A review of the Lake Baikal limpets, family Acroloxidae Thiele, 1931 (Mollusca: Pulmonata: Hygrophila), based on type specimens, with keys to the genera

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Abstract. We provide a comprehensive synopsis of Lake Baikal limpets, including summaries of their taxonomy and nomenclature, with emphasis on the identification of type species. We provide colour photographs of the type specimens of 24 valid species of the family Acroloxidae, including 22 species in 4 endemic or subendemic Baikalian genera, *Pseudancylastrum*, *Frolikhiancylus*, *Gerstfeldtiancylus*, and *Baicalancylus*, and 2 Siberian–Amur species in the Holarctic genus *Acroloxus* inhabiting shallow bays of Lake Baikal. Most of the species were described by the Russian malacologist Yaroslav I. Starobogatov between 1989 and 1991. The type species are stored in the collections of the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), the Limnological Institute of the Siberian Branch of the Russian Academy of Sciences (Irkutsk, Russia), the Zoological Museum of the Ivan Franko National University of Lviv (Ukraine), and the Freie Universität Berlin (Germany). We also present photographs of the holotypes of 2 species described by Starobogatov in 1989 and later synonymized. We provide topotype SEM images of species for which the type specimens are unavailable. Images of the teleoconch ultrastructure of 14 species as well as protoconchs of 11 species have not been published previously. Most of the topotypes are kept in collections of the Senckenberg Naturmuseum (Frankfurt am Main) and the Limnological Institute SB RAS. For each species, we describe their synonymy, type locality, type series, vertical and geographic distribution in Baikal, substrate preferences, ecology in brief (if at all), history of the usage of the name, and taxonomic remarks. We present a new identification key to *Gerstfeldtiancylus* spp. Specifically, we propose new characters, such as radula and jaw structure details, protoconch sculpture types, shell adductor topography, and relative sizes of parts of the male copulatory organ, in addition to traditional characters, such as teleoconch proportions. Identification keys to *Pseudancylastrum* and *Baicalancylus* spp. include well-defined species only.

Key words. Lake Baikal, limpets, Acroloxidae, taxonomy, type specimens, topotypes, identification key.

DOI. https://doi.org/10.1127/arch.moll/146/009-064

Introduction

The first collection of endemic molluscs of Lake Baikal was made by Richard K. Maack, a Russian naturalist, traveler, and teacher, who made 3 large-scale expeditions in Siberia and the Russian Far East between 1854 and 1860. This collection was described by Heinrich N. Gerstfeldt (1859) who accompanied Maack on his travels. Gerstfeldt described 12 species of terrestrial and freshwater molluscs, including 5 endemic Baikal species collected in a near-shore zone of the lake at the head of the Angara River (Sitnikova & Röpstorf 2004). One of these 5 endemic species is the acroloxid "*Ancylus*" *sibiricus,* originally placed in the "familia Limnaeacea" by Gerstfeldt (1859) without indication of the subgenus. He compared the basic shell characteristics with those of *Ancylus fluviatilis* O.F. Müller, 1774 and *Acroloxus lacustris* (Linnaeus, 1758).

DOI 10.1127/arch.moll/146/009-064

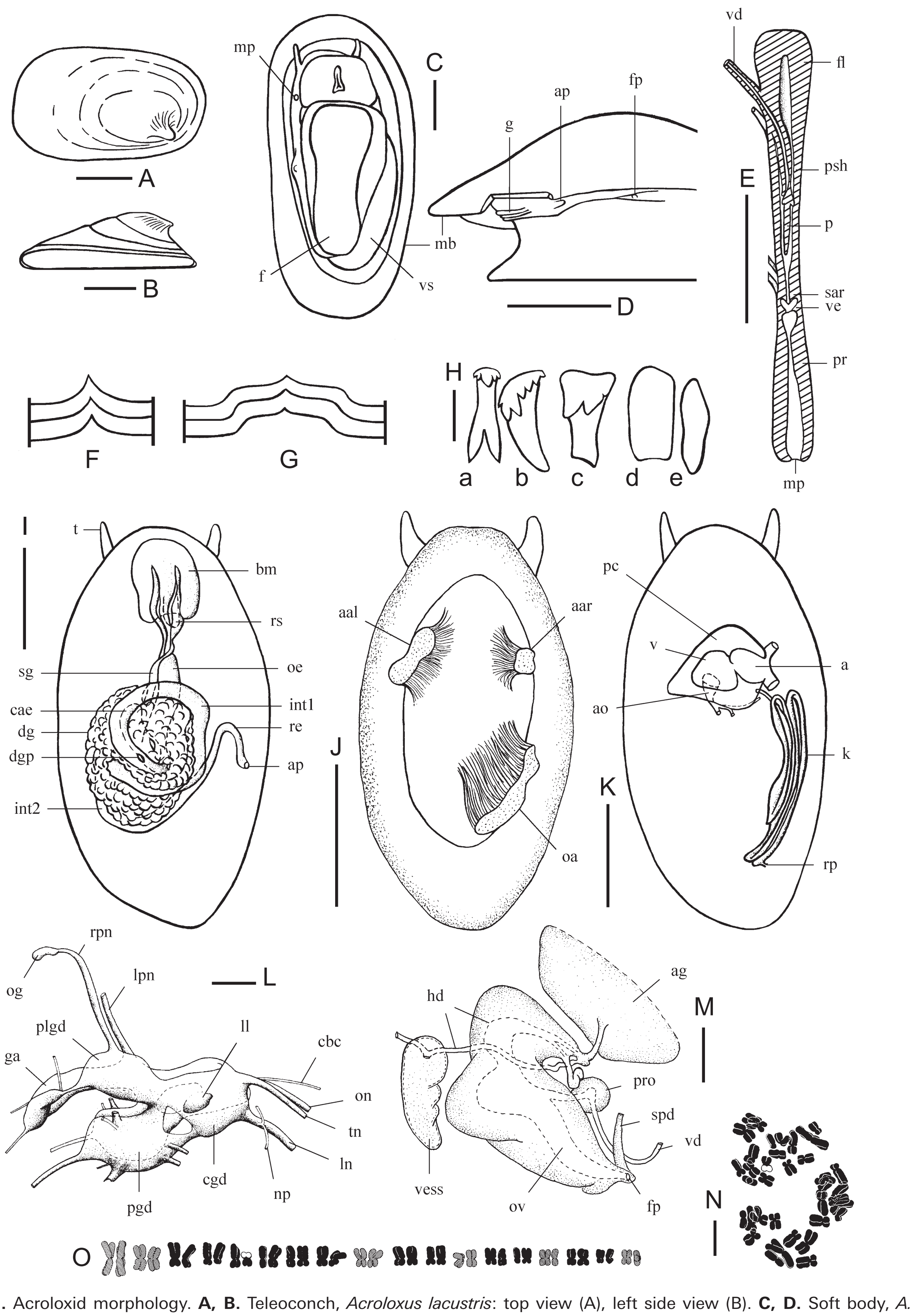

Figure 1. Acroloxid morphology. **A, B.** Teleoconch, *Acroloxus lacustris*: top view (A), left side view (B). **C, D.** Soft body, *A. lacustris*: bottom view (C); right side view (D). **E.** Longitudinally sectioned male copulatory organ, diagrammic, *A. lacustris*. **F, G.** Arrangement of the cross rows from the radula, diagrammic: *Pseudancylastrum* species (= *Ancylus sibiricus* sensu Dybowski 1875) (F); *Gerstfeldtiancylus* s. str. (= *Ancylus troschelii* sensu Dybowski 1875) and *Baicalancylus* species (G). **H.** Teeth: **Ha**, central tooth, *A. lacustris*; **Hb**, lateral teeth, *A. lacustris*; **Hc**, lateral teeth, *Pseudancylastrum* and *Kozhoviancylus* species; **Hd, He**, marginal teeth, *A. lacustris*. **I.** Digestive system, *A. lacustris*. **J.** Shell adductor muscles, *A. lacustris*. **K.** Excretory system and heart, *A. lacustris*. **L.** Central nervous system, right side view, *A. lacustris*. **M.** Central portion of the reproductive system, *A. lacustris*. **N.** Spermatogonial metaphase chromosomes, *A. lacustris*. **O.** Aligned spermatogonial chromosomes, karyogram, *A. lacustris*. Scale bars: length = 1 mm except H = 0.01 mm, L = 0.1 mm, M = 0.2 mm, N = 7 µm. A–E, Ha, Hb, Hd, He, I–M after Hubendick (1962), modified; F, G after Dybowski (1875); Hc after Shirokaya (2005); N, O after Burch (1962).

The other 4 endemic acroloxids, "*Ancylus*" *troschelii*, "*A.*" *renardii*, "*A.*" *kobeltii*, and "*A.*" *laricensis*, were described by Polish naturalist Wladysław Dybowski from 1875 to 1913 based on material collected by his brother Benedykt Dybowski. As a political exile in Kultuk Settlement, Benedykt gathered a rich collection of gastropods, disproving the opinion of zoologists of the time that the Baikal fauna is poor. This collection was sent to Wladysław, an associate professor at Dorpat University, who described most of the species and subspecies (36) as new. The descriptions were accompanied by detailed drawings of shells and, for some species, radulae and egg masses. The accuracy of Dybowski's drawings is so high that these illustrations are still used for identification. Based on the similarity with *A. lacustris* in having a left-shifted apex of the shell and openings of the body, situated on the right side, W. Dybowski (1875) attributed Baikal limpets to the subgenus *Velletia* Gray, 1840 (as "*Veletia*") in the "Sectio Limnophila Martens".

Having studied the molluscan collection of the Zoological Museum of the Imperial Academy of Sciences in Saint Petersburg, the German malacologist Stefan Clessin (1882) found, among other Baikalian limpets, shells from Southern Baikal with extremely left-curving apexes projecting beyond the aperture contour. He newly described them as "*Ancylus*" *dybowskii* and provided colour drawings of teleoconchs. Despite considerable differences in the position of their apexes, Clessin classified Baikalian limpets as belonging to the subgenus *Ancylastrum* Bourguignat, 1853 in the family Ancylidae Rafinesque, 1815.

From 1900 to 1902, during an expedition of the Imperial Academy of Sciences headed by Alexei A. Korotnev, unique material was collected in Lake Baikal. All specimens were transferred to the Zoological Museum of the Imperial Academy of Sciences (Saint Petersburg) and processed by the zoologist Wilhelm A. Lindholm. His work resulted in a monograph on molluscs of Baikal (Lindholm 1909), with descriptions of 48 new species and subspecies, including "*Ancylus*" *boettgerianus* with a costate shell found in Maloye More Strait. Lindholm (1909) thought acroloxids belonged to the family Lymnaeidae Rafinesque, 1815 (as "Limnaeidae"), but separated Baikalian species into a new subgenus, *Pseudancylastrum*.

In the 1930s, Baikalian molluscs were studied by scientists of the Siberian malacological school headed by Mikhail M. Kozhov, an eminent explorer of Lake Baikal and the head of the Zoology Department of the Irkutsk State University. Based on his collections obtained using a dredge and divers, as well as on numerous specimens gathered by the staff of the Baikalian Limnological Station, Kozhov reviewed molluscs of the lake and its adjacent waterbodies. The results were published in the monograph *Molluscs of Lake Baikal* (Kozhov 1936), which is still the only large-scale malacological review containing morphological, biological, and evolutionary data for Baikalian molluscs. Kozhov (1936) described 22 new species and subspecies, including a rare form of *Acroloxus lacustris*, *A. lacustris* var. *baicalensis*, new for the eastern Siberia fauna.

Kozhov (1936) examined acroloxids, at that time considered ancylids, and placed all endemic Baikalian species in the genus *Pseudancylastrum*. Having studied samples containing many specimens from different regions of Baikal, he remarked on the exceptional intraspecific variation of shell shapes in limpets and synonymized some species. In his opinion, the shell of "*Ancylus*" *dybowskii* is "… only an extreme variant of the shell of *Ps. sibiricum* induced by increased height and strong leftward inclination of the apex", whereas "*A.*" *renardi* is "… a form of individual variability of *Ps. troscheli* having no subspecies or race, let alone species status" (Kozhov 1936: 186–188). An analysis of about 100 specimens of costate "*Pseudancylastrum*" from Maloye More Strait and Southern Baikal, adjacent to the head of the Angara River, convinced him of the existence of a single costate species, for which, by priority, he retained the name *P. kobelti*. For 3 species, *P. sibiricum*, *P. troscheli*, and *P. kobelti*, Kozhov (1936) provided detailed descriptions of the horizontal and vertical distribution as well as the type of substrate. These same 3 species were subsequently mentioned in reviews of the Russian freshwater malacofauna by Vladimir I. Shadin as *Ancylus* O.F. Müller, 1773 (Shadin 1940) or as *Pseudancylastrum* (Shadin 1952).

The first anatomical data for Baikalian limpets were obtained by Swedish malacologist Bengt Hubendick (1962, 1969), who thoroughly examined their radula, as well as digestive, muscular, excretory, and reproductive systems, based on material provided by Kozhov, S.M. Popova, and Ya.I. Starobogatov. Unlike Kozhov, he considered "*A.*" *boettgerianus* and "*A.*" *kobeltii* 2 separate species and therefore recognized 4 species. The diagnoses presented by Hubendick (1969) were accompanied by excellent microscopic drawings, sometimes (e.g., with respect to the protoconch sculpture) comparable in detail to modern SEM images. In Hubendick's opinion, there was no justification for the separation of Baikalian species into the genus (or subgenus) *Pseudancylastrum*. He assigned all Baikalian limpets to the Holarctic genus *Acroloxus* Beck, 1837, family Acroloxidae.

The idea of an isolated position of acroloxids within freshwater pulmonates was first proposed by Bondesen (1950). Based on peculiarities of the egg cluster morphology, he transferred *Acroloxus* from Ancylidae to a separate family. The opinion of Bondesen was supported by Burch (1961, 1962), who studied the number and size of chromosomes in the haploid set of *A. lacustris*, as well as by Hubendick (1962, 1965), who revealed differences in the structure of digestive and reproductive systems of acroloxids. Acroloxidae anatomy is shown in Figure 1.

The taxonomic system of Acroloxidae was drastically revised by the Russian zoologist Ya.I. Starobogatov, who participated in 3 circum-Baikal expeditions of the Biological–Geographic Research Institute at Irkutsk State University and formed an extensive mollusc collection.

His work on acroloxids was based mostly on collections of the Zoological Institute of Russian Academy of Sciences, Saint Petersburg (ZIN), collected in Lake Baikal over more than a hundred years. First, Starobogatov (1967) proposed the endemic subgenus *Baicalancylus*, with "*Ancylus*" *laricensis* as the type species. Later, he found that *Pseudancylastrum sibiricum* and *P. troschelii* can be easily discriminated by shell shape and are so dissimilar with respect to reproductive system structure that they merit assignment into separate genera (Starobogatov 1989); the evident shell variation indicates the existence of far more species in Lake Baikal. Using his "comparative" (or template) method (Starobogatov & Tolstikova 1986), Starobogatov found 25 limpet species in Baikal, including 1 widespread species of the genus *Acroloxus* and 24 endemic species allocated to 3 genera (i.e., *Pseudancylastrum* Lindholm, 1909 [12 spp.], *Gerstfeldtiancylus* Starobogatov, 1989 [8 spp.], and *Baicalancylus* Starobogatov, 1967 [4 spp.]). According to Starobogatov (1970, 1989), all 3 genera are endemic to Baikal, though some authors (Zilch 1959–1960, Clarke 1970, 1973) include fossil European Upper Cretaceous acroloxids in the genus *Pseudancylastrum*.

The lack of ethanol-fixed materials prevented Ya.I. Starobogatov from studying in detail any anatomical differences between similar acroloxid species. Therefore, he used anatomical data only for genus-level diagnoses. Later, another Russian malacologist, Nikolai D. Kruglov, studied the structure of the male copulatory organ in 14 acroloxid species. He subdivided both *Pseudancylastrum* and *Gerstfeldtiancylus* each into 2 subgenera (Kruglov & Starobogatov 1991b), having proved that closely related limpet species exhibit different size ratios between parts of the male copulatory organ.

All subsequent studies of Baikalian acroloxids (1993–2016) were made by researchers of the Limnological Institute of the SB RAS, sometimes in cooperation with German colleagues from the Justus-Liebig-Universität (Giessen) and Freie Universität Berlin or with Russian scientists from the Institute of General and Experimental Biology of the SB RAS (Ulan-Ude) and the Institute of Biology and Soil Science, FEB RAS (now, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences, Vladivostok). Modern methods have been used, for example, scanning electron microscopy to analyze the protoconch and radula structures, and karyological and molecular approaches combined with the investigation of the microdistribution of invertebrates on various hard substrates using the "stone-unit" method, as suggested by Nakashizuka & Stork (2002). As a result, 3 new species and 1 new genus were described (Sitnikova et al. 1993, Shirokaya et al. 2003, Shirokaya 2007, Stelbrink et al. 2015), 1 limpet species previously undetected in the lake was recorded (Shirokaya et al. 2009), and 2 species were synonymized (Shirokaya 2005). The spatial distribution, macro- and fine-scale biotopical properties, and seasonal and annual dynamics of density and biomass were described (Shirokaya et al. 2008, Sitnikova et al. 2010, Maximova et al. 2012). The morphology of egg masses, duration of embryogenesis, and feeding range of Baikalian limpets have also been studied (Röpstorf et al. 2003, Shirokaya 2003, Shirokaya & Röpstorf 2003, Sitnikova & Shirokaya 2013). Mixoploidy has been found in some littoral acroloxids (Ostrovskaya et al. 2004). Based on nuclear and mitochondrial genome data, the timing of diversification events for endemic Baikalian limpets has been revealed (Albrecht et al. 2007, Stelbrink et al. 2015).

Presently, 27 species of the family Acroloxidae are known from Lake Baikal. Two of these are Siberian–Amur species belonging to the genus *Acroloxus*, 8 are subendemic species inhabiting Baikal and the Angara River, and 17 species are endemic to the lake (Table 1) (Starobogatov 1989, Kozhova & Erbaeva 1998, Shirokaya et al. 2008).

The taxonomic system of gastropods of Eurasian continental waterbodies developed by Starobogatov between 1970–2004 is widely used by Russian malacologists but has not been adopted in Western Europe (Bank et al. 2001, Falkner et al. 2001, Glöer 2002). Its application is limited by the lack of good illustrations of type specimens. In recent years, Russian malacologists have published on a number of molluscan types from European museums, including those of Jules-René Bourguignat in Geneva, Jacques P.R. Draparnaud in Vienna, Eduard von Martens in Berlin, O.F. Müller in Copenhagen, and Carl A. Westerlund in Stockholm and Göteborg (Glöer & Vinarski 2009, Lazutkina et al. 2009, 2010, Vinarski & Glöer 2009, Sitnikova et al. 2012, Vinarski et al. 2013, Nekhaev et al. 2015, Vinarski 2016, Vinarski & Eschner 2016), as well as types of freshwater pulmonates described by Ya.I. Starobogatov and others and stored in the ZIN (Vinarski 2009, Vinarski et al. 2012, 2013, Sitnikova et al. 2014a, b, c). Despite numerous publications on Baikalian limpets (see "History of the usage of the name" in the sections below), types of most acroloxid species are still illustrated by schematic pictures or line drawings (Starobogatov 1989), seriously hampering species identification.

When studying type series of acroloxids stored in the ZIN, we found that some specimens are partially or completely destroyed. This is probably attributed to their primary fixation with formaldehyde and subsequent transfer into ethyl alcohol. Shell surfaces preserved in ethanol become covered with crystals and flakes sedimented during fixation, and the shells become soft and decalcified (e.g., Figs 5E, 10Ea). Type specimens of some species are represented by dried shells without bodies or with dried bodies, which prevents comparisons of anatomical details among species with similar shells.

Another explanation for the lack of acceptance of Starobogatov's system is that conchological descriptions used only his comparative method (Starobogatov

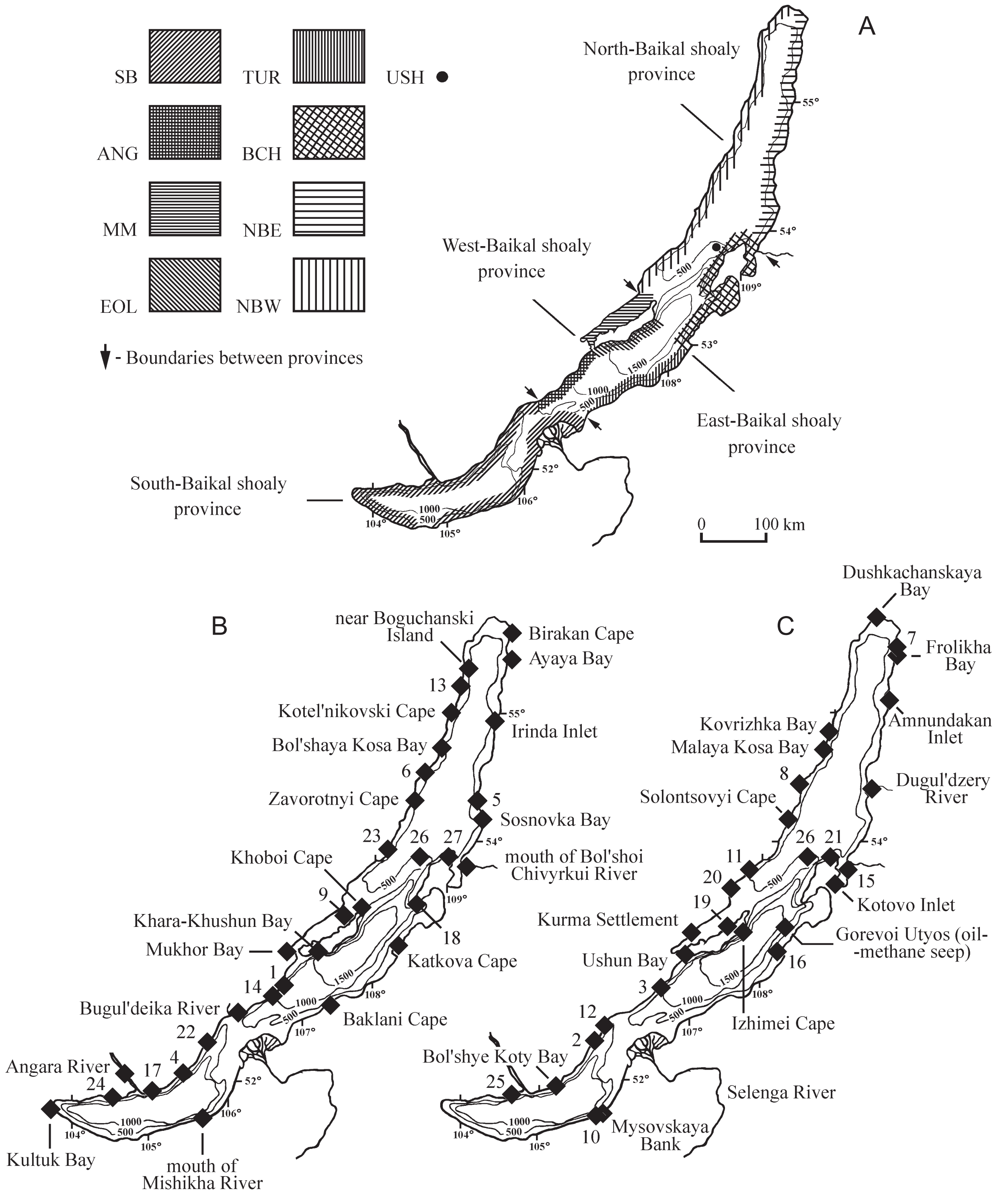

Figure 2. Schematic maps of Lake Baikal. **A.** Geographical regions of 4 shallow-water (0–100 m) provinces. The boundaries of the provinces and regions are indicated according to Starobogatov (1970), modified by Sitnikova (2006). Regions: South-Baikal (SB), Anginski (ANG), Malomorski (MM), East-Ol'khon (EOL), Turkinski (TUR), Barguzin-Chivyrkui (BCH), North-Baikal, eastern coast (NBE), North-Baikal, western coast (NBW), Ushkanski (USH). **B, C.** Localities of acroloxid species, after Shirokaya (2007, 2008), with additions: 1, Aya Bay (vicinity: Ulannur Cape); 2, Babushka Bay; 3, Birkhin Bay (vicinity: Khabsagai Cape); 4, near Bol'shoye Goloustnoye Settlement; 5, Davshe Bay; 6, Elokhin Cape; 7, Ireksokon Cape; 8, Kedrovyi Cape; 9, Khora-Undurskaya Inlet; 10, Klyuevka Settlement; 11, Kocherikovski Cape; 12, Krasnyi Yar Cape I, South Baikal; 13, Krasnyi Yar Cape II, North Baikal; 14, Krestovyi Cape; 15, Krutaya Inlet (vicinity: Malyi Kyltygei Island); 16, Listvennichnyi Island; 17, near Listvyanka Settlement (vicinities: Beriozovyi Cape and Baranchick Valley); 18, Nizhnee Izgolovie Cape, Svyatoi Nos Peninsula; 19, Njurgon Cape; 20, Ongurion Cape; 21, Orlovski Cape; 22, Peschanaya Bay (vicinity: Dyrovatyi Cape); 23, Pokojniki Cape; 24; Shumikha River (vicinity: Khabartui Cape); 25, Tolstyi Cape; 26, Ushkanji Islands; 27, Verkhnee Izgolovie Cape, Svyatoi Nos Peninsula; Boguchanski Island vicinity: Boguchanskaya Inlet; Bol'shye Koty Settlement vicinities: Sennaya Rivulet, Sennaya Valley, Malye Koty Valley, Varnachka Valley, and Zhilistsche Valley; Irinda Inlet vicinity: Pongonje Cape; Kotovo Inlet vicinity: a channel, connecting the Chivyrkui Bay with Lake Arangatui; Kultuk Settlement vicinity: Shaman Cape.

Table 1. Data on specimens Lake Baikal and Angara River Acroloxidae kept in scientific collections.

Museum or institution	Total no. of specimens	No. of type specimens	No. of specimens, ethanol preserved/dry	Acroloxid species	Zoogeographical status (Shirokaya 2005)
Zoological Institute of Russian Academy of Sciences (Saint Petersburg, Russia)	509	446[1]	334/175	*Acroloxus baicalensis* *A. orientalis* *Pseudancylastrum sibiricum* *P. beckmanae* *P. dybowskii* *P. olgae* *P. cornu* *P. korotnevi* *P. werestschagini* *"P." troschelii* *P. aculiferum* *P. poberezhnyi* *P. dorogostajskii* *P. irindaense* *Gerstfeldtiancylus gerstfeldti* *G. renardii* *G. kozhovi* *G. kotyensis* *G. ushunensis* *G. benedictiae* *G. capuliformis* *G. porfirievae* *G. pileolus* *Baicalancylus laricensis* *B. boettgerianus* *B. njurgonicus* *B. kobeltii*	Siberian-Amur Siberian-Amur Baikal subendemic Baikal subendemic Baikal subendemic Baikal endemic Baikal subendemic Baikal endemic Baikal subendemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic — Baikal subendemic — Baikal endemic Baikal endemic Baikal subendemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal subendemic
Limnological Institute, Siberian Branch of the Russian Academy of Sciences (Irkutsk, Russia)	104[2]	25	99/5	*F. frolikhae* *G. roepstorfi* *G. ushunensis*	Baikal endemic Baikal endemic Baikal endemic
Tomsk State Pedagogical University (Tomsk, Russia)	10	0	10/0	*A. baicalensis*	Siberian-Amur
Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (Vladivostok, Russia)	28	0	25/3	*A. orientalis*	Siberian-Amur
Benedykt Dybowski Zoological Museum, Ivan Franko National University of Lviv (Lviv, Ukraine)	86	2	0/86	*G. renardii* *"Ancylus" sibiricus* sensu W. Dybowski (lot includes several spp.) *P. sibiricum*	Baikal subendemic — Baikal subendemic
Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt am Main, Germany)	48 (most specimens are topotypes)	0	0/48	*P. sibiricum* *P. dybowskii* *P. olgae* *P. cornu* *P. korotnevi* *P. werestschagini* *"P." troschelii* *P. aculiferum* *P. poberezhnyi* *P. irindaense* *G. capuliformis* *G. porfirievae* *G. pileolus* *B. laricensis* *B. boettgerianus* *B. njurgonicus*	Baikal subendemic Baikal subendemic Baikal endemic Baikal subendemic Baikal endemic Baikal subendemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic Baikal endemic
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung (Berlin, Germany)	3	0	0/3	*F. frolikhae*	Baikal endemic
Institute of Geological Sciences, Freie Universität Berlin	13[3]	1	0/13	*P. sibiricum* *P. beckmanae* *P. dorogostajskii* *G. renardii* *G. kotyensis* *G. roepstorfi* *G. benedictiae* *B. boettgerianus* *B. kobeltii*	Baikal subendemic Baikal subendemic Baikal endemic Baikal subendemic Baikal endemic Baikal endemic Baikal subendemic Baikal endemic Baikal subendemic

[1]According to the ZIN systematic catalogue, 447 type specimens of Baikalian acroloxids are stored in the ZIN collection. One of 15 paralectotypes of *Baicalancylus boettgerianus*, ZIN 11/359-1935, was re-determined by Starobogatov (1989) as *B. laricensis* (non-type specimen ZIN 2/359-1935).
[2]The number of voucher specimens used in morphological study is given. The LIN collection includes c. 3,000 acroloxid specimens belonging to 27 species.
[3]Twelve shells and 1 radula preparation (SEM stubs).

& Tolstikova 1986). Unlike landmark approaches used by Western taxonomists (Conde-Padín et al. 2009, Dillon et al. 2013, Smith & Hendricks 2013, Butlin et al. 2014, Ross et al. 2014), this method allows for comparisons of shell geometry only in typical individuals of a species, morphologically similar to the holotype, and does not account for variation in shell shape. There are still no integrated keys that consider characters of embryonic and adult shells, molluscan anatomy, and peculiarities related to their distribution and ecology. This hampers the identification of sympatric species with similar teleoconchs.

Thus, our main aims are as follows: 1) to present colour photographs of the type specimens of Baikalian acroloxid species; 2) to provide SEM images of shells and radulae of topotypes and easily identified specimens, collected outside the type locality; 3) to compile references for the entire accumulated literature on Baikalian acroloxids; 4) to outline briefly the current taxonomic system, with problematic species highlighted; and 5) to develop dichotomous keys for the identification of acroloxid species or species groups inhabiting Lake Baikal.

Material and Methods

Materials examined. Materials for this work were obtained from molluscan collections stored in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (ZIN); Limnological Institute, Siberian Branch of the Russian Academy of Sciences, Irkutsk (LIN); the Benedykt Dybowski Zoological Museum, Ivan Franko National University of Lviv (ZMD); Tomsk State Pedagogical University (TSPU); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences, Vladivostok (FSCB); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); Institute of Geological Sciences, Freie Universität Berlin; and Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (ZMB) (Tables 1, 2).

In total, c. 3,000 specimens from the 3 Baikal basins were studied (Fig. 2), including 474 primary type specimens. Twenty-nine acroloxid species were studied, including 27 considered valid since Shirokaya (2005, 2007). Of these, 16 are endemic littoral species, 1 is an endemic abyssal species, 8 are subendemic littoral species also in the upper reach of the Angara River, and 2 are shallow-water non-endemic species. The type specimens kept in ZIN, including species synonymized after the revision of Starobogatov (1989), are summarized in accordance with the systematic catalogue of that institute.

We should briefly mention the system of inventory numbers used in the ZIN mollusc collection. In the late 19th century a card systematic catalogue was started (probably by Nikolai M. Knipovich and Solomon M. Herzenstein). For each species, a separate card, with several entries, was made and the locality and the identifier were cited for each sample. Thus, each sample was given a number which was unique only within a single species. Usually the card began with the accession of the type specimens, and therefore, most types are no. 1, but if the type specimens are absent, other, non-type specimens are no. 1. In the collection the lots are arranged taxonomically in accordance with the systematic catalogue numbers. Starting in the 1960s, a system of inventory numbers was initiated. These numbers were attributed to lots but not in taxonomic order. However, this work is incomplete, and inventory numbers are only available for most of the samples of marine gastropods and bivalves. Furthermore, samples accepted for storage in the ZIN collection are recorded with separate numbers in a book of accepted samples. Because freshwater and land molluscs in the collection have not yet been provided with inventory numbers, we give the ZIN no. ** (** = number in systematic catalogue) or ZIN **/** (** = numbers in systematic catalogue and the book of accepted samples). For example, ZIN no. 1 or ZIN 1/563-1995. Double numeration for the type specimens is obligatory.

Methods. Limpet shells were photographed in colour using the following digital cameras: Canon EOS 450D (Tokyo, Japan) with a macrolens (Canon Macro MP-E 65 mm), Canon EOS 60D with a universal optical adapter for reflex cameras mounted on a stereo microscope (LOMO MSP-2), and Panasonic Lumix DMC-FZ30 (Osaka, Japan).

For species identification, the measuring system suggested by Kruglov & Starobogatov (1991a) was used, in addition to Starobogatov's visual method for shell comparisons with holotype outlines using an MBS-1 stereomicroscope (LOMO PLC) connected to a camera

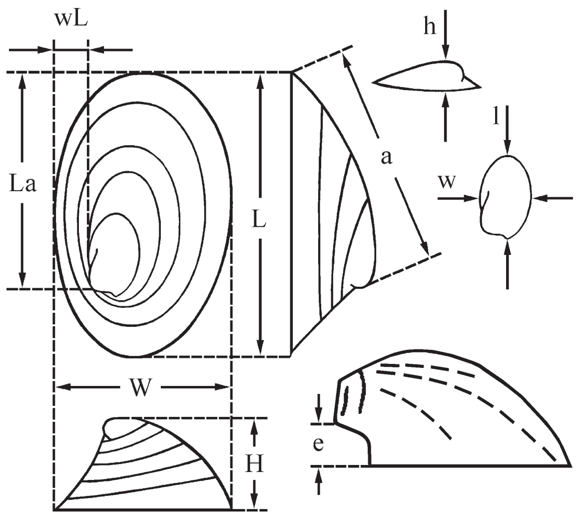

Figure 3. Measurements of an acroloxid shell, after Starobogatov (1989), Kruglov & Starobogatov (1991a), modified: L, length of aperture; La, distance from apex to the frontal apertural edge, projected on longitudinal axis of aperture; W, width of aperture; wL, distance from apex to left apertural edge; H, height of teleoconch; a, chord of longest slope; e, elevation of apex above apertural plane; l, length of protoconch; w, width of protoconch; h, height of protoconch.

Table 2. Compiled data on measurements (in mm) and indices of teleoconchs of the 2 acroloxid species, *Acroloxus baicalensis* and *A. orientalis*.

