

Taxonomic assessment of genetically-delineated species of radicine snails (Mollusca, Gastropoda, Lymnaeidae)

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Abstract

The article represents an overview of 29 biological species of the radicine snails (genera *Ampullaceana* Servain, 1882, *Bullastra* Bergh, 1901, *Racesina* Vinarski & Bolotov, 2018, *Kamtschaticana* Kruglov & Starobogatov, 1984, *Myxas* G.B. Sowerby I, 1822, *Orientogalba* Kruglov & Starobogatov, 1985; *Peregriana* Servain, 1882, *Radix* Montfort, 1810, and *Tibetoradix* Bolotov, Vinarski & Aksenova, 2018) recovered during our previous molecular taxonomic study (Aksenova et al. 2018a; Scientific Reports, 8: 11199). For each species, the following information is provided: scientific name, a (non-exhaustive) list of synonyms, type locality, type materials, shell and copulative apparatus morphology, distribution, and nomenclatural and taxonomic remarks. The colour images of shell(s) of each species are also given as well as illustrations of the copulatory apparatuses. We revealed a great conchological variation in the radicles, both intra- and interspecific, alongside with striking uniformity in the structure of their copulatory apparatuses. The latter was once thought to be a reliable tool for species delineation and identification in this snail group. The total of 29 species characterised here represents, probably, only a subset of the global taxonomic richness of the radicine snails, which approaches 50 species.

Key Words

aquatic pulmonates, distribution, Old World, phylogenetics, taxonomy

Introduction

Historically, systematics of freshwater pulmonate gastropods had relied on two basic sources of data – conchology and anatomy. The combined use of these sources allowed researchers to delineate species and higher taxa and to compile dichotomous keys for identification of snails (see, for example, Meier-Brook 1983; Taylor 2003; Kruglov 2005). Since the late 1990s, the novel methods of molecular phylogenetics and molecular taxonomy have been widely adopted by malacologists and today they represent a standard tool for species delimitation in different families of freshwater pulmonates. Though there is an almost full agreement that the molecular data are

more exact and ‘objective’ than the morphological ones, their extensive use has led to some problems in the practical taxonomy of aquatic Pulmonata. First, many taxa of snails, established on the basis of morphological information, proved non-valid due to the lack of genetic support (see, for example, Vinarski et al. 2016; Aksenova et al. 2017). On the other hand, some ‘good’ species defined genetically cannot be identified morphologically as the ranges of their conchological and anatomical variation overlap with those of closely-related species (Schniebs et al. 2011, 2013; Aksenova et al. 2018a). The cryptic speciation has also been detected within this group (Bargues et al. 2011; Standley et al. 2013). Lastly, the authors of some recent molecular works, focused on species diversi-

ty, prefer to deal with impersonal categories such as MOTUs (Pfenninger et al. 2006) and clades (von Oheimb et al. 2011; Clewing et al. 2016), instead of scientific names (Latin or latinised binomens) that would correspond to previously-described species of snails. In such cases, the proper taxonomic work remains unfinished since it is very difficult to find correspondence between the MOTUs or impersonal ‘clades’ and biological species, with their unique names. The use of such nameless entities makes it almost impossible to treat them in accordance with the internationally-adopted rules of zoological nomenclature and impedes the practical issues like conservation planning or studies of the snail-trematode interactions.

Recently, we published a paper (Aksenova et al. 2018a) devoted to the taxonomy, phylogeny and biogeography of the Old World radicine snails (subfamily Amphipepleinae Pini, 1877 of the family Lymnaeidae Rafinesque, 1815), based on an analysis of more than 2600 sequences of two mitochondrial (COI and 16S rRNA) and one nuclear (28S rRNA) gene. This analysis allowed us to propose a new taxonomic structure of the genus *Radix* Montfort, 1810 s. lato and to recover as many as 35 biological species of

radicines, based primarily on the molecular data. Since 2018, one more species of this group, *Radix dgebuadzei* Aksenova, Vinarski, Bolotov & Kondakov, 2019, has been described (Aksenova et al. 2019). A simplified phylogenetic tree of the recent Amphipepleinae recovered during our work is given in Fig. 1.

In that study (Aksenova et al. 2018a), we tried to link every genetically-defined clade of the genus or species rank to a certain taxonomic name. In particular, we managed to find proper names for formal designation of almost all MOTUs or clades delineated by previous workers (Pfenninger et al. 2006; von Oheimb et al. 2011; Clewing et al. 2016). However, in the previous paper, the emphasis was laid on phylogeny and historical biogeography (Aksenova et al. 2018a). Most issues, related to systematics and nomenclature of the radicines, remained unexplained.

The current study aims at taxonomic assessment of the genetically-defined species of the radicine snails. We tried to characterise them both morphologically and geographically and to give the readership some cues on how to identify these molluscs on the basis of their morphological characters. Additionally, we present here some

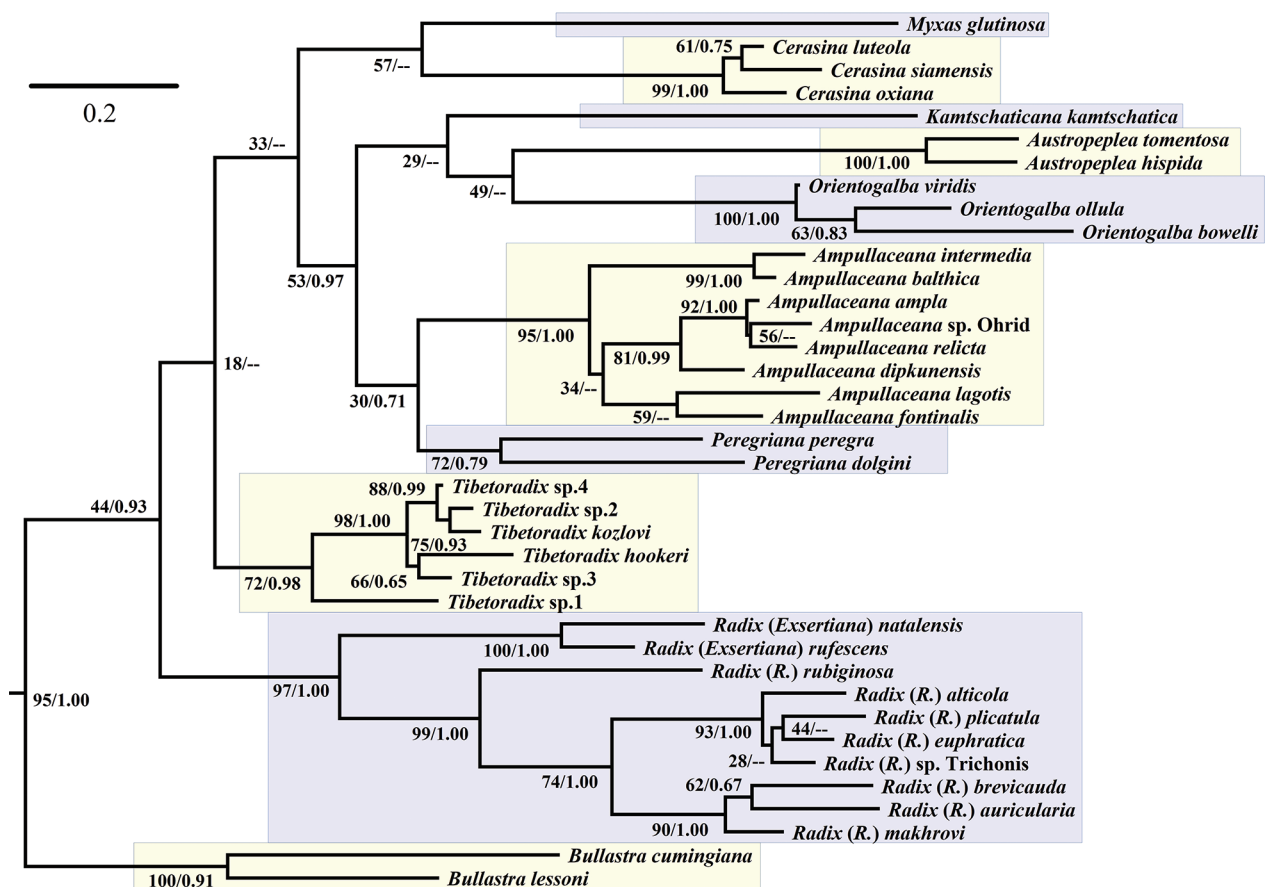


Figure 1. Majority rule consensus phylogenetic tree of the Amphipepleinae recovered from maximum likelihood analysis and obtained for the complete dataset of mitochondrial and nuclear sequences (three codons of COI + 16S rRNA + 28S rRNA). Black numbers near nodes are bootstrap support values/Bayesian posterior probabilities. The genus-level clades are highlighted in colour. The other Lymnaeidae and outgroup taxa are omitted (see Aksenova et al. 2018a for the complete phylogeny, sequence dataset and methodological details).

taxonomic and nomenclatorial considerations aimed to substantiate the taxonomic opinions proposed in the previous article (Aksenova et al. 2018a).

Material and methods

Out of 35 biological species of the radicles delineated by us (Aksenova et al. 2018a), we were able to study morphologically 29 taxa. The rest of the species were included in our analyses on the basis of sequences available from GenBank and we had none of our own or museum materials to examine their morphology. Such species as *Radix* sp., an (allegedly) endemic to Lake Trichonis of Greece (see Aksenova et al. 2018a) and some taxa from the Tibetan Plateau remain nameless and, though we are aware of their species status, the full absence of the material makes it impossible to form the type series and to designate the holotype as is required by the international rules of zoological nomenclature.

The snails for this study were either collected by the authors from various Old World countries (Russia, China, Tajikistan, Myanmar, Mongolia and some others) or examined in the collections of a series of European zoological institutions. The full enumeration of these repositories are given below, in the abbreviations list. In all cases, when it was possible, we tried to examine the type series of the studied species and to compare the holotype and paratypes (or syntypes) with the published descriptions and our own materials. During our work, we managed to reveal and study the type series (or possible syntypes) of 10 valid species. In some cases, high-quality photos of the type specimens were available for us (for exam-

ple, those published in Sitnikova et al. 2012). Besides, we were able to examine the type series of many nominal species considered below as synonyms. Additionally, we substantially benefited from the use of some comprehensive taxonomic publications, including high-quality overviews of the regional faunas (Brandt 1974; Brown 1994; Glöer 2002; Glöer and Pešić 2012; Glöer and Bössneck 2013) and from studies of the type series (Sitnikova et al. 2012, 2014; Vinarski 2016a).

The scheme of shell measurements is given in Fig. 2A. The praeputium:penis sheath ratio has been used as the characteristics of the proportions of the copulatory apparatus (see Fig. 2). This ratio (also known as the ‘index of the copulatory organ’, ICA) has been used for species delimitation in different genera of the Lymnaeidae (Falniowski 1980; Jackiewicz 1998; Kruglov 2005; Vinarski 2011; Standley et al. 2013). In total, 688 shells of 21 species were measured and 241 specimens of snails were dissected. All measurements in this paper are given in millimetres.

The accounts for particular species presented in the systematic part of this paper include the data on their original descriptions, type locality, type series and distribution. Additionally, we attempted to give morphological descriptions of species, with emphasis on those characters that may help in their identification. We avoided providing the full synonymies for each species since, in some cases, (for such widespread and long studied taxa as *Radix auricularia* or *Peregriana peregra*) it would generate enormous lists of synonyms. In most cases, we included into synonymy only names with extant type series or such taxa, whose original descriptions are detailed enough to warrant sure judgements on their taxonomic identity.

