunas differ in their species compositions, yet with considerable variation among systematic groups. The gastropod fauna and parts of the bivalve fauna (species of *Dreissena*, *Adacna* and *Hypanis*) found in the Late Pleistocene appear the same as those living in the Caspian Sea until the early 20th century (Yanina, 2012). On the contrary, the Late Pleistocene *Didacna* fauna does not contain any species that extends into the Holocene. The complete turnover within the genus *Didacna* has been traditionally used for a detailed biozonation of Quaternary Caspian deposits (Nevesskaja, 2007), yet the apparent stability of all other species is new and in marked contrast.

The stratigraphic age of the Selitrennoye fauna is revised here: the fauna is attributed to the regional Hyrcanian stage (Late Pleistocene, Marine Isotope Stage MIS5d-c). The sample contains a typical Middle-Late Pleistocene Caspian fauna; all genera are known from Khazarian, Hyrcanian and Khvalynian deposits (Krijgsman et al., 2019; Popov, 1983; Yanina, 2017). Previously, the fauna was attributed to the Late Pleistocene (MIS5) Late Khazarian regional stage (Neubauer et al., 2018; Yanina, 2013), but the lack of crassoidal *Didacna* indicator species (*Didacna nalivkini*, *D. delenda*, *D. ovalis*, *D. karabugasica*, *D. subovalis*, *D. ovatocrassa*, *D. schuraosenica*) is at odds with such an attribution. The index species of the Late Khazarian, *Didacna surachanica* (Fedorov, 1957; Nevesskaja, 2007; Yanina, 2005), is also lacking in the material. Of species characteristic of the early Khvalynian (*Didacna ebersini*, *D. parallella*, *D. protracta*, *D. praetrigonoides*, *D. delenda* and *D. zhukovi*) only *Didacna ebersini* is present in the Selitrennoye sample. The Hyrcanian faunas have been reported to contain the following *Didacna* species: *D. subcatillus*, *D. cristata*, *D. schuraosenica*, *D. pallasi* and *D. subcrassa* (Popov, 1983; Yanina, 2017), fitting the fauna reported here very well. Especially the occurrence of *D. cristata* together with *D. subcatillus* is typical for the Hyrcanian period (Popov, 1983). In the literature, it is mentioned that Hyrcanian faunas are often accompanied by the freshwater species *Corbicula fluminalis* (Sorokin et al., 2018; Svitoch, 2008; Yanina, 2012). That species however favors fresh water and very low salinities, well below those reconstructed for the Selitrennoye assemblage.

Outlook

Our approach to characterize composition and diversity in a fossil fauna to establish a baseline for comparison with biodiversity today will need to be extended to other habitats. So far, the Selitrennoye assemblage is the only completely documented Late Pleistocene in situ

Fig. 9. Shelly residue from the Caspian Sea floor on the North-Middle Caspian Basin transition offshore Kazakhstan (44°43.4 N, 50°13.2 E; water depth 8 m). The soft bottom fauna is dominated by Holocene invasives such as (1) *Abra segmentum*, (2) *Cerastoderma* spec. A sensu Wesselingh et al. (2019), and (3) *Mytilaster minimus*. Pontocaspian endemics occur in this sample: (4) *Monodacna albida* s.l., (5) *Didacna* spp., (6) *Dreissena caspia* and (7) *Turricaspia meneghiniana*, yet these all are discolored and presumably pre-20th century).

fauna from the Caspian Sea. Also, Holocene faunas require documentation and characterization for such comparisons. A well-resolved taxonomy is paramount for such studies, which is complicated by the paucity of suitable assemblages and the difficulties in determining species (Neubauer et al., 2018; Wesselingh et al., 2019). Establishing species boundaries is moreover hindered by the lack of live material of many of the modern endemic Caspian species that are necessary for combined molecular, anatomical and morphological analyses (Wesselingh et al., 2019). Shelly assemblages like the one documented here, whose taphonomic fidelity and depositional environment are well-constrained, offer a way forward to document biodiversity change and investigate its drivers. Taphonomic characterization of assemblages is an essential step to identify in-situ assemblages and allow for comparison with (pre-) Holocene baseline samples.

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