Source	Species (type)	L	La	W	wL	H	a	W/L	H/L	H/W	La/L	wL/W
Kozhov (1936)	*Acroloxus baicalensis* (holotype)	3.6	–	2.1	–	1.2	–	0.58	0.33	0.57	–	–
Shirokaya & Prozorova (original data)	*A. baicalensis* (neotype)	4.10	2.90	2.37	0.82	1.34	3.03	0.58	0.33	0.57	0.71	0.35
Kruglov & Starobogatov (1991a)	*A. orientalis* (holotype)	5.60	3.30	2.50	1.10	1.90	3.50	0.45	0.34	0.76	0.59	0.44
	A. orientalis (paratype no. 1)	3.80	–	2.00	–	0.95	–	0.53	0.25	0.48	–	–
	A. orientalis (paratype no. 2)	3.50	–	1.70	–	0.80	–	0.49	0.23	0.47	–	–
	A. orientalis (paratype no. 3)	3.10	–	1.65	–	0.75	–	0.53	0.24	0.46	–	–
	A. orientalis (paratype no. 4)	3.90	–	2.10	–	0.99	–	0.54	0.25	0.47	–	–
	A. orientalis (paratype no. 5)	2.50	–	1.30	–	0.60	–	0.52	0.24	0.46	–	–

lucida (Starobogatov & Tolstikova 1986). The shells were measured according to the scheme presented in Fig. 3. Measurements of holotypes and lectotypes were obtained from Starobogatov (1989). Shells of other type specimens and topotypes were measured based on photographs with scale bars using Image-Pro Plus. Protoconch characters were studied by scanning electron microscopy (Philips 525M, Amsterdam, Netherlands). SEM preparation techniques were described in Shirokaya et al. (2003).

Characters of the jaw, radula, shell adductors, and male copulatory organ were used to develop identification keys. For detailed SEM investigations, each radula was cleaned using bleach, rinsed in water, dehydrated in a graded series of ethanol, and further processed following standard methods (Shirokaya 2007). The jaw and surrounding soft tissues were cut from the body using a scalpel and immersed in a drop of Faure-Berlese fluid (gum chloral) on a slide. A cover glass was added and samples were kept for 10 d at room temperature. The anatomy was studied by dissection under an MBS-1 stereomicroscope, and the topography of shell adductors was drawn using a camera lucida. Azocarmine-stained copulatory organs were rinsed in distilled water, dried, and placed in clove oil for a few hours to observe structural details. The structure of the male copulatory organ was examined under a Nikon Optiphot-2 (Tokyo, Japan) compound microscope with a drawing tube. To describe egg masses, the terminology of Nekrassow (1927) and Bondesen (1950), revised and supplemented by Beriozkina & Starobogatov (1988), was applied.

The format of each species account follows the scheme used by Sitnikova et al. (2012) and Vinarski et al. (2013). Distances between the sampling sites were measured along the shoreline in accordance with Krivets et al. (1959) and Drizhenko & Kolotilo (1993). Individual records are not given for common species. Information on species synonymized since Starobogatov's (1989) revision is provided in Appendix 1.

Abbreviations. a, atrium; **aal**, left anterior adductor; **aar**, right anterior adductor; **ag**, albumen gland; **ao**, aorta; **ap**, anal pore; **bm**, buccal mass; **cae**, caecum; **cbc**, cerebro-buccal connectives; **cgd**, right cerebral ganglion; **dg**, digestive gland; **dgp**, digestive gland pore; **e**, elevation of the shell apex above the aperture plane; **f**, foot; **fl**, flagellum; **fp**, female genital pore; **g**, gill; **ga**, abdominal ganglion; **hd**, hermaphroditic duct; **int1**, first intestinal loop; **int2**, second intestinal loop; **k**, kidney; **ll**, lateral lobe; **ln**, labial nerve; **lpn**, left pallial nerve; **mb**, mantle border; **mp**, male genital pore; **np**, penis nerve; **oa**, original adductor; **oe**, oesophagus; **og**, osphradial ganglion; **on**, optical nerve; **ov**, oviduct; **p**, penis; **pc**, pericardium; **pgd**, right pedal ganglion; **plgd**, right pleuro-parietal ganglion; **pp**, penis papilla; **pr**, preputium; **prc**, preputium chamber; **pro**, prostate; **prp**, preputium pilasters; **prr**, preputium retractor; **psh**, penial sheath; **pshr**, penial sheath retractor; **re**, rectum; **rp**, renal pore; **rpn**, right pallial nerve; **rs**, radular sac; **sar**, sarcobelum; **sg**, salivary glands; **spd**, spermathecal duct; **t**, tentacle; **tn**, tentacle nerve; **v**, ventricle; **vd**, vas deferens; **ve**, velum; **vess**, vesicula seminalis; **vs**, visceral sac.

Taxonomic Account

Family Acroloxidae Thiele, 1931

Genus *Acroloxus* Beck, 1837

Type species. *Patella lacustris* Linnaeus, 1758, by subsequent designation (Herrmannsen 1846).

Diagnosis. Shell scutiform, fragile, with oval or elongated-oval aperture, 8–9 mm long in adults. Apex shifted leftward in respect to aperture longitudinal axis. Protoconch horn-shaped, with reticular microsculpture, locally becoming pitted. Male copulatory organ with short flagellum always situated at nearly right angle in respect to penis sheath and preputium. Penis sheath usually shorter than preputium or almost equally long. Penis short, massive, having a laterally located opening of vas deferens. Penis tip formed by a soft conical papilla. Preputium spherically inflated in its proximal part; sarcobelum located inside a muscular chamber together with velum (Hubendick 1962, Kruglov & Starobogatov 1991a).

Ecology. Depth, 0–4 m. Embryo development is normally synchronous. *Acroloxus* limpets feed by grazing on periphyton fouling stones and macrophytes. Main dietary components are diatom algae, bacteria, and phytodetritus (Stadnichenko 2004, Shirokaya et al. 2011, Galina V. Beriozkina pers. comm.).

Subgenus *Acroloxus* s. str.

Diagnosis. Dark pigment on dorsal mantle side not arranged into 2 transverse stripes ahead and behind apex (but rather evenly distributed). Spermathecal duct not exceeding pro-vagina length. Penis sheath cylindrical or slightly narrowing towards preputium; sheath walls of equal thickness along entire length. Sarcobelum weakly developed; velum absent. Syncapsule surface longitudinally striated (Kruglov & Starobogatov 1991a).

Acroloxus baicalensis Kozhov, 1936

Fig 4A, B

Acroloxus lacustris var. *baicalensis* Kozhov 1936: 184, Taf. VII, fig. 39.
Acroloxus baicalicus — Starobogatov 1989: 42.
Acroloxus lacustris — Golyshkina 1967: 77 (non Linnaeus, 1758).

Type locality (of neotype). Lake Baikal, Chivyrkui Bay, Kotovo Inlet, 53°38′06.7″N, 108°58′10.7″E. Former type locality (of lost holotype). Lake Baikal, Chivyrkui Bay, Krutaya Inlet (Kozhov 1936).

Types. Holotype lost. ZIN, neotype, designated here (ZIN 2/504–2014, dry shell, Fig. 4B): coll. Dmitri V. Matafonov and Nikolai M. Pronin, 21 July 2009, sample 5, at 1.4 m, on *Elodea canadensis* and silt, det. L.A. Prozorova. See also "Remarks," below.

Other material. LIN: 3 dry shells (SEM stub, topotypes), coll. data same as neotype, SEM images figured by Shirokaya et al. (2011: fig. 2G–L).

ZIN: 1 specimen (ZIN 1/278-1957, in alcohol), lower reaches of the Yenisei River, coll. Peter L. Pirozhnikov, 20 September 1935, sta. 105, sample 247, at 16 m, on stones, det. Ya.I. Starobogatov). Only ¾ of the shell's height remains intact but protoconch included. The lower ¼ is completely destroyed, the aperture outline cannot be determined (Fig. 4A). Teleoconch dimensions (in mm): length of aperture (L) = 4.20; distance from apex to the frontal apertural edge (projected on longitudinal axis of aperture) (La) = 3.30; width of aperture (W) = 2.50; distance from apex to left apertural edge (wL) = 0.80; height of teleoconch (H) = 1.50; distance from apex to the anterior apertural edge (chord of the longest slope) (a) = 3.50 (Kruglov & Starobogatov 1991a). The apex is situated at the border of left ⅓ of the aperture width (wL/W = 0.32) and behind the boundary of posterior ¼ of its length (La/L = 0.79). The shell is covered with rusty incrustation and the protoconch border cannot be seen. Therefore, the dimensions of the protoconch are not given.

TSPU, 10 specimens in total: 7 specimens (no numbers, in alcohol), Upper and Middle Chulym river drainage, coll. Pavel V. Maslennikov, quantitative sample, depth not indicated, on water plants (Vladimir N. Dolgin pers. comm.); 3 specimens (no numbers, in alcohol), Lake Kaibaduv, 57°30′4.9″N, 88°57′4.71″E, coll. P.V. Maslennikov, 30 June 2013, qualitative sample, depth not indicated, on stems of *Potamogeton* and *Sagittaria* (P.V. Maslennikov pers. comm.). Shell dimensions of these 10 specimens were not published.

Acroloxus baicalensis specimens from the Yenisei, Lena, and Kolyma rivers (coll. Anatoli D. Cheremnov?), which are mentioned in the contributions of Cheremnov (1972: Table "Species composition…") and Dolgin (2003–2015, see "History of the usage of the name") and, probably, kept in Zoological Museum of Khakassia State University, N.F. Katanov (Abakan, Russia), were not found (Anatoli A. Asochakov and Sergei V. Dragan pers. comm.).

History of the usage of the name.

Kozhov (1936), as *Acroloxus lacustris* var.: shell description and dimensions; distribution

Starobogatov & Streletskaya (1967): presence in ZIN collection; specific record; reasons for species status of Eastern Siberian form of *A. lacustris*

Cheremnov (1972): species records in Yenisei, Lena, and Kolyma river drainages

Kruglov & Starobogatov (1991a), as *Acroloxus* (*Acroloxus*): description of teleoconch; identification key

Sitnikova et al. (2004): type locality, distribution, zoogeographical and ecological data, presence in scientific collection

Starobogatov et al. (2004): identification key; distribution, biotope

Kantor & Sysoev (2005): distribution

Dolgin (1999): distribution within Subarctic and Arctic Siberia; detection in Lower Yenisei River; assigning of *A. baicalensis* to Middle Siberian zoogeographical group

Dolgin (2003): biotopic distribution in basins of northern Siberia; assigning of *A. baicalensis* to pelorheophilous ecological group

Dolgin (2009): distribution within Siberian provinces

Prozorova et al. (2009), as *Acroloxus* (*Acroloxus*): type locality, distribution, zoogeographical and ecological data

Shirokaya et al. (2009): first data on protoconch structure, boundaries of species range

Kantor et al. (2010): type locality, distribution

Shirokaya et al. (2011): data on shell ultrastructure, additional conchological characters revealed from study of topotypes, general distribution

Dolgin (2012): records from Upper Yenisei and Tuvinian lakes

Dolgin (2013): distribution in waters of different altitudinal zones of Sayan mountain system

Dolgin & Maslennikov (2015): species records in Upper Yenisei and Chulym river drainage

Maslennikov (2015): shell morphology, general distribution, first record in Middle Ob' river drainage, quantitative characteristics, biotope

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lower reaches of the Yenisei River to the Pacific Ocean.

Specific records. Dudinka Settlement and the upper reaches of Yenisei River; Upper and Middle Chulym river drainage, Sredneobskaya Zoogeographical Province of Siberian/Euro-Siberian subregion of the Palaearctic region (as proposed by Starobogatov [1970] and modified by Starobogatov [1986] and Dolgin [1999]); Kotovo and Krutaya inlets of Chivyrkui Bay, Lake Baikal; small lakes near the SE Baikal shore; Angara river basin; Shirokaya River, Ivano–Arakhlei lake–river system; Artyomovka River, Shtykovo Settlement, Shkotovski District, Primorye Territory (Kozhov 1936, Golyshkina 1967, Kruglov & Starobogatov 1991a, Sitnikova et al. 2004, Prozorova et al. 2009, Shirokaya et al. 2011, Dolgin & Maslennikov 2015, Maslennikov 2015).

Remarks. This species was described by Kozhov (1936) based on a single specimen initially stored in the collection of the Baikalian Museum of ISU (Irkutsk). In the mid-20th century, most material collected by employees of the Baikal Limnological Station and by M.M. Kozhov personally was transferred to ZIN. This material included type specimens of several species of gastropods. According to Vadim V. Takhteev (pers. comm.), who most recently inventoried the invertebrate collection of the Baikalian Museum (1995), the specimen of *A. baicalensis* is absent from the ISU collection. From 2012 to 2016, this specimen has not been found in the acroloxid type series stored in ZIN. Catalogue entries for these institutions do not include any records of this specimen.

The description of *A. baicalensis* published by Kozhov (1936) is rather brief and does not include embryonic shell characters, which are taxonomically important in freshwater limpets. Kozhov described the aperture shape and apex position, and provided only 3 teleoconch measurements (Table 2), but these features are not sufficient to distinguish this species from the conchologically similar *A. orientalis* Kruglov & Starobogatov, 1991, which occurs sympatrically in Chivyrkui Bay (Shirokaya et al. 2011). Despite thorough sampling in shallow bays and inlets of Lake Baikal, *A. baicalensis* has not been found since its description. The only record in 70 years was in a study of the gastropod fauna associated with dense aggregations of the alien aquatic weed *Elodea canadensis*, in which D.V. Matafonov found 2 separate species of *Acroloxus* in Kotovo Inlet (Matafonov et al. 2009; Shirokaya et al. 2009). Owing to the loss of the only type specimen of *A. baicalensis*, it is necessary to designate a neotype based on this material. We provide a detailed description below.

Description of neotype shell. Protoconch horn-shaped, relatively low (H/h = 5.36); its reticular sculpture less defined than that of endemic littoral Baikalian acroloxids. Protoconch dimensions (in mm): l = 0.76; w = 0.55; h = 0.25. A detailed description of the sculpture and initial plate of the protoconch of *A. baicalensis* was provided by Shirokaya et al. (2011). Teleoconch dimensions (in mm): L = 4.10; La = 2.90; W = 2.37; wL = 0.82; H = 1.34; a = 3.03. The aperture is elongated, oval (W/L = 0.58); its anterior edge is wider than the posterior edge. Shell flatter than that of the specimen from Lower Yenisei (H/L = 0.33, H/W = 0.57). Apex is situated at the border of the left ⅓ of the aperture width (wL/W = 0.35) and behind the boundary of the posterior ⅓ of its length (La/L = 0.71). Anterior shell slope evenly convex, sloping; posterior slope weakly concave, sloping; upper part of lateral slopes convex, steep (angle between slopes and aperture plane is 60–67.5°), lower part weakly convex, almost straight, sloping (angle between slopes and aperture plane is 43–47.5°) (Fig. 4B). Differences in the shapes of slopes and the aperture outline among acroloxids from Chivyrkui Bay of Baikal and the specimen from the Lower Yenisei are associated with different substrate types: the former were collected from stems and leaves of *Elodea*, whereas the latter was collected from a stone. The teleoconch morphology of the specimen designated here as the neotype corresponds most closely to the brief description of Kozhov (1936: 184) (see "Differential diagnosis"; Table 2: indices W/L, H/L, H/W).

Soft body. Dark pigmentation on the dorsal side of the mantle of *A. baicalensis* is not arranged in 2 transverse stripes located anteriorly and posteriorly with respect to the apex, as in the conchologically similar species *A. orientalis*, but it is not evenly distributed over the entire surface, as in most acroloxid species from rivers of Transbaikalia. The pigmentation forms an uneven ring around the visceral mass. The anatomy of this species is unknown.

Differential diagnosis. Based on shell morphology, *Acroloxus baicalensis* is most similar to *A. orientalis*. The protoconchs of both species are relatively low ($h/H \leq 0.20$) and horn-shaped with a weaker reticular sculpture than that of littoral endemic acroloxids. The posterior slope of the protoconch has both radial and concentric

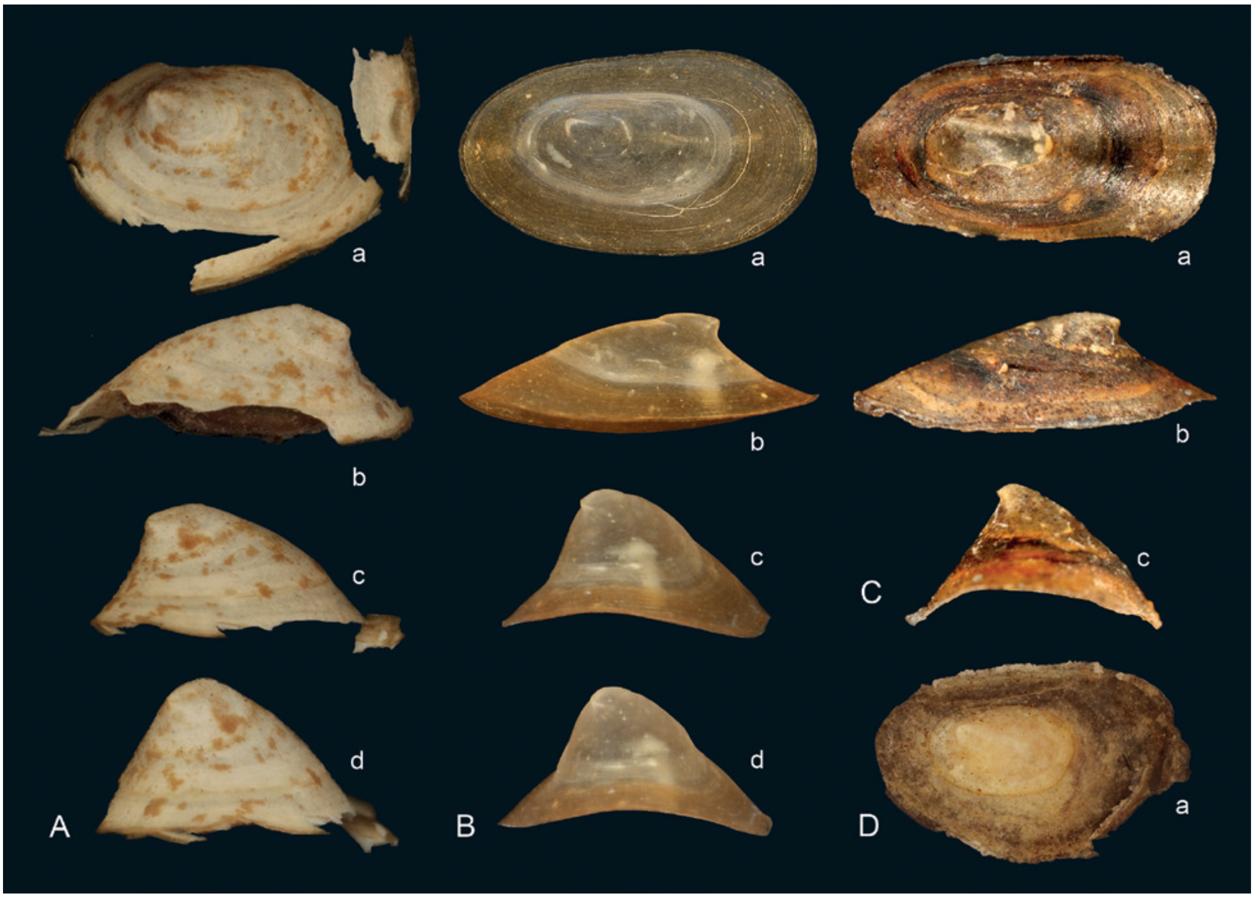

Figure 4. A. *Acroloxus baicalensis* Kozhov, Yenisei River, identified by Ya.I. Starobogatov: L = 4.20 mm, W = 2.50 mm, H = 1.50 mm. **B.** *A. baicalensis*, Kotovo Inlet, Chivyrkui Bay of Lake Baikal, neotype: L = 4.10 mm, W = 2.37 mm, H = 1.34 mm. **C.** *A. orientalis* Kruglov & Starobogatov, holotype: L = 5.60 mm, W = 2.50 mm, H = 1.90 mm; **D.** *A. orientalis*, paratype ZIN 2/145-1976: L = 3.80 mm; W = 2.00 mm; H = 0.95 mm. Teleoconch: **Aa–Da**, top view; **Ab–Db**, left side view; **Ac–Dc**, rear view, shell rotated clockwise so apex contours are clearly visible; **Ad–Dd**, rear view, shell mounted exactly perpendicular to the sample stage.

ribs. On the anterior slope, a weak reticular sculpture is replaced by punctae. The initial plate of the protoconch of both *Acroloxus* species is drop-shaped or oval. The rounded initial plate is typical of endemic Baikal species. The initial plates of *A. baicalensis* and *A. orientalis* have similar dimensions. Typical *A. orientalis* is characterized by a moderately high teleoconch (shell height (H) to aperture width (W) ratio ≤ 0.52), deep concavity below apex on the posterior-left slope, distinctly convex right slope, and equally rounded anterior and posterior aperture edges. *Acroloxus baicalensis* possesses a taller teleoconch (H/W ≥ 0.56) with a weak concavity below the apex and a nearly straight (or slightly convex) right slope. The aperture has a broader anterior edge. In both species, the anterior slope of the shell is slightly convex, whereas the posterior and left slopes are almost straight or slightly concave. The lower parts of the slopes of the teleoconch widen in limpets living on vegetative substrates. In *A. baicalensis*, the apex lies behind the border of the posterior ⅓ of the aperture length (La/L = 0.71–0.79) and at the border of the left ⅓ of the aperture width (wL/W = 0.32–0.35). In *A. orientalis*, the apex is only slightly shifted leftward with respect to the longitudinal axis of the shell (wL/W = 0.42–0.45) and lies anterior to the border of the aperture posterior ⅓ (La/L = 0.58–0.61).

In *A. orientalis*, the dorsal mantle pigmentation forms 2 transverse stripes in front of and behind the apex, but in *A. baicalensis*, the dark pigment forms an uneven ring.

The teleoconch of *A. lacustris*, a species distributed in Europe, Kazakhstan, and Western Siberia and not occurring east of the Altai Territory (KRUGLOV & STAROBOGATOV 1991a), differs from that of *A. baicalensis* by having a strongly convex right slope.

Subgenus *Amuracroloxus* Kruglov & Starobogatov, 1991

Type species. *Acroloxus likharevi* Moskvicheva, Kruglov & Starobogatov *in* KRUGLOV & STAROBOGATOV, 1991, by original designation (= *Acroloxus likharevi* Moskvicheva, Kruglov & Starobogatov *in* BOGATOV & ZATRAWKIN, 1991).

Diagnosis. Dark pigmentation on the mantle dorsal side arranged into 2 transverse stripes anteriorly and posteriorly of the apex. Length of spermathecal duct markedly exceeding pro-vagina length. Penis sheath conic, rapidly narrowing toward preputium, with thickened walls in narrowed part. Sarcobelum and, sometimes, velum rather developed. Syncapsule surface without longitudinal striation (Kruglov & Starobogatov 1991a, Prozorova 1991).

Acroloxus orientalis Kruglov & Starobogatov, 1991

Fig. 4C, D

Acroloxus (*Acroloxus*) *orientalis* Kruglov & Starobogatov 1991a: 75, fig. 2 (10).

Type locality. Brook connecting Lake Kotika with the Tym' River, Sakhalin (Kruglov & Starobogatov 1991a).

Types. ZIN: holotype and 5 paratypes. Holotype (ZIN 1/342-1938, dry shell): coll. Anatoli Ya. Taranets, 1934, no additional data. Right and rear slopes of shell markedly broken (Fig. 4Ca), its dimensions (in mm): L = 5.60; La = 3.30; W = 2.50; wL = 1.10; H = 1.90; a = 3.50 (Kruglov & Starobogatov 1991a). Paratypes: 5 specimens (ZIN 2/145-1976, in alcohol), Lake Krugloye, floodland of upper reaches of the Zeya River, Amurskaya Region, coll. Victor V. Bogatov, 28 August 1975, depth and substrate not indicated. All type specimens identified by N.D. Kruglov and Ya.I. Starobogatov. All paratypes are partially damaged. Dimensions of the paratype in best condition (in mm): L = 3.80; W = 2.0; H = 0.95 (Fig. 4D); Kruglov & Starobogatov (1991a).

Other material. FSCB, 28 specimens in total: 3 dry shells (FSCB 4155), Bibi River, Hokkaido, coll. L.A. Prozorova, 2001; 5 specimens (FSCB 123-02 and FSCB 134-02, in alcohol), Krasnaya River, tributary of the Tym' River, Sakhalin (topotypes), coll. L.A. Prozorova, 2002; 6 specimens (FSCB 6290, in alcohol), Khilok River, tributary of the Selenga River, Transbaikalia, coll. Mariana O. Sharyi-ool, 2004; 8 specimens (FSCB 4237, in alcohol), Zhyoltaya River, Primorski Krai, coll. Evgeni V. Kolpakov, 2001; 3 specimens (FSCB 7469, in alcohol), unnamed lake, Bira river basin, Birobidzhan City, Jewish Autonomous Region, Middle Priamurye, coll. Vera P. Makarenko, 2009; 3 specimens (FSCB 7851, in alcohol), Lake Tretje Lebedinoye, Khingan Nature Reserve, Amurskaya Region, Middle Priamurye, coll. Irina V. Balan, 2012. All specimens det. by L.A. Prozorova.

LIN, 9 specimens in total: 1 dry shell (FSCB 7893-3), Bibi River, Hokkaido, coll. Yuta Morii, 8 October 2015; 2 specimens (FSCB 123-02, in alcohol), flood plain lake in middle part of Tym' River, Sakhalin (topotypes), coll. L.A. Prozorova, 31 July 2002; 4 specimens (IBSS 7911b, in alcohol), Lake Vtoroye Lebedinoye, Khingan Nature Reserve, Amurskaya Region, Middle Priamurye, coll. I.V. Balan, 11 September 2016; 1 dry shell (SEM stub), Kotovo Inlet, Chivyrkui Bay, Lake Baikal, coll. D.V. Matafonov and N.M. Pronin, 21 July 2009, sample 5, at 1.4 m, on *Elodea canadensis* and silt; 1 dry shell (SEM stub), a channel, connecting the Chivyrkui Bay of Lake Baikal with Lake Arangatui, 53°37′40.4″N, 108°59′31.6″E, same coll. data, SEM images figured by Shirokaya et al. (2011: fig. 2B–C, E–F). All specimens det. by L.A. Prozorova.

History of the usage of the name.

Bogatov & Zatrawkin (1991), as *Acroloxus* (*Acroloxus*): detailed description of teleoconch, holotype dimensions and whereabouts, brief information about ecology of species, general distribution; identification key

Kruglov & Starobogatov (1991a), as *Acroloxus* (*Acroloxus*): description of teleoconch; identification key

Prozorova & Kolpakov (2004), as *Acroloxus* (*Amuracroloxus*) sp.: records from Northern Primorye

Starobogatov et al. (2004): identification key; distribution

Kantor & Sysoev (2005): distribution

Prozorova & Zasypkina (2005): distribution, including first record in Baikal basin and Transbaikalia

Zasypkina (2008): finding of *A. orientalis* in upper Amur river basin)

Prozorova et al. (2009), as *Acroloxus* (*Amuracroloxus*): zoogeographical and ecological data

Shirokaya et al. (2009), as *Acroloxus* (*Amuracroloxus*): first record in Baikal, protoconch structure, boundaries of species range

Kantor et al. (2010): type locality, presence of holotype in ZIN collection, distribution

Prozorova (2010), as *Acroloxus* (*Amuracroloxus*): first record of Acroloxidae in Japan, discussion of shell shape variability in *A. orientalis*; description of mantle pigment and male copulatory organ; transfer of species from subgenus *Acroloxus* to subgenus *Amuracroloxus* based on soft body morphology

Shirokaya et al. (2011), as *Acroloxus* (*Amuracroloxus*): discussion of shell shape variability, geographic and bathymetric distribution, biotope

Pietsch et al. (2012): distribution in Tym' and Poronai river basins, Sakhalin

Prozorova (2013a), as *Acroloxus* (*Amuracroloxus*): distribution in southern Russian Far East

Prozorova (2013b), as *Acroloxus* (*Amuracroloxus*): distribution, biogeography

General distribution. Lake Baikal to Sakhalin and Hokkaido, including northern tributaries of the Amur River.

Specific records. Khilok River of the Baikal basin, Buryatia (Prozorova & Zasypkina 2005); Bibi River of the Abira river system, vicinity of Tomakomai City (Hokkaido, Japan) (Prozorova 2010); Chivyrkui Bay, Lake Baikal and a channel connecting the bay with Lake Arangatui (Shirokaya et al. 2011); Poronai river basin, Sakhalin (Pietsch et al. 2012); small lakes in the Khingan Nature Reserve, Amurskaya Region (Balan & Prozorova original data); Bira river basin, Jewish Autonomous Region (Makarenko & Prozorova original data); Zhyoltaya River, Primorski Krai (Prozorova & Kolpakov 2004).

Remarks. Baikalian *A. orientalis* and *A. baicalensis* are characterized by pronounced variation in teleoconch morphology (Shirokaya et al. 2011). There is a set of specimens from Chivyrkui Bay with intermediate shell shapes, which may be evidence of cross-breeding or extensive intraspecific variation.

In our examination of the type series of *A. orientalis* and the species description (Kruglov & Starobogatov 1991a: 75), we found that the shell morphology of the holotype does not correspond to the species diagnosis. Our measurements of the holotype are H/W = 0.76 and H/L = 0.34 (Table 2), but the original diagnosis indicated H/W = 0.45–0.52 and H/L = 0.23–0.25. In 5 paratypes, these indices correspond to the diagnosis, but the other proportions of the teleoconch cannot be checked because Kruglov & Starobogatov (1991a) did not provide all measurements and the shells are now damaged or destroyed. The only character distinguishing most specimens of *A. orientalis* from *A. baicalensis*, including specimens from Kotovo Inlet and the Lower Yenisei River, is the position of the apex. However, according to Kozhov (1936) and Kruglov & Starobogatov (1991a), the aperture shape is also different, with *A. baicalensis* wider (W/L = 0.58–0.60) than *A. orientalis* (W/L = 0.45–0.54). In specimens found in Kotovo Inlet, the values of this index overlap: *A. baicalensis* W/L is 0.55–0.61 and *A. orientalis* W/L is 0.45–0.59 (Shirokaya et al. 2011). Interspecific differences in protoconch proportions and microsculpture have not been found.

In the absence of anatomical data, Kruglov & Starobogatov (1991a) included *A. orientalis* in the subgenus *Acroloxus* s. str. However, Prozorova (2010) found that, in Japanese specimens identified as this species, the dorsal mantle pigmentation forms 2 transverse stripes in front of and behind the apex; the spermathecal duct is longer than the pro-vagina; the width of the penis sheath is less than that of its glandular flagellum and sharply converged to the distal end; the sarcobelum is rather developed; and the velum is visible. These characters imply that *A. orientalis* belongs to the subgenus *Amuracroloxus*.

Because the anatomy of *A. baicalensis* is still unknown, we cannot verify whether *A. orientalis* and *A. baicalensis* belong to different subgenera. Moreover, the mantle pigmentation pattern used by Kruglov & Starobogatov (1991a) to delineate subgenera varies considerably within species of acroloxids inhabiting Chivyrkui Bay. The shell characters as well as the geographic distributions do not allow us to clearly separate these 2 species. In our opinion, all of the specimens examined represent a single widely variable species, *A. baicalensis*. However, until we obtain anatomical and molecular data, we provisionally regard both species as valid.

Genus *Pseudancylastrum* Lindholm, 1909

Type species. *Ancylus sibiricus* Gerstfeldt, 1859, by original designation.

Diagnosis. Shell brownish grey, without sculpture. Shell shape of an oblique cap with leftward shifted apex. Anterior and right slopes always convex. In littoral species, protoconch horn-shaped with reticulate microsculpture; in an abyssal species, cap-shaped, with pitted microsculpture. Central tooth of radula narrow, bearing 2 asymmetric cusps; lateral teeth broad, with 2 large symmetric cusps. Number of lateral teeth in a transverse row not exceeding 7 on each side of the central tooth. Odontophore dark grey in living specimens. Prostate globular. Male copulatory organ with narrow and very long flagellum stretched along the body. Penis sheath longer than preputium, penis short and massive; opening of vas deferens laterally situated and penis apex formed by a soft papilla. Preputium inflated proximally, forming a chamber with muscular walls containing sarcobelum and sometimes also velum (Starobogatov 1989, Kruglov & Starobogatov 1991b, Shirokaya et al. 2003, Shirokaya & Röpstorf 2004).

Ecology. Depth, 1.5–40 m. Embryo development inside syncapsule is asynchronous. Adult snails feed mainly on benthic diatom algae (Röpstorf et al. 2003, Shirokaya 2003, Shirokaya & Röpstorf 2003).

Subgenus *Pseudancylastrum* s. str.

Diagnosis. Anterior teleoconch slope convex, posterior slope concave below apex, then weakly concave or straight. Protoconch horn-shaped, with reticulate microsculpture. Expanded proximal part of preputium forms a muscular chamber; sarcobelum weakly developed, velum absent (Kruglov & Starobogatov 1991b, Shirokaya et al. 2003).

Pseudancylastrum sibiricum (Gerstfeldt, 1859)

Figures 5B, 12G

Ancylus sibiricus, part. Gerstfeldt 1859: 23, fig. 30 — Crosse 1860: 403; Bourguignat 1862: 204; Westerlund 1877: 99; Crosse & Fischer 1879: 163; Westerlund 1885: 95.
Ancylus (*Pseudancylastrum*) *sibiricus*, part. — Lindholm 1909: 27; Starostin 1926: 2, 14; Kozhov 1931: 64; Shadin 1933: 130, fig. 99.
Ancylus (*Pseudancylastrum*) *troscheli*, part. — Lindholm 1909: 28.
Acroloxus sibiricus — Hubendick 1969: 58, figs 5–16, 30, 37.

Type locality. Angara River, near Irkutsk City.

Types. ZIN, lectotype (ZIN no. 1, dry shell), designated by Starobogatov (1989: 46): coll. R. Maack, 1854, depth not indicated, on stones, initially identified by H.N. Gerstfeldt. Shell in good condition (Fig. 5B), its dimensions (in mm): L = 4.55; La = 4.0; W = 3.50; wL = 0.60; H = 2.40; a = 4.55 (Starobogatov 1989). Eight paralectotypes (ZIN no. 2 and ZIN no. 3) were assigned to other species by Starobogatov (1989). See "Remarks", below.

Other material. ZIN, 20 specimens in total: 5 dry shells (ZIN no. 5), Angara River (topotypes), coll. and det. M.M.

Kozhov, no additional data; 1 specimen (ZIN 6/548-1985, in alcohol), opposite Sennaya Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 28 June 1954, at 2.5 m, on stone; 1 specimen (ZIN 7/548-1985, in alcohol), same locality and coll., 16 June 1954, at 4–6 m, on stone; 1 specimen (ZIN 8/545-1985, in alcohol), Mysovskaya Bank, coll. S.M. Popova, 30 July 1957, at 4 m, substrate not indicated; 2 specimens (ZIN 9/545-1985, in alcohol), same locality, collector and sampling data, at 8 m, on stone; 7 specimens (ZIN 10/547-1985, in alcohol), Bugul'deika River, coll. Evgeni S. Poberezhnyi, 30 August 1979, at 5–7 m, on sand and stones; 1 specimen (ZIN 11/548-1985, in alcohol), opposite Zhilistsche Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 30 June 1954, at 9 m, on stone; 1 dry shell (ZIN 12/359-1935), near Listvyanka Settlement, coll. A.A. Korotnev expedition, 19 June 1901, sta. 12, at 5.6–22.2 m, on stone, initially identified by Lindholm (1909) as "*Ancylus* (*Pseudancylastrum*) *troscheli* no. 4"; 1 specimen (ZIN no. 13, in alcohol), Baikal, no additional data. All specimens (re)determined by Ya.I. Starobogatov.