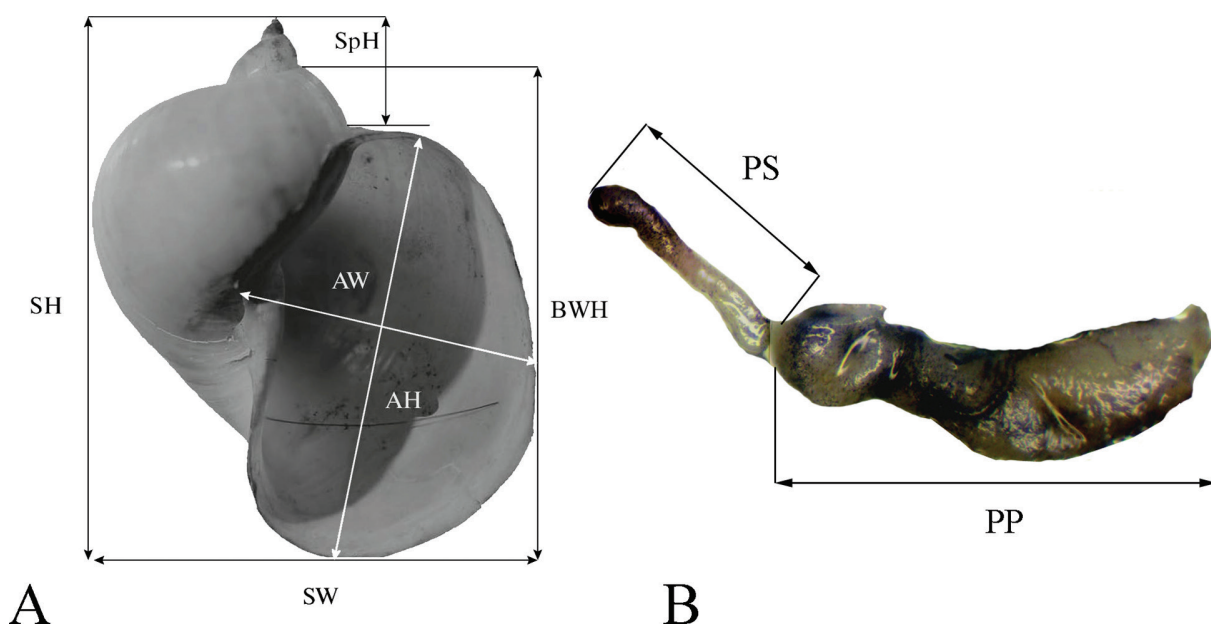


Figure 2. The scheme of measurements of the shell (A) and the parts of the copulatory apparatus (B). Abbreviations: SH – shell height; SW – shell width; SpH – spire height; BWH – body whorl height; AH – aperture height; AW – aperture width; PP – length of praeputium; PS – penis sheath length. A – after Vinarski (2016b).

List of abbreviations

The acronyms for the zoological repositories: **NHMUK** – Museum of Natural History, London, UK; **NMNH** – National Museum of Natural History, Paris, France; **ZISP** – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; **ZMB** – Natural History Museum of Berlin/Museum für Naturkunde, Germany; **ZMUC** – Zoological Museum of the Copenhagen University, Denmark; **NHMW** – Natural History Museum of Vienna, Austria; **NMG** – Natural History Museum of Gothenburg, Sweden; **SMF** – Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt-am-Main, Germany; **SNSD** – Senckenberg Naturhistorische Sammlung Dresden, Germany; **RMBH** – Russian Museum of Biodiversity Hotspots, Federal Center for Integrated Arctic Research of the Russian Academy of Sciences, Arkhangelsk, Russia; **LMBI** – Laboratory for Macroecology and Biogeography of Invertebrates, Saint-Petersburg State University, Russia.

The abbreviations for the shell and anatomical structures and measurements: **WN** – whorls number; **SH** – shell height; **SW** – shell width; **SpH** – spire height; **BWH** – body whorl height; **AH** – aperture height; **AW** – aperture width; **PP** – length of praeputium; **PS** – penis sheath length; **ICA** – the index of the copulatory apparatus (= PP:PS).

TL – type locality.

Systematic part

Genus *Radix* Montfort, 1810

Subgenus *Radix* s. str.

Radix Montfort 1810: 266.

Gulnaria Turton 1831: 117 (partim).

Cerasina Kobelt 1881: 297.

Auriculariana Servain 1882: 29.

Acuminatiana Bourguignat 1889: 155.

Desertiradix Kruglov and Starobogatov 1989: 23.

Iraniradix Kruglov and Starobogatov 1989: 23.

Nipponiradix Kruglov and Starobogatov 1989: 25.

Okhotiradix Kruglov and Starobogatov 1989: 28.

Pamiriradix Kruglov and Starobogatov 1989: 22.

Thermoradix Kruglov and Starobogatov 1989: 19.

Ussuriradix Kruglov and Starobogatov 1989: 24.

Type species. *Helix auricularia* Linnaeus, 1758

1. *Radix (Radix) auricularia* (Linnaeus, 1758)

Figs 3A; 4A.

Helix auricularia Linnaeus 1758: 774, 775.

Lymnaea auricularia – Hubendick 1951: 151, figs 96, 97, 99 (partim).

Lymnaea (Radix) auricularia – Kruglov and Starobogatov 1993a: 85, fig. 10E; Jackiewicz 1998: 47, figs 64, 65, pl. II, X.7, XI, 1, 2; Kruglov 2005: 250, figs 137(I)–139; Andreeva et al. 2010: 99, fig. 48.

Lymnaea (Radix) hadutkae Kruglov and Starobogatov 1989: 22, figs 1(12), 2(7); 1993a: 85, fig. 11D.

Lymnaea (Radix) hakusyensis Kruglov and Starobogatov 1989: 20, figs 1(8), 2(6); 1993a: 88, fig. 11G.

Lymnaea (Radix) thermobaicalica Kruglov and Starobogatov 1989: 20, figs 1(10), 2(8); 1993a: 85, fig. 11E.

Lymnaea (Radix) thermokamtschatica Kruglov and Starobogatov 1989: 22, figs 1(9), 2(9); 1993a: 85, fig. 11F.

Radix auricularia – Glöer 2002: 213, fig. 241; Welter-Schultes 2012: 52, textfig; Vinarski and Kantor 2016: 318; Aksenova et al. 2016: 16, figs 1F, G; 2; Glöer 2019: 236, fig. 294.

TL. Europe.

Types. Possibly lost (Vinarski and Kantor 2016).

This species is common in Eurasia, sporadically distributed in North Africa, introduced into North America and New Zealand (Hubendick 1951; Charleston and Climo 1979; Burch 1989; Brown 1994; Kruglov 2005; Andreeva et al. 2010). It has many times been characterised in literature, both conchologically and anatomically (Jackiewicz 1998; Glöer 2002; Kruglov 2005). The typical form of this snail has an ear-shaped shell with shortened spire and greatly expanded body whorl (see Fig. 3A). However, *R. auricularia* exhibits wide variation in shell shape and proportions (Vinarski 2016b). It may form local and ecological races, including dwarf races of geothermal springs, which had been accepted as valid species (Bolotov et al. 2014; Aksenova et al. 2016, 2017).

The structure of the copulatory apparatus of *R. auricularia* is quite typical for the genus. The praeputium is oblong, cylindrical and rather thick; its width is virtually equal along its whole length (see Fig. 4A). The penis sheath is much narrower, with a bulbous swelling on its distal end. The lengths of the praeputium and the penis sheath of *R. auricularia* are nearly equal, though in some populations, there is a substantial variation in the ICA values (Vinarski 2011).

A characteristic trait of this species, which distinguishes it from the remaining radicles of Europe, is the presence of freckles on the foot and praeputium (Glöer 2019).

2. *Radix (Radix) alticola* (Izzatullaev, Kruglov & Starobogatov, 1983)

Figs 3B, C; 4B; Table 1

Lymnaea (Radix) alticola Izzatullaev et al. 1983: 53, figs 1, 2; Kruglov and Starobogatov 1993a: 85, fig. 11C; Kruglov 2005: 261, figs 146(1)–148; Sitnikova et al. 2014: 25, fig. 8D.

Radix (Radix) alticola – Vinarski and Kantor 2016: 320.

TL. Tajikistan, a hot spring near the Yashilkul' Lake (approximately 37°47'00"N, 72°51'00"E).

Types. ZISP (Vinarski and Kantor 2016). The holotype is illustrated by Sitnikova et al. (2014). We studied both the holotype and the paratypes of *R. alticola*.

According to our data (Aksenova et al. 2018a), *R. alticola* is endemic to the High Asia mountains; found in Tajikistan (from several sites, including the type locality)