Before 2013, the ZIN catalogue card of *P. sibiricum* erroneously included 1 dry shell (ZIN no. 4) from the Angara River collected by Gustav I. Radde, 1855. In fact, Radde collected 7 specimens initially identified by Carl A. Westerlund and Leopold von Schrenck as *Ancylus* (*Ancylastrum*) *sibiricus*. In 1985, 3 of these specimens were re-identified by Starobogatov as *Pseudancylastrum dybowskii* (Clessin, 1882) and added to the card of the latter as ZIN no. 1. The 4 remaining shells were identified by him as *G. benedictiae* Starobogatov, 1989 and included into its paratypes as ZIN no. 18. Presently there are no records in the ZIN catalogue card of *P. sibiricum* listed as no. 4.

Institute of Geological Sciences, Freie Universität Berlin: 1 dry shell (SEM stub), upper Angara River, near Irkutsk City, Akademgorodok (topotype), 52° 15′ 10.8″ N, 104° 16′ 58.1″ E, coll. P. Röpstorf (scuba diving), early 2000, at 3 m, on stone (Shirokaya et al. 2003: fig. 5A–C).

SMF: 2 dry shells, Lake Baikal, Birkhin Bay, 52° 43′ 11.76″ N, 106° 32′ 17.78″ E, coll. Igor V. Khanaev (scuba diving), 19 July 2004, at 12 m, on gabbroid stones, det. Alena A. Shirokaya (Fig. 12G).

LIN: 454 specimens (in alcohol), from 3 Baikal basins.

History of the usage of the name.

Gerstfeldt (1859), as *Ancylus sibiricus*: shell description; comparison to *A. fluviatilis* and *A. lacustris*; geographic distribution

Crosse (1860), as *Ancylus sibiricus*: shell description and dimensions; distribution

Bourguignat (1862), as *Ancylus sibiricus*: the author, describing shell morphology, erroneously stated that the apex is turned rightward, and compared the species to North American *Ancylus elatior* Anthony, 1855, now *Rhodacmea elatior*

Westerlund (1877), as *Ancylus sibiricus*: shell dimensions

Crosse & Fischer (1879), as *Ancylus sibiricus*: distribution

Westerlund (1885), as *Ancylus sibiricus*: shell dimensions; distribution

Lindholm (1909), as *Ancylus* (*Pseudancylastrum*) *sibiricus*: records from Baikal with depth and bottom type; description of adult and juvenile shells; zoogeographic affinities

Dybowski (1910), as *Ancylus sibiricus*: bathymetrical distribution; biotope

Starostin (1926), as *Ancylus* (*Pseudancylastrum*) *sibiricus*: records from Baikal with depth and bottom type

Kozhov (1931), as *Ancylus* (*Pseudancylastrum*) *sibiricus*: records from Baikal with depth and sediment distribution

Thiele (1931): morphology of radula

Shadin (1933), as *Ancylus* (*Pseudancylastrum*) *sibiricus*: shell description and dimensions; distribution

Kozhov (1936): detailed description of teleoconch and radula; discussion of shell shape variability; comparison to "*A.*" *troschelii* sensu Dybowski and "*A.*" *dybowskii* sensu Clessin; data on horizontal and vertical distribution as well as associate bottom type

Shadin (1952): description of shell, distribution, biotope

Golyshkina (1963): records in Irkutsk water reservoir; bottom type distribution

Golyshkina (1967): depth and bottom type distribution in upper Angara River, 130 km from its source

Golyshkina (1969): records from head of Angara River

Hubendick (1969), as *Acroloxus sibiricus*: teleoconch and protoconch description (light microscopy), morphology of soft body, radula, pseudobranch, copulatory organ, and shell adductors; taxonomic position; phylogeny

Clarke (1970), as *Acroloxus* (*Pseudancylastrum*): distribution

Clarke (1973), as *Acroloxus* (*Pseudancylastrum*): distribution

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of lectotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): structure of male copulatory organ

Kozhova & Erbaeva (1998): subendemism of *P. sibiricum*: records in upper and middle Angara River, as well as in Irkutsk water reservoir

Shirokaya et al. (2003): description of adult shell, protoconch and radula (SEM data), additional taxonomically important characters, polytomic identification key to species

Ostrovskaya et al. (2004): phenomenon of intra-clonal mixoploidy occurring in a form of mosaic specimens

Shirokaya & Röpstorf (2004), as *Pseudancylastrum* (*Pseudancylastrum*): description of alimentary system and shell adductor muscles, additional taxonomically important characters, polytomic key

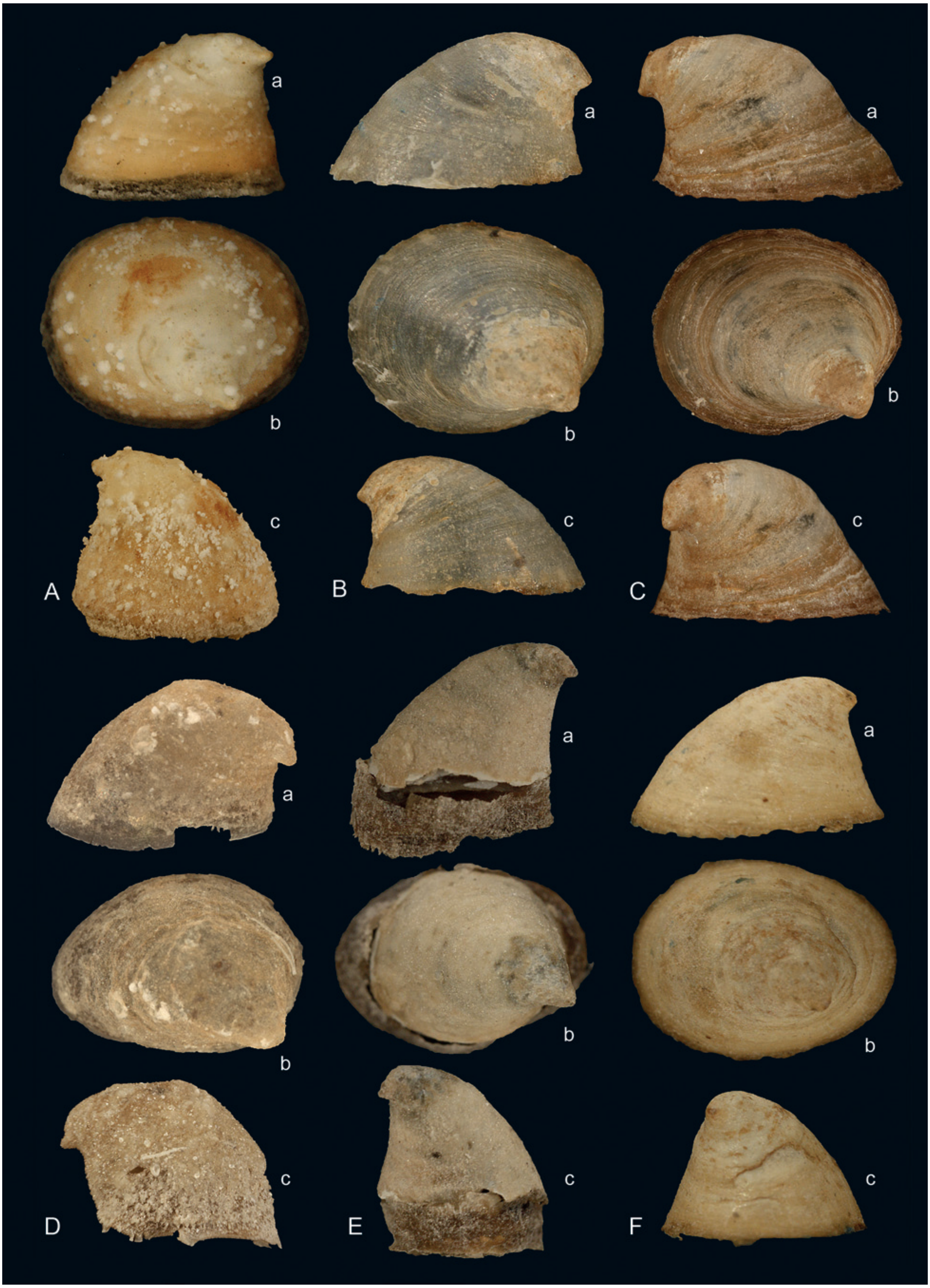

Figure 5. A. *Pseudancylastrum beckmanae* Starobogatov, holotype: L = 5.30 mm, W = 4.50 mm, H = 4.00 mm. **B.** *P. sibiricum* (Gerstfeldt), lectotype: L = 4.55 mm, W = 3.50 mm, H = 2.40 mm. **C.** *P. dybowskii* sensu Starobogatov 1989, the largest specimen from Radde's collection: L = 5.10 mm, W = 4.30 mm, H = 3.00 mm. **D.** *P. olgae* Starobogatov, holotype: L = 5.00 mm, W = 3.60 mm, H = 3.20 mm. **E.** *P. cornu* Starobogatov, holotype: L = 5.00 mm, W = 4.20 mm, H = 4.50 mm. **F.** *P. korotnevi* Starobogatov, holotype: L = 4.30 mm, W = 3.20 mm, H = 2.50 mm. Teleoconch: **Aa**, **Ba**, **Da**–**Fa**, left side view; **Ca**, right side view; **Ab–Fb**, top view; **Ac–Fc**, rear view.

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): information on type material and type locality; distribution, zoogeographical and ecological data

Starobogatov et al. (2004): identification key; distribution; biotope

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): detailed diagnosis of species; phylogenetic relationships

Vin'kovskaya (2006): presence of species in exhibition of Irkutsk Regional Museum of Local History, containing dry shells (SEM stubs), shells with soft bodies in ethyl alcohol, and photographs

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality; presence of lectotype in ZIN collection; distribution

Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on quantitative characteristics

Maximova et al. (2012): seasonal quantitative dynamics of snails in 3 hydrodynamically different stony littoral areas of Lake Baikal

Sitnikova (2012): identification key; brief description of teleoconch

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper and middle reaches of the Angara River. A common species living on entire open littoral of the lake (Starobogatov 1989, Shirokaya et al. 2008).

Ecology. Depth, 2–20 m. The greatest population density, up to 943 individuals m^{-2}, was recorded in Birkhin Bay, at 10–12 m, on multilayered rounded stones and boulders underlain by fine, slightly silted sand (Shirokaya et al. 2008). In the littoral zone this species occurs seasonally. In spring and summer limpets inhabit both the surf zone (depth 2–5 m) and zone of weakened breakers (5–20 m), but in autumn, they live only in shallower zone (Maximova et al. 2012).

Remarks. Emendation of initial spelling "*sibiricus*" for "*sibiricum*" (Kozhov 1936) is obligatory according to Article 34.2 of the Code (ICZN 1999).

One of the 7 paralectotypes of *P. sibiricum* (ZIN no. 2, labelled as "Angara River and Lake Baikal, near Kultuk Settlement") is the holotype of *P. aculiferum* Starobogatov, 1989; the other 6 (ZIN no. 2) are paratypes of *G. benedictiae* (ZIN no. 3). The eighth paralectotype of *P. sibiricum* (ZIN no. 3) was erroneously labelled "Tomsk" (Western Siberia) by R. Maack and is a paratype of *P. werestschagini* Starobogatov, 1989 (ZIN no. 3).

Pseudancylastrum beckmanae Starobogatov, 1989

Figures 5A, 12F

Pseudancylastrum beckmanae Starobogatov 1989: 49, fig. 1(*4*).

Type locality. Lake Baikal, Solontsovyi Cape.

Types. ZIN: holotype and 20 paratypes. Holotype (ZIN 1/546-1985, in alcohol): coll. expedition of Biological–Geographic Institute of Irkutsk State University (BGI ISU), 2 September 1966, at 18–40 m, on stone. The shell is covered with crust of white crystals precipitated from fixing fluid, and it is gradually decaying (Fig. 5A). Its dimensions (in mm): L=5.30; La=4.90; W=4.50; wL=0.50; H=4.0; a=5.90 (Starobogatov 1989). Paratypes: 1 specimen (ZIN 2/546-1985, in alcohol), coll. data same as holotype; 9 specimens (ZIN 3/546-1985, in alcohol), Bol'shaya Kosa Bay, coll. same expedition, 3 September 1966, at 5–12 m, substrate not indicated; 1 specimen (ZIN 4/546-1985, in alcohol), Malaya Kosa Bay, coll. same expedition, 3 September 1966, at 4 m, on stone; 9 specimens (ZIN 5/546-1985, in alcohol), Kedrovyi Cape, coll. same expedition, 2 September 1966, at 4–12 m, on stones.

Other material. Institute of Geological Sciences, Freie Universität Berlin: 1 dry shell (SEM stub), Lake Baikal, near Listvyanka Settlement, 51°51′00.49″N, 104°51′59.97″E, coll. P. Röpstorf (scuba diving), October 1998, at 15 m, on stone, det. A.A. Shirokaya (Fig. 12F).

LIN: 230 specimens (in alcohol and dry), Northern Baikal.

History of the usage of the name.

Starobogatov (1989): teleoconch description; data on type material including shell dimensions of holotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): structure of male copulatory organ

Shirokaya (2003): peculiarities of post-embryonal growth; time to reach maturity; lifespan; differences in diet of juvenile and mature individuals

Shirokaya & Röpstorf (2003): morphology of syncapsules, period of reproduction, duration of embryogeny, developmental stages

Shirokaya et al. (2003): description of adult shell, protoconch and radula (SEM data); additional taxonomically important characters; polytomic identification key to species)

Shirokaya & Röpstorf (2004), as *Pseudancylastrum* (*Pseudancylastrum*): description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic key

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): data on type material and type locality; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): specified and supplemented diagnosis; phylogenetic relationships

Shirokaya et al. (2008): geographic and bathymetric distribution, biotope

Kantor et al. (2010): type locality; presence of holotype in ZIN collection; distribution

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper part of the Angara River. Disjunctive range.

Specific records in Lake Baikal. Elokhin Cape; Zavorotnyi Cape; Kotel'nikovski Cape; Svyatoi Nos Peninsula; mouth of the Bol'shoi Chivyrkui River; Bol'shoi Ushkani Island (Starobogatov 1989, Shirokaya et al. 2008, Shirokaya original data).

Ecology. Depth, 1.5–20 m. The greatest population density, up to 147 individuals m^{-2}, was recorded at Elokhin Cape, at 15 m, on bedrock, including vertical rock surfaces (Shirokaya et al. 2008). Egg masses are laid on upper and lateral surfaces of stones. The syncapsule contains 4–10 eggs; the development of embryos is asynchronous (Shirokaya & Röpstorf 2003). In culture, oviposition occurs in June, hatching of juveniles in December. Juveniles feed on cyanobacteria, fungi, and phytoplankton (green, diatom, and dynophyte algae, as well as their spores). Benthic diatoms form the bulk of the diet in mature animals (Shirokaya 2003).

Pseudancylastrum dybowskii **(Clessin, 1882)**

Figures 5C, 11A, 13B

Ancylus dybowskii Clessin 1882: 38, Taf. VII, fig. 1(*1*).
Pseudancylastrum sibiricum, part. — Kozhov 1936: 185, Taf. VII, figs 34–36; Shadin 1952: 203.

Type locality. Southern Baikal.

Types. Whereabouts unknown.

Other material. ZIN, 4 specimens in total: 3 dry shells (ZIN no. 1), Angara River, near Irkutsk City, coll. G. Radde, 1855, initially identified by C.A. Westerlund and L. Schrenck as *Ancylus* (*Ancylastrum*) *sibiricus,* re-identified by Ya.I. Starobogatov, 1985, as *Pseudancylastrum dybowskii*, dimensions (in mm) of largest shell (Fig. 5C): L = 5.10; La = 4.80; W = 4.30; wL = 0.50; H = 3.0; a = 5.60; 1 specimen (ZIN 2/546-1985, in alcohol), Solontsovyi Cape, coll. BGI ISU expedition, 2 September 1966, at 10 m, substrate not indicated, det. Ya.I. Starobogatov.

SMF, 2 specimens in total: 1 dry shell, Lake Baikal, Davshe Bay, 54°20′31.47″N, 109°29′43.91″E, coll. I.V. Khanaev and Alexander B. Kupchinski (scuba diving), 14 July 2002, at 3.5 m, on rounded stones covered with encrusting sponges (Fig. 13Ba); 1 dry shell, Lake Baikal, Khabsagai Cape, 52°44′38.91″N, 106°34′33.28″E, same collectors, 18 July 2002, at 6–9 m, on angular stones (5–30 cm in diameter) and boulders (0.7–1.5 m in diameter) covered with sponges and *Chaetocladiella* sp., on sandy-pebble bottom (Fig. 13Bb). Both specimens identified by A.A. Shirokaya.

LIN: 11 specimens (in alcohol) and 1 dry shell (SEM stub), Northern and Middle Baikal.

History of the usage of the name.
Clessin (1882), as *Ancylus*: teleoconch description and dimensions; locality; assignment of Baikalian limpets to *Ancylastrum*
Westerlund (1885), as *Ancylus*: teleoconch description and dimensions
Lindholm (1909), as *Ancylus* (*Pseudancylastrum*)?: teleoconch description, bathymetrical and regional distribution, zoogeographical characteristics (= *Baicalancylus laricensis* sensu Starobogatov 1967, 1989)
Shadin (1933), as *Ancylus* (*Pseudancylastrum*): teleoconch description and dimensions
Starobogatov (1989): teleoconch description; data on type locality; shell dimensions of ZIN collection collected by G.I. Radde, 1855, and expedition of BGI ISU, 1966; discussion on shell variability; distribution; biotope
Kozhova & Erbaeva (1998): subendemism of *P. dybowskii* (record in upper Angara River)
Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): type locality and distribution; zoogeographical and ecological data; presence in ZIN collection
Starobogatov et al. (2004): identification key; distribution; biotope
Kantor & Sysoev (2005): distribution
Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): differential diagnosis
Shirokaya et al. (2008): geographic and bathymetric distribution; biotope
Kantor et al. (2010): type locality; distribution
Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper part of the Angara River. Disjunctive range.

Specific records in Lake Baikal. Davshe Bay; Khabsagai Cape (Shirokaya et al. 2008, Shirokaya original data). Unknown in Southern Baikal (Starobogatov 1989).

Ecology. Depth, 2.5–10 m (Starobogatov 1989). Found at 40 m (Khabsagai Cape, coll. I.V. Khanaev and A.B. Kupchinski, 18 July 2002) on grey sand and pebbles (det. A.A. Shirokaya).

Remarks. Type specimens of gastropods described by Clessin (1882) are dispersed among several European natural history museums, for example, London and Stuttgart (Ira Richling pers. comm.). Malacological collections in some of them were partially destroyed during the Second World War (e.g., most basommatophorans in the Senckenberg Naturmuseum, Frankfurt am Main, and Stuttgart Staatliches Museum für Naturkunde) (Dance 1986, Vinarski et al. 2012, Ronald Janssen pers. comm.). There are now no types of "*A*." *dybowskii* remaining in any European museum. Perhaps, they were also destroyed in the 1940s. Hubendick (1969) was of the same opinion. Here, we provide a drawing of the type specimen of "*Ancylus*" *dybowskii* reproduced from Clessin (1882)

(Fig. 11A). Its dimensions (in mm): L=4.5; W=3.8; H=3.2 (other measurements were not indicated by Clessin).

Pseudancylastrum olgae Starobogatov, 1989

Figures 5D, 12H

Pseudancylastrum olgae Starobogatov 1989: 48, fig. 1(*3*).

Type locality. Lake Baikal, near Klyuevka Settlement.

Types. ZIN: holotype and 3 paratypes. Holotype (ZIN 1/545-1985, in alcohol): coll. S.M. Popova, 29 July 1957, at 8 m, on stone. Shell almost destroyed, its surface covered with white crystals precipitated from fixing fluid (Fig. 5D). Its dimensions (in mm): L=5.0; La=4.40; W=3.60; wL=0.30; H=3.20; a=5.0 (Starobogatov 1989). Paratypes: 2 specimens (ZIN 2/545-1985, in alcohol), coll. data same as holotype; 1 specimen (ZIN 3/545-1985, in alcohol), Mysovskaya Bank, same collector, 30 July 1957, at 8 m, on stone. All type specimens identified by Ya.I. Starobogatov.

Other material. SMF, 3 specimens in total: 1 dry shell, Lake Baikal, Davshe Bay, 54°20′31.47″N, 109°29′43.91″E, coll. I.V. Khanaev and A.B. Kupchinski, 14 July 2002, at 6 m, on rounded stones covered with encrusting sponges (Fig. 12Ha); 1 dry shell, Lake Baikal, Khabsagai Cape, 52°44′38.91″N, 106°34′33.28″E, same collectors, 18 July 2002, at 6–9 m, on angular stones (5–30 cm in diameter) and boulders (0.7–1.5 m in diameter) covered with sponges and *Chaetocladiella* sp., on sandy-pebble bottom (Fig. 12Hb); 1 dry shell, Lake Baikal, Krasnyi Yar Cape I, South Baikal, 52°25′36.6″N, 105°53′14.2″E, same collectors, 18 July 2002, at 9 m, on angular boulders covered with branched sponges (Fig. 12Hc). All specimens identified by A.A. Shirokaya.

LIN: 11 specimens (in alcohol), from 3 Baikal basins.

History of the usage of the name.

Starobogatov (1989): teleoconch description; data on type material including shell dimensions of holotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): assignment of species to nominotypical subgenus based on shell characters

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): information on type material and type locality; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): comparative diagnosis

Shirokaya et al. (2008): occurrences

Kantor et al. (2010): type locality; presence of holotype in ZIN collection; distribution

General distribution. Lake Baikal. Disjunctive range.

Specific records in Lake Baikal. Khabsagai Cape; Davshe Bay; Krasnyi Yar Cape I (Shirokaya et al. 2008).

Ecology. Depth, 2–10 m; on stones and pebbles. A rare species.

Pseudancylastrum cornu Starobogatov, 1989

Figures 5E, 13A

Pseudancylastrum cornu Starobogatov 1989: 50, fig. 1(*5*).

Type locality. Southern Baikal, without further locality details.

Types. ZIN, holotype (ZIN no. 1, in alcohol): coll. A.A. Korotnev expedition, no additional data, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *troscheli*. Lower ⅓ of shell completely destroyed (Fig. 5E). Shell dimensions (in mm): L=5.0; La=3.40; W=4.20; wL=0.20; H=4.50; a=5.90 (Starobogatov 1989).

Other material. SMF, 6 specimens in total: 1 dry shell, Lake Baikal, littoral of Tonki Island, vicinity of a sealery, 53°51′25.6″N, 108°42′36.7″E, coll. P. Röpstorf (scuba diving), 12 September 2002, at 20 m, on rocks and boulders; 4 dry shells, Lake Baikal, N of Zavorotnyi Cape, 54°18′05.1″N, 108°30′09.9″E, coll. I.V. Khanaev, Valeri F. Skudenko and Igor Yu. Parfeevets (scuba diving), 30 June 2003, at 5–10 m, on stones (Fig. 13A); 1 dry shell, Lake Baikal, littoral of Boguchanski Island, 55°25′58.07″N, 109°13′40.39″E, same collectors, at 15 m, on rounded stones covered with encrusting sponges. All specimens identified by A.A. Shirokaya.

LIN: 74 specimens (in alcohol), Northern Baikal.

History of the usage of the name.

Starobogatov (1989): teleoconch description; data on type material, including shell dimensions of holotype; distribution

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): assignment to nominotypical subgenus based on shell sharacters

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): data on type material and type locality; zoogeographical data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): differential diagnosis

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality; presence of holotype in ZIN collection; distribution

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper part of the Angara River. Disjunctive range.

Specific records in Lake Baikal. Elokhin Cape; littoral of Boguchanski Island; Kotel'nikovski Cape; N of Zavorotnyi Cape; Ushkanji Islands; upper reaches of the Angara River (Shirokaya et al. 2008).

Ecology. Depth, 1.5–25 m. The greatest population density, up to 25 individuals m^{-2}, was recorded in Northern Baikal, at 7–10 m, on pebbles and boulders, on sandy bottom (Shirokaya et al. 2008).

Remarks. The indication by Starobogatov (1989) that W.A. Lindholm identified the holotype of *P. cornu* as "*Ancylus dybowskii*" was in error. Only 1 acroloxid specimen in all material collected by the A.A. Korotnev expedition was identified by Lindholm (1909) as "*A.* (*Pseudancylastrum*) ? *dybowskii*". This specimen was the holotype of *Baicalancylus laricensis* (1901, collected at Listvyanka Settlement, on stones, depth 6.4–10.7 m, sta. 13a) (Starobogatov 1989).

The ZIN catalogue indicates that the only specimen of *P. cornu* from Southern Baikal was identified by Lindholm as "*A.* (*P.*) *troscheli* Dyb.". There is no original label in the lot. In Southern Baikal, *A. troscheli* (sensu Lindholm 1909) was found by A.A. Korotnev in 2 bays: Listvennichnyi, including Baranchick Valley, and Kultuk. One of these bays probably is the exact type locality of *P. cornu*.

Pseudancylastrum korotnevi Starobogatov, 1989

Figures 5F, 12C

Pseudancylastrum korotnevi Starobogatov 1989: 51, fig. 1(*6*).
Ancylus sibiricus, part.—Dybowski 1875: 61, Taf. IV, figs 38–40, Taf. VII, figs 11, 14.
Ancylus (*Pseudancylastrum*) *sibiricus*, part.—Lindholm 1909: 27.
Ancylus (*Pseudancylastrum*) *troscheli*, part.—Lindholm 1909: 28.

Type locality. Lake Baikal, Kocherikovski Cape.

Types. ZIN: holotype and 9 paratypes. Holotype (ZIN 1/359-1935, dry shell): coll. A.A. Korotnev expedition, 14 July 1902, sta. 165, at 5.6–7.4 m, on stones, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *troscheli*. Shell in good condition (Fig. 5F), its dimensions (in mm): L = 4.30; La = 3.40; W = 3.20; wL = 1.0; H = 2.50; a = 4.0 (Starobogatov 1989). Paratypes: 1 dry shell (ZIN 2/359-1935), coll. data same as holotype, initially identified by W.A. Lindholm as *A.* (*P.*) *troscheli*; 6 dry shells (ZIN 3/359-1935), Kultuk Bay, coll. same expedition, 16 August 1902, sta. 13a, at 3.7–31.5 m, substrate not indicated, initially identified by W.A. Lindholm as *A.* (*P.*) *sibiricus*; 1 specimen (ZIN 4/548-1985, in alcohol), opposite Zhilistsche Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 20 June 1954, at 9 m, on stone; 1 dry shell (ZIN no. 5), Lake Baikal, coll. B. Dybowski, no additional data, initially identified by W. Dybowski (1875) as *A. sibiricus*. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF, 3 specimens in total: 2 dry shells, Lake Baikal, between Tolstyi Cape and Shumikha River (near collection sites of paratypes ZIN 3/359-1935 and ZIN 4/548-1985), 51°47′48.20″N, 104°31′42.12″E, coll. I.Yu. Parfeevets and I.V. Khanaev, 5 July 2001, at 1.5–2.5 m, on boulders and pebbles (Fig. 12Ca); 1 dry shell, Lake Baikal, Khabsagai Cape, 52°44′38.91″N, 106°34′33.28″E, coll. I.V. Khanaev and A.B. Kupchinski, 18 July 2002, at 2.5 m, on multilayered boulders (to 1.5 m in diameter) and stones covered with sponge and *Chaetocladiella* sp. and powdered with fine sand (Fig. 12Cb). All specimens identified by A.A. Shirokaya.

LIN: 25 specimens (in alcohol), Southwestern Baikal.

History of the usage of the name.
Starobogatov (1989): type material including shell dimensions of holotype and largest paratype from Kultuk; teleoconch; variability of shell shape; distribution; ecological data
Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): assignment of species to nominotypical subgenus based on shell sharacters
Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): type material and type locality; zoogeographical and ecological data
Kantor & Sysoev (2005): distribution
Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): differential diagnosis
Shirokaya et al. (2008): horizontal distribution
Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution
Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal. Disjunctive range.

Specific records in Lake Baikal. Khabsagai Cape; Khabartui Cape; between Tolstyi Cape and Shumikha River (Shirokaya et al. 2008).

Ecology. Depth, 1.5–10 m. A rare species.

Pseudancylastrum werestschagini Starobogatov, 1989

Figures 6A, 12E

Pseudancylastrum werestschagini Starobogatov 1989: 53, fig. 1(*8*).
Ancylus sibiricus, part.—Gerstfeldt 1859: 23; Clessin 1882: 37, Taf. III, fig. 10.
Ancylus (*Pseudancylastrum*) *sibiricus*, part.—Lindholm 1909: 27.
Ancylus (*Pseudancylastrum*) *troscheli*, part.—Lindholm 1909: 28.
Ancylus (*Pseudancylastrum*) *sibiricus*, part.—Shadin 1933: 130, fig. 99.
Pseudancylastrum sibiricum, part.—Kozhov 1936: 185, Taf. VII, figs 34–36; Taf. X, figs 1, 17.

Type locality. Lake Baikal, opposite Varnachka Valley, Bol'shye Koty Bay.

Types. ZIN: holotype and 74 paratypes. Holotype (ZIN 1/547-1985, dry shell): coll. E.S. Poberezhnyi, August 1978, at 3–5 m, on stones. Shell in good condition (Fig. 6A), its dimensions (in mm): L = 6.80; La = 5.0; W = 5.30; wL = 1.10; H = 3.60; a = 6.20 (Starobogatov 1989). Paratypes: 13 dry shells (ZIN 2/547-1985), coll. data same as holotype; 1 dry shell (ZIN no. 3), erroneously labelled "Tomsk", actually, Angara River, coll. R. Maack, 1854, no additional data, initially identified by H.N. Gerstfeldt as *Ancylus sibiricus* (syntype ZIN no. 5 of the latter); 2 dry shells (ZIN 4/359-1935), opposite Baranchick Valley, Listvennichnyi Bay, coll. A.A. Korotnev expedition, 9 June 1902, sta. 2a, at 5.6–13 m, on stones, initially identified by Lindholm (1909) as *A.* (*P.*) *sibiricus*; 1 dry shell (ZIN no. 5), Angara River, coll. and det. M.M. Kozhov (as *A. sibiricus*), no additional data; 2 specimens (ZIN no. 6, in alcohol), Lake Baikal, sta. 16, no additional data, initially identified by Ilia M. Likharev as "*P. sibiricum* no. 12"; 16 specimens (ZIN 7/68-1964, in alcohol), Listvennichnyi Bay, coll. expedition of Limnological Institute, at 3–10 m, sampling data and substrate not indicated; 5 specimens (ZIN 8/137-1973, in alcohol), same locality, coll. A.A. Korotnev expedition, 19 June 1901, sta. 12, at 5.6–22.2 m, on stones, initially identified by Lindholm (1909) as "*A.* (*P.*) *sibiricus* no. 14"; 15 specimens (ZIN 9/548-1985, in alcohol), opposite Zhilistsche Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 16 September 1966, at 15 m, on rocks and stones; 2 specimens (ZIN 10/548-1985, in alcohol), same locality and collector, 20 June 1954, at 9 m, on stones; 1 specimen (ZIN no. 11, in alcohol), Southern Baikal, no additional data; 1 specimen (ZIN 12/548-1985, in alcohol), Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 20 June 1954, at 9 m, on stones; 5 specimens (ZIN 13/548-1985, in alcohol), same locality and collector, 15 June 1954, at 3 m, on stones; 3 specimens (ZIN 14/548-1985, in alcohol), same locality and collector, July 1954, at 10 m, on stones; 4 specimens (ZIN 15/547-1985, in alcohol), same locality, coll. E.S. Poberezhnyi, August 1977, at 3–5 m, on stones; 1 specimen (ZIN 16/548-1985, in alcohol), opposite Sennaya Valley, same locality, coll. Ya.I. Starobogatov, 28 June 1954, at 2.5 m, on stone; 1 damaged specimen (ZIN 17/548-1985, in alcohol), opposite Malye Koty Valley, same locality and collector, 25 August 1966, at 5–8 m, on stone; 1 dry shell (ZIN 18/359-1935), Listvennichnyi Bay, coll. A.A. Korotnev expedition, 19 June 1901, sta. 12, at 5.6–22.2 m, on stone, initially identified by Lindholm (1909) as "*A.* (*P.*) *troscheli* no. 4". All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF, 3 specimens in total: 2 dry shells, Khabsagai Cape, 52°44′38.91″N, 106°34′33.28″E, coll. I.V. Khanaev and A.B. Kupchinski (scuba diving), 18 July 2002, at 2.5 m, on multilayered boulders (to 1.5 m in diameter) and stones covered with sponge and *Chaetocladiella* sp. and powdered with fine sand (Fig. 12Ea, c); 1 dry shell, Beriozovyi Cape (c. 15 km SW of Bol'shye Koty Bay, topotype), 51°50′38.03″N, 104°53′46.58″E, coll. Kirill M. Ivanov and Sergei Petrov (scuba diving), 26 June 2002, at 10 m, on stones covered with encrusting sponges (Fig. 12Eb). All specimens identified by A.A. Shirokaya.

LIN: 17 specimens (in alcohol and dry), western shore of South and Middle Baikal.

History of the usage of the name.

Starobogatov (1989): teleoconch description; data on type material including shell dimensions of holotype; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): structure of male copulatory organ

Kozhova & Erbaeva (1998): subendemism of *P. werestschagini*: record of species in upper Angara River

Shirokaya (2003): peculiarities of post-embryonal growth; terms of maturity, life span; diet differences between mature and juvenile individuals

Shirokaya & Röpstorf (2003): morphology of syncapsules, terms of reproduction, duration of embryogeny, developmental stages

Ostrovskaya et al. (2004): phenomenon of intra-clonal mixoploidy, occurring in a form of mosaic specimens

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): information on type material and type locality, distribution, zoogeographical and ecological data

Starobogatov et al. (2004): identification key, distribution; biotope

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): specified and supplemented diagnosis

Shirokaya et al. (2008): horizontal distribution; biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

Maximova al. (2012): seasonal quantitative dynamics of gastropods in 3 hydrodynamically different stony littoral areas of Lake Baikal

General distribution. Lake Baikal and the upper Angara River (Starobogatov 1989, Shirokaya et al. 2008).

Specific records in Lake Baikal. Khabsagai Cape (Shirokaya et al. 2008).

Ecology. Depth, 3–20 m; on multilayered stones. Limpets crowd on the undersides of the uppermost layers of stones and on the upper surfaces of underlying layers of stones (Sitnikova et al. 2004, Shirokaya et al. 2008). In spring and autumn, this littoral species occurs mostly in the zone of weakened breakers, at 5–20 m (Maximova et al. 2012). Egg masses are laid on the tops and sides of stones. The number of eggs in a syncapsule varies (3–10), and development of embryos is asynchronous (Shirokaya & Röpstorf 2003). In culture, oviposition occurs in June and hatching of juveniles in October to December. Juveniles feed on cyanobacteria, water fungi, and phytoplankton (green, dynophyte, and diatom algae, as well as their spores). Benthic diatoms are the bulk of diet in mature molluscs (Shirokaya 2003).

"Pseudancylastrum" troschelii (W. Dybowski, 1875)

Figures 6B, 12A

Ancylus troschelii, part. W. Dybowski 1875: 64, Taf. IV, figs 35–37.
Ancylus troscheli — Crosse & Fischer 1879: 163; Clessin 1882: 56, Taf. IX, fig. 1; Westerlund 1885: 95.