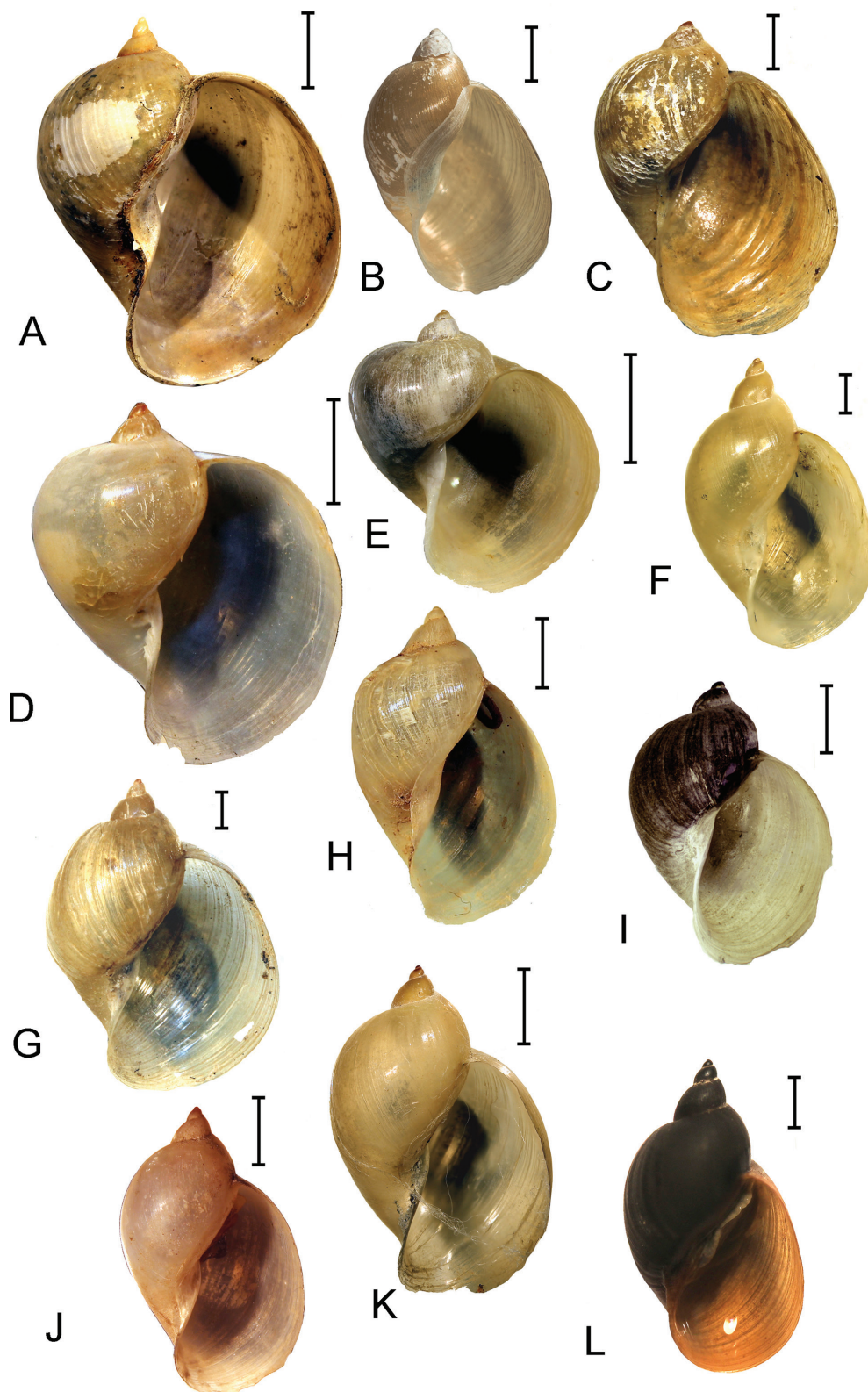


Figure 3. Shells of species in the genus *Radix*. **A.** *Radix auricularia* (28.08.2013, Kazakhstan, Karaganda Region, Suresai River; LMBI); **B.** *R. alticola* (20.06.2012, Tajikistan, a hot spring near Djelandy village; LMBI); **C.** *R. alticola* (01.07.2016, Tajikistan, a warm brook near Dzhaushangoz village; LMBI); **D.** *R. brevicauda* (Kashmir, a syntype; NHMUK); **E.** *R. brevicauda* (05.08.1948, Tajikistan, Pamir Mts., Shaimak village, in a warm spring; ZISP); **F.** *R. euphratica* (26.06.2016, Tajikistan, Dushanbe, a fountain near the President's palace; LMBI); **G.** *R. euphratica* (04.07.2016, Tajikistan, a roadside ditch near Kurban-Shakhid village; LMBI); **H.** *R. euphratica* (without date, Iraq, Bagdad; NHMUK); **I.** *R. makhrovi*, the holotype (China, Tibet, a roadside ditch west of the Lhasa River mouth; ZISP); **J.** *R. plicatula*, a probable syntype (China, Chusan, NHMUK); **K.** *R. plicatula* (26.07.2017, China, Uyghuria, Bagrash-kol' Lake; LMBI); **L.** *R. plicatula* (26.11.2014, China, Beijing, an artificial pond in the former Emperor's summer palace; LMBI). Scale bars: 2 mm (**B–C, F–L**), 5 mm (**A, D–E, K**).



Figure 4. Copulatory apparatuses of the species of the genus *Radix*. **A.** *Radix auricularia* (19.07.2007, Russia, Tyumen' Region, Vylposl channel near Labytnangi Town); **B.** *R. alticola* (01.07.2016, Tajikistan, a warm brook near Dzhaushangoz village); **C.** *R. euphratica* (04.07.2016, Tajikistan, a roadside ditch near Kurban-Shakhid village); **D.** *R. makhrovi*, a paratype (after Aksenova et al. 2018a, modified). **E.** *R. plicatula* (26.11.2014, China, Beijing, an artificial pond in the former Emperor's summer palace). **F.** *R. rubiginosa* (Malaysia, Kuala-Lumpur); **G.** *R. rufescens* (24.11.2016, Myanmar, Yetho River, near the dam). **H.** *R. natalensis* (05.08.2018, Uganda, crater lake Kyamwiga). Scale bars: 2 mm.

and Nepal. In mountain Tajikistan (Pamir), this species inhabits hot springs and satellite streams with relatively warm water.

The shell shape of *R. alticola* is similar to that of *R. auricularia*, but the former species is of much smaller size; its shell height does not exceed 16 mm (see Table 1), whereas the shells of *R. auricularia* may reach 35–40 mm in height. The proportions of the copulatory organ of *R. alticola* are very similar to *R. auricularia* (compare Fig. 3A and 3B).

3. *Radix (Radix) brevicauda* (G.B. Sowerby II, 1872)

Fig. 3D, E; Table 1

Limnaea brevicauda G.B. Sowerby II 1872: pl. XV, fig. 105.

Limnaea brevicauda – Hanley and Theobald 1876: 64, pl. 158, fig. 7;

Annandale and Rao 1925: 157, figs 1–6.

Lymnaea (Radix) brevicauda – Subba Rao 1989: 134, figs 302, 303.

Radix brevicauda – Glöer and Bössneck 2013: 153, figs 61–63.

TL. The type locality was originally stated as 'Australia' (Sowerby 1872). It is, however, erroneous. Hanley and Theobald (1876) gave the proper type locality: Kashmir.

Types. NHMUK. The syntypes were inspected by us.

R. brevicauda inhabits Northern India (Kashmir), Nepal, China (Western Tibet and Himalaya Range) and, probably, Tajikistan (Pamir Mts.) [Subba Rao 1989; Glöer and Bössneck 2013; Aksenova et al. 2018a]. The record of this species from Tajikistan is based on numerous shells from ZISP collection (see Fig. 3E), virtually identical with the syntypes of *R. brevicauda*. This species has not been registered from the ex-USSR territory (Vinarski and Kantor 2016) and hereby we, for the first time, include it in the malacofauna of the former Soviet Union. However, this record is still not corroborated genetically.

The shell of *R. brevicauda* is ear-shaped, with low spire and greatly expanded aperture. Generally, in many ways, it resembles the shell of *R. auricularia* and Glöer and Bössneck (2013: 153) note that there are no substantial differences between the two species, which are probable

Table 1. Morphological characterisation of shells and copulative apparatuses of several species in the genus *Radix*.

Character / index	Species / locality																		
	<i>R. alticola</i>			<i>R. euphratica</i>			<i>R. brevicauda</i>			<i>R. plicatula</i>			<i>R. natalensis</i>		<i>R. rufescens</i>				
	Tajikistan, Zor-Kul Lake (paratypes)	Tajikistan, a warm brook near Dzhaushangoz village*	LMBI	Tajikistan, Dushanbe, a fountain near President's palace*	LMBI	Tajikistan, a roadside ditch near Kurban-Shakhid village*	LMBI	Tajikistan, a warm spring near a pond near the former Emperor's palace*	LMBI	China, Beijing, a pond near the Bagrashkol' Lake*	LMBI	China, Uyghuria, Kiyamwiga crater lake**,**	LMBI	Uganda, the Kiyamwiga crater lake**,**	LMBI	India, "Khipru, Sind"	NHMUK	Myanmar, River near the dam*	LMBI
Repository	ZISP	LMBI	LMBI	LMBI	LMBI	ZISP	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI	LMBI
Number of specimens measured (dissected)	45 (0)	44 (16)	4(3)	21(15)	21(0)	29(11)	16(9)	26(20)	40(0)	12(6)									
Whorls number	3.00–3.75	3.00–3.75	3.87–4.25	3.25–4.12	3.25–4.00	3.75–4.00	3.50–4.12	3.25–3.75	3.75–4.75	3.87–4.50									
Shell height, mm (SH)	3.40±0.18	3.30±0.17	4.06±0.16	3.71±0.21	3.48±0.19	4.08±0.21	3.76±0.23	3.51±0.15	4.17±0.21	4.22±0.22									
	9.0–13.9	9.4–15.3	12.6–15.1	12.5–20.0	9.8–15.3	13.6–20.7	12.9–22.6	13.6–18.8	37.9–43.4	17.5–28.9									
	10.9±1.0	11.9±1.4	13.9±1.1	14.8±2.1	12.1±1.5	16.5±1.5	15.8±3.1	16.2±1.3	39.9±1.6	23.2±3.8									
Shell width, mm (SW)	6.4–10.5	7.8–13.2	8.4–9.3	7.6–13.4	8.4–13.0	7.9–14.2	8.2–14.6	8.0–13.0	17.8–20.8	9.1–13.6									
	8.1±0.8	9.5±1.2	8.9±0.4	9.7±1.5	10.3±1.4	10.4±1.6	10.1±2.1	10.5±1.0	18.8±1.0	11.0±1.4									
Spire height, mm (SpH)	1.4–2.8	2.0–4.0	3.8–4.5	2.7–5.2	2.2–4.2	3.4–6.8	2.7–7.0	2.8–4.7	10.6–14.8	4.5–10.8									
	2.1±0.3	2.6±0.4	4.1±0.3	3.7±0.8	2.8±0.5	4.7±0.9	4.4±1.2	3.7±0.5	12.7±1.1	7.7±1.8									
Body whorl height, mm (BWH)	8.4–12.8	8.7–14.2	10.1–12.2	11.0–17.6	8.9–13.8	11.7–18.0	11.5–20.3	12.3–17.5	32.8–37.4	15.6–25.2									
	9.9±0.9	10.9±1.3	11.7±1.1	13.1±1.9	10.9±1.4	14.4±1.5	14.1±2.8	14.8±1.2	34.7±1.2	20.1±3.3									
Aperture height, mm (AH)	7.6–11.4	7.7–12.9	9.1–12.2	9.4–15.1	7.7–11.7	8.8–16.0	9.4–16.1	10.2–14.6	27.0–31.2	12.7–19.1									
	9.1±0.9	9.6±1.2	10.1±0.9	11.4±1.6	9.6±1.2	11.8±1.7	11.6±2.2	12.6±1.0	28.9±1.2	15.5±2.2									
Aperture width, mm (AW)	5.0–8.5	5.2–10.4	5.8–7.3	5.8–11.8	5.5–8.8	6.3–12.4	6.1–10.5	6.0–9.3	12.3–16.3	6.5–11.3									
	6.3±0.7	6.4±1.1	6.5±0.6	7.5±1.5	7.0±1.0	8.2±1.4	7.5±1.6	7.9±0.7	14.4±0.9	8.6±1.4									
Praepitium length, mm (PP)	–	3.2–5.6	2.8–3.6	3.2–4.9	–	3.4–6.5	3.0–5.4	3.1–4.9	–	2.8–4.2									
	–	4.1±0.6	3.2±0.9	3.9±1.1	–	4.3±0.9	4.2±0.9	4.3±0.5	–	3.4±1.0									
Penis sheath length, mm (PS)	–	3.2–5.1	2.9–3.5	2.2–3.9	–	3.6–9.2	3.6–7.8	3.0–5.5	–	2.2–3.6									
	–	4.2±0.6	3.2±0.6	3.1±1.1	–	5.8±1.2	5.5±1.3	4.5±0.6	–	2.9±1.0									
SW/SH	0.65–0.81	0.72–0.87	0.62–0.67	0.61–0.73	0.79–0.94	0.53–0.76	0.55–0.72	0.57–0.71	0.44–0.50	0.41–0.52									
	0.74±0.03	0.80±0.04	0.64±0.03	0.66±0.03	0.85±0.04	0.63±0.05	0.64±0.04	0.65±0.04	0.47±0.02	0.48±0.03									
SpH/SH	0.13–0.24	0.18–0.27	0.28–0.32	0.20–0.30	0.18–0.28	0.20–0.42	0.20–0.33	0.19–0.27	0.27–0.38	0.26–0.37									
	0.19±0.02	0.22±0.02	0.30±0.02	0.25±0.03	0.23±0.02	0.31±0.05	0.28±0.04	0.23±0.02	0.32±0.02	0.33±0.04									
BWH/SH	0.87–0.93	0.88–0.98	0.80–0.86	0.83–0.94	0.87–0.92	0.83–0.95	0.86–0.92	0.86–0.93	0.84–0.89	0.80–0.90									
	0.90±0.01	0.91±0.02	0.84±0.03	0.89±0.02	0.90±0.01	0.87±0.02	0.89±0.02	0.91±0.02	0.87±0.01	0.86±0.02									
AH/SH	0.65–0.81	0.75–0.85	0.70–0.74	0.70–0.86	0.72–0.86	0.59–0.86	0.69–0.81	0.74–0.82	0.69–0.77	0.63–0.75									
	0.74±0.03	0.81±0.02	0.73±0.02	0.77±0.04	0.80±0.03	0.71±0.06	0.74±0.04	0.78±0.02	0.73±0.02	0.67±0.04									
AW/AH	0.59–0.83	0.66–0.91	0.63–0.67	0.57–0.78	0.67–0.81	0.63–0.78	0.56–0.73	0.57–0.67	0.45–0.55	0.50–0.61									
	0.69±0.04	0.72±0.04	0.65±0.02	0.65±0.05	0.73±0.03	0.70±0.04	0.64±0.05	0.62±0.02	0.50±0.03	0.55±0.04									
ICA	–	0.81–1.18	0.93–1.16	1.10–1.69	–	0.54–0.96	0.64–0.90	0.84–1.13	–	1.09–1.27									
	–	0.97±0.11	1.01±0.12	1.25±0.18	–	0.76±0.14	0.79±0.08	0.96±0.07	–	1.19±0.06									