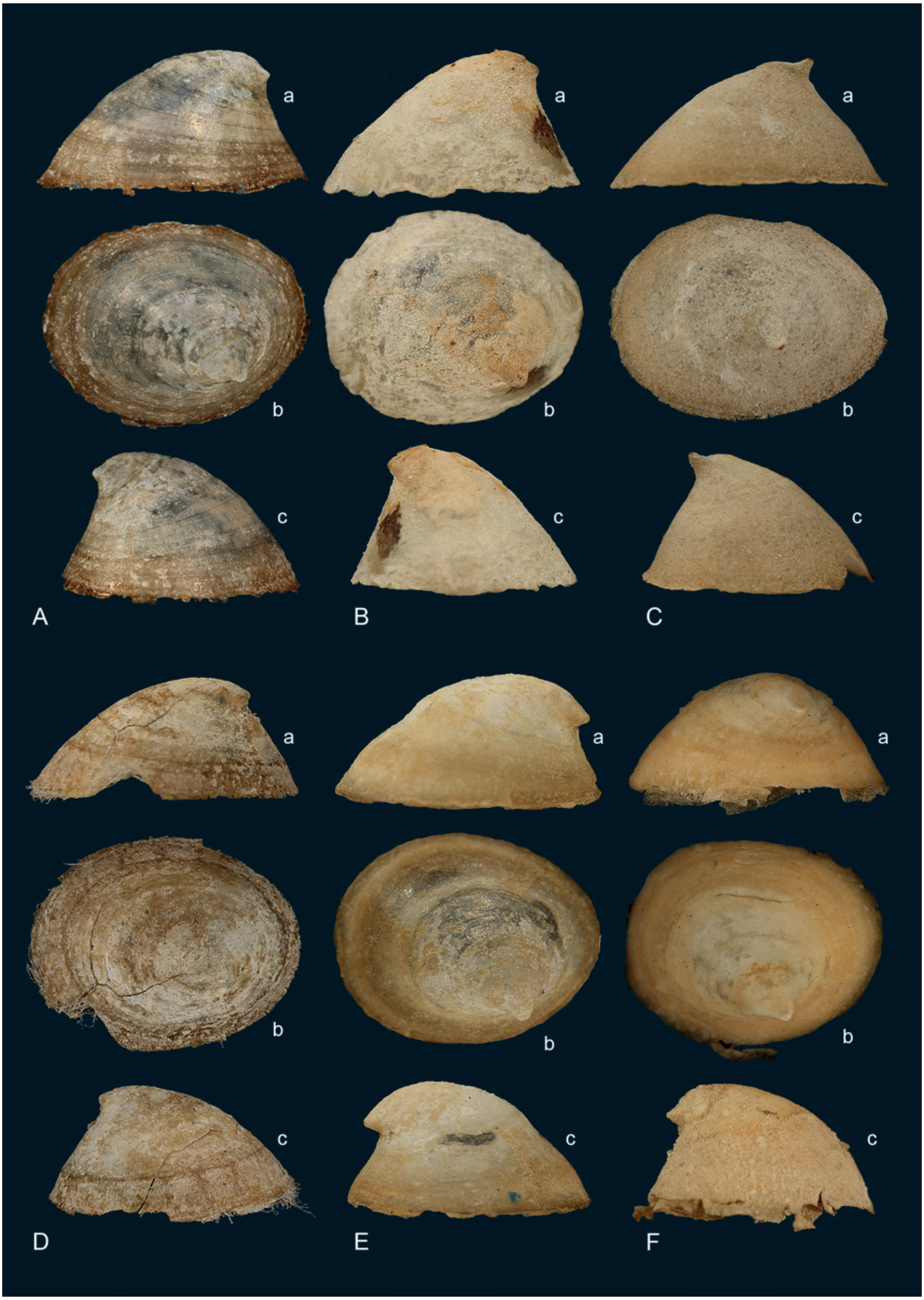

Figure 6. A. *Pseudancylastrum werestschagini* Starobogatov, holotype: L = 6.80 mm, W = 5.30 mm, H = 3.60 mm. **B.** "*P.*" *troschelii* (W. Dybowski), lectotype: L = 7.00 mm, W = 5.70 mm, H = 3.60 mm. **C.** *P. aculiferum* Starobogatov, holotype: L = 6.50 mm, W = 4.80 mm, H = 3.00 mm. **D.** *P. poberezhnyi* Starobogatov, holotype: L = 5.60 mm, W = 4.70 mm, H = 2.40 mm. **E.** *P. dorogostajskii* Starobogatov, holotype: L = 5.90 mm, W = 4.50 mm, H = 2.50 mm. **F.** *P. irindaense* Starobogatov, holotype: L = 6.20 mm, W = 4.90 mm, H = 3.40 mm. Teleoconch: **Aa–Fa**, left side view; **Ab–Fb**, top view; **Ac–Fc**, rear view.

Ancylus (*Pseudancylastrum*) *sibiricus*, part.—Lindholm 1909: 27.
Ancylus (*Pseudancylastrum*) *troscheli*—Shadin 1933: 130, fig. 100.
Pseudancylastrum troscheli—Starobogatov 1989: 54, fig. 1(*9*).
Pseudancylastrum (*Pseudancylastrum*) *troscheli*—Kruglov & Starobogatov 1991b: 84; Shirokaya 2005: 8; Shirokaya et al. 2008: 534, fig. 2, tab. 1.

Type locality. Southern Baikal. Probably Kultuk Settlement (Starobogatov 1989).

Types. ZIN: lectotype and 4 paralectotypes, all designated by Starobogatov (1989: 54). Lectotype (ZIN no. 1, dry shell): coll. B. Dybowski, no additional data, det. W. Dybowski. Shell in relatively good condition (Fig. 6B), its dimensions (in mm): L = 7.0; La = 4.80; W = 5.70; wL = 1.80; H = 3.60; a = 6.30 (Starobogatov 1989). Paralectotypes: 4 dry shells (ZIN no. 2), coll. data same as lectotype.

Other material. ZIN, 8 specimens in total: 2 dry shells (ZIN no. 3), Bol'shye Koty Bay, coll. and det. M.M. Kozhov, at 21–25 m, sampling data and substrate not indicated; 1 dry shell (ZIN 4/359-1935), opposite Baranchick Valley, Listvennichnyi Bay, coll. A.A. Korotnev expedition, 9 June 1902, sta. 2a, at 5.6–13 m, on stone, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *sibiricus*; 1 specimen (ZIN 5/548-1985, in alcohol), Bol'shye Koty Bay, coll. and det. Ya.I. Starobogatov, 21 June 1954, at 6 m, on silted sand; 4 dry shells (ZIN 6/359-1935), Kultuk Bay (topotypes), coll. A.A. Korotnev expedition, 16 August 1902, sta. 13a, at 3.7–31.5 m, on stones and sand. All specimens (re)determined by Ya.I. Starobogatov.

SMF: 2 dry shells, Lake Baikal, littoral of Tonki Island, vicinity of a sealery, 53° 51′ 25.6″ N, 108° 42′ 36.7″ E, coll. P. Röpstorf (scuba diving), 12 September 2002, at 10–20 m, on stones and peaks of underwater rocks (Fig. 12A).

History of the usage of the name. To understand the development of the species comprehension, we have included here some synonymous names that evolved due to incorrect subsequent spelling of the species name.

Dybowski (1875), as *Ancylus*: teleoconch and radula description

Westerlund (1877), as *Ancylus*: shell description and dimensions; distribution

Crosse & Fischer (1879), as *Ancylus troscheli*: distribution; comparison shell and radula to "*A.*" *sibiricus*

Clessin (1882), as *Ancylus troscheli*: shell description and dimensions; distribution; taxonomic position

Dybowski (1884), as *Ancylus*: shell and radula, including tooth dimensions; bathymetric distribution

Westerlund (1885), as *Ancylus troscheli*: description and dimensions of shell; distribution

Dybowski (1910), as *Ancylus*: bathymetric distribution; biotope

Starostin (1926), as *Ancylus* (*Pseudancylastrum*): geographic and bathymetric distribution

Shadin (1933), as *Ancylus* (*Pseudancylastrum*) *troscheli*: teleoconch description and dimensions; distribution

Starobogatov (1989), as *Pseudancylastrun troscheli*: teleoconch description; information on type material including shell dimensions of lectotype; discussion of shell shape variability; specific records; bathymetric distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*) *troscheli*: belongs to nominotypical subgenus, based on shell characters

Takhteev et al. (2000), as *Pseudancylastrum troscheli*: record of species from Baikal-Lena Nature Reserve, Northern Baikal

Shirokaya et al. (2003), as "*Ancylus*" or "*Acroloxus*": taxonomic position

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): type material and type locality; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): geographic and bathymetric distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*) *troscheli*: differential diagnosis

Shirokaya et al. (2008), as *Pseudancylastrum troscheli*: horizontal distribution

Kantor et al. (2010): type locality, presence of lectotype in ZIN collection, distribution

General distribution. Lake Baikal.

Specific records in Lake Baikal. Kultuk Bay; near Listvyanka and Bol'shoye Goloustnoye Settlements; Bol'shye Koty Bay (Starobogatov 1989, Sitnikova et al. 2004); littoral of Malye Uskanji Islands (Shirokaya original data).

Ecology. Depth, 5–25 m; on small to medium-sized stones (Starobogatov 1989).

Remarks. The taxonomic position of "*P.*" *troschelii* is still uncertain. According to Starobogatov (1989), the shape and position of the protoconch are the main generic characters of Baikal-endemic limpets, but since its description by W. Dybowski (1875), Lake Baikal acroloxids with different shell shapes, as well as protoconch morphologies and positions, were identified as *troschelii.* For example, the shell morphology of *Pseudancylastrum* (or *Acroloxus*) *troscheli*, described by Kozhov (1936: Taf. VII, figs 37, 38), Shadin (1952: fig. 119), and Hubendick (1969: 57, figs 1, 2), is identical to that of *Gerstfeldtiancylus gerstfeldti* Starobogatov, 1989. That is, both have a cap-shaped, medially located protoconch. *Ancylus troscheli*, mentioned in the earlier publication of Shadin (1933: 130, fig. 100), conchologically corresponds to *P. sibiricum* sensu lato; the protoconch is horn-shaped and shifted left of centre. Even the author of the species, W. Dybowski (1875, 1884), illustrated *A. troschelii* using specimens with different protoconch shapes and positions. The left lateral view of the shell in his figure 35 (W. Dybowski 1875: Taf. IV) shows a horn-shaped protoconch, and the ventral view in figure 37 (same plate) shows a cap-shaped protoconch. Later, W. Dybowski (1884: fig. 1a, b) showed a shell with the apex acuminate, but directed hindward. Illustrations of the "*A.*" *troschelii* shell published by the above-cited authors are given here in Figure 11Ba–Bk, Bm, Bn).

"*Ancylus*" *troschelii* (sensu Dybowski) anatomically corresponds to species of the nominotypical subgenus *Gerstfeldtiancylus*, which is characterized by the radula bearing narrow lateral teeth having long cutting edges and the transverse row of teeth undulate, with an obtuse angle in the centre (Dybowski 1875: Taf. VII, fig. 12b, c, 15; 1884: fig. 5).

Structural peculiarities of the digestive, muscular, and reproductive systems of "*Acroloxus troscheli*" illustrated by Hubendick (1962: figs 30–33, 1969: figs 1–4, 29, 36; here, Fig. 11Bl), coincide with those of *G. gerstfeldti* (= *G. renardii*; Shirokaya et al. [2003]). Salivary glands are long and thin throughout. The radular sac length is ⅓–¼ of the body length. The 2 anterior adductor muscles are small. The posterior muscle is thin and arched. The male copulatory organ has a terminally located opening of the vas deferens (Shirokaya et al. 2003, Shirokaya & Röpstorf 2004).

The absence of good drawings (Dybowski 1875) of the type specimens of "*A.*" *troschelii* allowed Kozhov (1936), Shadin (1952), and Hubendick (1969) to consider "*A.*" *renardii* as a junior synonym of "*A.*" *troschelii*, based on a lack of variation in the number of teeth in a transverse radular row and the lack of significant differences in teleoconch morphology. They believed that the position of the apex was variable and not a species-specific character, and defined *Pseudancylastrum* (or *Acroloxus*) *troscheli* as having a smooth shell with a blunt apex located almost medially and behind the middle. However, Starobogatov (1989) considered that species with such an apex belong to the genus *Gerstfeldtiancylus*, and transferred "*A.*" *troschelii* to the genus *Pseudancylastrum* based on his study of type specimens, which are closer to *P. sibiricum* sensu lato.

Because the type specimens of "*P.*" *troschelii* are dried, anatomical study of this material is impossible. To correctly establish the genus to which *"P." troschelii* belongs, it is necessary to determine whether all the specimens used by Dybowski (1875, 1884) to characterize shells and radulae had the same protoconchs and whether the ZIN specimens labelled as "*Pseudancylastrum troscheli*" are those studied by him. For now, we place this species in *Pseudancylastrum* in accordance with Starobogatov (1989).

Pseudancylastrum aculiferum Starobogatov, 1989

Figures 6C, 12B

Pseudancylastrum aculiferum Starobogatov 1989: 55, fig. 1(*10*).
Ancylus sibiricus, part. — Gerstfeldt 1859: 23.
Ancylus (*Pseudancylastrum*) *sibiricus*, part. — Lindholm 1909: 27.
Pseudancylastrum (*Pseudancylastrum*) *aculiferum* — Kruglov & Starobogatov 1991b: 84; Sitnikova et al. 2004: 992; Shirokaya 2005: 8.

Type locality. Primary label: "Angara and Baikal". According to Starobogatov (1989), near Kultuk Settlement.

Types. ZIN: holotype and 7 paratypes. Holotype (ZIN no. 1, dry shell): coll. R. Maack, 1854, no additional data, initially identified by H.N. Gerstfeldt as *Ancylus sibiricus*. It is simultaneously a paralectotype of *P. sibiricum* (one of the 7 specimens listed as no. 2 in the card of the latter species). Shell in good condition (Fig. 6C), its dimensions (in mm): L = 6.50; La = 4.10; W = 4.80; wL = 1.50; H = 3.0; a = 5.50 (Starobogatov 1989). Paratypes: 5 dry shells (ZIN 2/359-1935), Kultuk Bay, coll. A.A. Korotnev expedition, 16 August 1902, sta. 13a, at 3.7–31.5 m, on stones and sand, initially identified by W.A. Lindholm as *A.* (*Pseudancylastrum*) *sibiricus*; 1 dry shell (ZIN 3/359-1935), near Kurma Settlement, Maloye More Strait, coll. same expedition, 30–31 July 1902, sta. 113a, at 9.3 m, on stone; 1 dry shell (ZIN 4/359-1935), opposite Baranchick Valley, Listvennichnyi Bay, coll. same expedition, 9 June 1902, sta. 2a, at 5.6–13 m, on stone, initially identified by W.A. Lindholm as *A.* (*P.*) *sibiricus*. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. ZIN: 1 specimen (ZIN 5/546-1985, in alcohol), S of Bol'shoi Ushkani Island, coll. BGI ISU expedition, 1 September 1966, at 10 m, substrate not indicated.

SMF: 2 dry shells, Lake Baikal, between Tolstyi Cape and Shumikha River (c. 61.5 km NE of Kultuk Bay, topotypes), 51° 47′ 48.20″ N, 104° 31′ 42.12″ E, coll. I.Yu. Parfeevets and I.V. Khanaev, 5 July 2001, at 14 m, on stones and boulders (to 1 m in diameter) on sandy-silt and sandy-pebble bottom, det. A.A. Shirokaya (Fig. 12B).

LIN: 83 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype ZIN 3/359-1935; data on additional material in the collection of ZIN; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): species assigned to nominotypical subgenus based on shell characters

Shirokaya & Röpstorf (2003): morphology of syncapsules, terms of reproduction, duration of embryogeny, developmental stages

Ostrovskaya et al. (2004): phenomenon of intra-clonal mixoploidy (mosaic specimens were found)

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): presence of species in scientific collection; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): differential diagnosis

Shirokaya et al. (2008): geographic and bathymetric distribution, biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection, distribution

Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on density and biomass

Maximova et al. (2012): seasonal quantitative dynamics of snails in 3 hydrodynamically different stony littoral areas of Lake Baikal

Sitnikova (2012): identification key; brief description of teleoconch

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Western side of the south basin, and boundary area between middle and northern basins of Lake Baikal.

Specific records in Lake Baikal. Bol'shye Koty Bay; Khabsagai Cape; Maloye More Strait; Svyatoi Nos Peninsula; littoral of Ushkanji Islands (Starobogatov 1989, Shirokaya et al. 2008).

Ecology. Depth, 1.5–36 m; in rubble-debris zone, on sharp-edged boulders, as well as in bedrock areas (Shirokaya et al. 2008). No large aggregations. In the littoral zone this species occurs seasonally. In spring and summer limpets inhabit the surf zone (2–5 m), but in autumn, they are deeper (5–20 m) (Maximova et al. 2012). Egg masses are laid on the tops and sides of stones. The number of eggs in a syncapsule varies (3–6), and the development of embryos is asynchronous (Shirokaya & Röpstorf 2003). In culture, oviposition occurs in April and juveniles hatch in October.

Pseudancylastrum poberezhnyi Starobogatov, 1989

Figures 6D, 12D

Pseudancylastrum poberezhnyi Starobogatov 1989: 56, fig. 1(*11*).
Ancylus sibiricus, part.—W. Dybowski 1884: 148, Taf. IV, figs 3, 6–7.
Ancylus (*Pseudancylastrum*) *sibiricus*, part.—Lindholm 1909: 27.
Acroloxus (*Baicalancylus*) *laricensis*, part.—Starobogatov 1967: 295, fig. 5.

Type locality. Lake Baikal, Bol'shye Koty Bay.

Types. ZIN: holotype and 20 paratypes. Holotype (ZIN 1/547-1985, dry shell): coll. E.S. Poberezhnyi, August 1978, at 3–5 m, on stone. Shell cracked (Fig. 6D), its dimensions (in mm): L = 5.60; La = 4.80; W = 4.70; wL = 0.80; H = 2.40; a = 5.10 (Starobogatov 1989). Paratypes: 1 dry shell (ZIN 3/548-1985), Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 21 June 1954, at 6 m, on silted sand; 1 dry shell (ZIN 4/359-1935), Kultuk Bay, coll. A.A. Korotnev expedition, 16 August 1902, sta. 13a, at 3.7–31.5 m, substrate not indicated, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *sibiricus*; 1 dry shell (ZIN 5/359-1935), coll. data same as ZIN 4/359-1935; 1 specimen (ZIN 6/548-1985, in alcohol), Bol'shye Koty Bay, coll. Ya.I. Starobogatov (dredge), July 1954, at 10 m, on stone; 2 specimens (ZIN 7/548-1985, in alcohol), same locality and collector, 16 June 1954, at 4–6 m, on stones; 2 specimens (ZIN 8/548-1985, in alcohol), same locality and collector, 15 June 1954, at 9 m, on stones; 2 specimens (ZIN 9/548-1985, in alcohol), same locality and collector, 18 June 1954, at 12 m, on stones; 2 specimens (ZIN 10/548-1985, in alcohol), same locality and collector, 9 July 1954, at 8 m, on stones; 1 specimen (ZIN 11/546-1985, in alcohol), Bol'shaya Kosa Bay, coll. BGI ISU expedition, 9 September 1966, depth not indicated, on stones and sand; 6 specimens (ZIN 12/546-1985, in alcohol), Malaya Kosa Bay, coll. same expedition (scuba diving), 3 September 1966, at 10 m, on stones; 1 specimen (ZIN 13/546-1985, in alcohol), Irinda Inlet, coll. same expedition, 10 September 1966, at 5 m, on stone. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF: 3 dry shells, Bol'shye Koty Bay (topotypes). 51°54′09.17″N, 105°04′03.92″E, coll. P. Röpstorf (scuba diving), 30 June 2002, at 14 m, on stones, det. A.A. Shirokaya (Fig. 12D).

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype ZIN 13/546-1985; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Pseudancylastrum*): structure of male copulatory organ

Sitnikova et al. (2004), as *Pseudancylastrum* (*Pseudancylastrum*): presence of species in scientific collection; records in Lake Baikal; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Pseudancylastrum*): specified and supplemental differential diagnosis

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality; presence of holotype in ZIN collection; distribution

Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on density and biomass

General distribution. Lake Baikal.

Specific records in Lake Baikal. Listvennichnyi Bay; littoral of Ushkanji Islands (Sitnikova et al. 2004).

Ecology. Depth, 3–36 m; in rubble-debris zone, on sharp-edged boulders, as well as in bedrock areas (Shirokaya et al. 2008). No large aggregations.

Subgenus *Parancylastrum* Kruglov & Starobogatov, 1991

Type species. *Pseudancylastrum dorogostajskii* Starobogatov, 1989, by original designation.

Diagnosis. Anterior and posterior shell slopes convex. Protoconch horn-shaped, with reticulate microsculpture.

Strong sarcobelum and a well-developed velum situated inside expanded part of preputium (Kruglov & Starobogatov 1991b, Shirokaya et al. 2003).

Pseudancylastrum dorogostajskii Starobogatov, 1989

Figures 6E, 13C

Pseudancylastrum dorogostajskii Starobogatov 1989: 57, fig. 1(*12*).
Ancylus (*Pseudancylastrum*) *sibiricus*, part. — Lindholm 1909: 27.

Type locality. Lake Baikal, opposite Baranchick Valley, near Listvyanka Settlement.

Types. ZIN: holotype and 36 paratypes. Holotype (ZIN 1/359-1935, dry shell): coll. A.A. Korotnev expedition, 9 June 1902, sta. 2a, at 5.6–13 m, substrate not indicated, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *sibiricus*. Shell in good condition (Fig. 6E), its dimensions (in mm): L = 5.90; La = 4.0; W = 4.50; wL = 0.80; H = 2.50; a = 5.20 (Starobogatov 1989). Paratypes: 3 dry shells (ZIN 2/359-1935), coll. data same as holotype; 1 dry shell (ZIN 3/359-1935), Kultuk Bay, coll. same expedition, 16 August 1902, sta. 13a, at 3.7–31.5 m, on stones and sand; 12 dry shells (ZIN 4/359-1935), near Kurma Settlement, Maloye More Strait, coll. same expedition, 30–31 July 1902, sta. 113a, at 1.4–9.3 m, on stones; 1 specimen (ZIN 5/548-1985, in alcohol), Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 21 June 1954, at 6 m, on silted sand; 12 specimens (ZIN 6/546-1985, in alcohol), Ireksokon Cape, coll. BGI ISU expedition, 2 September 1966, at 3–8 m, on stones; 1 specimen (ZIN 7/548-1985, in alcohol), opposite Malye Koty Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov and S.M. Popova, 25 August 1966, at 5–8 m, on stone; 1 specimen (ZIN 8/546-1985, in alcohol), opposite Dugul'dzery river mouth, coll. BGI ISU expedition, 10 September 1966, depth not indicated, on sand; 2 specimens (ZIN 9/546-1985, in alcohol), 2 km S of Orlovski Cape, Svyatoi Nos Peninsula, coll. same expedition, 12 September 1966, at 5 m, on stones; 3 specimens (ZIN 10/546-1985, in alcohol), Khora-Undurskaya Inlet, coll. same expedition, 30 August 1966, at 5–10 m, on stones. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. Institute of Geological Sciences, Freie Universität Berlin: 1 dry shell (SEM stub), near Listvyanka Settlement (topotype), 51° 51′ 00.49″ N, 104° 51′ 59.97″ E, coll. P. Röpstorf (scuba diving), October 1998, at 15 m, on lateral surface of stone, det. A.A. Shirokaya (Fig. 13C).

LIN: 642 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name.

Starobogatov (1989): type material; teleoconch description, including shell dimensions of holotype and largest paratype from Maloye More Strait; variability of shell shape; distribution; biotope

Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Parancylastrum*): structure of male copulatory organ

Shirokaya et al. (2003): description of adult shell, protoconch and radula (SEM data); additional taxonomically important characters; polytomic identification key to species

Shirokaya & Röpstorf (2004), as *Pseudancylastrum* (*Parancylastrum*): description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic key

Sitnikova et al. (2004), as *Pseudancylastrum* (*Parancylastrum*): information on type material and type locality, distribution, zoogeographical and ecological data; syncapsule morphology

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Pseudancylastrum* (*Parancylastrum*): specified and supplemented species diagnosis; phylogenetic relationships

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

Sitnikova (2012): identification key; brief description of teleoconch

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal. A common species living on entire open littoral of the lake (Starobogatov 1989, Shirokaya et al. 2008).

Ecology. Depth, 3–35 m. The greatest population density, up to 247 individuals m^{-2}, was recorded near Katkova Cape, on multilayered rounded stones and boulders (Shirokaya et al. 2008). Syncapsules usually contain 7 egg capsules (Sitnikova et al. 2004).

Pseudancylastrum irindaense Starobogatov, 1989

Figures 6F, 13D

Pseudancylastrum irindaense Starobogatov 1989: 52, fig. 1(*7*).
Ancylus (*Pseudancylastrum*) *sibiricus*, part. — Lindholm 1909: 27.

Type locality. Lake Baikal, Irinda Inlet.

Types. ZIN: holotype and 4 paratypes. Holotype (ZIN 1/546-1985, in alcohol): coll. BGI ISU expedition, 10 September 1966, at 5 m, on stone. Shell gradually decaying (Fig. 6F), its dimensions (in mm): L = 6.20; La = 4.30; W = 4.90; wL = 0.50; H = 3.40; a = 5.50 (Starobogatov 1989). Paratypes: 4 specimens (ZIN 2/359-1935, in alcohol), Lake Baikal, near Kurma Settlement, Maloye More Strait, coll. A.A. Korotnev expedition, 30–31 July 1902, at 9.3 m, on stones, initially identified by Lindholm (1909) as "*Ancylus sibiricus* no. 9". All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF: 3 dry shells, Irinda Inlet (topotypes), 54° 50′ 41.49″ N, 109° 40′ 31.70″ E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets (scuba diving), 4 July 2003, at 4.8 m, on undersides of stones covered with *Ulothrix zonata*, det. A.A. Shirokaya (Fig. 13D).

LIN: 1 specimen (in alcohol), Lake Baikal, near Krasnyi Yar Cape I, 52°25′36.6″N, 105°53′14.2″E, coll. I.V. Khanaev and A.B. Kupchinski, 18 July 2002, at 9 m, on boulders.

History of the usage of the name.
Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype; distribution; biotope
Kruglov & Starobogatov (1991b), as *Pseudancylastrum* (*Parancylastrum*): assignment to *Parancylastrum* based on shell characters
Sitnikova et al. (2004), as *Pseudancylastrum* (*Parancylastrum*): type material and type locality, zoogeographical and ecological data
Kantor & Sysoev (2005): distribution
Shirokaya (2005), as *Pseudancylastrum* (*Parancylastrum*): differential diagnosis
Shirokaya et al. (2008): horizontal distribution
Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

General distribution. Lake Baikal.

Specific records in Lake Baikal. Krasnyi Yar Cape I (our data).

Ecology. Depth, 2–10 m; on large stones (Starobogatov 1989). A rare species.

Genus *Frolikhiancylus* Sitnikova & Starobogatov *in* Sitnikova, Fialkov & Starobogatov, 1993

Type species. *Pseudancylastrum* (*Frolikhiancylus*) *frolikhae* Sitnikova & Starobogatov *in* Sitnikova, Fialkov & Starobogatov, 1993, by original designation and monotypy.

Diagnosis. Anterior and posterior shell slopes convex, left slope nearly straight and vertical. Protoconch cap-shaped, with pitted microsculpture. Penis sheath long, proximally equal in width to glandular flagellum. Penial papilla not well evident. Preputium globularly inflated, followed by narrow cylindrical part. Sarcobelum weakly developed, velum absent (Sitnikova et al. 1993, Shirokaya et al. 2003).

Ecology. Depth, 95–1,000 m. The development of embryos is synchronous. Mixotrophic feeding: vegetable detritus, methane oxidising, and sulphur bacteria (Sitnikova & Shirokaya 2013).

Frolikhiancylus frolikhae (Sitnikova & Starobogatov *in* Sitnikova, Fialkov & Starobogatov, 1993)

Figures 10D, 13E

Pseudancylastrum (*Frolikhiancylus*) *frolikhae* Sitnikova & Starobogatov *in* Sitnikova, Fialkov & Starobogatov 1993: 134, fig. 1.
Frolikhiancylus frolikhae — Stelbrink et al. 2015: 3, fig. 2, electronic supplementary material: 3, tables S1, 4–5, figs S1, 7, S2.

Type locality. Lake Baikal, underwater hydrothermal vent in Frolikha Bay.

Types. LIN: holotype and 15 paratypes. Holotype (LIN no. 263, in alcohol), coll. expedition of the manned deep water submersible “Pisces”, 1990–1991, at 340–420 m, on stones covered with sponges and mud of medium consistence. Shell in good condition, aperture slightly broken (Fig. 10D), its dimensions (in mm): L=2.50; La=1.50; W=1.75; wL=0.0; H=0.95; a=1.85 (Sitnikova et al. 1993). Paratypes: 15 specimens (LIN no. 264, in alcohol), coll. data same as holotype. All type specimens identified by T.Ya. Sitnikova.

Other material. ZMB: 3 dry shells (SEM stub, ZMB/Moll. 103.129a+b; Röpstorf & Riedel 2004), Lake Baikal, Pokojniki Cape, Baikal-Lena Nature Reserve, 1 km N of meteorological station “Solnechnaya”, coll. V.V. Takhteev and P. Röpstorf (Ekman grab), 26 July 1996, at 95–115 m, on stones, on the sandy-silt and sandy-pebble bottom. Two specimens figured (Fig. 13E).

LIN: 48 specimens (in alcohol), Frolikha Bay (topotypes), 55°30′59.77″N, 109°45′55.68″E, coll. Tatiana Ya. Sitnikova, Alexander V. Egorov, Victor M. Pl’usnin, Evgeni S. Chernyaev, and Victor A. Nishcheta, the expedition of the manned deep water submersible “Mir”, 2008–2010, at 402–430 m, on coarse pebble, gravel with patches of sponge, submerged wood, saprolegnia, and filamentous bacteria; 1 specimen (in alcohol), oil-methane seep Gorevoi Utyos, 53°17′03.26″N, 108°25′58.86″E, same collectors and sampling data, at 870–912 m, on bitumen.

History of the usage of the name.
Sitnikova et al. (1993), as *Pseudancylastrum* (*Frolikhiancylus*): teleoconch and male copulatory organ description, differential diagnosis, dimensions of holotype and 1 paratype
Adov et al. (1998), as *Pseudancylastrum*: species finding at northwestern shore of Baikal
Takhteev et al. (2000), as *Pseudancylastrum*: records in Baikal; bathymetric distribution; biotope
Shirokaya et al. (2003), as *Pseudancylastrum*: description of adult shell, protoconch and radula (SEM data); additional taxonomically important characters; polytomic identification key to species
Röpstorf & Riedel (2004), as *Pseudancylastrum*: description of teleoconch, protoconch, and radula (SEM data); discussion on feeding range and foraging
Sitnikova et al. (2004), as *Pseudancylastrum* (*Frolikhiancylus*): information on type material and type locality, distribution, zoogeographical and ecological data
Kantor & Sysoev (2005), as *Pseudancylastrum*: distribution
Shirokaya (2005), as *Pseudancylastrum* (*Frolikhiancyl-*

us): specified and supplemented differential diagnosis; phylogenetic relationships

Shirokaya et al. (2008), as *Pseudancylastrum*: geographic and bathymetric distribution

Kantor et al. (2010), as *Pseudancylastrum*: type locality, presence of holotype in LIN collection, distribution

Sitnikova et al. (2010): record in Middle Baikal, in Gorevoi Utyos oil seep; isotope analysis of tissue, discussion on role of methanotrophic bacteria in feeding

Zemskaya et al. 2012, as *Pseudancylastrum*: discussion on feeding spectrum of *P. frolikhae*, as based on data on stable isotopes in tissue

Sitnikova & Shirokaya (2013), as *Pseudancylastrum* (*Frolikhiancylus*): discussion of shell shape variability; reproductive strategy; egg mass morphology; finding of ectosymbiotic bacteria on shells and egg masses of *P. frolikhae*; first record of gregarines in freshwater gastropods; distribution and trophic relationships of limpets

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Middle and Northern Baikal.

Specific records in Lake Baikal. Pokojniki Cape; Gorevoi Utyos oil seep.

Ecology. Depth, 95–912 m; in areas of thermal water release and oil seeps, on gravel-pebble bottom. This species is the deepest known of any freshwater pulmonate gastropod (Sitnikova 2006, Sitnikova & Shirokaya 2013). Egg masses nearly entirely cover substrates. Egg masses contain 1–3 embryos, with synchronous development. Mixotrophic feeding; food includes, besides vegetable detritus, methane oxidising and sulphur bacteria. Endemic gregarines in the mid-gut.

Remarks. Based on characters of the shell and male copulatory organ, this species was initially assigned to the genus *Pseudancylastrum*. However, the cupped protoconch and terminal position of the vas deferens opening are not typical for that genus. The depth of occurrence as well as light-stable isotopes in animal tissues, which demonstrate the food spectrum of "*P.*" *frolikhae*, allowed us to allocate it to the genus *Frolikhiancylus*. The uniqueness of *F. frolikhae* is confirmed by mitochondrial (COI and 16S rRNA) and nuclear (28S rRNA and H3) data (Stelbrink et al. 2015).

Genus *Gerstfeldtiancylus* Starobogatov, 1989

Type species. *Gerstfeldtiancylus gerstfeldti* Starobogatov, 1989, by original designation; (=*"Ancylus" renardii* W. Dybowski, 1884, according to Shirokaya [2005]).

Diagnosis. Shell grey, lacking sculpture, high-capuliform, with wide, rounded apex, directed hindward, and slightly shifted to the left in some species. Anterior and lateral slopes always convex, posterior slope concave, weakly convex, or straight. Protoconch cap-shaped, with reticulate microsculpture. Prostate globular. Male copulatory organ with long flagellum; penis short, with a terminally located opening of vas deferens; papilla absent. Preputium retractors very strong (Starobogatov 1989, Kruglov & Starobogatov 1991b, Shirokaya et al. 2003).

Ecology. Depth, 2–40 m. The development of embryos is asynchronous. Limpet feed mainly on benthic diatom algae and phytodetritus (Shirokaya 2005).

Subgenus *Gerstfeldtiancylus* s. str.

Diagnosis. Shell large, with maximal width of aperture in adults being no less than 5 mm. Odontophore pink or red in living individuals. Glandular flagellum gradually passing to penis sheath; wall of the latter also with dispersed large glandular cells (Kruglov & Starobogatov 1991b, Shirokaya & Röpstorf 2004).

Gerstfeldtiancylus renardii (W. Dybowski, 1884)

Figsure 7D, 14A

Ancylus renardii W. Dybowski 1884: 157, Taf. IV, figs 2, 4.

Ancylus sibiricus, part. — W. Dybowski, 1875: 61 (non Gerstfeldt 1859).

Ancylus troschelii — W. Dybowski 1884: 156, Taf. IV, figs 1, 5 (non W. Dybowski 1875).

Ancylus (*Pseudancylastrum*) *troscheli*, part. — Lindholm 1909: 28; Kozhov 1931: 65.

Ancylus (*Pseudancylastrum*) *renardi* — Shadin 1933: 131, fig. 102.