*Sample studied genetically. ** The short-spined morph of *R. natalensis*.

synonyms. However, Annandale and Rao (1925) reported the structure of the jaw and radula of *R. brevicauda* is distinct from that of *R. auricularia*. The anatomical structure of the discussed species, described and illustrated by Glöer and Bössneck (2013), is typical for the genus *Radix*. Our molecular analysis recovered *R. brevicauda* as a species sister to *R. auricularia* (Aksenova et al. 2018a).

We may indicate some conchological differences between *R. auricularia* and *R. brevicauda*. The latter species is of smaller size, the largest syntype shell is 18.1 mm (our data) and Glöer and Bössneck (2013) mention that *R. brevicauda* may reach 20 mm in height. Next, the columellar depression in shells of *R. brevicauda* is very prominent, whereas, in *R. auricularia*, it is typically weakly developed (compare Fig. 2A and 2D, E). Lastly, the spire whorls in *R. auricularia* are usually flattened, while in *R. brevicauda* these are visibly convex and rounded.

Nomenclature remark. The name *Limnaea brevicauda* Sowerby is the oldest available one to designate a lymnaeid species, sister to *R. auricularia*, restricted in its distribution to the Central Asia mountain regions. The taxonomic identity of *R. brevicauda*, as well its close affinity to *R. auricularia*, was confirmed by the inspection of the extant syntypes.

4. *Radix (Radix) euphratica* (Mousson, 1874)

Figs 3F–H; 5C. Table 1

Limnaea euphratica Mousson 1874: 40, 41.

Limnaea tenera race *euphratica* – Annandale and Prashad 1919b: 113, pl. XIII, figs 3–5.

Limnaea gedrosiana Annandale and Prashad 1919a: 48, pl. VII, figs 2–4; Annandale and Prashad 1919b: 107.

Limnaea gedrosiana var. *rectilabrum* Annandale and Prashad 1919a: 49, pl. VI, figs 1–6

Limnaea iranica Annandale and Prashad 1919a: 43, pl. VII, fig. 1.

Limnaea gedrosiana – Likharev and Starobogatov 1967: 171, fig. 3.

Limnaea (Pseudosuccinea) gedrosiana – Annandale and Rao 1925: 172; Subba Rao 1989: 130, fig. 295.

Limnaea (Pseudosuccinea) gedrosiana f. *rectilabrum* – Annandale and Rao 1925: 173.

Limnaea (Pseudosuccinea) iranica – Annandale and Rao 1925: 172.

Limnaea (Radix) euphratica – Kruglov and Starobogatov 1993a: 88, fig. 12F; Kruglov 2005: 273, figs 160, 163.

Limnaea (Radix) gedrosiana – Kruglov and Starobogatov 1993a: 90, fig. 14A; Kruglov 2005: 284, figs 164(8), 176.

Limnaea (Radix) rectilabrum – Kruglov and Starobogatov 1993a: 90, fig. 13G; Kruglov 2005: 283, figs 164(7), 175.

Radix gedrosiana gedrosiana – Glöer and Pešić 2012: 42.

Radix gedrosiana rectilabrum – Glöer and Pešić 2012: 42.

Radix euphratica – Aksenova et al. 2018a: 4.

Radix (Radix) euphratica – Vinarski and Kantor 2016: 321.

Radix (Radix) gedrosiana – Vinarski and Kantor 2016: 322.

Radix (Radix) rectilabrum – Vinarski and Kantor 2016: 324.

Radix euphratica – Glöer 2019: 239, fig. 298.

TL. Iraq, vicinity of Es-Samava Town (approximately 31°19'00"N, 45°17'00"E).

Types. Not traced, but probably in the Zürich Zoological Museum (Vinarski and Kantor 2016).

We recorded *R. euphratica* genetically from such remote countries as Iraq and Turkey in the west and southwest and Tajikistan in the northwest, also it has been identified from samples collected in the Krasnodar Region of Russia and Georgia (Aksenova et al. 2018a; see Fig. 5C). The records of this species in literature cover also Afghanistan, India, Iran, Pakistan, Azerbaijan, Tajikistan, Uzbekistan and Turkmenistan (Annandale and Rao 1919a, b; Likharev and Starobogatov 1967; Subba Rao 1989; Kruglov and Starobogatov 1993a; Glöer and Pešić 2012). The range of *R. euphratica* seems to be rather wide, stretching from the Middle East to northern India. The northernmost localities of this snail are known in the Caucasian region, in Georgia and European Russia (Aksenova et al. 2018a).

Conchologically, *R. euphratica* may be distinguished from the species of *Radix* described above by its relatively oblong ovate-conical shell, with high spire and weakly-inflated body whorl. The maximum shell height is around 20.0 mm (see Table 1). The columellar depression is weakly developed and, in some specimens, may be not visible. The tangential line of spire is almost straight or weakly concave that allows us to distinguish this species from the three species of *Radix* discussed above (see Fig. 3). The morphology of the copulatory apparatus is typical for the genus (see Fig. 4).

Nomenclature remark. Several nominal species of radicles, with type localities situated in the Middle East or the east of Central Asia, were described in the late 19th – first half of the 20th century. The oldest of them are *Limnaeus tener* Küster, 1862, *Limnaea auricularia* var. *persica* Bourguignat in Issel, 1865 and *Limnaea euphratica* Mousson, 1874. The types of *L. tener* are lost, while the holotype of *L. auricularia* var. *persica* is extant (Sitnikova et al. 2012). *L. tener* and *L. auricularia* var. *persica* share the same shell shape; these are ear-shaped, with low spire and enlarged aperture (see Fig. 5A, B). Both species were described from Iran and their conchological similarity, as well as the overlap in geographical distribution, may indicate these forms are conspecific (or represent the intraspecific morphs of *R. auricularia*). Though the type series of *R. euphratica* is most probably lost, the shells of this species collected in Iraq (NHMUK) look like shells of snails from Tajikistan studied by us both genetically and morphologically (compare Fig. 3F, G and 3I). It allowed us to select the name *Limnaea euphratica* Mousson, 1874 for designation of this species, since the shell habitus of both *L. tener* and *L. auricularia* var. *persica* is different from that of snails from Iraq.

The absence of shell picture in the original description of *L. euphratica* (Mousson, 1874) may be compensated by the author's remark that the shell shape of this species "approaches ... some species of the eastern India [such as] *L. succinea* Desh." (Mousson 1874: 40). Hubendick (1951) regarded *L. succinea* as a synonym of *Limnaea luteola*, whose habitus indeed resembles that of *L. euphratica*, but looks rather different from shells of either *L. tener* or *L. auricularia* var. *persica*.

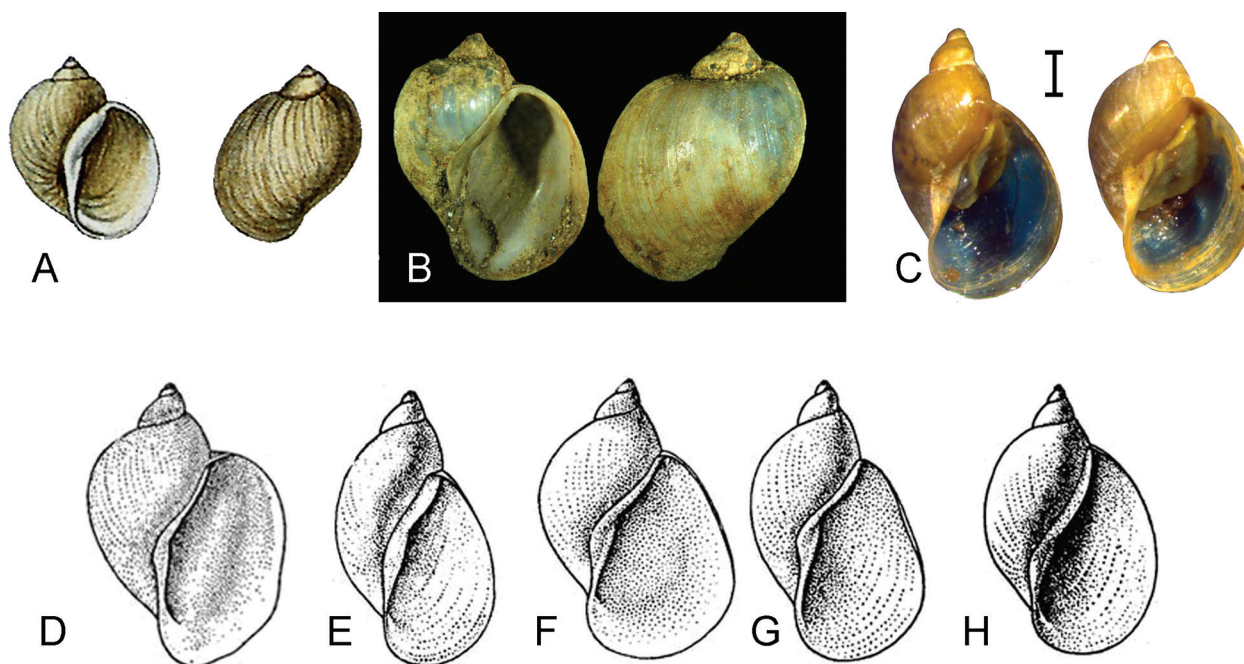


Figure 5. Shells of the Central Asian representatives of the genus *Radix*. **A.** *Radix tener*, the type (after Küster 1862, slightly modified); **B.** *R. persica*, the holotype (after Sitnikova et al. 2012); **C.** *R. euphratica* (30.08.2013, Russia, Krasnodar Region, Yaseni River, scale bar 2 mm; RMBH); **D.** *R. tener* race *euphratica* (Iraq, Samara, after Annandale and Prashad 1919b); **E.** *R. gedrosiana*, a syntype (Pakistan, Baluchistan, Quetta, a pond in the Residency garden; after Annandale and Prashad 1919a); **F, G.** *R. rectilabrum* (Pakistan, Northern Baluchistan, Pishin district, Kushdil Khan reservoir; after Annandale and Prashad 1919a); **H.** *R. iranica*, the holotype (from the “Persian Baluchistan”; after Annandale and Prashad 1919a).