Pseudancylastrum troscheli, part. — Kozhov 1936: 187, Taf. VII, figs 37, 38, Taf. X, figs 2, 3; Shadin 1952: 203, fig. 119.

Acroloxus (*Pseudancylastrum*) *troscheli* — Hubendick 1962: 47, figs 29–33.

Acroloxus troscheli part. — Hubendick 1969: 55, figs 1–4, 29, 36.

Gerstfeldtiancylus gerstfeldti — Starobogatov 1989: 60, fig. 2(*1*).

Gerstfeldtiancylus (*Gerstfeldtiancylus*) *gerstfeldti* — Kruglov & Starobogatov 1991b: 85, fig. 2(*1*); Shirokaya et al. 2003: 133, 137, figs 3A, B, 14A–F, tabs. 2, 3, 6–8; Sitnikova et al. 2004: 994.

Type locality. Southern Baikal (Starobogatov 1989).

Types. ZMD: lectotype and 1 paralectotype, both designated here. Lectotype (ZB-M 562 (CD-82), dry shell): coll. B. Dybowski, no additional data, det. W. Dybowski. Shell in good condition, with slightly broken aperture and a fractured protoconch (Fig. 7D), its dimensions (in mm): L = 8.46; La = 5.41; W = 6.30; wL = 2.78; H = 4.0; a = 7.22 (our data). Paralectotype (ZB-M 563 (CD-82), dry shell): coll. data same as lectotype. Both type specimens re-identified by T.Ya. Sitnikova as *Gerstfeldtiancylus renardii*.

Other material. Institute of Geological Sciences, Freie Universität Berlin: 1 dry shell (SEM stub), Lake Baikal, near Listvyanka Settlement (topotype), 51° 51′ 00.49″ N, 104° 51′ 59.97″ E, coll. P. Röpstorf (scuba diving), October 1998, at 15 m, on stones, det. A.A. Shirokaya (Fig. 14A).

LIN: 180 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name. We include some synonymous names as well as erroneous identifications to better understand the development of the interpretation of this species.

DYBOWSKI (1884), as *Ancylus*: description of shell and radula

WESTERLUND (1890), as *Ancylus*: description of shell and radula

HUBENDICK (1962), as *Acroloxus* (*Pseudancylastrum*) *troscheli*: structure of pseudobranch, shell adductors, excretory system, radula, alimentary system, male copulatory organ, and reproductive system

HUBENDICK (1969), as *Acroloxus troscheli*: ultrastructure of protoconch and teleoconch; description of mantle pigment, pseudobranch, shell adductors, radula, and male copulatory organ; synonymy; taxonomic position; horizontal and vertical distribution, biotope

STAROBOGATOV (1989), as *Gerstfeldtiancylus gerstfeldti*: teleoconch description; discussion of shell shape variability; distribution; biotope

KRUGLOV & STAROBOGATOV (1991b), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*) *gerstfeldti*: structure of male copulatory organ

RÖPSTORF et al. (2003), as *Gerstfeldtiancylus kozhovi*: radula morphology and feeding spectrum

SHIROKAYA et al. (2003), as *Gerstfeldtiancylus gerstfeldti*: description of adult shell, protoconch and radula (SEM data); taxonomic position: suggestion to consider *G. gerstfeldti* as a junior synonym of *G. renardii*

SHIROKAYA & RÖPSTORF (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic identification key to species

SITNIKOVA et al. (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*) *gerstfeldti*: distribution, zoogeographical and ecological data

KANTOR & SYSOEV (2005), as *Gerstfeldtiancylus gerstfeldti*: distribution

SHIROKAYA (2005), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): specified and supplemented species diagnosis; phylogenetic relationships

SHIROKAYA et al. (2008): geographic and bathymetric distribution; biotope

KANTOR et al. (2010): type locality; presence of syntypes in ZMD collection; distribution

SITNIKOVA et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on quantitative characteristics

MAXIMOVA et al. (2012): seasonal quantitative dynamics of gastropods in 3 hydrodynamically different stony littoral areas of Lake Baikal

SITNIKOVA (2012): identification key; brief description of teleoconch

STELBRINK et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper part of the Angara River. A common species living on entire open littoral of the lake (SHIROKAYA et al. 2008).

Ecology. Depth, 2–25 m; on multilayered, waterworn stones and boulders. In spring and autumn, this species mostly occurs in the zone of weakened breakers, at 5–20 m (MAXIMOVA et al. 2012). KOZHOV (1931: 65) wrongly gave the depth range for this species as 1.5–150 m.

Remarks. According to the ZIN systematic catalogue, 4 non-type specimens of *G. renardii* sensu STAROBOGATOV (1989) are stored in collection: 2 specimens in poor condition (ZIN no. 1, in alcohol, shells dried separately), Southern Baikal, no additional data, initially identified by W.A. Lindholm as *Ancylus renardi* (Fig. 8); 1 specimen (ZIN 2/548-1985, in alcohol), opposite Varnachka Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov and S.M. Popova, August 1966, at 4–8 m, on stone; 1 specimen (ZIN 3/546-1985, in alcohol, shell dried separately), Bol'shaya Kosa Bay, coll. BGI ISU expedition, 3 September, 1966, at 12–70 m, on stones and sand (Fig. 7C). Without viewing any type specimens, STAROBOGATOV (1989) identified them as *G. renardii*, the flat shell of which had an apex located immediately in the medial part of the teleoconch (as described by DYBOWSKI [1884]). Comparing 2 type specimens of "*Ancylus*" *renardii* stored in ZMD, drawings of the shell and radula of this species provided by W. DYBOWSKI (1884: Taf. IV, figs 2, 4), and those of *G. renardii* sensu STAROBOGATOV (1989: 61, fig. 2(*4*), 64; here, Figs 7C, 8), we concluded that the latter are not "*A.*" *renardii* W. Dybowski. We assigned them to *G. roepstorfi* Shirokaya, Röpstorf & Sitnikova, 2003 (SHIROKAYA et al. 2003).

Gerstfeldtiancylus roepstorfi Shirokaya, Röpstorf & Sitnikova, 2003

Figures 7C, E, 8, 14B

Gerstfeldtiancylus roepstorfi SHIROKAYA, RÖPSTORF & SITNIKOVA 2003: 117–118, 122, 125, 131, 134–136, figs 3C–D, 4A–J, 15B, tables 2–3, 6–8.

Gerstfeldtiancylus renardii — STAROBOGATOV 1989: 64, fig. 2(*4*) (non W. DYBOWSKI 1884).

Gerstfeldtiancylus (*Gerstfeldtiancylus*) *renardii* — KRUGLOV & STAROBOGATOV 1991b: 87, fig. 2(*4*) (non W. DYBOWSKI 1884); SITNIKOVA et al. 2004: 995.

Type locality. Lake Baikal, littoral of Ushkanji Islands.

Types. LIN: holotype and 3 paratypes. Holotype (LIN no. 898, in alcohol): coll. P. Röpstorf, 12 September 2002, at 13 m, on stones and rocks. Shell in good condition (Fig. 7E), its dimensions (in mm): L = 11.70; La = 8.80; W = 9.50; wL = 5.0; H = 4.90; a = 9.0 (SHIROKAYA et al. 2003). Paratypes: 3 specimens (LIN no. 899), coll. data same as holotype.

Institute of Geological Sciences, Freie Universität Berlin, 1 paratype (no number, dry shell, SEM stub): littoral of Tonki Island, Malye Uskanji Islands, vicinity of a sealery, 53° 51′ 25.6″ N, 108° 42′ 36.7″ E, coll. P. Röpstorf (scuba diving), 5 July 2000, at 20 m, on stones and rocks, det. T.Ya. Sitnikova. Photographs of protoconch, teleoconch, and radula of that specimen have been published

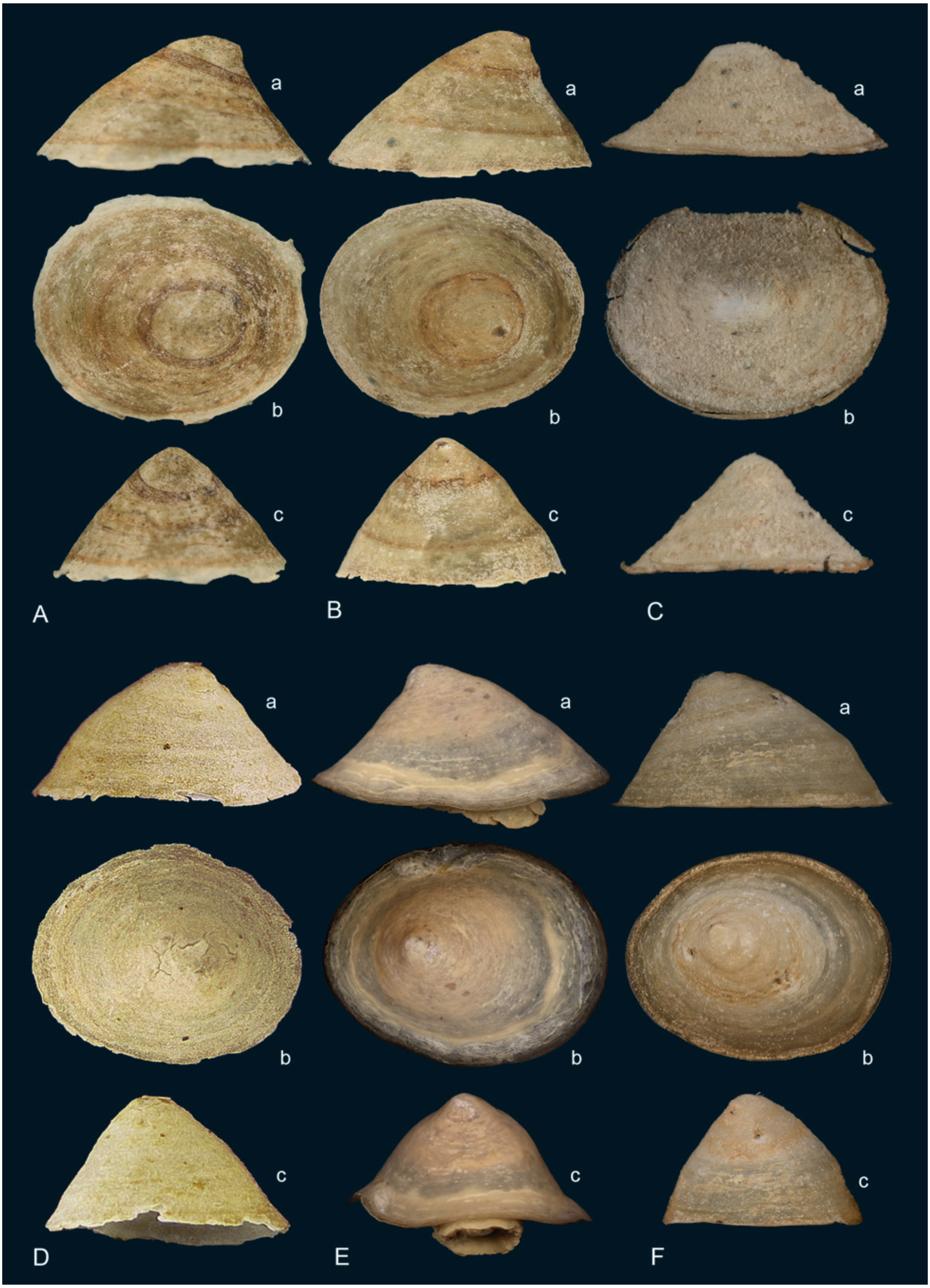

Figure 7. A. *Gerstfeldtiancylus kotyensis* Starobogatov, holotype: L = 6.30 mm, W = 5.20 mm, H = 3.20 mm. **B.** *G. kozhovi* sensu Starobogatov (1989), holotype: L = 8.60 mm, W = 7.10 mm, H = 4.70 mm. **C.** *G. renardii* sensu Starobogatov (1989), ZIN 3/546-1985 (= *G. roepstorfi*, after Shirokaya et al. [2003]), L = 3.75 mm, W = 2.90 mm, H = 1.45 mm. **D.** *G. renardii* (W. Dybowski), lectotype: L = 8.46 mm, W = 6.30 mm, H = 4.00 mm. **E.** *G. roepstorfi* Shirokaya, Röpstorf & Sitnikova, holotype, with soft body: L = 11.70 mm, W = 9.50 mm, H = 4.90 mm. **F.** *G. ushunensis* Shirokaya, topotype: L = 7.98 mm, W = 6.15 mm, H = 4.03 mm. Teleoconch: **Aa**, **Ba**, **Da**, left side view; **Ca**, **Ea**, **Fa**, right side view; **Ab**–**Fb**, top view; **Ac**–**Fc**, rear view.

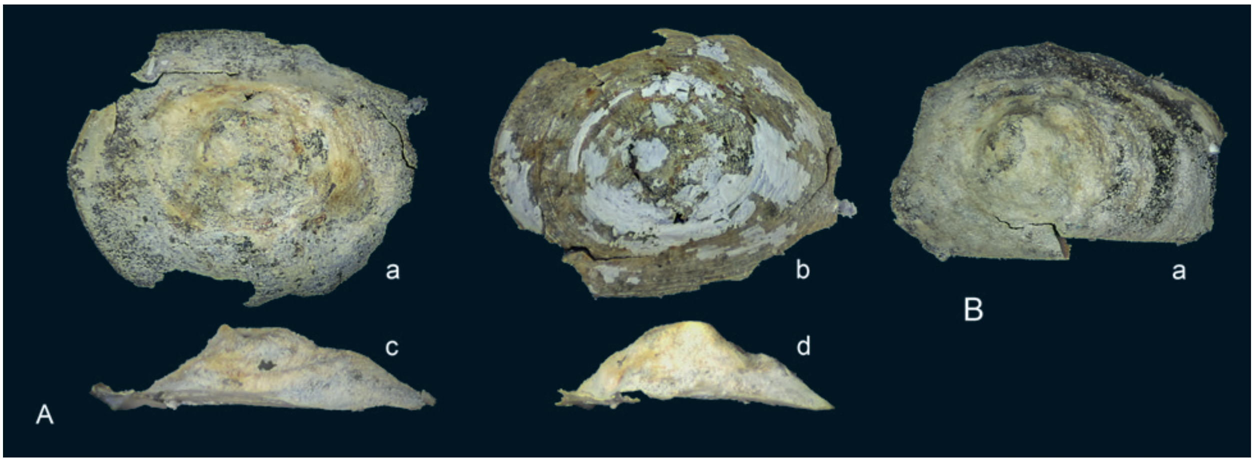

Figure 8. *Gerstfeldtiancylus renardii* sensu Starobogatov (1989), ZIN no. 1, identified by W.A. Lindholm (= *G. roepstorfi*, after Shirokaya et al. [2003]). **A.** First specimen, L = 4.50 mm, W = 2.80 mm, H = 1.50 mm. **B.** Second specimen. Teleoconch: **Aa**, **Ba**, top view; **Ab**, bottom view; **Ac**, right side view; **Ad**, rear view.

in Shirokaya et al. (2003: fig. 4A–J). Here we provide only the shell image (Fig. 14B).

Other material. ZIN, 4 specimens in total: 2 specimens in poor condition (ZIN no. 1, in alcohol, shells dried separately), Southern Baikal, no additional data, initially identified by W.A. Lindholm as *Ancylus renardi*, shell dimensions of largest specimen (in mm): L = 4.5, La = 2.8, W = 2.8, wL = 1.4, H = 1.5, a = 2.8 (Starobogatov 1989), Fig. 8; 1 specimen (ZIN 2/548-1985, in alcohol), opposite Varnachka Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov and S.M. Popova, August 1966, at 4–8 m, on stones; 1 specimen (ZIN 3/546-1985, in alcohol, shell dried separately), Bol'shaya Kosa Bay, coll. BGI ISU expedition, 3 September 1966, at 12–70 m, on stones and sand, shell dimensions (in mm): L = 3.75, La = 2.3, W = 2.9, wL = 1.45, H = 1.45, a = 2.7 (Starobogatov 1989), Fig. 7C. All specimens (re)determined by Ya.I. Starobogatov as *G. renardii*.

LIN: 15 specimens (no numbers, dry shells, SEM stubs), Bol'shoi Ushkani Island (topotypes), c. 53° 50′ 57.8″ N, 108° 36′ 39.6″ E, coll. P. Röpstorf, 12 September 2002, at 15–20 m, on stones and rocks; 5 specimens (no numbers, in alcohol), Krestovyi Cape, c. 52° 38′ 47.41″ N, 106° 26′ 20.58″ E, coll. I.Yu. Parfeevets and A.B. Kupchinski, 13 July 2001, at 18 m, on stones.

History of the usage of the name. To understand the development of the species comprehension, some synonymous names are included.

Starobogatov (1989), as *Gerstfeldtiancylus renardii*: teleoconch description; information on non-type material in ZIN collection; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*) *renardii*: structure of male copulatory organ

Shirokaya et al. (2003): description of protoconch, teleoconch and radula (SEM data); information on type material including shell dimensions of holotype and largest paratype; polytomic identification key to species; discussion of shell shape variability; distribution; biotope

Shirokaya & Röpstorf (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): description of alimentary system, shell adductor muscles, and additional taxonomic characters; polytomic identification key to species

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*) *renardii*: specific records; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005): differential diagnosis; phylogenetic relationships

Shirokaya (2007): morphology of shell; alimentary system and male copulatory organ; geographic and bathymetric distribution; biotope; evolutionary trends

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality, presence of holotype in LIN collection; distribution

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal. Disjunctive range (Shirokaya et al. 2008).

Specific records in Lake Baikal. Bol'shye Koty Bay; Krestovyi Cape; Bol'shaya Kosa Bay (Shirokaya 2007).

Ecology. Depth, 4–25 m; on vertical sides of rocks and upper-lateral surfaces of stones (Starobogatov 1989, Shirokaya et al. 2003). A rare species.

***Gerstfeldtiancylus kotyensis* Starobogatov, 1989**

Figures 7A, 13G

Gerstfeldtiancylus kotyensis Starobogatov 1989: 63, fig. 2(*3*).
Ancylus (*Pseudancylastrum*) *troscheli*, part. — Lindholm 1909: 28 (non W. Dybowski 1875).

Gerstfeldtiancylus kozhovi — Starobogatov 1989: 62, fig. 2(*2*).
Gerstfeldtiancylus (*Gerstfeldtiancylus*) *kozhovi* — Kruglov & Starobogatov 1991b: 85, fig. 2(*2*); Shirokaya et al. 2003: 122, 125, 129–131, 134–137, tables 2, 3, 6–8, figs 12A–G, 15B; Shirokaya & Röpstorf 2004: 63–64, 68–69, tables 1, 2, fig. 5A–D; Sitnikova et al. 2004: 995; Shirokaya 2005: 10.

Type locality. Lake Baikal, Bol'shye Koty Bay.

Types. ZIN: holotype and 20 paratypes. Holotype (ZIN no. 1, dry shell): coll. M.M. Kozhov, July 1928, at 25–40 m, substrate not indicated. Shell with broken margins (Fig. 7A), its dimensions (in mm): L = 6.30; La = 4.70; W = 5.20; wL = 2.60; H = 3.20; a = 5.20 (Starobogatov 1989). Paratypes: 1 specimen (ZIN 2/70-1896, in alcohol), Boguchanskaya Inlet, coll. Yuli N. Wagner, sampling data not indicated, at 44.8 m, on stones, sand, and clay; 6 specimens (ZIN 3/546-1985, in alcohol), Dyrovatyi Cape, coll. BGI ISU expedition, 28 August 1966, sta. 2, at 18–60 m, on gravel; 1 specimen (ZIN 4/548-1985, in alcohol), Bol'shye Koty Bay, coll. Ya.I. Starobogatov, July 1954, at 10 m, on stone; 3 specimens (ZIN 5/548-1985, in alcohol), opposite Malye Koty Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov and S.M. Popova, 25 August 1966, at 5–8 m, substrate not indicated; 1 specimen (ZIN 6/545-1985, in alcohol), Mysovkaya bank, coll. S.M. Popova, 30 August 1957, at 4 m, substrate not indicated; 2 specimens (ZIN 7/546-1985, in alcohol), Kedrovyi Cape, coll. BGI ISU expedition, 2 September 1966, at 4–12 m, on stones; 2 specimens (ZIN 8/548-1985, in alcohol), Peschanaya Bay, coll. Alexander F. Alimov, August 1966, at 10 m, substrate not indicated; 2 specimens (ZIN 9/548-1985, in alcohol), N of Elokhin Cape, coll. Ya.I. Starobogatov, 12 September 1976, at 10–12 m, on big stones and sand; 1 specimen (ZIN 10/70-1896, in alcohol), Dushkachanskaya Bay, coll. Yu.N. Wagner, sampling data not indicated, at 15.5–16.2 m, on small stones and sand; 1 specimen (ZIN no. 11, in alcohol), Lake Baikal, sta.16, no additional data. All specimens determined by Ya.I. Starobogatov.

Other material. Institute of Geological Sciences, Freie Universität Berlin, 2 specimens in total: 1 dry shell (no number, SEM stub), littoral of Tonki Island, vicinity of a sealery, 53°51′25.6″N, 108°42′36.7″E, coll. P. Röpstorf (scuba diving), 12 September 2002, at 20 m, on boulders (Fig. 13Ga, b, e); 1 dry shell (no number, SEM stub), Bol'shye Koty Bay (topotype), 51°53′57.79″N, 105°03′56.50″E, coll. I.Yu. Parfeevets and A.B. Kupchinski (scuba diving), 5 July 2001, at 2–6 m, on upper and lateral surfaces of stones (Fig. 13Gc, d). Both specimens identified by A.A. Shirokaya.

LIN: 248 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name. To understand the development of the species comprehension, some synonymous names are included.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype from Kedrovyi Cape; distribution; biotope
Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): structure of male copulatory organ
Shirokaya & Röpstorf (2003), as *Gerstfeldtiancylus kozhovi*: morphology of syncapsules, terms of reproduction, duration of embryogeny, developmental stages
Shirokaya et al. (2003): description of adult shell, protoconch, and radula (SEM data); additional taxonomic characters; polytomic identification key to species
Shirokaya & Röpstorf (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): description of alimentary system and shell adductor muscles, additional taxonomically important characters, polytomic key
Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): information on type material and type locality; distribution; zoogeographical and ecological data
Kantor & Sysoev (2005): distribution
Shirokaya (2005), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): specified and supplemented diagnosis of species; phylogenetic relationships
Shirokaya (2007): shell, alimentary system and male copulatory organ morphology; geographic and bathymetric distribution; biotope; evolutionary trends
Shirokaya et al. (2008): geographic and bathymetric distribution; biotope
Kantor et al. (2010): type locality; presence of holotype in ZIN collection, distribution
Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on quantitative characteristics
Sitnikova (2012): identification key; brief description of teleoconch
Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal. A common species living on entire open littoral of the lake (Starobogatov 1989, Shirokaya et al. 2008).

Ecology. Depth, 2–40 m; on hard bottoms. The greatest population density, up to 112 individuals m^{-2}, was recorded in Ushun Bay, Malye Ol'khonskie Vorota, at 5–15 m, on multilayered rounded stones and boulders in places with bedrock (Shirokaya et al. 2008). Eggs masses are mostly laid on the lateral surfaces of stones. The number of eggs in a syncapsule varies from 5 or 6 to 10, embryos develop asynchronously (Shirokaya & Röpstorf 2003). In culture, oviposition occurs in April and hatching of juveniles in October. The diet of adults mostly consists of benthic diatom algae of the genus *Cocconeis* Ehrenberg (Shirokaya 2005). The diet of juveniles is unknown.

Gerstfeldtiancylus ushunensis Shirokaya, 2007

Figures 7F, 13F

Gerstfeldtiancylus ushunensis Shirokaya 2007: 55–67, tables 1–2, figs 1, 3A–K, 4A–C, 5A–H, 6F–G, 7A–C.

Type locality. Lake Baikal, Malye Ol'khonskie Vorota, Ushun Bay, 53° 00′ 54″ N, 106° 56′ 96″ E.

Types. ZIN: holotype and 10 paratypes. Holotype (ZIN 1/521-2006, dry shell, SEM stub): coll. I.V. Khanaev and V.F. Skudenko, 7 July 2003, at 20–22 m, on stones. Shell in good condition, its dimensions (in mm): L = 7.20; La = 4.20; W = 5.80; wL = 2.50; H = 3.0; a = 5.50 (Fig. 13F). Paratypes: 9 dry shells (ZIN 2/521-2006), coll. data same as holotype; 1 dry shell (ZIN 3/521-2006), coll. I.V. Khanaev and V.F. Skudenko, 7 July 2003, at 4 m, on stones. All type specimens identified by A.A. Shirokaya.

LIN, 5 paratypes: 2 dry shells (LIN no. 904, SEM stub), coll. data same as holotype; 3 dry shells (LIN no. 905, SEM stub), locality, collectors, and sampling data same as holotype, at 4 m, on stones.

Other material. LIN: 30 specimens (in alcohol; mostly juveniles, topotypes), coll. data same as holotype; shell dimensions (in mm) of adult specimen (Fig. 7F): L = 7.98; La = 5.58; W = 6.15; wL = 2.09; H = 4.03; a = 6.62 (our data).

History of the usage of the name.

Shirokaya (2007): description of protoconch, teleoconch, radula, shell adductor muscles, male copulatory organ (SEM data), egg masses; information on type material including shell dimensions of holotype and 15 paratypes; distribution and habitat; evolutionary trends

Shirokaya et al. (2008): geographic and bathymetric distribution, biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on quantitative characteristics

General distribution. Lake Baikal. Local endemic of East-Ol'khon District (Shirokaya et al. 2008). Unknown outside Malye Ol'khonskie Vorota.

Ecology. Depth, 4–25 m. The greatest population density, up to 114 individuals m^{-2}, was recorded at 20–22 m, on multilayered rounded boulders (Shirokaya 2007).

Subgenus *Kozhoviancylus* Kruglov & Starobogatov, 1991

Type species. *Gerstfeldtiancylus benedictiae* Starobogatov, 1989, by original designation.

Diagnosis. Shell small, with maximum aperture width in adults being no more than 3.5 mm. Odontophore dark grey in living individuals. Penis sheath thin-walled, without large glandular cells, separated from flagellum by a constriction (Kruglov & Starobogatov 1991b, Shirokaya & Röpstorf 2004).

Gerstfeldtiancylus benedictiae Starobogatov, 1989

Figures 9B, C, 14F

Gerstfeldtiancylus benedictiae Starobogatov 1989: 65, fig. 2(*6*).
Ancylus sibiricus, part. — Gerstfeldt 1859: 23.
Ancylus (*Pseudancylastrum*) *troscheli*, part. — Lindholm 1909: 28 (non W. Dybowski 1875).

Type locality. Lake Baikal, near Listvyanka Settlement.

Types. ZIN: holotype and 79 paratypes. Holotype (ZIN 1/543-1985, dry shell): coll. A.A. Korotnev expedition, 19 June 1901, sta. 15a, at 5.6–22.2 m, on stone covered with algae, initially identified by Lindholm (1909) as *Ancylus* (*Pseudancylastrum*) *troscheli*. Shell in poor condition, periostracum fractured (Fig. 9B), its dimensions (in mm): L = 3.30; La = 3.0; W = 2.70; wL = 1.20; H = 4.90; a = 3.10 (Starobogatov 1989). Paratypes: 1 dry shell (ZIN 2/543-1985), coll. data same as holotype; 6 dry shells (ZIN no. 3), Angara River, coll. R. Maack, 1854, depth and substrate not indicated, initially identified by H.N. Gerstfeldt as *Ancylus sibiricus*; 2 dry shells (ZIN 4/543-1985), Kultuk Bay, coll. A.A. Korotnev expedition, 26 June 1902, sta. 37a, at 3.7–9.3 m, on stones; 1 dry shell (ZIN 5/543-1985), opposite Baranchick Valley, near Listvyanka Settlement, coll. same expedition, 1902, at 5.6–11.1 m, on stone; 3 dry shells (ZIN 6/543-1985), Kocherikovski Cape, coll. same expedition, 14 July 1902, sta. 165, at 5.6–7.4 m, on stones; 7 specimens (ZIN 7/548-1985, in alcohol), Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 25 August 1966, at 4–6 m, on stones; 1 specimen (ZIN 8/546-1985, in alcohol), Irinda Lnlet, coll. BGI ISU expedition, 10 September 1966, at 10 m, on stone; 4 specimens (ZIN 9/546-1985, in alcohol), between Gorevoi Utyos and Katkova Cape, coll. same expedition, 13 September 1966, at 5 m, on stones; 37 specimens (ZIN 10/546-1985, in alcohol), entrance to Mukhor Bay, coll. same expedition, 17 September 1966, at 6 m, on gravel and sand; 1 specimen (ZIN 11/546-1985, in alcohol), Irinda Inlet, coll. same expedition, 10 September 1966, at 5–10 m, on stone; 2 specimens (ZIN 12/548-1985, in alcohol), opposite Varnachka Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov and S.M. Popova, 25 August 1966, at 4–8 m, on stones; 1 specimen (ZIN 13/546-1985, in alcohol), Ongurion Cape, coll. BGI ISU expedition, 31 August 1966, at 8–16 m, on stone; 3 specimens (ZIN 14/547-1985, in alcohol), Bol'shye Koty Bay, coll. E.S. Poberezhnyi, August 1977, at 3–5 m, substrate not indicated; 3 specimens (ZIN 15/546-1985, in alcohol), Boguchanski Island, coll. BGI ISU expedition, 5 September 1966, at 12 m, on stones; 1 specimen (ZIN 16/546-1985, in alcohol), Zavorotnyi Cape, coll. same expedition, 6 July 1955, sta. 557, at 4 m, on stone; 2 specimens (ZIN 17/240-1969, in alcohol), Babushka Bay, coll. A.F. Alimov, 10 August 1966, at 10 m, substrate not indicated; 4 dry shells (ZIN no. 18), Angara River, near Irkutsk City, coll. G.I. Radde, 1855, depth and substrate not indicated, initially identified by C.A. Westerlund and L. Schrenck as *Ancylus* (*Ancylastrum*) *sibiricus*. All type specimens (re)determined by Ya.I. Starobogatov. Because the holotype is in poor condition, we provide a photograph of paratype no. 18 (Fig. 9C). Its dimen-

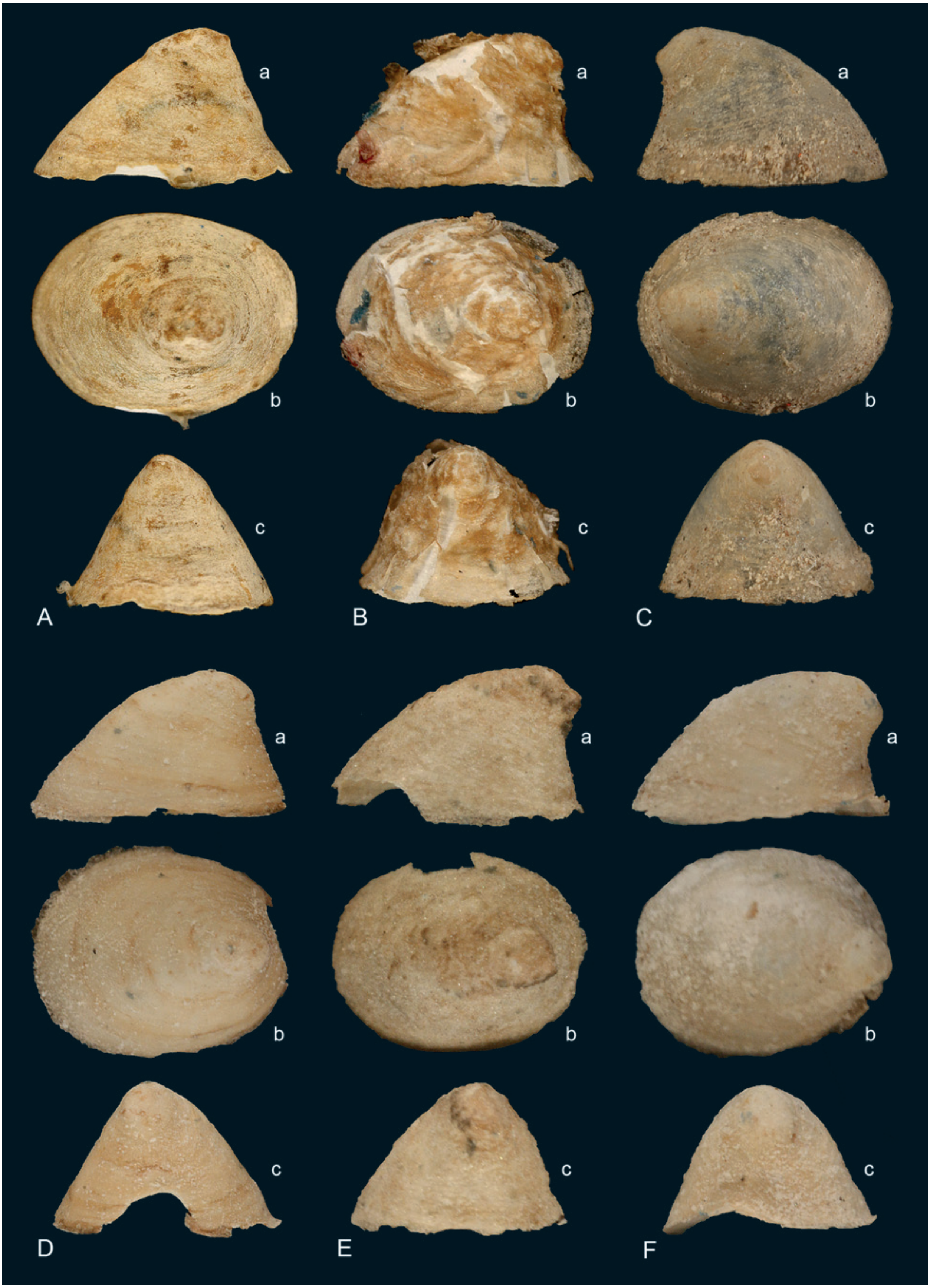

Figure 9. A. *Gerstfeldtiancylus gerstfeldti* sensu Starobogatov (1989), holotype (= *G. renardii*, after Shirokaya et al. [2003]): L = 7.70 mm, W = 5.80 mm, H = 4.90 mm. **B.** *G. benedictiae* Starobogatov, holotype: L = 3.30 mm, W = 2.70 mm, H = 4.90 mm. **C.** *G. benedictiae*, paratype ZIN no. 18: L = 3.17 mm, W = 2.54 mm, H = 2.01 mm. **D.** *G. capuliformis* Starobogatov, holotype: L = 3.90 mm, W = 3.10 mm, H = 2.05 mm. **E.** *G. porfirievae* Starobogatov, holotype: L = 2.75 mm, W = 2.20 mm, H = 2.00 mm. **F.** *G. pileolus* Starobogatov, holotype: L = 2.50 mm, W = 2.00 mm, H = 1.50 mm. Teleoconch: **Aa**, **Ba**, **Da**, **Ea**, **Fa**, left side view; **Ca**, right side view; **Ab–Fb**, top view; **Ac–Fc**, rear view.

sions (in mm): L = 3.17, La = 2.94, W = 2.54, wL = 1.16, H = 2.01, a = 3.34.