Based on the original descriptions and the study of specimens from available museum collections (ZISP, NHMUK, NMNH and NHMW), we consider the three taxa from the Middle East, described by Annandale and Prashad (1919), as junior synonyms of *R. euphratica*. These are *Limnaea gedrosiana*, *L. gedrosiana* var. *rectilabrum* and *L. iranica* (see Fig. 5D–H). These three species are conchologically very similar and their shell traits correspond well to *R. euphratica* from Iraq (see Fig. 3I). Specimens of *Radix rectilabrum* sensu Kruglov and Starobogatov 1993a from Tajikistan and Uzbekistan studied by us (Aksenova et al. 2018a) proved to be genetically indistinguishable from snails sampled in Iraq.

The taxonomic identity of *Limnaea tenera* and conchologically similar species (*Limnaea persica*, *Limnaea cor* Annandale et Prashad, 1919) needs a further research by means of an integrative taxonomic analysis of the topotypic specimens.

5. *Radix (Radix) makhrovi* Bolotov, Vinarski & Aksenova, 2018

Figs 3I; 5D.

Radix makhrovi Aksenova et al. 2018a: 9, fig. 7E, G, I.

TL. China, Tibet, a roadside ditch west of the Lhasa River mouth, Brahmaputra River basin.

Types. ZISP (holotype, paratypes), RMBH (paratypes).

This species, endemic to Tibet, is fully described in our previous paper (Aksenova et al. 2018a), therefore, we give here only pictures of its shell and copulatory organ.

6. *Radix (Radix) plicatula* (Benson in Cantor, 1842)

Figs 3J–L; 4E; 5D.

- Limnaea plicatula* Cantor 1842: 487.
- Limnaea swinhoi* H. Adams 1866: 319, pl. 33, fig. 13.
- Limnaeus plicatulus* – Martens 1867: 221.
- Limnaea yunnanensis* Nevill 1877: 26, 27.
- Limnaeus chefouensis* Clessin 1878–1886: 391, Taf. 55, fig. 6.
- Limnaeus heudi* Clessin 1878–1886: 394, Taf. 55, fig. 10.
- ? *Limnaea annamitica* Watterbled 1886: 57, pl. IV, fig. 4.
- Limnaea (Gulnaria) pettiti* Jones and Preston 1904: 142, fig. 3.
- Limnaea (Gulnaria) whartoni* Jones and Preston 1904: 142, fig. 1.
- Limnaea (Gulnaria) lumleyi* Jones and Preston 1910: 11, textfig.
- Limnaea (Gulnaria) schwilpi* Jones and Preston 1910: 10, textfig.
- Limnaea (Gulnaria) sinensis* Jones and Preston 1910: 11, textfig.
- Radix plicatulus* – Yen 1939: 65, Taf. 5, fig. 40.
- Radix swinhoi* – Yen 1939: 66, Taf. 5, fig. 43.
- Radix plicatula* – Aksenova et al. 2018a: 4

TL. China, Chusan Island.

Types. Probable syntypes are kept in NHMUK (see Taxonomic remark below).

The actual range of *R. plicatula* is not ascertained yet. In our molecular analysis, we studied samples of this spe-

cies from Beijing, southern and western China that may indicate it is distributed throughout the country. The presence of *R. plicatula* in adjacent states (Laos, Vietnam) is also very probable, although, as far as we can judge, it is absent from India (Subba Rao 1989). The records of *R. auricularia swinhoei* (Adams) from Thailand (Brandt 1974) may refer to this species, but a special study is needed to check it.

The shell of *R. plicatula* is rather oblong, with relatively high spire and moderately inflated body whorl (see Fig. 3J–L). The copulative apparatus is typical for this genus (see Fig. 5D). In all individuals dissected in this study, the penis sheath was slightly longer than the praeputium (see Table 1), thus ICA < 1.0.

Taxonomic remark. *Radix plicatula* is almost indistinguishable from *R. euphratica* by its shell habitus (compare Fig. 2F and 2L) and the copulatory organ structure, but molecular analyses have revealed that the two species are distinct and their ranges are almost non-overlapping (Aksenova et al. 2018a). We found the shells of this species, collected in the type locality, in NHMUK (accession No. 42.9.30.50.51.487). These possibly once belonged to Benson's collection and may be considered the probable syntypes (see Fig. 3F). Their morphology is very similar to that in *R. plicatula* snails examined genetically by us. Having studied the type series of some nominal species of *Radix* described from China and South-East Asia (kept in NHMUK, NMNH and ZMB), we ascertained they are junior synonyms of *R. plicatula* (see Vinarski 2016a and synonymy above).

7. *Radix (Radix) rubiginosa* (Michelin, 1831)

Figs 4F; 6A–C.

- Limnoeus rubiginosus* Michelin 1831: 22.
Limnaeus succineus var. *javanicus* Mousson 1849: 42.
Limnaeus singaporinus Küster 1862: 35, pl. 6, fig. 17.
Limnaea crosseana Mabilie and Le Mesle 1866: 130, pl. 7, fig. 5.
Limnaeus javanicus – von Martens 1867: 222.
Limnaeus javanicus var. *intumescens* von Martens 1867: 223.
Limnaeus javanicus var. *obesus* von Martens 1867: 223.
Limnaeus javanicus var. *rubiginosus* – von Martens 1867: 224.
Limnaea javanica var. *subteres* von Martens 1881: 88, figs 6, 7.
Limnaea javanica var. *angustior* von Martens 1881: 88, pl. 16, fig. 8.
Limnaea javanica var. *porrecta* von Martens 1881: 89, figs 9, 10.
Limnaea bongsonensis Bullen 1906: 14, pl. II, figs 5, 6.
Lymnaea auricularia rubiginosa – Hubendick 1951: 154, figs 342, 342;
 Brand 1974: 229, pl. 16, fig. 95 (partim).
Lymnaea rubiginosa – van Benthem Jutting 1959: 116.
Radix rubiginosa – Aksenova et al. 2018a: 4

TL. The East-Indies. “The original specimens are said to come from Bogor in Java” (Brandt 1974: 230).

Types. Probably lost. We failed to find them in NMNH collection.

This species is endemic to Southeast Asia. Its findings supported by molecular evidence are known from

a vast territory, i.e. Thailand, Singapore, Indonesia up to Lesser Sundas (Flores) and Mascarenes (Réunion) [Aksenova et al. 2018a]. It has also been recorded from Cambodia, Laos and Vietnam (Brandt 1974). However, the identification of *R. rubiginosa*, based on shell only, may be misleading. As Brandt (1974: 230) stated, “this race has often been confused with *L. luteola* Lamarck”. Therefore, the actual range of *R. rubiginosa* is not satisfactorily outlined since many historical recordings of it were shell-based.

A high conical spire, almost straight tangential line and weakly-inflated body whorl are the most characteristic conchological traits of *R. rubiginosa* (see Fig. 6A–C) helping one to distinguish it from the rest of congeners inhabiting the south of Asia. The variation in the proportions of the copulatory organ of this species has not been studied. We dissected four specimens collected from different parts of the *R. rubiginosa* range (Thailand, Malaysia, Philippines). In all cases, the penis sheath was shorter than the praeputium (see Fig. 4F) and the ICA values varied between 1.02 and 1.59.

Taxonomic remark. *R. rubiginosa* has an extensive synonymy and a special study is required to clarify the taxonomic identity of numerous nominal species of *Radix*, described from Indonesia and adjacent countries. Some of these names, such as *Radix quadrasii* (Möllendorff, 1898) of Philippines, have been used in recent literature, but may well be synonyms of *R. rubiginosa* (see, for example, Stelbrink et al. 2019).

Subgenus *Exsertiana* Bourguignat, 1883

Exsertiana Bourguignat 1883: 88.

Raffrayana Bourguignat 1883: 88.

Radix (Exsertiana) – Aksenova et al. 2018a: 6, 9

Type species. This subgenus contains two molecularly-defined species of *Radix* having an almost entirely tropical distribution – *Radix natalensis* (Krauss, 1848) and *R. rufescens* (Gray, 1822).

Remark. Bourguignat (1883: 88), in his lengthy article devoted to classification of continental molluscs of Abyssinia, established two new groups of species within the genus *Limnaea* – *Exsertiana* and *Raffrayana*. He did not give any diagnoses for the two taxa, only lists of species included there. In both cases, these species are currently recognised as junior synonyms of *R. natalensis* (fide Hubendick 1951; Brown 1994). We selected *Exsertiana* as a name for designation of a lymnaeid clade containing *R. natalensis*. Since Bourguignat (1883) did not indicate the type species for *Exsertiana*, we designate here *Limnaeus natalensis* var. *exsertus* Martens, 1866 as the type taxon for this subgenus. This species is usually regarded as identical to *R. natalensis* (Hubendick, 1951), though Mandahl-Barth (1954) accepted it as a valid species, closely related to the latter.

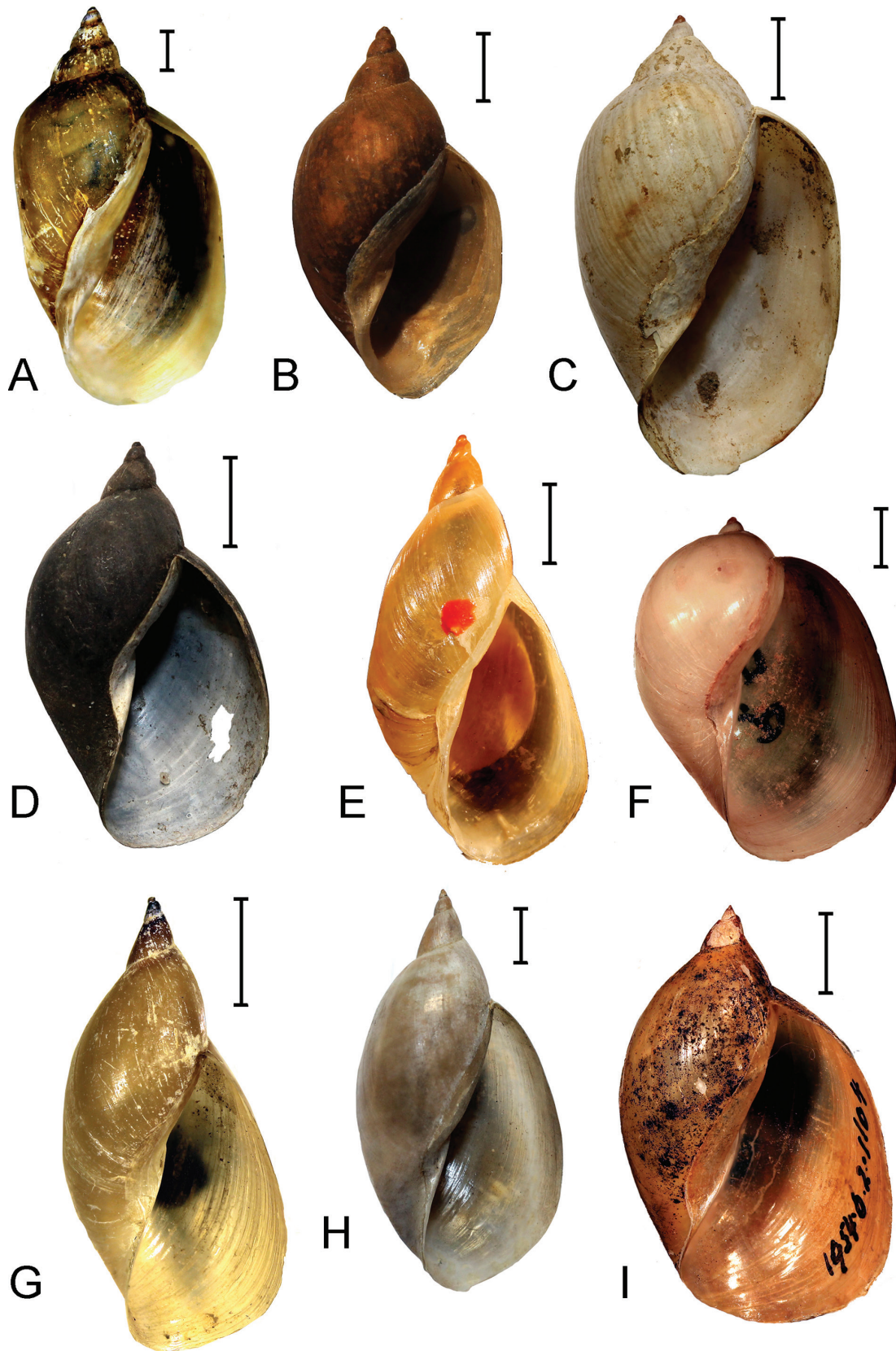


Figure 6. Shells of species of the subgenera *Radix* s. str. and *Exsertiana*. **A.** *Radix rubiginosa* (Malaysia, Kuala-Lumpur; LMBI); **B.** *R. rubiginosa* (1846, Indonesia, Java Island, “Batavia”; ZMUC); **C.** *R. rubiginosa* var. *intumescens* (Indonesia, Java Island, Surabaya; ZMB); **D.** *R. natalensis* (= *Limnaea undussumae*) (Congo, Undussuma; ZMB). **E.** *R. natalensis* (= *Limnaea arabica* Smith; the holotype; NHMUK); **F.** *R. natalensis* f. *gravieri* (10.03.1966, Ethiopia, lower Avash valley, swamp between Assaita and Dubte; NHMUK). **G.** *R. rufescens* (24.11.2016, Myanmar, Yetho River, near the dam; LMBI); **H.** *R. rufescens* var. *patula* (India, Ganges River; ZMB); **I.** *R. rufescens* var. *chlamys* (India, Moradabad; probably syntype; NHMUK). Scale bars: 2 mm (A, B, E, F), 5 mm (C, D, G, I).

8. *Radix (Exsertiana) natalensis* (Krauss, 1848)

Figs 4H; 6D–F; Table 1

Limnaeus natalensis Krauss 1848: 85.
Limnaea hovarum Tristram 1863: 61.
Limnaeus natalensis var. *exsertus* von Martens 1866: 101, pl. 3, figs 8, 9.
Limnaea electa Smith 1882: 385.
Limnaea caillaudi Bourguignat 1883: 89, figs 100, 101.
Limnaea exserta – Bourguignat 1883: 90.
Limnaea gravieri Bourguignat 1885: 23.
Limnaea nyansae von Martens 1892: 16.
Limnaea arabica Smith 1894a: 142, fig. 3.
Limnaea elmeteitensis Smith 1894b: 167, fig. 5.
Limnaea humerosa von Martens 1897: 135, pl. 6, fig. 1.
Limnaea undussumae von Martens 1897: 135, pl. I, fig. 18; pl. VI, figs 2, 5.
Limnaea kempfi Preston 1912: 190, pl. 32, fig. 1.
Limnaea (Radix) elmeteitensis – Germain 1919: 186.
Limnaea (Radix) gravieri – Germain 1919: 186.
Limnaea (Radix) natalensis – Germain 1919: 185.
Limnaea (Radix) tchadiensis – Germain 1919: 186.
Limnaea (Radix) vignoni – Germain 1919: 186.
Lymnaea exserta – Mandahl-Barth 1954: 71, fig. 32a–c.
Lymnaea natalensis natalensis – Mandahl-Barth 1954: 67, fig. 30a, b.
Lymnaea natalensis caillaudi – Mandahl-Barth 1954: 68, fig. 31a–h.
Lymnaea natalensis nyansae – Mandahl-Barth 1954: 70, fig. 30c–h.
Lymnaea (Radix) natalensis – Brown 1994: 166, figs 76a, b; 79a.
Radix natalensis – Neubert 1998: 354; Lotfy and Lotfy 2015: 29; Glöer 2019 p. 241, fig. 301.

TL. South Africa, Natal.

Types. Probably lost. We failed to find them either in ZMB collection or in other institutions (NMNH, NHMUK) known to contain vast collections of African aquatic snails.

R. natalensis is widely distributed in the sub-Saharan Africa as well as in the Nile Basin of Northern Africa (van Damme 1984; Brown 1994; Lotfy and Lotfy 2015). It also occurs in Arabia (Neubert 1998) and Atlantic and Indian Ocean islands: Anjouan (Comores), Madagascar (Brown 1994; Stothard et al. 2000) and the Cabo Verde Islands (Aksenova et al. 2018a).

The shell of this species is (in its typical form) ovate-conical, with somewhat oblong and narrow spire and ovoid body whorl (see Fig. 6D, E). However, some varieties of *R. natalensis* possess an almost spheroid shell with very low spire (see Fig. 6F). The shell height is up to 23 mm (Lotfy and Lotfy 2015).

We studied anatomically a sample of *R. natalensis* collected from the crater lake Kyamwiga in Uganda and found that the soft body anatomy of this snail is generally the same as in the species of *Radix* discussed above. Praeputium is relatively narrow and oblong, darkly pigmented (grey), whereas the penis sheath is typically light coloured and much narrower and a little longer than the praeputium (see Fig. 4H); the ratio of their lengths is 0.96 ± 0.07 (see Table 1).

The intraspecific shell variation in *R. natalensis* is very prominent (see Fig. 6) that led some authors to split this species into several ones (Germain 1919; Mandahl-Barth

1954). Another outcome of this enormous variation is a plethora of nominal species and variety of names proposed to designate the African *Radix* snails. The synonymy given above represents a small part of this abundance of names (see Germain 1919 for a fuller list of these).

9. *Radix (Exsertiana) rufescens* (Gray in Sowerby, 1822)

Figs 4, G; 6, G–I; Table 1

Lymnaea acuminata Lamarck 1822: 160 (invalid; a junior homonym of *Lymnaea acuminata* Brogniart, 1810).
Limnaea rufescens Sowerby 1822: 44, pl. 178, fig. 2.
Limnaeus chlamys Benson 1836: 744.
Limnaeus amygdalum Troschel 1837: 168.
Limnaeus nucleus Troschel 1837: 171.
Limnaeus patulus Troschel 1837: 167.
Limnaeus prunum Troschel 1837: 170.
Limnaeus sulcatulus Troschel 1837: 167.
Limnaeus amygdalum – Küster 1862: 35, pl. 6, figs 15, 16.
Limnaea acuminata var. *rufescens* – Nevill 1877: 27.
Limnaea acuminata – Annandale and Prashad 1919c: 140, pl. V, fig. 1; Germain 1924: 27, figs 23–28.
Limnaea acuminata var. *nana* Annandale and Prashad 1919c: 141, pl. IV, fig. 1.
Limnaea chlamys – Annandale and Prashad 1919c: 142, pl. V, fig. 3; pl. V, fig. 2.
Limnaea (Pseudosuccinea) acuminata – Annandale and Rao 1925: 177.
Lymnaea auricularia rufescens – Hubendick 1951: 157, fig. 344.
Lymnaea (Pseudosuccinea) acuminata – Subba Rao 1989: 126, figs 254–265, 272.
Radix acuminata – Glöer and Bössneck 2013: 152, figs 52–54, 58–60.
Radix (Exsertiana) rufescens – Aksenova et al. 2018a: 9.

TL. “The East Indies”.

Types. Probably lost.

The range of this species covers the central part of the tropical Asia; it is known from India, Nepal and Myanmar, but absent from Thailand (Brandt 1974; Subba Rao 1989; Glöer and Bössneck 2013; Aksenova et al. 2018a).

The shell of *R. rufescens* is large, its height may approach 45 mm (see Table 1). Most probably, it is the largest member of the genus. Hubendick (1951: 56) described its shape in such words: “[shell is] extremely high and slender. Even the body whorl and the aperture are slender”. However, this description is fully applicable only to the typical morph of this species. There are varieties with inflated body whorl and not slender aperture (see Fig. 6I). This high variability allowed some authors to split several intraspecific morphs or even separate species within the *R. rufescens* s. lato (Troschel 1837; Annandale and Prashad 1919c; Subba Rao 1989).

Some shells of *R. rufescens* look almost indistinguishable from shells of certain varieties of *R. natalensis* (compare Fig. 5E and 5H). It is problematic to draw a sharp boundary between the two species on the basis of their conchological characters. *R. natalensis* and *R. rubiginosa*

represent a pair of closely-related vicariant species isolated by the Middle East, where no representatives of *Exsertiana* occur. Similar to *R. natalensis*, the relative height of the spire is the most variable shell trait in *R. rufescens*.

The next three genera discussed (*Ampullaceana*, *Peregriana* and *Kamtschaticana*) represent the parts of the former subgenus *Peregriana* s. lato classified within the genus *Lymnaea* (Kruglov and Starobogatov 1993b; Kruglov 2005) or the genus *Radix* (Vinarski 2013; Vinarski and Kantor 2016). From the morphological point of view, these three genera cannot be distinguished on the basis of either shell or anatomical characters (Aksenova et al. 2018a) and they share the same *Bauplan* of the reproductive system. That is why previous authors considered them as the members of a single subgenus (*Peregriana*; see Kruglov and Starobogatov 1993b; Kruglov 2005) or even lumped them into a single polymorphic species, *Lymnaea peregra* s. lato (see Hubendick 1951).

Genus *Ampullaceana* Servain, 1882

Ampullaceana Servain 1882: 53; Aksenova et al. 2018a: 11.
Biformiana Servain 1882: 47.
Bouchardiana Servain 1882: 53.
Caenisiana Servain 1882: 56.
Effusiana Servain 1882: 49.
Nivalisiana Servain 1882: 54.
Ohridlymnaea Kruglov and Starobogatov 1993b: 166.

Type species. *Limnaeus ampullaceus* Rossmäßler, 1835 = ? *Ampullaceana balthica* (Linnaeus, 1758). According to Kruglov and Starobogatov (1993b), *L. ampullaceus* is a valid species allied to *A. balthica*.

10. *Ampullaceana ampla* (W. Hartmann, 1821)

Figs 7A, B; 8A; Table 2

Limnaeus hartmanni Studer 1820: 93 (nom. nudum).
Limnaeus auricularia var. *ampla* Hartmann 1821: 250, Taf. II, fig. 29.
Limnaea ampla – Hartmann 1840–1844: 69, pl. 17.
Gulnaria hartmanni – Hartmann 1840–1844: 71, pl. 18.
Gulnaria monnardi Hartmann 1840–1844: 72, pl. 19.
Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).
Lymnaea (Peregriana) patula – Kruglov and Starobogatov 1993b: 166, fig. 6D (*Lymnaea*), non Da Costa 1778; Kruglov 2005: 351, figs 236(4–5); 241, 242.
Lymnaea tobolica Lazareva 1967: 200, figs 4, 8.
Radix ampla – Glöer 2002: 215, fig. 243; Glöer 2019: 235, fig. 293.
Radix (Peregriana) ampla – Vinarski and Kantor 2016: 327.
Ampullaceana ampla – Aksenova et al. 2018a: 4.