Other material. Institute of Geological Sciences, Freie Universität Berlin, 3 specimens in total: 1 dry shell (no number, SEM stub), upper part of the Angara River, near Irkutsk City, Akademgorodok (same site as paratypes ZIN no. 3 and ZIN no. 18), 52° 15′ 10.8″ N, 104° 16′ 58.1″ E, coll. P Röpstorf (scuba diving), early 2000, at 3 m, on stone (Fig. 14Fa, b); 1 dry shell (no number, SEM stub), mouth of Sennaya Rivulet, Bol'shye Koty Bay (same site as paratypes ZIN 7/548-1985, ZIN 12/548-1985 and ZIN 14/547-1985), 51° 53′ 55.07″ N, 105° 07′ 23.19″ E, same collector and sampling data, at 15 m, on stone (Fig. 14Fc); 1 dry shell (no number, SEM stub), Shaman Cape, near Kultuk Settlement (same site as paratypes ZIN 4/543-1985), 51° 41′ 42.42″ N, 103° 42′ 25.60″ E, same collector and sampling data, at 5 m, on stone. All specimens identified by P. Röpstorf.

LIN: 525 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name.

Starobogatov 1989: teleoconch description; information on type material including shell dimensions of holotype; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Kozhoviancylus*): structure of male copulatory organ

Sitnikova (1991): morphology and size of syncapsules; embryogeny

Kozhova & Erbaeva (1998): subendemism of *G. benedictiae*: record from upper Angara River

Shirokaya et al. (2003): description of adult shell, protoconch, and radula (SEM data); additional taxonomically important characters; polytomic identification key to species

Shirokaya & Röpstorf (2004), as *Gerstfeldtiancylus* (*Kozhoviancylus*): description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic key

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Kozhoviancylus*): information on type material and type locality; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Kozhoviancylus*): specified and supplemented species diagnosis; phylogenetic relationships

Shirokaya (2007): jaw morphology; geographic and bathymetric distribution, biotope; evolutionary trends

Shirokaya et al. (2008): geographic and bathymetric distribution, biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

Sitnikova et al. (2010): influence of abiotic environmental factors (geomorphological and hydrodynamic) on quantitative characteristics

Maximova et al. (2012): seasonal quantitative dynamics of gastropods in 3 hydrodynamically different stony littoral areas of Lake Baikal

Sitnikova (2012): identification key; brief description of teleoconch; association with substrate type

General distribution. Lake Baikal and the upper part of Angara River. A common species living on entire open littoral of the lake (Starobogatov 1989, Kozhova & Erbaeva 1998, Shirokaya et al. 2008).

Ecology. Depth, 1.5–40 m. A generally dominant species on boulder-pebble substrate with local outcrops of basic rocks (up to 237 individuals m^{-2}, Ushun Bay), sandy-pebble (up to 196 specimens m^{-2}, same bay) and sandy-boulder substrates (up to 182 specimens m^{-2}, Birkhin Bay) (Shirokaya 2007). The shells of living rissooideans coated by algae are also used as a substrate (Starobogatov 1989). Limpets attach their syncapsules on large gastropod shells, particularly of *Benedictia* spp. and *Parabaikalia florii* (W. Dybowski, 1875), as well as on upper surface of stones. The number of eggs in a syncapsule varies from 1–3, and the development of embryos is asynchronous (Shirokaya & Röpstorf 2003). In culture, oviposition occurs in April and hatching of juveniles in October.

Remarks. Six paratypes of *G. benedictiae* (ZIN no. 3) are simultaneously paralectotypes of *P. sibiricum* (ZIN no. 2) (Starobogatov 1989); 4 paratypes of *G. benedictiae* (ZIN no. 18) have been previously recorded in the ZIN systematic catalogue cards as "other material" of *P. sibiricum* (ZIN no. 4, initially identified by C.A. Westerlund and L. Schrenck, re-identified by Ya.I. Starobogatov).

Gerstfeldtiancylus capuliformis **Starobogatov, 1989**

Figures 9D, 14C

Gerstfeldtiancylus capuliformis Starobogatov 1989: 65, fig. 2(5).

Type locality. Lake Baikal, Zavorotnyi Cape.

Types. ZIN: holotype and 13 paratypes. Holotype (ZIN 1/546-1985, dry shell): coll. BGI ISU expedition, 6 July 1955, sta. 557, at 4 m, on pebbles and stones. Shell with broken posterior slope (Fig. 9Dc), its dimensions (in mm): L = 3.90; La = 3.40; W = 3.10; wL = 1.55; H = 2.05; a = 3.70 (Starobogatov 1989). Paratypes: 7 specimens (ZIN 2/546-1985, 1 dry shell and 6 specimens in alcohol), coll. data same as holotype; 1 specimen (ZIN 3/548-1985, in alcohol), same locality, coll. Ya.I. Starobogatov, 2 September 1966, at 4 m, on silt; 1 specimen (ZIN 4/546-1985, in alcohol), Amnundakan Inlet, coll. BGI ISU expedition, 10 September 1966, at 10 m, on sand covered with blue-green algae; 4 specimens (ZIN 5/546-1985, in alcohol), Zavorotnyi Cape, coll. same expedition, 7 July 1955, sta. 561, at 3 m, on pebbles. All type specimens identified by Ya.I. Starobogatov.

Other material. SMF, 4 specimens in total: 2 dry shells, littoral of Tonki Island, vicinity of a sealery, 53°

51′25.6″N, 108°42′36.7″E, coll. I.V. Khanaev and A.B. Kupchinski (scuba diving), 12 July 2002, at 9–15 m, on 1-layered boulders (to 1.5–2 m in diameter) and angular stones covered with Lubomirskiidae sponges, on the silty-sand bottom (Fig. 14Ca); 2 dry shells, N of Zavorotnyi Cape (topotypes), 54°18′05.1″N, 108°30′09.9″E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets, 30 June 2003, at 5–10 m, on rounded stones covered with sponges (Fig. 14Cb). All specimens identified by A.A. Shirokaya.

LIN: 1 dry shell (SEM stub), N of Zavorotnyi Cape (topotype), 54°18′05.1″N, 108°30′09.9″E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets, 30 June 2003, at 5–10 m, on rounded stones covered with sponges (Fig. 14Cc); 27 specimens (in alcohol), Middle and Northern Baikal. All specimens identified by A.A. Shirokaya.

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Kozhoviancylus*): structure of male copulatory organ

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Kozhoviancylus*) *caputiformis*: information on type material and type locality; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005), as *Gerstfeldtiancylus caputiformis*: distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Kozhoviancylus*) *caputiformis*: differential diagnosis; distribution

Shirokaya et al. (2008), as *Gerstfeldtiancylus caputiformis*: geographic and bathymetric distribution; biotope

Kantor et al. (2010), as *Gerstfeldtiancylus caputiformis*: type locality, presence of holotype in ZIN collection; distribution

General distribution. Northern and middle basins of Lake Baikal.

Specific records in Lake Baikal. Eastern shore of Ol'khon Island; littoral of Ushkanji Islands; mouth of the Bol'shoi Chivyrkui River; Katkova Cape; Irinda and Davshe bays; Pongonje Cape.

Ecology. Depth, 3–12 m. The greatest population density, up to 25 individuals m^{-2}, was recorded near Katkova Cape, at 8 m, on single-layered rounded boulders lying on sand, as well as on bedrock (Shirokaya et al. 2008). A rare species.

Gerstfeldtiancylus porfirievae Starobogatov, 1989

Figures 9E, 14E

Gerstfeldtiancylus porfirievae Starobogatov 1989: 66, fig. 2(*7*).
Ancylus (*Pseudancylastrum*) *troscheli*, part. — Lindholm 1909: 28 (non W. Dybowski 1875).

Type locality. Lake Baikal, Kocherikovski Cape.

Types. ZIN: holotype and 5 paratypes. Holotype (ZIN 1/543-1985, dry shell): coll. A.A. Korotnev expedition, 14 July 1902, sta. 165, at 5.6–7.4 m, on stone, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *troscheli*. Shell with broken aperture (Fig. 9Ea, b), its dimensions (in mm): L = 2.75; La = 2.70; W = 2.20; wL = 0.80; H = 2.0; a = 2.90 (Starobogatov 1989). Paratypes: 4 specimens (ZIN 2/546-1985, in alcohol), entrance to Mukhor Bay, coll. BGI ISU expedition, 17 September 1966, at 6 m, on sand and gravel; 1 specimen (ZIN 3/546-1985, in alcohol), Kedrovyi Cape, coll. same expedition, 2 September 1966, at 4–12 m, on stone. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF: 1 dry shell, Kovrizhka Bay, N side of Muzhinai Cape (65 km N of Kedrovyi Cape, where the paratype ZIN 3/546-1985 was collected), 54°51′13.74″N, 108°54′38.12″E, coll. T.Ya. Sitnikova (trawling), 20 October 1995, at 4.5–6.5 m, on silt, silty sand and algae, det. A.A. Shirokaya (Fig. 14E).

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Kozhoviancylus*): structure of male copulatory organ)

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Kozhoviancylus*): type locality, distribution, zoogeographical and ecological data; presence in scientific collection

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Kozhoviancylus*): species diagnosis

Shirokaya et al. (2008): horizontal distribution

Kantor et al. (2010): type locality; presence of holotype in ZIN collection, distribution

General distribution. Northern Baikal.

Specific records in Lake Baikal. Kovrizhka Bay; littoral of Ushkanji Islands (Shirokaya et al. 2008).

Ecology. Depth, 4–13 m; on gravel-pebble bottom, on sand and stones (Shirokaya et al. 2008). A rare species.

Gerstfeldtiancylus pileolus Starobogatov, 1989

Figures 9F, 14D

Gerstfeldtiancylus pileolus Starobogatov 1989: 67, fig. 2(*8*).

Type locality. Lake Baikal, Zavorotnyi Cape.

Types. ZIN: holotype and 35 paratypes. Holotype (ZIN 1/546-1985, dry shell), coll. BGI ISU expedition, 6 July 1955, sta. 557, at 4 m, on pebbles and stones. Shell in good condition (Fig. 9F), its dimensions (in mm): L = 2.50; La = 2.30; W = 2.0; wL = 1.0; H = 1.50; a = 2.50 (Starobogatov 1989). Paratypes: 21 specimens (ZIN 2/546-1985, 1 dry shell and 20 specimens in alcohol), coll. data same as holotype; 14 specimens (ZIN 3/546-

1985, in alcohol), same locality and collectors, 2 July 1955, sta. 561, at 3 m, on pebbles. All type specimens identified by Ya.I. Starobogatov.

Other material. SMF: 3 dry shells, Kotel'nikovski Cape (107 km N of Zavorotnyi Cape, topotypes), 55° 05′ 14.65″ N, 109° 06′ 17.39″ E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets (diving scoop), 1 July 2003, at 3–15 m, on pebbles and small 1-layered boulders completely covered with encrusting sponges, on sandy-gruss bottom, det. A.A. Shirokaya (Fig. 14D).

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Kozhoviancylus*): structure of male copulatory organ)

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Kozhoviancylus*): type locality, distribution, zoogeographical and ecological data; presence in scientific collection

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Kozhoviancylus*): species diagnosis

Shirokaya et al. (2008): horizontal distribution

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

General distribution. Western shore of North Baikal.

Specific records in Lake Baikal. North of Kotel'nikovski Cape (Shirokaya et al. 2008).

Ecology. Depth, 3–15 m; on stony-pebble substrate underlain by gruss. Stones at the collection sites were covered with encrusting sponges (I.V. Khanaev pers. comm.). A rare species.

Genus *Baicalancylus* Starobogatov, 1967

Type species. *Ancylus dybowskii* var. *laricensis* W. Dybowski, 1913, by original designation.

Diagnosis. Shell cap-shaped, small, brown, with radial costate sculpture. Height varying from moderately high to flat. Apex directed hindward, leftward, and downward (i.e., towards aperture). Apical part lacks sculpture and separated from sculptured part by a ring-shaped bulge. Anterior slope always convex, left and right slopes concave or straight, posterior slope can be concave, convex or straight (in different species). Aperture margins wavy. Protoconch large, cap-shaped, with reticulate microsculpture. Odontophore dark grey in living specimens. Male copulatory organ with relatively short glandular appendage not exceeding 0.75 of total length of penis sheath and preputium. Flagellum situated sharply laterally from penis sheath. The latter is shorter than preputium, penis very short, fusiform, with terminal opening of vas deferens (papilla is absent). Preputium slightly inflated proximally, with weakly developed sarcobelum in its muscular chamber. Velum absent (Starobogatov 1967, 1989, Kruglov & Starobogatov 1991b, Shirokaya et al. 2003, Shirokaya & Röpstorf 2004).

Ecology. Depth, 1–20 m. Adult snails feed mainly on benthic diatom algae (Röpstorf et al. 2003).

Baicalancylus laricensis (W. Dybowski, 1913)

Figures 10E, F, 15B

Ancylus dybowskii var. *laricensis* W. Dybowski 1913: 140.
Ancylus (*Pseudancylastrum*) ? *dybowskii* — Lindholm 1909: 28 (non Clessin 1882).
Ancylus (*Pseudancylastrum*) *boettgerianus*, part. — Lindholm 1909: 28.
Pseudancylastrum kobelti, part. — Kozhov 1936: 188 (non W. Dybowski 1885); Shadin 1952: 204.

Type locality. Lake Baikal, near Listvyanka Settlement.

Types. ZIN, holotype (ZIN 1/543-1985, dry shell, body dried separately): coll. A.A. Korotnev expedition, 19 June 1901, sta. 13a, at 5.6–18.5 m, on stone, initially identified by Lindholm (1909) as "*Ancylus* (*Pseudancylastrum*) ? *dybowskii*". Shell completely decalcinated, the remaining periostracum strongly deformed (Fig. 10Ea). Starobogatov (1989) did not give the teleoconch measurements.

Other material. ZIN: 1 dry shell (ZIN 2/359-1935), Malyi Kyltygei Island, Chivyrkui Bay, coll. A.A. Korotnev expedition, 10 July 1902, sta. 111, at 1.9–5.6 m, substrate not indicated, det. by Starobogatov (1989) as *B. laricensis* (and a paralectotype, ZIN 11/359-1935, of *B. boettgerianus*). Shell in good condition, costate, with cap-shaped protoconch (Fig. 10F), aperture slightly broken, periostracum locally peeled, shell dimensions (in mm): L = 4.10; La = 3.60; W = 3.20; wL = 0.10; H = 1.70; a = 4.0; e = 1.0 (Starobogatov 1989).

SMF: 5 dry shells, S of Katkova Cape, 53° 09′ 34.49″ N, 108° 24′ 12.93″ E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets (scuba diving), 6 July 2003, at 12.5 m, on boulders (to 1 m in diameter), on the sandy bottom, det. A.A. Shirokaya (Fig. 15B).

LIN: 26 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name.

Dybowski (1913), as *Ancylus dybowskii* var.: introduction of replacement name for *A.* (*Pseudancylastrum*) ? *dybowskii* Clessin sensu Lindholm, 1909

Lindholm (1909), as *Ancylus* (*Pseudancylastrum*) ? *dybowskii*: collection site; teleoconch description and dimensions; comparison to "*A.*" *sibiricus*; horizontal and vertical distribution of species in Baikal; zoogeographical affinities

Starobogatov (1967), as *Acroloxus* (*Baicalancylus*): description of teleoconch and male copulatory organ; designation as type species for new subgenus *Baicalancylus*

Starobogatov (1989): teleoconch description; information on type and additional material in ZIN collection;

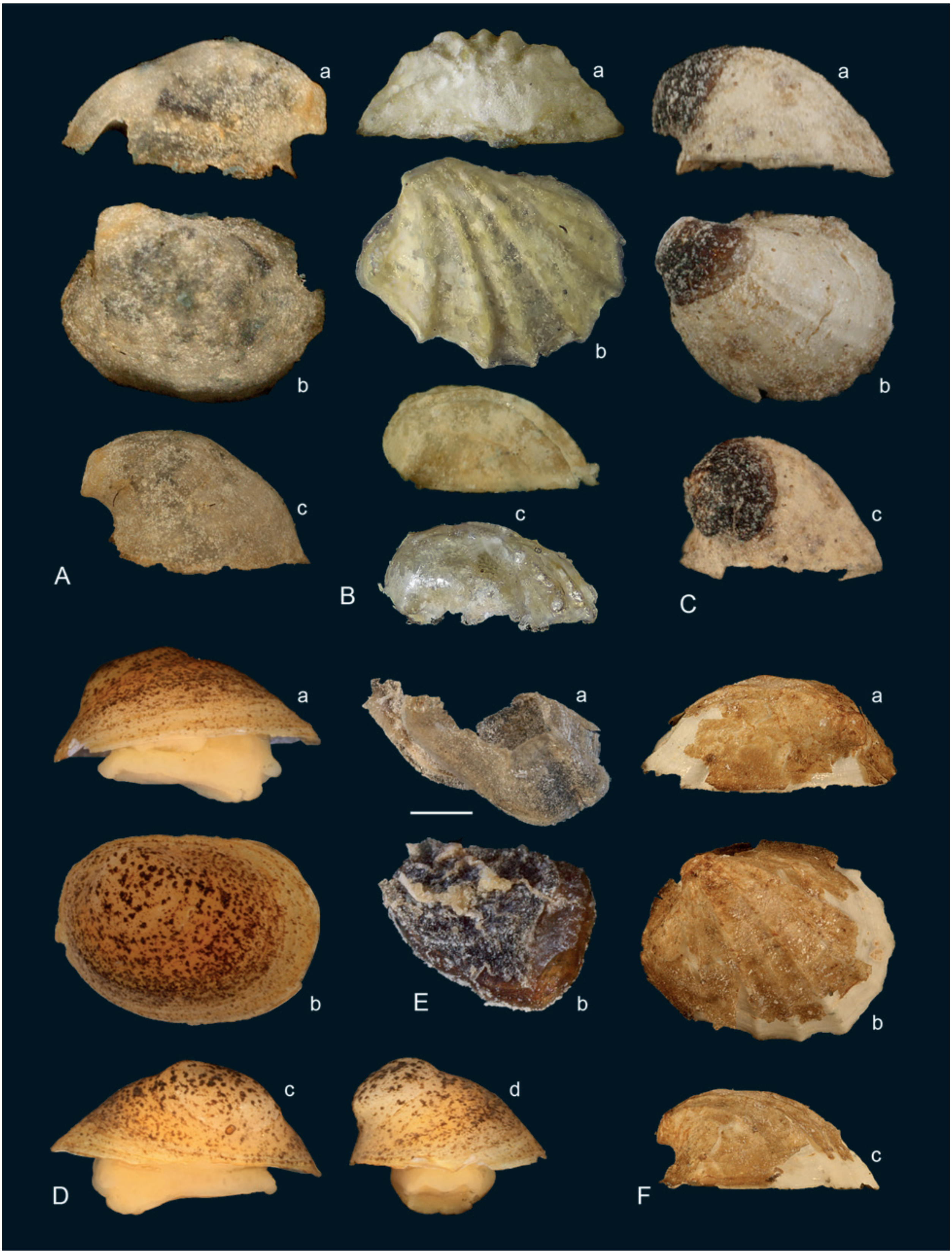

Figure 10. A. *Baicalancylus njurgonicus* Starobogatov, holotype: L = 3.00 mm, W = 2.30 mm, H = 1.60 mm. **B.** *B. boettgerianus* (Lindholm), one of paralectotypes ZIN 2/543-1985, the most similar to lectotype depicted by Starobogatov (1989: 61): L = 2.44 mm, W = 1.76 mm, H = 1.08 mm. **C.** *B. kobeltii* (W. Dybowski), non-type specimen ZIN 1/546-1985: L = 2.10 mm, W = 1.80 mm, H = 1.20 mm. **D.** *Frolikhiancylus frolikhae* (Sitnikova & Starobogatov), holotype: L = 2.50 mm, W = 1.75 mm, H = 0.95 mm. **E.** *Baicalancylus laricensis* (W. Dybowski), holotype, photograph taken in 2014: soft body length (dry) = 2.23 mm. **F.** *B. laricensis* sensu Starobogatov (1989), non-type specimen ZIN 2/359-1935 (= *B. boettgerianus* sensu Lindholm [1909]), paralectotype ZIN 11/359-1935: L = 4.10 mm, W = 3.20 mm, H = 1.70 mm. Teleoconch: **A–C, F**; **D**, with soft body. **Ea**, periostracum. **Eb**, dry soft body. **Aa, Ba**, **Dc**, **Fa**, left side view; **Ca**–**Ea**, right side view; **Ab–Fb**, top view; **Ac–Cc**, **Dd**, **Fc**, rear view; **Bc** (upper), photograph taken 22 February 2013; **Bc** (lower): phototograph taken 17 April 2014. Scale bar (for Ea only): Ea = 1 mm.

discussion of shell shape variability; distribution; biotope

Sitnikova et al. (2004): information on type material and type locality; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005): extended species diagnosis; macrobiotopical differentiation: association of *B. laricensis* and *B. njurgonicus* Starobogatov, 1989 with different types of hard bottom

Shirokaya et al. (2008): geographic and bathymetric distribution; biotope

Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

General distribution. Lake Baikal. Disjunctive range.

Specific records in Lake Baikal. Bol'shye Koty Bay; mouth of the Bol'shoi Chivyrkui River; Katkova Cape; Listvennichnyi Island; littoral of Ushkanji Islands (Shirokaya et al. 2008, our data).

Ecology. Depth, 2–20 m. The greatest population density, up to 73 individuals m^{-2}, was recorded near Katkova Cape, at 11.5 m, on rock outcrops (Shirokaya et al. 2008).

Remarks. *Ancylus dybowskii* var. *laricensis* was introduced by W. Dybowski (1913) as a replacement name for *Ancylus dybowskii* sensu Lindholm (1909), non Clessin (1882), which was based on a single specimen that was not figured by any of these authors. Neither Starobogatov (1989), who published a detailed diagnosis of the species, nor subsequent taxonomists (Shirokaya et al. 2003) were aware of the condition of the holotype (Fig. 11Cc). In the 1980s, its shell was already partially destroyed. Based on patterns of teleoconch deformations, Starobogatov (1989) reconstructed the holotype shell (Fig. 11Cd), which appeared to be similar to a specimen of *B. laricensis* from Chivyrkui Bay (ZIN 2/359-1935, Fig. 11Ce–g).

In addition to 2 specimens stored in the ZIN collection, Starobogatov (1989) assigned to *B. laricensis* a large ribless specimen from Ireksokon Cape (Fig. 11Ca, b). This specimen was illustrated by Hubendick (1969: figs 19, 20), having been identified by him as *Acroloxus boettgerianus*. Despite considerable variation in the expression of the ribs on adult shells, all species of *Baicalancylus* are characterized by a cap-shaped or faceted protoconch (Starobogatov 1989, Shirokaya et al. 2003). A specimen of "*Acroloxus*" *boettgerianus* from Ireksokon Cape possesses a horn-shaped protoconch and a smooth teleoconch with an aperture length of about 4 mm, indicating that it belongs to the genus *Pseudancylastrum*. This assignment is supported by a figure of the radula (Hubendick 1969: 64, fig. 31; here: Fig. 16A) that shows 3–5 broad bicuspid lateral teeth on both sides of the central tooth, which is also characteristic of *Pseudancylastrum* and *Kozhoviancylus* spp. (Shirokaya et al. 2003). Lateral teeth inclination to the central tooth at an acute or a right angle; the line of lateral teeth is clearly separated from the line of marginal teeth. The radula of *Baicalancylus* possesses 13–18 narrow lateral teeth on each side from the central tooth; they bear 1–4 terminal cusps and many wrinkles on the cutting edge. A transverse tooth row forms a wavy line with an obtuse angle in the centre; there is no clear boundary between lateral and marginal teeth (Fig. 15Cf).

Lindholm (1909) assigned the holotype of *B. laricensis* to "*Ancylus*" (*Pseudancylastrum*) *dybowskii*. Judging from his description, he clearly distinguished specimens corresponding to "*A.*" *sibiricus* sensu lato (smooth shell with an acute apex) and "*A.*" *boettgerianus*–"*A.*" *kobeltii* (ribbed teleoconch with obtuse apex). The ribless holotype of *B. laricensis* probably had a horn-shaped protoconch, but its poor condition does not allow this to be determined. Figures published by Starobogatov (1989: 61, figs 9, 10), show that the holotype (in its condition at that time and its reconstruction) looks ribbed, but this may be due to the shell wrinkling during the drying process.

We do not know the exact specimen dissected by Starobogatov (1967: 288, fig. 5) to illustrate the male copulatory organ of "*Acroloxus*" *laricensis*. The bodies of the holotype and the specimen from Chivyrkui Bay are dried, and it is now impossible to determine whether they were dissected. In species of *Baicalancylus* that have been studied (*B. boettgerianus* and *B. kobeltii*), the opening of the vas deferens is terminal, there is no penis papilla, and the flagellum is short (Fig. 16B, D, E; Kruglov & Starobogatov 1991b, Shirokaya 2005). The male copulatory organ of *B. laricensis*, dissected by Ya.I. Starobogatov (Fig. 16C), possesses a long flagellum and a laterally located opening of the vas deferns with the penial papilla present.

Therefore, of all specimens attributed to *B. laricensis*, we can only definitively assign to the genus *Baicalancylus* to one of them, that is, the specimen collected by A.A. Korotnev at Malyi Kyltygei Island (see "Other material"). This specimen was used by Starobogatov (1989) to make a template for identification by the comparative method. Since Starobogatov (1989), the holotype has not been used as a basis for identification of this species.

Owing to the poor condition of the holotype of *B. laricensis*, which is not useful for the characterization of the species, a neotype is needed. However, this is impossible because the species is not identifiable from the original publication (Dybowski 1913), which lacked illustrations and diagnostic characters. The Lindholm's (1909) description of this species corresponds to a third of *Pseudancylastrum* species (Starobogatov 1989); it shows characters of the genus, but not the species.

The specimen from Chivyrkui Bay, a paralectotype of *B. boettgerianus,* differs from Lindholm's (1909) description with respect to the elevation of apex above the aperture plane. The apex in typical *B. boettgerianus* lies below the middle of the shell height (e/H < ½); in *B.*

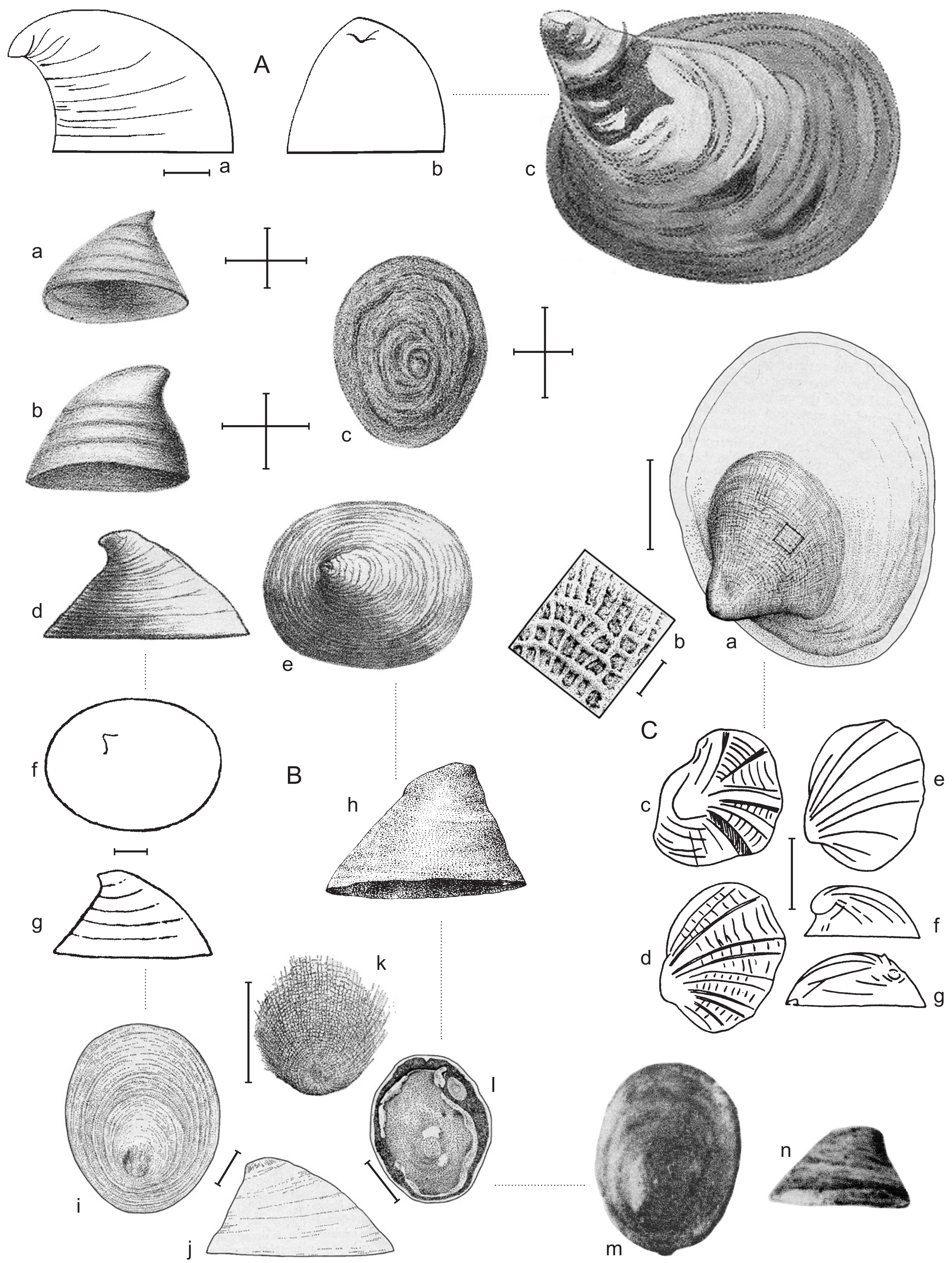

Figure 11. A. "*Ancylus*" *dybowskii* Clessin (1882: Taf. 7, fig. 1). **B.** "*Ancylus*" *troschelii* W. Dybowski: **Ba–Bc**, after Dybowski (1875); **Bd**, **Be**, after Dybowski (1884); **Bf**, **Bg**, after Shadin (1933); **Bh**, after Shadin (1952); **Bi–Bl**, after Hubendick (1969); **Bm**, **Bn**, after Kozhov (1936). **Ca, Cb.** "*Acroloxus*" *boettgerianus* sensu Hubendick (1969) (= *Baicalancylus laricensis* sensu Starobogatov [1989], Ireksokon Cape). **Cc, Cd.** *B. laricensis*, holotype, after Starobogatov (1989): **Cc**, picture of shell made in the 1980s; **Cd**, shell reconstruction depicted by Starobogatov. **Ce–Cg.** *B. laricensis* sensu Starobogatov (1989), non-type specimen, ZIN 2/359-1935 (= *B. boettgerianus* sensu Lindholm [1909], paralectotype ZIN 11/359-1935). Teleoconch: **Ac**, **Be**, **Bf**, **Bi**, **Bm**, **Ca**, **Cc–Ce**, top view; **Aa**, **Cf**, rear view; **Bg**, rear (?) view; **Ab**, **Ba**, **Bb**, **Bh**, **Bn**, **Cg**, left side view; **Bc**, bottom view; **Bd**, right (?) side view; **Bj**, right side view. Protoconch: **Bk**, top view; **Cb**, fragment. **Bl**, soft body. Scale bars: length = 1 mm except for Cb = 0.1 mm; Cc–Cg = 2 mm.

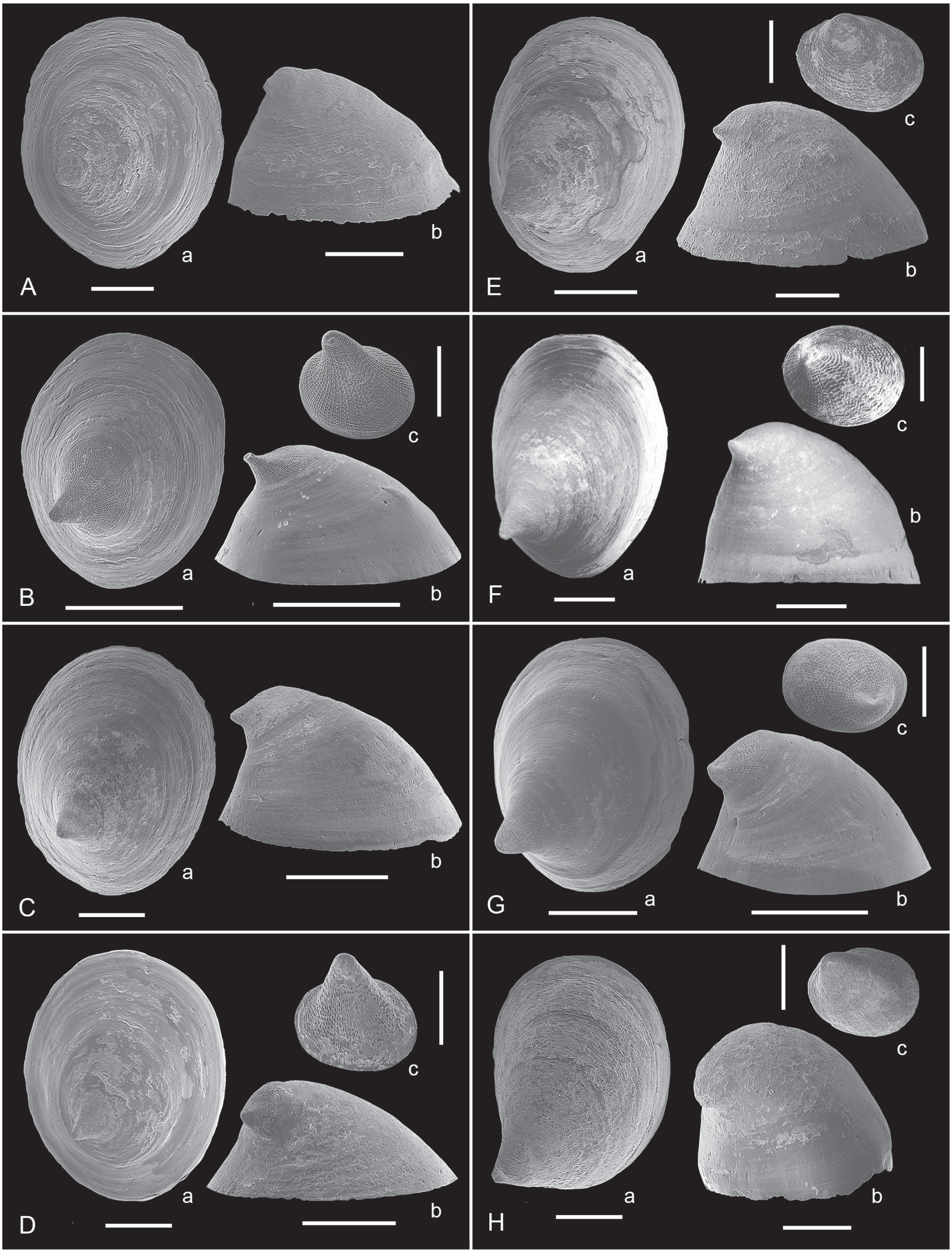

Figure 12. Topotypes and easily identified non-topotypic specimens of *Pseudancylastrum* species from Lake Baikal. **A.** *P. troschelii* (Dybowski): littoral of Malyi Ushkani Island, vicinity of a sealery. **B.** *P. aculiferum* Starobogatov (topotypes): between Tolstyi Cape and Shumikha River. **C.** *P. korotnevi* Starobogatov: **Ca**, between Tolstyi Cape and Shumikha River near sampling sites of paratypes ZIN 3/359-1935 and ZIN 4/548-1985); **Cb**, Khabsagai Cape. **D.** *P. poberezhnyi* Starobogatov (topotypes): Bol'shye Koty Bay. **E.** *P. werestschagini* Starobogatov: **Ea**, **Ec**, Khabsagai Cape; **Eb**, Beriozovyi Cape (topotype). **F.** *P. beckmanae* Starobogatov: near Listvyanka Settlement. **G.** *P. sibiricum* (Gerstfeldt): Birkhin Bay. **H.** *P. olgae* Starobogatov: **Ha**, Davshe Bay; **Hb**, Khabsagai Cape; **Hc**, Krasnyi Yar Cape, South Baikal. Teleoconch: **Aa–Ha**, top view; **Ab–Hb**, rear view. Protoconch: **Bc**, **Dc–Hc**, top view. Different views for each species refer to different shells. Scale bars: length = 1 mm except for Dc–Fc, Hc = 0.5 mm; Gc = 0.4 mm.

laricensis sensu Starobogatov (1989) it lies in the middle or above the middle (e/H ≥ ½). In the specimen from Chivyrkui Bay, e/H = 0.59 (Fig. 10Fc).

According to Article 75.5 of the Code (ICZN 1999), the species name *Baicalancylus laricensis* Dybowski, 1913 is a nomen dubium. Therefore, the existing name-bearing type can be set aside, and designation of a neotype can be suggested to the Commission. The species *Baicalancylus laricensis* sensu Starobogatov (1989), non W. Dybowski (1913), should be redescribed, with a new name and a new diagnosis, which we will present in a separate publication.

Baicalancylus boettgerianus (Lindholm, 1909)

Figures 10B, 15C

Ancylus (*Pseudancylastrum*) *boettgerianus*, part. Lindholm 1909: 28–29, Taf. II, figs 37, 38.
Pseudancylastrum kobelti, part.—Kozhov 1936: 188, Taf. VII, figs 30–32 (non W. Dybowski 1885); Shadin 1952: 204.

Type locality. Lake Baikal, Maloye More Strait, near Kurma Settlement.

Types. ZIN: 14 paralectotypes, designated by Starobogatov (1989: 71). According to the ZIN systematic catalogue, the lectotype (ZIN 1/543-1985, dry shell, designated by Starobogatov (1989: 71), coll. by A.A. Korotnev expedition, 30–31 July 1902, sta. 113a, at 1.4–9.3 m, on stone, its dimensions (in mm): L = 2.70; La = 2.40; W = 2.0; wL = 0.20; H = 1.0; a = 2.50; e = 0.30) is stored in ZIN. We did not to find it. Paralectotypes: 5 dry shells (ZIN 2/543-1985), coll. data same as lectotype; 5 dry shells (ZIN 3/359-1935), coll. data same as lectotype; 3 dry shells (ZIN 4/543-1985), Malyi Kyltygei Island, coll. same expedition, 10 July 1902, sta. 111, at 1.9–5.6 m, on stones; 1 dry shell (ZIN 5/359-1935), coll. data same as paralectotypes ZIN 4/543-1985. All type specimens identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *boettgerianus*. Due to the probable loss of the lectotype, we provide a shell photograph of 1 of the 5 paralectotypes ZIN 2/543-1985 (Fig. 10B). Its dimensions (in mm): L = 2.44; La = 1.98; W = 1.76; wL = –0.17; H = 1.08; a = 2.20; e = 0.12 (Shirokaya & Sitnikova original data).

Other material. ZIN, 23 specimens in total: 1 dry shell (ZIN 6/359-1935), Maloye More Strait (topotype), coll. A.A. Korotnev expedition, 1902, sta. 77, depth and substrate not indicated, identified by W.A. Lindholm as *A.* (*P.*) *boettgerianus*, erroneously indicated by Starobogatov (1989) as "a paralectotype no. 6"; 8 dry shells (ZIN no. 7), Njurgon Cape (topotypes), coll. M.M. Kozhov, 1934, at 3 m, on stones; 9 specimens (ZIN 8/546-1985, in alcohol), Khora-Undurskaya Inlet (topotypes), coll. BGI ISU expedition, 30 August 1966, at 5–10 m, on stones; 3 specimens (ZIN 8/359-1935, in alcohol), coll. data same as specimens ZIN 8/546-1985 (topotypes); 1 specimen (ZIN 9/546-1985, in alcohol), between Gorevoi Utyos and Katkova Cape, coll. same expedition, 13 September 1966, at 5 m, on stone; 1 specimen (ZIN 10/546-1985, in alcohol), Ireksokon Cape, coll. same expedition, 7 September 1966, at 3–8 m, on stone. Specimens ZIN no. 7, ZIN 8/359-1935, ZIN 8/546-1985, ZIN 9/546-1985, ZIN 10/546-1985 identified by Ya.I. Starobogatov.

SMF, 3 specimens in total: 1 dry shell, Nizhnee Izgolovie Cape, Svyatoi Nos Peninsula (68.5 km SW of Malyi Kyltygei Island, where paralectotypes ZIN 4/543-1985 and ZIN 5/359-1935 were collected), 53°29′38.79″N, 108°30′57.73″E, coll. I.Yu. Parfeevets and A.B. Kupchinski (scuba diving), 13 July 2001, at 8.5 m, on the 1- or 2-layered stones covered with sponges and *Draparnaldioides* sp., on grey silty sand (Fig. 15Ca; 2 dry shells, mouth of the Bol'shoi Chivyrkui River (9 km NE of Malyi Kyltygei Island), 53°49′19.70″N, 109°12′27.05″E, same collectors, 11 July 2001, at 4–4.5 m, on lateral surfaces of stones (Fig. 15Cb–e). All specimens identified by A.A. Shirokaya.

Institute of Geological Sciences, Freie Universität Berlin, 2 specimens in total: 1 dry shell (SEM stub), Nizhnee Izgolovie Cape, Svyatoi Nos Peninsula (68.5 km SW of Malyi Kyltygei Island, where paralectotypes ZIN 4/543-1985 and ZIN 5/359-1935 were collected), 53°29′38.79″N, 108°30′57.73″E, coll. and det. P. Röpstorf, early 2000, at 8.5 m, on stone (Shirokaya et al. 2003: fig. 9A–E); 1 radula preparation (SEM stub), littoral of Bol'shoi Ushkani Island, 53°50′57.8″N, 108°36′39.6″E, coll. Sergei V. Selyandin (scuba diving), 15 October 1995, at 3 m, on multilayered stones, det. A.A. Shirokaya (Fig. 15Cf).

LIN: 89 specimens (in alcohol; dry, SEM stubs), from 3 Baikal basins.

History of the usage of the name.

Lindholm (1909), as *Ancylus* (*Pseudancylastrum*): description of teleoconch; specific records; geographic and bathymetric distribution

Starostin (1926), as *Ancylus* (*Pseudancylastrum*): geographic and bathymetric distribution

Kozhov (1931), as *Ancylus* (*Pseudancylastrum*): description of teleoconch; specific records; bathymetric distribution; biotope

Shadin (1933), as *Ancylus* (*Pseudancylastrum*): teleoconch description and dimensions; distribution

Hubendick (1969), as *Acroloxus*: teleoconch and protoconch description (light-optical data); morphology of soft body, radula, pseudobranch, and copulatory organ; topography of shell adductors; taxonomic position; phylogeny

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of lectotype and 2 paralectotypes from Kurma; information on additional, non-type material stored in ZIN collection; discussion of shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b): structure of male copulatory organ

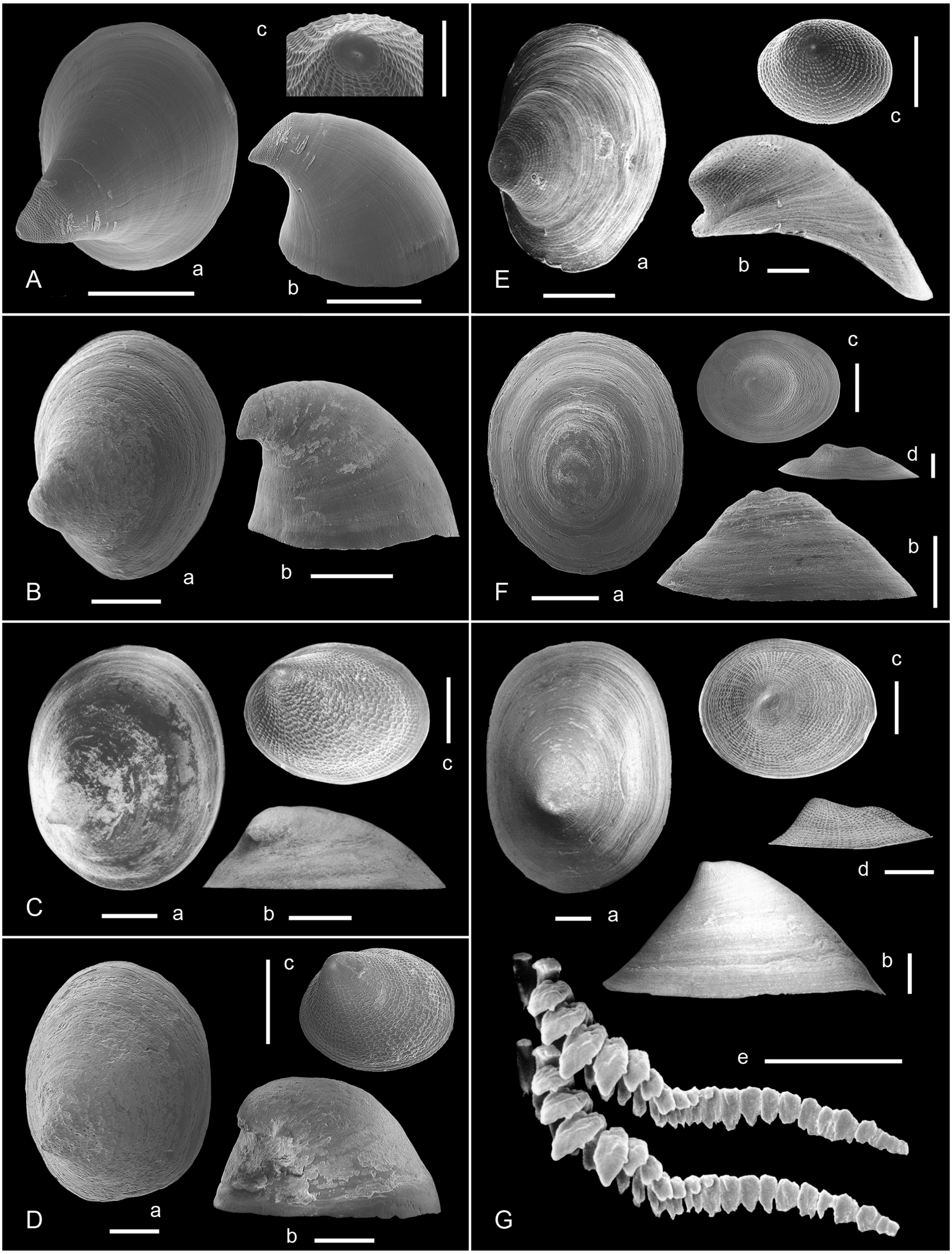

Figure 13. Types, topotypes, and easily identified non-topotypic specimens of *Pseudancylastrum*, *Frolikhiancylus*, and *Gerstfeldtiancylus* spp. from Lake Baikal. **A.** *P. cornu* Starobogatov (juvenile specimens): north of Zavorotnyi Cape. **B.** *P. dybowskii* (Clessin): **Ba**, Davshe Bay; **Bb**, near Khabsagai Cape. **C.** *P. dorogostajskii* Starobogatov (topotype): near Listvyanka Settlement. **D.** *P. irindaense* Starobogatov (topotypes): Irinda Inlet. **E.** *F. frolikhae* (Sitnikova & Starobogatov): Pokojniki Cape, after Röpstorf & Riedel (2004). **F.** *G. ushunensis* Shirokaya (holotype): Ushun Bay, after Shirokaya (2007). **G.** *G. kotyensis* Starobogatov: **Ga**, **Gb**, **Ge**, littoral of Tonki Island, vicinity of a sealery; **Gc**, **Gd**, Bol'shye Koty Bay (topotype). Teleoconch: **Aa–Ga**, top view; **Ab–Eb**, rear view; **Fb**, **Gb**, right side view. Protoconch: **Ac**, **Cc–Gc**, top view; **Fd**, **Gd**, right side view. Different views for each species refer to different shells. Radula fragment: **Ge**. Scale bars: length = 1 mm except for Cc, Dc, Ea, Gc, Gd = 0.5 mm; Ac, Eb = 0.2 mm; Ec = 0.4 mm; Fa, Fb) = 2 mm; Fd = 0.25 mm; Ge = 0.1 mm.

Shirokaya et al. (2003): description of adult shell, protoconch and radula (SEM data); additional taxonomically important characters; polytomic identification key to species
Shirokaya & Röpstorf (2004): description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic key
Sitnikova et al. (2004): information on type material and type locality; distribution; zoogeographical and ecological data
Kantor & Sysoev (2005): distribution
Shirokaya (2005): detailed and extended species diagnosis; morphological-physiological differentiation of species: distinctions in male copulatory organ structure in *B. boettgerianus* and *B. kobeltii*; phylogenetic relationship)
Shirokaya et al. (2008): geographic and bathymetric distribution, biotope
Kantor et al. (2010): type locality; presence of lectotype in ZIN collection, distribution
Sitnikova (2012): identification key; brief description of teleoconch
Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal. A widely distributed species, though not yet known for southeastern and northwestern shores of Baikal, as well as for the Anginski District.

Ecology. Depth, 1–20 m; on rocky and stony substrates. The species density was up to 6 individuals m^{-2} in Bol'shye Koty Bay, 3.5 m, on a sandy-rubble bottom (Shirokaya et al. 2008), and up to 33 individuals m^{-2} in Ushun Bay, 4 m, on single-layered boulders and on bedrock (Shirokaya original data).

Remarks. The Alexei A. Korotnev expedition collected 19 paralectotypes of *B. boettgerianus* (ZIN 2/543-1985 and ZIN 3/359-1935; dry shells, det. W.A. Lindholm) near Kurma Settlement as well as 7 paralectotypes of *B. boettgerianus* (ZIN 4/543-1985, ZIN 5/359-1935, ZIN 11/359-1935, and ZIN 12/359-1935; dry shells, det. W.A. Lindholm) in the littoral of Malyi Kyltygei Island (Starobogatov 1989). Nine of the 14 specimens of ZIN 2/543-1985, as well as 2 specimens from ZIN 12/359-1935, were assigned by Starobogatov (1989) to *B. njurgonicus* as paratypes of the latter (ZIN 2/543-1985 and ZIN 3/359-1935). The paralectotype of *B. boettgerianus* ZIN 11/359-1935 was re-identified by Starobogatov (1989) as *B. laricensis* (ZIN 2/359-1935).

Baicalancylus njurgonicus Starobogatov, 1989

Figures 10A, 15A

Baicalancylus njurgonicus Starobogatov 1989: 72, fig. 2(*13*).
Ancylus (*Pseudancylastrum*) *boettgerianus*, part. — Lindholm 1909: 28.
Pseudancylastrum kobelti, part. — Kozhov 1936: 188 (non W. Dybowski 1885); Shadin 1952: 204.

Type locality. Lake Baikal, Njurgon Cape.

Types. ZIN: holotype and 12 paratypes. Holotype (ZIN no. 1, dry shell): coll. M.M. Kozhov, 1934, at 3 m, on stone. Shell with broken aperture (Fig. 10Aa, b), its dimensions (in mm): L = 3.0; La = 2.50; W = 2.30; wL = 0.40; H = 1.60; a = 3.0; e = 0.80 (Starobogatov 1989). Paratypes: 9 dry shells (ZIN 2/543-1985), near Kurma Settlement, coll. A.A. Korotnev expedition, 30–31 July 1902, sta. 113a, at 1.4–9.3 m, on stones, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *boettgerianus*; 2 dry shells (ZIN 3/359-1935), Malyi Kyltygei Island, coll. same expedition, 10 July 1902, sta. 111, at 1.9–5.6 m, on stones, initially identified by W.A. Lindholm as *A.* (*P.*) *boettgerianus*; 1 specimen (ZIN 4/546-1985, in alcohol), Khora-Undurskaya Inlet, coll. BGI ISU expedition, 30 August 1966, at 5–10 m, on stone. All type specimens (re)determined by Ya.I. Starobogatov.

Other material. SMF, 3 specimens in total: 2 dry shells, S of Katkova Cape, 53° 09′ 34.49″ N, 108° 24′ 12.93″ E, coll. I.V. Khanaev, V.F. Skudenko and I.Yu. Parfeevets (scuba diving), 6 July 2003, at 5 m, on rounded multilayered boulders (to 0.5 m in diameter) covered with *Nostoc*, *Tetraspora,* and sponges, on brown sand (Fig. 15Aa, c, d); 1 dry shell, littoral of Bol'shoi Ushkani Island, 53° 50′ 57.8″ N, 108° 36′ 39.6″ E, coll. S.V. Selyandin (scuba diving), 15 October 1995, at 3 m, on multilayered stones (Fig. 15Ab, e). All specimens identified by A.A. Shirokaya.

LIN: 8 specimens (in alcohol and dry), from middle and northern Baikal basins.

History of the usage of the name.
Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype from Kurma; discussion of shell sculpture variability; distribution; biotope
Sitnikova et al. (2004): type locality, distribution, zoogeographical and ecological data; presence in scientific collection
Kantor & Sysoev (2005): distribution
Shirokaya (2005): detailed diagnosis of species; macrobiotopic distribution
Shirokaya et al. (2008): geographic and bathymetric distribution; biotope
Kantor et al. (2010): type locality, presence of holotype in ZIN collection; distribution

General distribution. North and middle basins of Baikal.

Specific records in Lake Baikal. Mouth of the Bol'shoi Chivyrkui River; littoral of Ushkanji Islands; Katkova Cape (Shirokaya et al. 2008).

Ecology. Depth, 2–12 m; on rocky bottom. The greatest density, up to 17 individuals m^{-2}, was recorded near Katkova Cape, on multilayered rounded stones and boulders, in cracks or pits of their upper-lateral surfaces (Shirokaya et al. 2008). A rare species.

***Baicalancylus kobeltii* (W. Dybowski, 1885)**

Figures 10C, 14G

Ancylus kobeltii W. Dybowski 1885: 313, Taf. II, figs 1–7.
Ancylus (*Pseudancylastrum*) *kobelti* — Shadin 1933: 131.
Acroloxus kobelti — Hubendick 1969: 62, figs 24–28.
Baicalancylus kobelti — Starobogatov 1989: 73, fig. 2(*14*); Shirokaya et al. 2003: 122, fig. 10A–H, tables 1, 3, 5, 7–8; Shirokaya & Röpstorf 2004: 67, fig. 7D–F, tables 1–2; Sitnikova et al. 2004: 998; Kantor & Sysoev 2005: 195; Shirokaya 2005: 12.

Type locality. Angara River (probably near Listvyanka Settlement).

Types. According to W. Dybowski (1885), syntypes are stored in "Museum der Universität Lemberg" (ZMD now) (but see Remarks).

Other material. ZIN: 1 dry shell (ZIN 1/546-1985) with broken aperture (Fig. 10Cc), Khora-Undurskaya Inlet, coll. BGI ISU expedition, 30 August 1966, at 5–10 m, on stones. Its dimensions (in mm): L = 2.10; La = 2.30; W = 1.80; wL = 0.10; H = 1.20; a = 2.30; e = 0.50 (Starobogatov 1989: fig. 2(*14*)). According to the ZIN systematic catalogue, this lot includes 2 specimens. One specimen, in alcohol, is lost (figured by Hubendick 1969).

Institute of Geological Sciences, Freie Universität Berlin: 1 dry shell (SEM stub), upper part of the Angara River, near Irkutsk City, Akademgorodok (64 km NW of Listvyanka Settlement, topotype), 52° 15′ 10.8″ N, 104° 16′ 58.1″ E, coll. and det. P. Röpstorf (scuba diving), early 2000, at 3 m, on stone (Fig. 14G).

LIN: 46 specimens (in alcohol and dry), from 3 Baikal basins.

History of the usage of the name. To understand the development of the species comprehension, we have included here some synonymous names that evolved due to incorrect subsequent spelling of the species name.

Dybowski (1885), as *Ancylus*: site of collection; detailed description of shell and radula

Dybowski (1913), as *Ancylus*: *"A." boettgerianus* is a synonym of "*A.*" *kobeltii*

Shadin (1933), as *Ancylus* (*Pseudancylastrum*) *kobelti*: teleoconch description and dimensions; distribution

Kozhov (1936), as *Pseudancylastrum kobelti*: teleoconch description; distribution

Shadin (1952), as *Pseudancylastrum kobelti*: identification key; teleoconch description and dimensions; distribution

Golyshkina (1967), as *Pseudancylastrum kobelti*: recorded 92 km downstream from Lake Baikal in Angara River

Hubendick (1969), as *Acroloxus kobelti*: teleoconch and protoconch description (light-optical data), morphology of soft body, radula, pseudobranch, and copulatory organ; topography of shell adductors; taxonomic position; phylogeny

Starobogatov (1989), as *Baicalancylus kobelti*: teleoconch description; information on additional (non-type) material in ZIN collection; shell dimensions of specimen from Khoboi Cape; distribution; biotope

Kozhova & Erbaeva (1998), as *Baicalancylus* (*Pseudancylastrum*) *kobelti*: record from upper Angara

Röpstorf et al. (2003), as *Baicalancylus kobelti*: radular morphology and feeding spectrum

Shirokaya et al. (2003), as *Baicalancylus kobelti*: description of adult shell, protoconch and radula (SEM data); additional taxonomically important characters; polytomic identification key to species

Shirokaya & Röpstorf (2004), as *Baicalancylus kobelti*: description of alimentary system and shell adductor muscles; additional taxonomically important characters; polytomic key

Sitnikova et al. (2004), as *Baicalancylus kobelti*: type locality, distribution, zoogeographical and ecological data; presence of species in scientific collections

Kantor & Sysoev (2005), as *Baicalancylus kobelti*: distribution

Shirokaya (2005), as *Baicalancylus kobelti*: detailed and expanded species diagnosis; morpho-physiological differentiation of species: differences in male copulatory organ structure between *B. kobeltii* and *B. boettgerianus*; phylogenetic relationships

Shirokaya et al. (2008), as *Baicalancylus kobelti*: geographic and bathymetric distribution; biotope

Kantor et al. (2010), as *Baicalancylus kobelti*: type locality, distribution

Sitnikova (2012): identification key; brief description of teleoconch

Stelbrink et al. (2015): mitochondrial and nuclear genome data; phylogenetic relationships

General distribution. Lake Baikal and the upper part of the Angara River (Starobogatov 1989, Kozhova & Erbaeva 1998). A widely distributed species, though not yet known for southeastern and northwestern lake shores (Shirokaya et al. 2008).

Ecology. Depth, 1–20 m; on rocks (Starobogatov 1989, Shirokaya original data). The greatest population density, up to 39 individuals m^{-2}, was recorded near the mouth of Bol'shoi Chivyrkui River, on multilayered rounded stones and boulders (Shirokaya et al. 2008). Both in Lake Baikal and the Angara River, adult snails feed mainly on benthic diatom algae (85% of the bolus). The stomach also contains small amounts of macrophyte fragments (up to 7%), planktonic diatoms (up to 4%), and pine pollen (up to 4%) (Röpstorf et al. 2003). Feeding of juveniles is unknown.

Remarks. In the late 1980s, Russian malacologists were unaware of the location of the type specimens of "*Ancylus" dybowskii*, "*A.*" *renardii*, and "*A.*" *kobeltii* (Starobogatov 1989). In 2003, while working with the gastropod collection of the Lviv Zoological Museum (Ukraine), T.Ya. Sitnikova found 2 syntypes of "*A.*" *renardii* in samples mostly catalogued as "*Ancylus sibiricus*." We cannot state that the type series of "*A.*" *kobeltii* is lost without a more thorough study of these specimens.

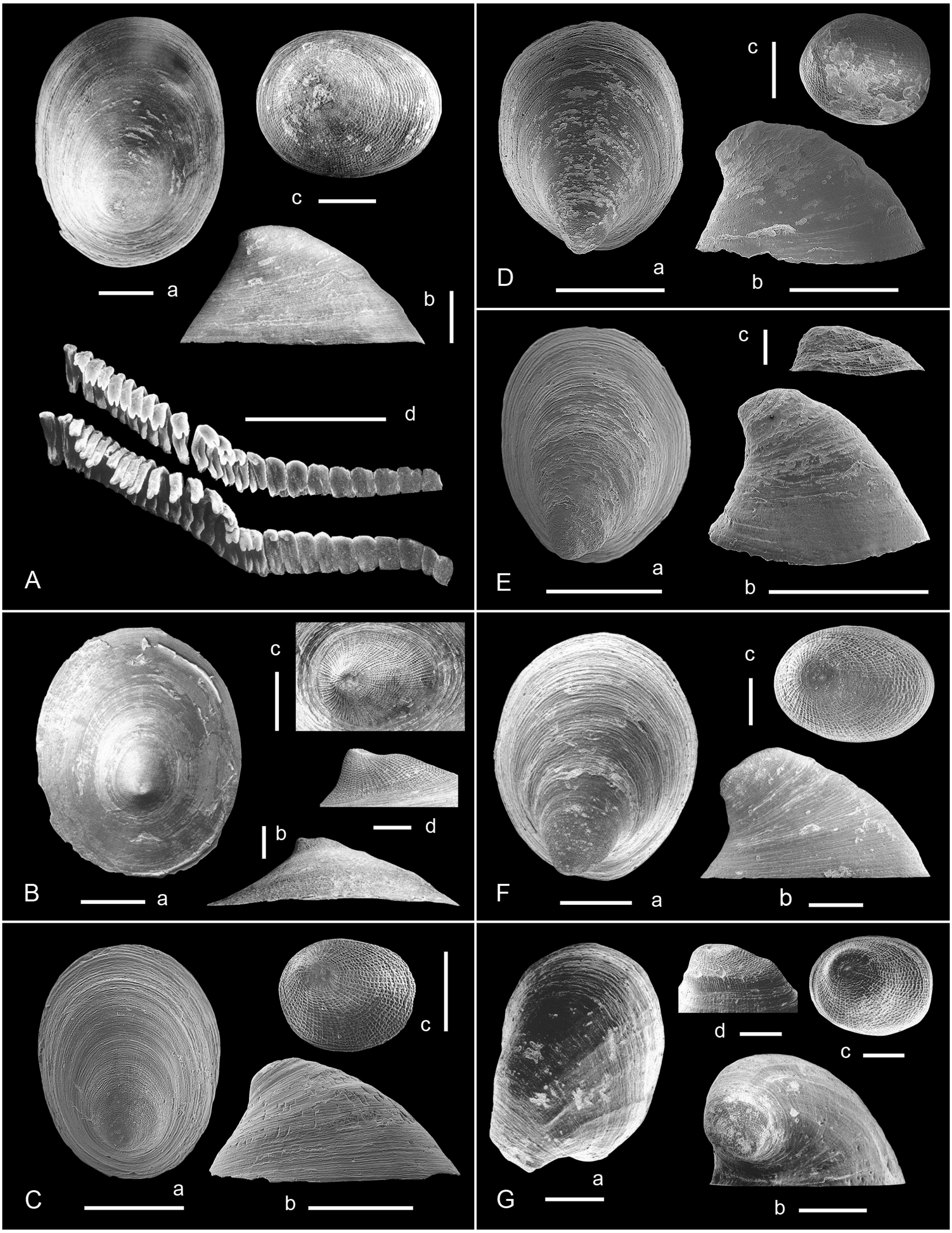

Figure 14. Types, topotypes, and easily identified non-topotypic specimens of *Gerstfeldtiancylus* and *Baicalancylus* spp. from Lake Baikal. **A.** *G. renardii* (W. Dybowski) (topotype): near Listvyanka Settlement. **B.** *G. roepstorfi* Shirokaya, Röpstorf & Sitnikova (paratype): littoral of Malye Uskanji Islands. **C.** *G. capuliformis* Starobogatov: **Ca**, littoral of Tonki Island; **Cb**, **Cc**, Zavorotnyi Cape (topotypes). **D.** *G. pileolus* Starobogatov (topotypes): Kotel'nikovski Cape. **E.** *G. porfirievae* Starobogatov: Kovrizhka Bay (near the collection site of paratype ZIN 3/546-1985). **F.** *G. benedictiae* Starobogatov (same sites as paratypes ZIN no. 3, ZIN no. 18, ZIN 7/548-1985, ZIN 12/548-1985, and ZIN 14/547-1985): **Fa**, **Fb**, upper part of the Angara River; **Fc**, mouth of Sennaya Rivulet. **G.** *B. kobeltii* (W. Dybowski) (topotype): upper part of the Angara River. Teleoconch: **Aa–Ga**, top view; **Ab–Fb**, right side view; **Gb**, rear view. Protoconch: **Ac–Dc**, **Fc–Gc**, top view; **Bd**, **Ec**, **Gd**, right side view. Different views for each species refer to different shells. Radula fragment: **Ad**. Scale bars: length = 1 mm except for Ac, Bd, Fa, Fb, Ga, Gb = 0.5 mm; Ad, Ec = 0.1 mm; Ba = 2 mm; Cc = 0.25 mm; Dc, Fc, Gc, Gd = 0.2 mm.

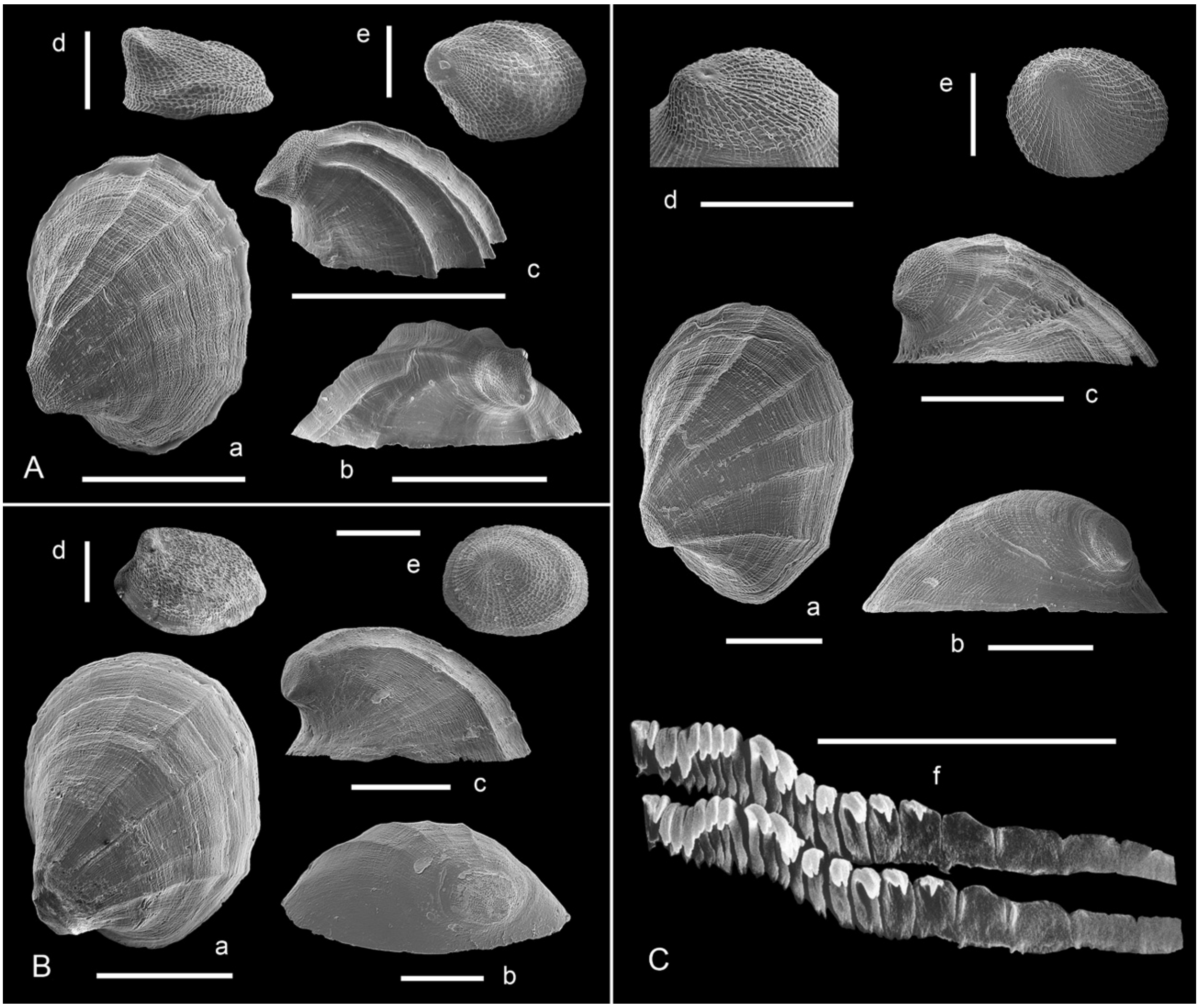

Figure 15. Easily identified non-topotypic specimens of *Baicalancylus* spp. from Lake Baikal. **A.** *B. njurgonicus* Starobogatov. **B.** *B.* cf. *laricensis* (W. Dybowski). **C.** *B. boettgerianus* (Lindholm) (**Ca–Ce**, from near collection site of paralectotypes ZIN 4/543-1985 and ZIN 5/359-1935). Teleoconch: **Aa–Ca**, top view; **Ab–Cb**, left side view; **Ac–Cc**, rear view. Protoconch: **Ad–Cd**, right side view; **Ae–Ce**, top view. Different views for each species refer to different shells. Radula fragment: **Cf**. Scale bars: length = 1 mm except for Ad, Ae, Bd = 0.2 mm; Be, Cd = 0.5 mm; Ce = 0.3 mm; Cf = 0.05 mm.

Discussion

The Acroloxidae is a family of Holarctic freshwater limpets with a disjunct distribution across the Northern Hemisphere (Starobogatov 1970, Stelbrink et al. in press). According to Kruglov & Starobogatov (1991a), the family is represented by 6 Recent genera: *Acroloxus*, incorporating the majority of Palaearctic and Nearctic species; *Pseudancylastrum*, *Gerstfeldtiancylus*, and *Baicalancylus* containing Lake Baikal endemic/subendemic species; and *Dinarancylus* Starobogatov, 1991 and *Costovelletia* Starobogatov, 1991 for the Balkan Peninsula endemics. The latter 2 genera, restricted to Lake Ohrid and caves of the Dinar Mountains, respectively, are usually synonymized with *Acroloxus* by Western malacologists (Stelbrink et al. in press). A recent molecular study of Baikalian acroloxids (Stelbrink et al. 2015) supported the separation from *Acroloxus* of the Baikal endemic genera, including *Frolikhiancylus*. Altogether, at least 50 acroloxid species are known (Kruglov & Starobogatov 1991a, Shirokaya 2005, Kantor et al. 2010), including 2 species recently described from the Anatolian Lake Eğirdir (Shirokaya et al. 2012) and northern Iran (Glöer & Pešić 2012). Lake Baikal is the major world centre of acroloxid speciation, harbouring half of the global species diversity.