TL. Germany, Bavaria, Rhein River near Reineck.

Lectotype. Naturmuseum Saint-Gallen, Switzerland (designated in Vinarski and Glöer 2007).

A. ampla is distributed in Europe (except the northernmost and southernmost latitudes), Western Siberia

and the southern part of Eastern Siberia (Glöer 2002, 2019; Vinarski and Glöer 2007; Andreeva et al. 2011; Welter-Schultes 2012). The shell of this species is relatively large, with low spire and very expanded aperture; conchologically, *A. ampla* can sometimes be confused with *R. auricularia*; however, the former species has straight or virtually absent columellar fold, which is not characteristic for *R. auricularia*. Shell height may reach 30–32 mm. The lengths of the praeputium and the penis sheath in this species are roughly equal (see Fig. 8A), with ICA close to 1.00. In a sample of *A. ampla* ($n = 52$), collected from several water-bodies of Russia, ICA was equal to 0.88 ± 0.13 (min – max = 0.51–1.21).

11. *Ampullaceana balthica* (Linnaeus, 1758)

Figs 7C, D; 8B; Table 2

Helix balthica Linnaeus 1758: 775.
Turbo patulus Da Costa 1778: 95, pl. V, fig. 17.
Limnaeus ovatus Draparnaud 1805: 50, pl. II, figs 30, 31, 33.
Limnaeus vulgaris Pfeiffer 1821: 89, Taf. IV, fig. 22.
Limnaea geysericola Beck 1837: 114.
Limnaea ovata var. *inflata* Kobelt 1871: 164, Taf. IV, fig. 12.
Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).
Radix ovata auct.
Lymnaea (Peregriana) balthica – Kruglov and Starobogatov 1983b: 1468, fig. 2(11); 1993b: 165, fig. 4C.
Radix balthica – Glöer 2002: 217, fig. 245; Schniebs et al. 2011: 664, figs 4–8; Glöer 2019: 237, fig. 296.
Radix (Peregriana) balthica – Vinarski and Kantor 2016: 329.
Ampullaceana balthica – Aksenova et al. 2018a: 4.

TL. Sweden, the Baltic Sea shore (Linnaeus 1758). The locality of the neotype is “Sweden, Stockholm” (see Kruglov and Starobogatov 1983b for details).

Neotype. ZISP (designated in Kruglov and Starobogatov 1983b).

This is one of the most common and widespread species of radicine snails in Europe (Aksenova et al. 2018a). A single representative of the radicine pond snails was found in Iceland (Bolotov et al. 2017). The species is common in various regions of the Northern Palearctic; distributed in Europe, Siberia and Central Asia (Andreeva et al. 2010; Schniebs et al. 2011; Vinarski et al. 2017). *A. balthica* is characterised by a rather wide variation, both in conchological and anatomical traits (summarised in Schniebs et al. 2011). The taxonomic identity of this species is based on the neotype (illustrated in Schniebs et al. 2011, fig. 8).

12. *Ampullaceana dipkunensis* (Gundrizer & Starobogatov, 1979)

Figs 7E, F; 8C; Table 2

Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).
Lymnaea dipkunensis Gundrizer and Starobogatov 1979: 1134, fig. 1(4).

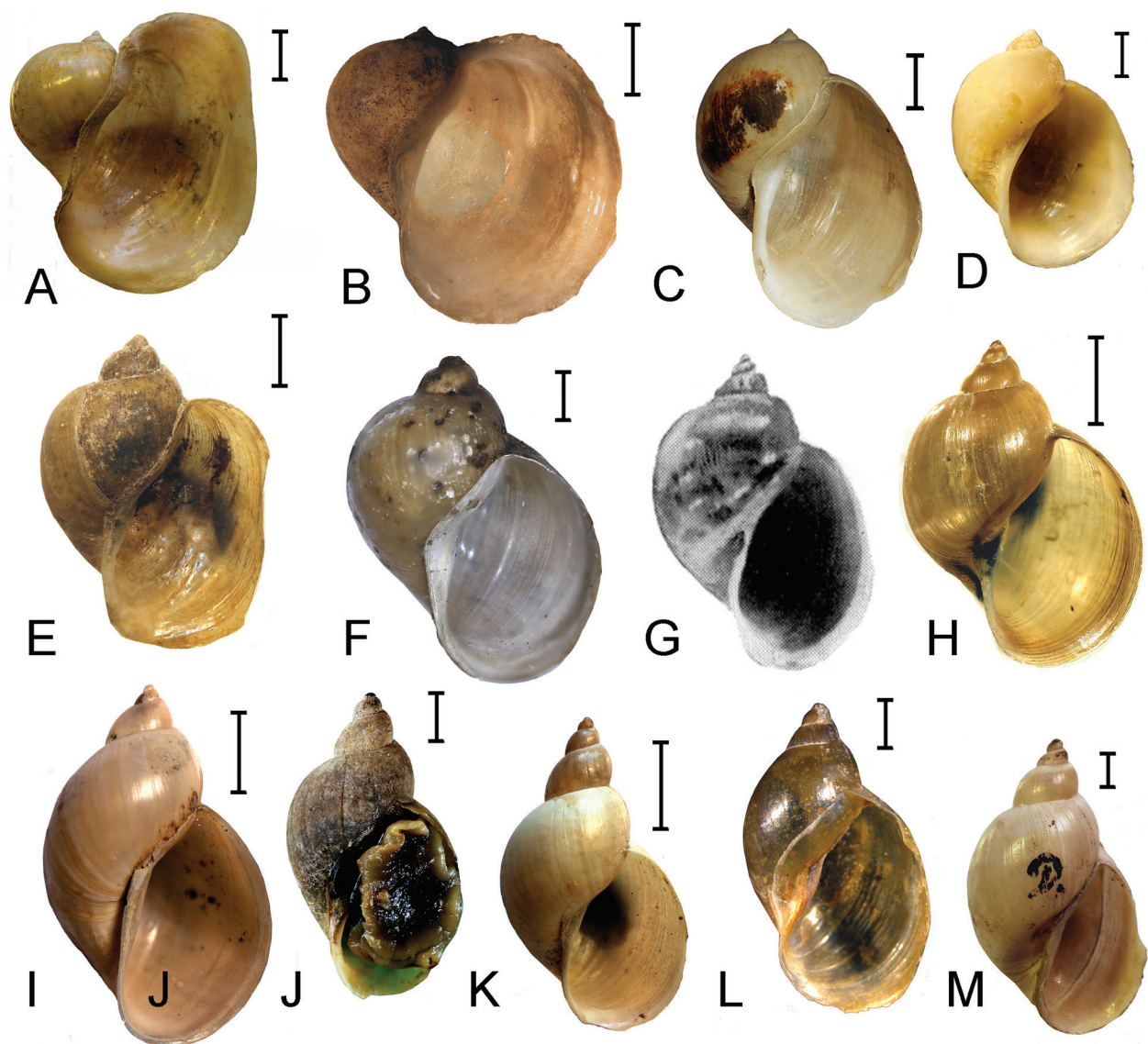


Figure 7. Shells of species of the genera *Ampullaceana* and *Peregriana*. **A.** *Ampullaceana ampla* (Austria, Wallersee Lake; NHMW). **B.** *A. ampla* (Germany, Neckarsteinach; NHMUK). **C.** *A. balthica* (14.12.1946, Denmark, Furesø Lake; ZMUC). **D.** *A. balthica* (Sweden, Stockholm; NMG). **E.** *A. dipkunensis* (Russia, Arkhangelsk Region, Nyandomka River; LMBI). **F.** *A. dipkunensis*, the holotype (07.07.1977, Russia, Krasnoyarsk Territory, Gornoye Lake; ZISP). **G.** *Limneus fontinalis*, the lectotype (after Forcart 1957). **H.** *A. fontinalis* (18.08.2017, Russia, Rostov Region, Veselovskoye Reservoir; LMBI). **I.** *Limneus intermedius* (France, Lyon; NHMW). **J.** *A. lagotis* (Russia, Leningrad Region, Lava River near Troitskoye; ZISP). **K.** *A. lagotis* (Austria, Bùrgenland, Bodersdorf; NHMW). **L.** *Peregriana dolgini* (Russia, Republic of Buryatia, Kironskiy Spring; RMBH). **M.** *P. peregra* (France, from Draparnaud's collection; NHMW). Scale bars: 2 mm (**D–F, J, L, M**), 5 mm (**A–C, H, I, K**). **G** – scale bar absent from the original publication.

Lymnaea (*Peregriana*) *dipkunensis* – Kruglov and Starobogatov 1993b: 164, fig. 2B (partim).

Lymnaea (*Peregriana*) *tumida* – Kruglov and Starobogatov 1993b: 166, fig. 6G, non Held 1836 (partim).

Radix (*Peregriana*) *dipkunensis* – Vinarski and Kantor 2016: 332 (partim).

Radix (*Peregriana*) *tumida* – Vinarski and Kantor 2016: 336, non Held 1836 (partim).

Ampullaceana cf. *dipkunensis* – Aksenova et al. 2018a: 4.

TL. Russia, Krasnoyarsk Territory, Gornoye Lake in the floodplain of the Kureika River upstream of the mouth of the Dipkun River.

Holotype. ZISP (see Sitnikova et al. 2014).

A species characterised by a broad shell with well-developed aperture, relatively-low spire and inflated body whorl. Its range covers European North of Russia and Eastern Europe (Aksenova et al. 2018a). Anistratenko et al. (2018) mentioned it (as *Radix tumida*) from the Western Ukraine. Specimens, morphologically identified as *R. tumida*, are known from the Urals, Western and Eastern Siberia (Gundrizer 1984; Kruglov 2005; Khokhutkin et al. 2009; Andreeva et al. 2010).