Of the 27 valid species of Baikalian limpets, the protoconch ultrastructure has been studied in 24 species and the radula in 11 (SEM data). Teleoconch morphology has been described for all species, but intraspecific variation of shell shape has only been studied in 10 species. The anatomy of the digestive and muscular systems is described for 10 species, and the structure of the male copulatory organ is known for 17 species. The reproductive system is completely characterized in only 1 species. Detailed data, including quantitative indices, related to the geographic, vertical, and biotopic distribution are available for 19 species. Abundance

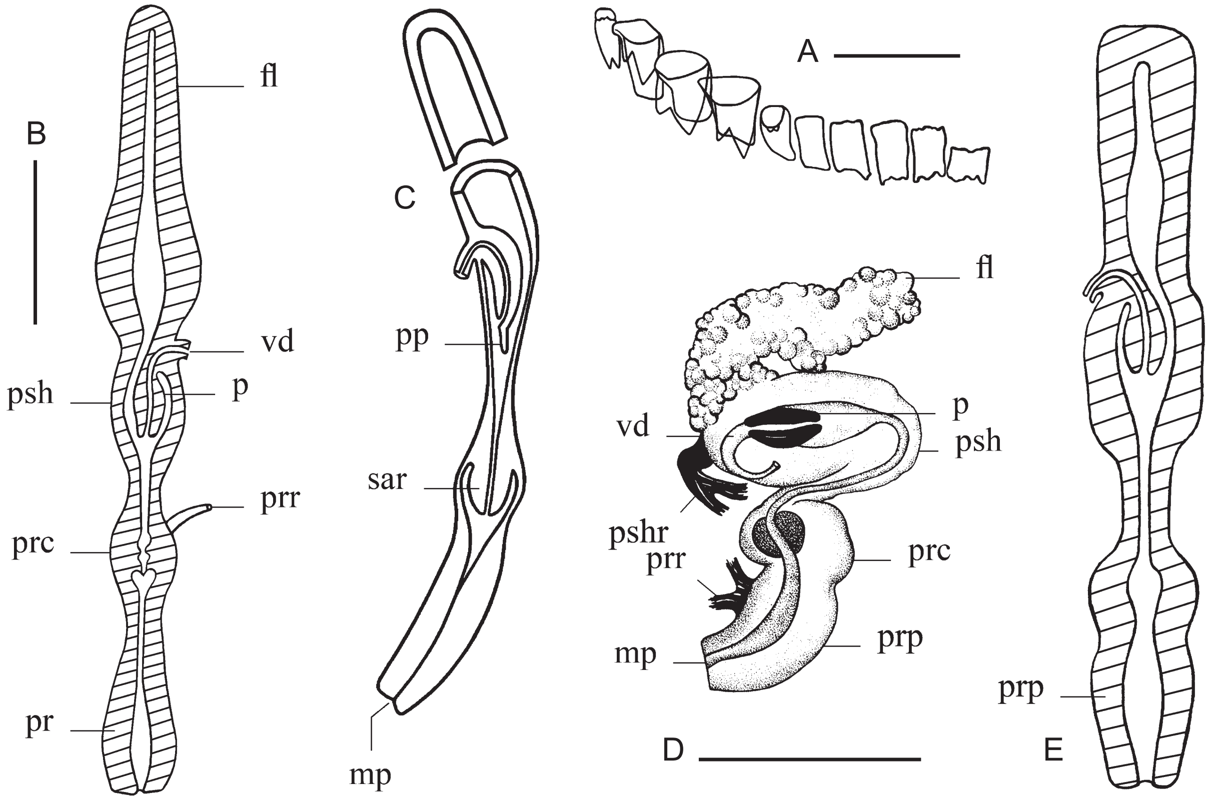

Figure 16. A. Radula fragment of *Baicalancylus laricensis* (W. Dybowski), after Hubendick (1969). **B–E.** Male copulatory organ (B–C, E, diagrammatic): **B**, *B. boettgerianus* (Lindholm), after Kruglov & Starobogatov (1991b), modified; **C**, *B. laricensis*, after Starobogatov (1967); **D, E**, *B. kobeltii* (W. Dybowski) (Shirokaya original data). Scale bars: A = 0.05 mm; B = 0.5 mm; D = 0.3 mm (no scale bars for C, E).

and biomass (seasonal and annual) dynamics have been studied in 8 species. Life history characteristics, including feeding, reproduction, and life span, have been obtained for 6 acroloxid species, and the karyotype is known for 3 of them. Therefore, detailed morphological and ecological information is available for ⅔ of Baikalian acroloxid species. Eight species are known only from sporadic records.

Of the 4 endemic genera, *Gerstfeldtiancylus* is the best known. Its species can be easily distinguished based on anatomical characters as well as protoconch shape and sculpture. These molluscs are undemanding with respect to maintenance in an aquarium, enabling descriptive analyses of the life cycles of common species (Shirokaya & Röpstorf 2003). As for the genus *Baicalancylus*, data on the anatomy and distribution in Baikal are known for 2 easily conchologically identifiable species. Ecological data are sparse.

The genus *Pseudancylastrum* requires revision, as it is the most diverse and least studied among Baikalian acroloxid genera. Samples of *Pseudancylastrum* often include hundreds of specimens collected at the same site. Most *Pseudancylastrum* species present considerable variation in the slopes of the teleoconch and the position of the apex, which hampers species identification by both descriptive and quantitative methods.

Based on examinations of type series of acroloxids stored in ZIN (Shirokaya original data), we believe that the shape of shell slopes cannot be used for the discrimination of related species or, in some cases, even for distinguishing subgenera. According to Kruglov & Starobogatov (1991b), in *Pseudancylastrum* s. str. the posterior slope of the teleoconch is concave under the apex and then weakly concave or straight, but in the subgenus *Parancylastrum* the posterior slope is convex. The type series of *P.* (*Pseudancylastrum*) *aculiferum* includes specimens with a weakly concave posterior slope (paratype ZIN 3/359-1935) and those with distinctly convex slopes (holotype and a non-type specimen collected south of the Bol'shoi Ushkani Island, ZIN 5/546-1985).

Available ecological data are also insufficient to distinguish conchologically similar species of the genus *Pseudancylastrum*. Despite macro- and microbiotopic differentiation (maximum values for the abundance of species are associated with substrate type or surface differences on the same stone; see "Ecology"), related species can occur sympatrically (e.g., *P. sibiricum* and *P. werestschagini* in Bol'shye Koty Bay, *P. beckmanae* and *P. cornu* at Elokhin Cape, and *P. sibiricum* and *P. dorogostajskii* at Katkova Cape) (Shirokaya et al. 2008). All

Pseudancylastrum species live in littoral and sublittoral zones to a depth of 40 m.

Species of *Pseudancylastrum* s. str. are not strictly differentiated with respect to breeding seasons. For instance, oviposition and hatching occur in April and October, respectively, in *P. aculiferum*, but in June and December, respectively, in *P. beckmanae* (Shirokaya & Röpstorf 2003). *Pseudancylastrum werestschagini* lays eggs in both April and June, and juveniles hatch from October to December. Embryonic development in all studied species spans 6 months. The diet is basically similar in all shallow-water species, with benthic diatoms prevailing in the gut content.

In the first major revision of Baikalian acroloxids, Starobogatov (1989) published a dichotomous key to endemic species based on teleoconch proportions and indices. At the same time, interspecific variation in these indices had not been evaluated in a statistical framework. A factor analysis performed for conchologically similar species (Shirokaya et al. 2003) did not reveal significant differences in the *P. sibiricum–P. beckmanae* group. Thus, the calculation of shell indices based on type specimens leads to erroneous species identifications. For example, *B. laricensis*, according to Starobogatov's key, differs from *B. njurgonicus* in the distance between the apex and anterior apertural margin in the projection on the longitudinal axis of the shell (La/L). This index should be ≤ 0.70 in the former species and ≥ 0.75 in the latter species. La/L is 0.88 in the Chivyrkui Bay specimen identified by Starobogatov (1989) as *B. laricensis* (ZIN 2/359-1935).

We attempted to develop a polytomic key to species (Shirokaya et al. 2003, Shirokaya & Röpstorf 2004) based on the structure of the protoconch, radula, and various anatomical characters (i.e., number of jaw plates, shape of lateral teeth of radula, proportions of various parts of the digestive system, and area of muscular adductors of the shell). We found that all *Pseudancylastrum* species possess a horn-shaped protoconch with reticulate microsculpture. We did not observe differences in their radular morphology. All species had broad bicuspid lateral teeth, and a transverse row having a maximum of 7 lateral teeth on each side from the central tooth. Of the 14 characters of the digestive and muscular systems, 11 appeared identical in *P. sibiricum*, *P. beckmanae*, and *P. dorogostajskii* (Shirokaya & Röpstorf 2004).

Descriptions of embryonic shell morphology and anatomical characters are lacking for some species, for example, "*P.*" *troschelii* and *B. laricensis*. Anatomical features were not included in the original descriptions, and the type material stored in ZIN either lack soft bodies or are dried, making dissection impossible. The holotype of *B. laricensis* lacks a protoconch. It is difficult to designate neotypes for such species in the absence of distinguishing characters.

Based on an analysis of c. 2,000 specimens collected in various geographic regions of Baikal (Shirokaya et al. 2008), we found that the currently available keys are unable to identify some species of *Pseudancylastrum* and *Baicalancylus*. In the absence of molecular genetic data, we provisionally divide *Pseudancylastrum* species into 4 groups based on the leftward shift and degree of inclination of the apex. Groups *P. sibiricum–P. beckmanae* and *P. olgae–P. dybowskii* have the apex closer to the left apertural margin than to the longitudinal axis of the shell, and groups *P. korotnevi–P. troschelii*, *P. werestschagini–P. poberezhnyi* have an apex situated closer to the centre of the aperture. Easily identifiable species include *P. cornu*, with an extremely tall shell (H/L = 0.90) and an apex that is strongly shifted leftward (the angle to the longitudinal axis of the aperture is not less than 68°), *P. aculiferum*, with an apex directed obliquely upward, like a thorn, and *P. dorogostajskii*, with an apex that looks like a parrot's bill. *Pseudancylastrum irindaense* is probably a morph of *P. dorogostajskii* because their holotypes are very similar. Of 4 species of the genus *Baicalancylus*, only *B. kobeltii* can be easily identified by its small, but tall shell with a massive protoconch. The other 3 species of the genus are connected by many intermediate morphs.

Khokhutkin & Vinarski (2013) thought it impossible to develop functional dichotomous keys to acroloxid species based on only shell morphology. This belief was demonstrated by an example of numerous samples of 3 *Acroloxus* species (*A. lacustris*, *A. oblongus* (Lightfoot, 1786), and *A. shadini* Kruglov & Starobogatov, 1991) from the Urals and Western Siberia. Using the published key (Kruglov & Starobogatov 1991a), Khokhutkin & Vinarski (2013) identified all 3 species, which only differ in 2 shell indices, but an analysis of teleoconch variation using a principal components analysis did not support the species-level identity of *A. oblongus* and *A. shadini*. Additionally, they found a lack of ecological niche divergence among coexisting species in the same microbiotope.

Over 25 years have passed since the publication of Starobogatov's (1989) key to Baikalian acroloxids, and the taxonomic composition of the family has changed. Accordingly, we present a new key what integrates data on the embryonic and adult shell, jaw, radular teeth, muscular system, and male copulatory organ (Appendix 2). The key will serve to identify all species and subgenera of the genus *Gerstfeldtiancylus*, as well as easily distinguishable species and species groups within *Pseudancylastrum* and *Baicalancylus*. However, because of a lack of clear differences in shell shape and a lack of soft body morphological data, we do not provide subgeneric characters for *Acroloxus* and *Pseudancylastrum*.

Acknowledgements

We express our cordial gratitude to Dr Andrei Zatushevski (Zoological Museum of the Ivan Franko National University of Lviv, Ukraine) for photographing the lectotype of *G. renardii*, Dr Pavel V. Maslennikov and Prof. Vladimir N. Dolgin (Tomsk State Pedagogical University, Russia) for information on *A. baicalensis* from the Chulym river drainage, Dr Anatoli A. Asochakov and Dr Sergei V. Dragan (Khakassia State University, N.F. Katanov, Abakan, Russia) for the opportunity to explore the catalogue of Cheremnov's collection of freshwater molluscs. Special thanks go to Lydia L. Yarokhnovich (ZIN, Saint Petersburg, Russia) for her constant assistance in working with acroloxid collections, Dr Matthias Glaubrecht and Christine Zorn (Museum für Naturkunde, Berlin, Germany) for data on the deep-water Baikalian acroloxids stored in that museum, Dr Ronald Janssen (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany), Dr Ira Richling (Staatliches Museum für Naturkunde, Stuttgart, Germany), Dr Jonathan Ablett (Natural History Museum, London), and Dr Peter Röpstorf for the information about the condition of Clessin's type collections in European museums. We are grateful to Dr Galina V. Beriozkina (Smolensk State University, Russia) for the information on the life cycles of Palaearctic Acroloxidae, which is used for compilation of the extended diagnoses. Much advice, which considerably improved the manuscript, were provided by Prof. Vadim V. Takhteev (Irkutsk State University, Russia), Prof. Maxim V. Vinarski (Saint Petersburg State University, Russia), Prof. Oleg A. Timoshkin (Limnological Institute SB RAS, Russia), and Dr Alexander V. Sysoev (Zoological Museum of Moscow State University, Russia). SEM images of shells were made at the Centre for joint researches "Ul'tramicroanaliz" of LIN (Irkutsk), as well as at the Institute of Geological Sciences, Freie Universität Berlin. The English version of this manuscript was translated by Dr Alexander V. Sysoev, Dr Larisa A. Prozorova, and Prof. Oleg A. Timoshkin. Comprehensive editing was made by Dr Patrick Hughes (Bioedit Ltd.). This work was supported by the State Projects of the Siberian Branch of the Russian Academy of Sciences (no. VI.51.1.10; "Current state, biodiversity and ecology of the coastal zone of Lake Baikal" and no. 0345-2016-0009 (AAAA-A16-116122110067-8) "Large-scale changes in ecology and biodiversity of the communities of the coastal zone of Lake Baikal …"), RFBR projects (nos 12-04-00503-a, 14-44-04126, and 15-29-02515), the Grants-in-Aid for Scientific Research (KAKENHI) (no. 15H05112), and a DAAD-scholarship (no. A0984347).

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Appendix 1

Species synonymized since the revision of Starobogatov (1989)

Gerstfeldtiancylus gerstfeldti **Starobogatov, 1989**

Figure 9A

Gerstfeldtiancylus gerstfeldti Starobogatov 1989: 60, fig. 2(*1*).
Ancylus sibiricus, part.— W. Dybowski 1875: 61 (non Gerstfeldt 1859).
Ancylus troschelii— W. Dybowski 1884: 156, Taf. IV, figs 1, 5 (non W. Dybowski 1875).
Ancylus (*Pseudancylastrum*) *troscheli*, part.— Lindholm 1909: 28; Kozhov 1931: 65.
Pseudancylastrum troscheli, part.— Kozhov 1936: 187, Taf. VII, figs 37, 38, Taf. X, figs 2, 3; Shadin 1952: 203, fig. 119.
Acroloxus (*Pseudancylastrum*) *troscheli*— Hubendick 1962: 47, figs 29–33.
Acroloxus troscheli— Hubendick 1969: 55, figs 1–4, 29, 36.

Type locality. Lake Baikal, near Listvyanka Settlement.

Types. ZIN: holotype and 25 paratypes. Holotype (ZIN 1/359-1935, dry shell): coll. A.A. Korotnev expedition, 19 June 1901, sta. 12, at 5.6–22.2 m, on stone, initially identified by W.A. Lindholm as *Ancylus* (*Pseudancylastrum*) *troscheli*. Shell in good condition (Fig. 9A), its dimensions (in mm): L = 7.70; La = 6.0; W = 5.80; wL = 2.80; H = 4.90; a = 7.20 (Starobogatov 1989). Paratypes: 2 dry shells (ZIN 2/359-1935), opposite Baranchick Valley, Listvennichnyi Bay, coll. same expedition, 1902, sta. 4b, at 5.6–11.1 m, on stones, initially identified by W.A. Lindholm as *A.* (*P.*) *troscheli*; 1 dry shell (ZIN 3/359-1935), Kultuk Bay, coll. same expedition, 16 August 1902, sta. 13a, at 31.5 m, substrate not indicated; 1 dry shell (ZIN 4/359-1935), Kocherikovski Cape, coll. same expedition, 14 July 1902, sta. 165, at 5.6–7.4 m, on stone, initially identified by W.A. Lindholm as *A.* (*P.*) *troscheli*; 2 dry shells (ZIN 5/543-1985), coll. data same as holotype; 3 dry shells (ZIN no. 6), Bol'shye Koty Bay, coll. M.M. Kozhov, at 21–25 m, sampling data and substrate not indicated; 4 dry shells (ZIN no. 7), Lake Baikal, coll. B. Dybowski, no additional data, initially identified by W. Dybowski as *A. sibiricus*; 1 specimen (ZIN no. 8, in alcohol), Southern Baikal, no additional data; 1 specimen (ZIN 9/548-1985, in alcohol), opposite Zhilistsche Valley, Bol'shye Koty Bay, coll. Ya.I. Starobogatov, 16 September 1966, at 15 m, on rocks; 3 specimens (ZIN 10/548-1985, in alcohol), opposite Malye Koty Valley, same bay, coll. Ya.I. Starobogatov and S.M. Popova, 25 August 1966, at 5–6 m, substrate not indicated; 4 specimens (ZIN 11/548-1985, in alcohol), opposite Zhilistsche Valley, coll. Ya.I. Starobogatov, 20 June 1954, at 9 m, on stones; 1 specimen (ZIN 12/545-1985, in alcohol), Mysovskaya Bank, coll. S.M. Popova, 30 July 1957, at 4 m, substrate not indicated; 1 dry shell (ZIN 13/543-1985), opposite Baranchick Valley, coll. A.A. Korotnev expedition, 1901, sta. 17, at 7.4–9.3 m, on stones and sand; 1 dry shell (ZIN 14/543-1985), Boguchanskaya Inlet, coll. same expedition, 27 July 1902, sta. 112, at 3.7–5.6 m, on stone. All type specimens (re)determined by Ya.I. Starobogatov.

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype from Boguchanskaya Inlet; discussion on shell shape variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): structure of male copulatory organ

Shirokaya et al. (2003): description of adult shell, protoconch, and radula (SEM data); additional taxonomically important characters; polytomic identification key to species; taxonomic position, synonymization of *G. gerstfeldti* with *G. renardii* (Dybowski)

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): information on type locality and type material; distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): synonymy; distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): synonymization with *G. renardii* (Dybowski)

Remarks. A principal components analysis of shell shape (Shirokaya et al. 2003) showed that, based on teleoconch measurements and indices, *G. gerstfeldti* is similar to 2 other species of the subgenus *Gerstfeldtiancylus* s. str., i.e., *G. kozhovi* sensu Starobogatov (1989) (= *G. kotyensis* Starobogatov, 1989, after Shirokaya et al. [2003]) and *G. renardii* (W. Dybowski). Moreover, the teleoconch measurements of 1 paratype of *G. gerstfeldti*, found in Boguchanskaya Inlet (NW Baikal), coincide completely with those of the holotype of *G. kozhovi* from Bol'shye Koty Bay (south basin) (Starobogatov 1989). However, there is a clear difference in the radular morphology between these 2 species: in *G. kozhovi* (= *G. kotyensis*), a transverse row contains 5–9 broad lateral teeth on each side from the central tooth, and 13–15 marginal teeth, whereas *G. gerstfeldti* has 12–20 narrow lateral teeth and 8–10 marginal ones (Shirokaya et al. 2003). The same radula pattern, with numerous narrow lateral teeth, is characteristic of "*Ancylus*" *renardii* (Dybowski 1884: Taf. IV, fig. 4) and "*Acroloxus*" *troschelii* (Hubendick 1969: fig. 29). The latter was believed by Hubendick to be a senior synonym of "*A.*" *renardii*. Based on a comparative analysis of the teleoconchs of 2 type specimens of *G. renardii*, which were unknown to Ya.I. Starobogatov (1989: 64), with the type series of *G. gerstfeldti* as well with the numerous samples of the latter species collected during circum-Baikalian expeditions (1999–2004) (Shirokaya original data), we did not find substantial differences between the 2 species, except for the shape of the posterior shell slope, which is more inclined in *G. renardii* (Fig. 7Da), but upright and nearly vertical in *G. gerstfeldti* (Fig. 9Aa).

According to Article 23.3 of the Code (ICZN 1999), the species name *G. gerstfeldti* is regarded as a junior synonym of *G. renardii* (W. Dybowski) (Shirokaya 2005).

Gerstfeldtiancylus kozhovi Starobogatov, 1989

Figure 7B

Gerstfeldtiancylus kozhovi Starobogatov 1989: 62, fig. 2(*2*).
Ancylus (*Pseudancylastrum*) *troscheli*, part.— Lindholm 1909: 28 (non W. Dybowski 1875).

Type locality. Lake Baikal, Bol'shye Koty Bay.

Types. ZIN: holotype and 28 paratypes. Holotype (ZIN no. 1, dry shell): coll. M.M. Kozhov, July 1928, at 25–40 m, substrate not indicated. Shell in good condition (Fig. 7B), its dimensions (in mm): L = 8.60; La = 5.90; W = 7.10; wL = 2.80; H = 4.70; a = 7.70 (Starobogatov 1989). Paratypes: 1 dry shell (ZIN no. 2), coll. data same as holotype; 1 dry shell (ZIN no. 3), Lake Baikal, coll. M.M. Kozhov, no additional data; 1 dry shell (ZIN 4/543-1985), opposite Baranchick Valley, Listvennichnyi Bay, coll. A.A. Korotnev expedition, 22 July 1901, sta. 17, at 7.4–9.3 m, on stones and sand; 1 dry shell (ZIN 5/543-1985), same locality and coll., 19 June 1901, sta. 12, at 5.6–22.2 m, on stone; 4 specimens (ZIN 6/548-1985, in alcohol), opposite Zhilistsche Valley, Bol'shye Koty Bay, coll. Ya. I. Starobogatov, 16 September 1966, at 15 m, on rock; 1 juvenile specimen (ZIN 7/546-1985, in alcohol), 2 km S of Orlovski Cape, Svyatoi Nos Peninsula, coll. BGI ISU expedition, 12 September 1966, at 5 m, on stone; 2 specimens (ZIN 8/546-1985, in alcohol), Ongurion Cape, coll. same expedition, 31 August 1966, at 8–16 m, on stones; 8 specimens (ZIN 9/546-1985, in alcohol), Dyrovatyi Cape, coll. same expedition, 28 August 1966, sample 2, at 18–60 m, on gravel; 3 specimens (ZIN 10/546-1985, in alcohol), Boguchanski Island, coll. same expedition, 5 September 1966, at 12 m, on stones; 1 specimen (ZIN no. 11, in alcohol), Southern Baikal, no additional data; 2 juvenile specimens (ZIN 12/546-1985, in alcohol), entrance to Mukhor Bay, coll. BGI ISU expedition, 17 September 1966, at 6 m, on gravel and sand; 1 specimen (ZIN 13/546-1985, in alcohol), between Izhimei Cape and Ulannur Inlet, Ol'khon Island, coll. same expedition, 13 September 1966, at 21 m, on stones and sand; 2 specimens (ZIN 14/548-1985, in alcohol), Babushka Bay, coll. A.F. Alimov, 10 August 1966, at 10 m, substrate not indicated. All type specimens identified by Ya.I. Starobogatov.

History of the usage of the name.

Starobogatov (1989): teleoconch description; information on type material including shell dimensions of holotype and paratype from Baranchick Valley; discussion on shell variability; distribution; biotope

Kruglov & Starobogatov (1991b), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): structure of male copulatory organ

Shirokaya et al. (2003): description of adult shell, protoconch and radula (SEM data); polytomic identification key to species; taxonomic position: *G. kozhovi* can be considered as a synonym of either *G. renardii* or *G. kotyensis*, or it is a possible hybrid of latter 2 species, because it combines their characters and lives sympatrically with them

Shirokaya & Röpstorf (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): description of alimentary system and shell adductor muscles; polytomic key; taxonomic position: absence of significant differences in anatomy confirms necessity to synonymize *G. kozhovi* and *G. kotyensis*

Sitnikova et al. (2004), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): information on type locality and type material, distribution; zoogeographical and ecological data

Kantor & Sysoev (2005): distribution

Shirokaya (2005), as *Gerstfeldtiancylus* (*Gerstfeldtiancylus*): taxonomic position: *G. kozhovi* is a subjective synonym of *G. kotyensis*

Remarks. Shell dimensions and indices for specimens that can be identified by comparative method (Starobogatov & Tolstikova 1986) as *G. kozhovi* are similar to those for *G. renardii* and *G. kotyensis* (Shirokaya et al. 2003). The size of the *G. kozhovi* holotype is the same as that of paratype ZIN 14/543-1985 of *G. gerstfeldti* Starobogatov, which is a junior synonym of *G. renardii* (Dybowski) (Shirokaya 2005). *Gerstfeldtiancylus renardii* and *G. kotyensis* differ substantially in radular morphology. The lateral teeth of *G. renardii* have narrow cutting edges, and the number in a transverse row varies from 26–38; the radula of *G. kotyensis* possesses 10–18 wide lateral teeth. There are no known differences between *G. kotyensis* and *G. kozhovi* in radula, digestive system, or muscular adductors of the shell. In *G. renardii*, the salivary glands are thin, the caecum is short, and the first intestinal loop lies above the radular sac; in *G. kozhovi* and *G. kotyensis*, the caecum is long, the salivary glands are initially expanded, and the first intestinal loop is shifted rightward. The surface of the posterior adductor in *G. renardii* is 4 times larger than that of each of the anterior adductors, whereas this index is 1.5–2 larger in *G. kozhovi* and *G. kotyensis* (Shirokaya & Röpstorf 2004). According to Kruglov & Starobogatov 1991b, the male copulatory organ of *G. kozhovi* differs from that of *G. kotyensis* by the relative length of the preputium and the shape of the glandular flagellum. *Gerstfeldtiancylus gerstfeldti* (=*G. renardii*) differs from the above-mentioned species by the shape of the penis sheath and by the relative length of the flagellum. Owing to limited material, it was only possible to dissect a single specimen of each species (Kruglov & Starobogatov 1991b). We examined 9 specimens of *G. kotyensis*, 7 *G. renardii*, and 4 *G. kozhovi*. To compare measurements and male copulatory organ indices among the 3 species, we used a factor analysis (Shirokaya et al. 2003). According to this analysis, *G. renardii* is separated from both *G. kozhovi* and *G. kotyensis*, whereas the latter 2 species are represented by overlapping clouds.

Because *G. kotyensis* and *G. kozhovi* were described simultaneously, we consider them as the subjective synonyms (ICZN 1999, Article 61.3.1). Following Recommendation 24A as First Reviser (ICZN, Article 24), we select *G. kotyensis* to take precedence and best preserve the stability of the nomenclature. The morph that matches this name is distributed throughout Lake Baikal. We did not detect significant differences among populations of *G. kotyensis*. The morphological diagnosis of the species (Starobogatov 1989: 63) facilitates its identification in different areas of the lake.

Appendix 2

Identification key to Lake Baikal limpets

1(4) Shell buckler-shaped, laterally compressed; aperture oval or elongated-ovate (W/L ≤ 0.60); initial plate of the protoconch drop-shaped or oval . . . **Genus *Acroloxus***

2(3) Shell with slight concavity below apex on posterior-left slope; right slope straight (or weakly convex); apex visibly shifted to the left of the shell midline (wL/W = 0.32–0.35) and projects onto the aperture within the posterior ⅓ (La/L > 0.70); the aperture oval with a broader anterior edge; dark pigmentation on dorsal body side arranged in an uneven ring; egg mass (syncapsule) surface with longitudinal striation
. . . . ***A. baicalensis***; Fig. 4A, B

3(2) Shell with deep concavity below apex on posterior-left slope; right slope distinctly convex; apex slightly shifted to the left of the shell midline (wL/W = 0.42–0.45) and projects onto the aperture within the anterior ⅔ (La/L < 0.65); front and back aperture edges equally rounded, whereas its lateral sides nearly parallel to each other; mantle pigmentation on the dorsal body side forms 2 transverse lines in front of and behind the apex; egg mass (syncapsule) surface without longitudinal striation . . . . ***A. orientalis***; Fig. 4C, D

4(1) Shell cap-shaped, elevated; aperture rounded-ovate (W/L ≥ 0.70); initial plate of the protoconch rounded

5(6) Protoconch with pitted microsculpture; teleoconch and syncapsules are fouled mainly by filamentous and rod-shaped bacteria; depth, 100–1,000 m
. . . . **Genus *Frolikhiancylus***; only 1 sp., *F. frolikhae*; Figs 10D, 13E

6(5) Protoconch with reticulate microsculpture; teleoconch and syncapsules are fouled mainly by diatoms; depth, 1–40 m

7(38) Teleoconch with only visible growth lines; aperture with smooth (even) margins

8(23) Shell apex oriented to the left at 8 o'clock position; shell greenish-yellow or yellowish-brown; protoconch horn-shaped; vas deferens opening located laterally, tip of the penis possesses soft papilla
. . . . **Genus *Pseudancylastrum***

9(20) Right slope of teleoconch strongly convex; apex lies much closer to left apertural margin than to its centre (wL/W ≤ 0.24)

10(15) Geometrically, back view of the shell fits into a triangle with narrow base and a high left-skewed apex

11(12) Shell apex shifted to very left aperture edge
. . **spp. group *P. sibiricum*** (including *P. beckmanae*); Figs 5A, B, 12F, G

12(11) Shell apex significantly protrudes beyond the contour of aperture

13(14) Teleoconch extremely high (H/L up to 0.90); apex located on the level of upper ¼ of the shell height; angle between apex and longitudinal axis of aperture is not less than 68° in adult individuals
. . . . ***P. cornu***; Figs 5E, 13A

14(13) Teleoconch fairly high (H/L = 0.57–0.73); apex located on the level of upper ⅓ of the shell height; angle between apex and longitudinal axis of aperture is not > 65° in adult individuals
. . . . . . **spp. group *P. olgae*** (including *P. dybowskii*); Figs 5C, D, 11A, 12H, 13B

15(10) Geometrically, back view of the shell fits into a semicircle

16(17) Left slope of teleoconch straight or slightly convex, with the exception of concavity below apex; apex hamiform, bent down
. . . . **spp. group *P. dorogostajskii*** (including *P. irindaense*); Figs 6E, F, 13C, D

17(16) Left slope of teleoconch straightened

18(19) Teleoconch fairly low (H/L = 0.40–0.44, H/W = 0.48–0.51); posterior slope weakly convex
. . . . ***P. poberezhnyi***; Figs 6D, 12D

19(18) Teleoconch moderately high (H/L = 0.49–0.54, H/W = 0.65–0.68); posterior slope slightly concave
. . . . ***P. werestschagini***; Figs 6A, 12E

20(9) Right slope of teleoconch weakly convex or straight; apex slightly shifted to the left from the longitudinal axis of aperture (wL/W > 0.30)

21(22) Concavity below apex on the anterior-right slope of teleoconch strongly expressed, whereby the apex looks like thorn directed obliquely upwards
. . . . ***P. aculiferum***; Figs 6C, 12B

22(21) Concavity below apex on the anterior-right slope of teleoconch indistinct; apex directed downward
. . . **spp. group *P. korotnevi*** (including *P. troschelii*); Figs 5F, 6B, 12A, C

23(8) Shell apex directed hindward; shell grey or grey-green; protoconch cap-shaped; vas deferens opening located terminally (penial papilla lacking)
. . . . **Genus *Gerstfeldtiancylus***

24(31) Shell large, maximum width of aperture in adults not < 5 mm; flagellum gradually passing into the penis sheath . . . . **Subgenus *Gerstfeldtiancylus***

25(26) Posterior slope of teleoconch slightly convex, protoconch flattened (H/h = 8.5); dorsal part of jaw with plates; globular chamber of preputium contains, besides sarcobelum, a well discernible velum; right ½ of shell posterior adductor is substantially elongated and directed forward, its surface arch-shaped; extra-syncapsular tunic very broad
. . . . ***G. ushunensis***; Figs 7F, 13F

26(25) Posterior slope of teleoconch concave or straight; protoconch relatively high (H/h = 4–5); dorsal part of jaw without plates; velum absent; position of the posterior shell adductor bilaterally symmetrical; extra-syncapsular tunic relatively narrow

27(30) Diameter of initial plate of the protoconch not exceeding 0.2 mm; concavity below apex on the anterior slope of teleoconch weakly expressed or absent; shell moderately high (H/L = 0.45–0.65), anterior slope convex; the number of jaw plates < 70

28(29) Cross row of radula includes not > 18 lateral teeth and not < 26 marginal teeth; lateral teeth with a broad cutting edge . . . . ***G. kotyensis***; Figs 7A, 13G

29(28) Cross row of radula includes not < 24 lateral teeth and not > 20 marginal teeth; lateral teeth with a narrow cutting edge . . . . ***G. renardii***; Figs 7D, 14A

30(27) Diameter of initial plate of the protoconch not < 0.26 mm; concavity below apex on the anterior slope of teleoconch well visible; shell relatively low (H/L = 0.30–0.47), anterior slope straight; the number of jaw plates > 70 . . . . ***G. roepstorfi***; Figs 7C, E, 8, 14B

31(24) Shell small, maximum width of aperture in adults not > 3.5 mm; penis sheath separated from flagellum by a constriction . . . . . . **Subgenus *Kozhoviancylus***

32(35) Apex lying exactly above the shell medial line

33(34) Shell height not > 0.55 of the aperture length; angle between posterior slope of shell and plane of aperture < 60° . . . . ***G. capuliformis***; Figs 9D, 14C

34(33) Shell height not < 0.55 of the aperture length; angle between posterior slope of shell and plane of aperture > 65° . . . . ***G. pileolus***; Figs 9F, 14D

35(32) Apex slightly shifted leftward (distance from initial plate of protoconch to left margin of aperture not exceeding 0.9 of distance from initial plate to right margin of aperture)

36(37) Apex lying almost above the posterior edge of aperture; posterior slope of the shell straight, with the exception of concavity below apex . . . . ***G. porfirievae***; Figs 9E, 14E

37(36) Distance from apex to posterior edge of aperture 0.1–0.2 of its length (as projected to the plane of aperture); posterior slope of the shell evenly concave over the entire length . . . . ***G. benedictiae***; Figs 9B, C, 14F

38(7) Teleoconch with radial ribs; aperture edges undulating . . . . **Genus *Baicalancylus***

39(40) Protoconch massive, cap-shaped, faceted, relatively high (h/H ≥ ⅔); shell apex slightly shifted leftward (angle between apex and longitudinal axis of aperture being not > 40°) and markedly projects outside posterior margin of aperture (La/L nearly 1.10); ring-shaped bulge along the protoconch edge indistinct, shell ribs weak; aperture rounded . . . . ***B. kobeltii***; Figs 10C, 14G

40(39) Protoconch small, cap-shaped, faceted, relatively low (h/H = ⅛–¼); shell apex distinctly shifted leftward (angle between apex and longitudinal axis of aperture being not < 45°) and not reaching posterior margin of aperture (La/L ≤ 0.95); ring-shaped bulge along the protoconch edge distinct, shell ribs well visible; aperture oval . . . . **spp. group *B. boettgerianus*** (including *B. laricensis* and *B. njurgonicus*); Figs 10A, B, E, F, 15A, B, C

Manuscript submitted 6 June 2016
Revised manuscript accepted 14 December 2016