Conchologically, *A. dipkunensis* resembles *A. ampla*, but differs from the latter by a slightly higher spire and less

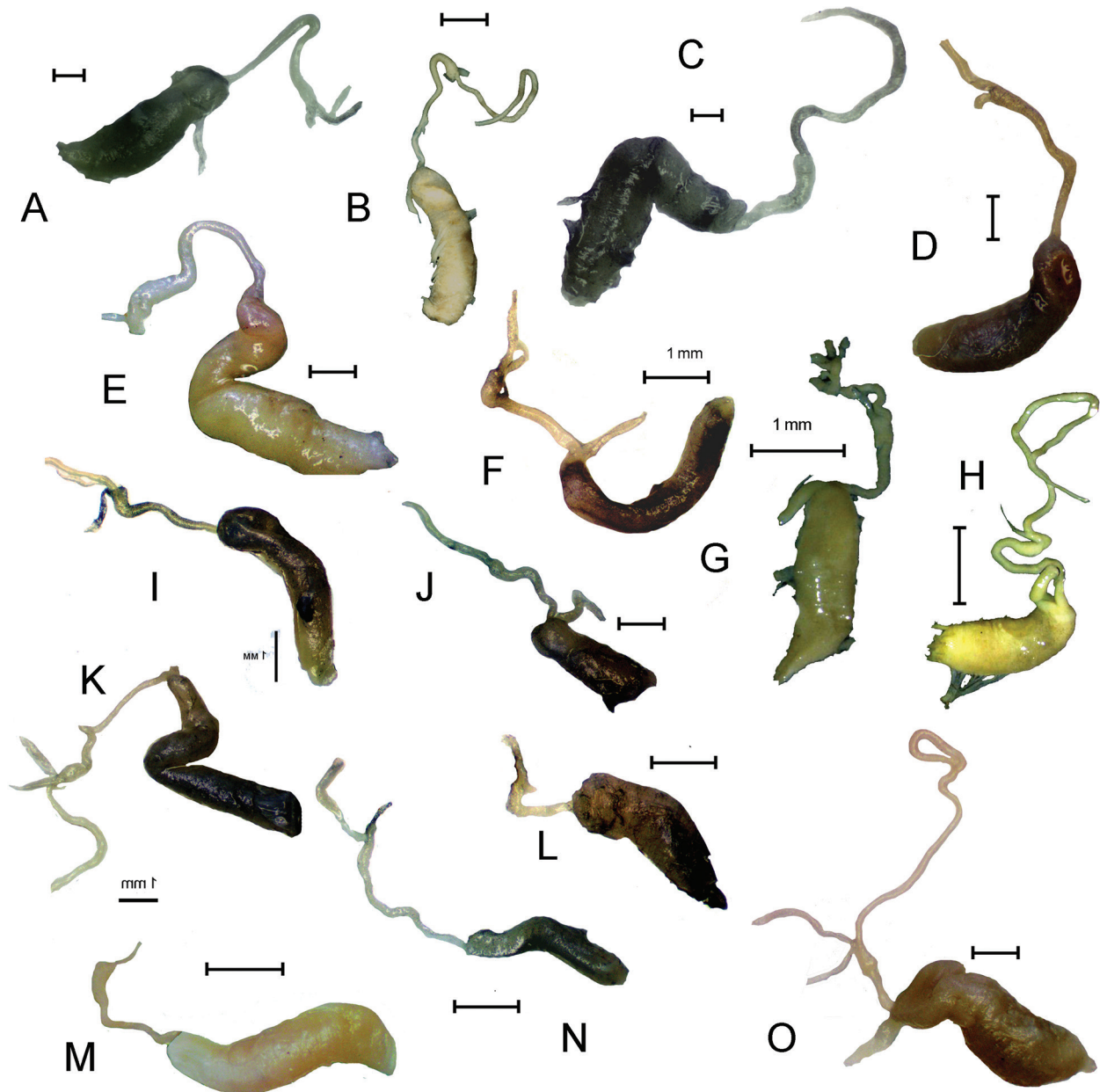


Figure 8. Copulatory apparatuses of the species in the genera *Ampullaceana*, *Peregriana*, *Kamtschaticana*, *Tibetoradix*, *Racesina*, *Orientogalba* and *Bullastra*. **A.** *Ampullaceana ampla* (11.07.2017, Ukraine, Transcarpathian Region, Irshava River). **B.** *A. balthica* (Germany, Mecklenburg-Vorpommern, lake Torgelower See). **C.** *A. dipkunensis* (15.09.2016, Ukraine, Transcarpathian Region, Tisa River). **D.** *A. fontinalis* (20.08.2017, Russia, Rostov Region, Severskiy Donets River). **E.** *A. lagotis* (29.06.2016, Tajikistan, a stream in the Panj River floodplain). **F.** *Peregriana dolgini* (13.07.2015, Russia, Tyumen' Region, a floodplain of the Tol'ka oxbow). **G.** *Peregriana peregra* (01.07.2006, Russia, Omsk Region, vicinity of Chernoluchye settlement). **H.** *Kamtschaticana kamtschatica* (12.04.2014, Russia, Kamchatka Peninsula, Valley of Geysers). **I.** *Tibetoradix hookeri* (09-10.2012, China, Tibet, a brook, 250 km N of Lhasa). **J.** *T. kozlovi* (after Aksyonova et al. 2018a, modified). **K.** *Racesina oxiana* (04.07.2016, Tajikistan, a roadside ditch near Kurban-Shakhid village). **L.** *R. siamensis* (24.11.2016, Myanmar, a water reservoir on the Yetho River). **M.** *Ampullaceana relicta relicta* (2005, Ohrid Lake). **N.** *Orientogalba ollula* (08.07.2010, China, Shaanxi Province, a roadside ditch near Yandi village). **O.** *Bullastra cumingiana* (Philippines, Luzon Island, Lake Sampaloc). Scale bars: 1 mm. **B** – after Schniebs et al. (2011), modified.

inflated aperture. Besides, Kruglov (2005) reported some differences in the proportions of the copulatory organs of these two snails. As was stated above, the penis sheath in *A. ampla* is slightly longer than the praeputium, whereas, in *A. dipkunensis*, one may observe an opposite state. According to Kruglov (2005), the praeputium of *R. tumida* is around

1.7 times longer than the penis sheath. In a sample containing 103 specimens of this species, collected from four localities in Russia, the mean ICA value was 1.84 ± 0.22 (limits of variation: 1.37–2.44) [Vinarski, unpublished data].

Taxonomic remark. Aksenova et al. (2018a) genetically studied some specimens of radicine snails identified

Table 2. Morphological characterisation of shells and copulative apparatuses of several species in the genera *Ampullaceana* and *Peregrina*.

Character / index	Species / locality									
	<i>A. ampla</i> Russia, Omsk Region, floodplain of the Irtysh River	<i>A. balthica</i> Russia, Altay Region, Buria River	<i>A. dipkumensis</i> Russia, Tyumen' Region, floodplain of the Tobol River	<i>A. fontinalis</i> Russia, Rostov Region, Severskiy Donets River*	<i>A. intermedia</i> Kazakhstan, Bolscheye Chebachiye Lake	<i>A. lagotis</i> Russia, Leningrad Region, Lava River near Troitskoye	Tajikistan, a stream in the floodplain of the Panj River*	<i>P. dolgini</i> Russia, Tyumen' Region, Taz River basin*	<i>P. peregra</i> Germany, a pond near Hammergut Town	
Repository	LMBI	LMBI	LMBI	LMBI	LMBI	ZISP	LMBI	LMBI	LMBI	
Number of specimens measured (dissected)	60(0)	28(25)	32(30)	33(17)	30(0)	13(0)	14(12)	16(11)	11(0)	
Whorls number	3.50-4.25	3.62-4.75	4.00-4.75	3.50-4.25	4.00-4.50	4.00-4.50	4.00-4.50	3.75-4.00	3.75-4.12	
Shell height, mm (SH)	3.79±0.19	4.22±0.26	4.37±0.16	3.83±0.18	4.21±0.17	4.32±0.17	4.18±0.17	3.81±0.10	3.94±0.12	
Shell width, mm (SW)	16.1-26.7	14.7-22.6	17.5-27.6	11.3-15.4	13.3-19.4	12.5-16.4	10.4-15.1	9.2-11.7	7.8-11.4	
Spire height, mm (SpH)	18.7±1.9	18.3±2.3	20.8±2.3	12.8±1.0	15.5±1.7	14.7±1.3	12.2±1.1	10.2±0.8	9.7±1.0	
Body whorl height, mm (BWH)	13.7-22.8	10.4-16.4	12.5-19.0	7.2-9.9	8.0-12.6	7.5-10.8	6.8-10.2	5.6-7.6	5.0-6.7	
Aperture height, mm (AH)	15.8±1.7	13.5±1.7	15.3±1.5	8.4±0.7	9.9±1.2	9.0±1.0	7.8±0.9	6.4±0.6	6.0±0.5	
Aperture width, mm (AW)	1.9-5.3	2.8-5.3	2.6-4.5	3.2-5.1	4.5-7.1	4.7-6.6	3.5-5.0	2.7-4.2	2.3-4.1	
Praepitium length, mm (PP)	3.0±0.6	4.2±0.6	3.6±0.5	4.0±0.5	5.5±0.7	5.8±0.7	4.4±0.4	3.4±0.4	3.3±0.5	
Penis sheath length, mm (PS)	14.8-25.0	13.7-19.1	15.7-24.5	9.6-12.9	11.1-16.2	10.1-15.5	8.8-12.3	7.6-10.1	6.7-9.5	
	17.3±1.8	16.2±1.7	18.6±2.0	11.1±0.8	13.2±1.4	12.3±1.6	10.1±0.9	8.6±0.8	8.2±0.9	
	13.8-23.1	10.6-16.3	13.1-23.4	7.1-10.7	8.0-13.0	7.8-11.1	7.1-10.4	5.4-9.0	5.4-7.8	
	16.2±1.8	13.9±1.7	17.0±2.2	9.0±0.7	10.0±1.2	9.3±1.0	8.1±0.9	6.7±0.9	6.5±0.7	
	10.3-19.0	8.1-12.5	10.3-16.3	4.8-7.1	5.8-10.4	5.4-7.7	4.1-7.4	3.9-6.0	3.2-4.6	
	12.7±1.6	10.2±1.4	12.3±1.3	5.9±0.5	7.3±0.9	6.3±0.8	5.4±0.8	4.9±0.5	4.0±0.5	
	-	5.2-16.0	5.5-13.0	3.1-5.7	-	-	2.3-4.0	2.3-3.15	-	
	-	10.3±2.3	9.8±1.3	4.3±0.7	-	-	3.2±0.5	2.8±0.3	-	
	-	4.4-10.5	2.7-6.7	3.3-5.5	-	-	1.6-2.6	2.0-3.6	-	
	-	6.0±1.6	5.0±0.7	4.0±0.6	-	-	2.1±0.3	2.7±0.4	-	
	0.77-0.94	0.66-0.84	0.68-0.81	0.59-0.72	0.59-0.69	0.52-0.67	0.59-0.68	0.58-0.69	0.59-0.65	
	0.84±0.04	0.74±0.04	0.74±0.03	0.66±0.03	0.64±0.03	0.60±0.04	0.64±0.03	0.63±0.03	0.62±0.02	
	0.11-0.21	0.17-0.30	0.14-0.20	0.26-0.38	0.31-0.41	0.31-0.42	0.33-0.41	0.23-0.42	0.30-0.38	
	0.16±0.02	0.23±0.03	0.17±0.02	0.31±0.03	0.36±0.03	0.39±0.03	0.36±0.02	0.33±0.05	0.34±0.03	
	0.89-0.97	0.79-0.98	0.84-0.95	0.83-0.89	0.82-0.88	0.66-0.83	0.79-0.85	0.74-0.89	0.82-0.86	
	0.93±0.01	0.89±0.04	0.90±0.02	0.87±0.02	0.85±0.02	0.80±0.04	0.82±0.01	0.84±0.03	0.85±0.01	
	0.77-0.96	0.68-0.86	0.66-0.89	0.64-0.75	0.58-0.64	0.51-0.69	0.62-0.69	0.58-0.76	0.63-0.71	
	0.87±0.04	0.76±0.04	0.83±0.05	0.70±0.03	0.65±0.03	0.63±0.04	0.66±0.02	0.66±0.05	0.67±0.03	
	0.66-0.89	0.65-0.84	0.61-0.86	0.59-0.73	0.66-0.80	0.61-0.73	0.58-0.74	0.67-0.85	0.51-0.71	
	0.79±0.04	0.73±0.05	0.72±0.05	0.65±0.03	0.73±0.04	0.68±0.03	0.66±0.04	0.67±0.06	0.61±0.06	
ICA	-	1.18-2.55	1.62-2.38	0.88-1.20	-	-	1.29-1.77	0.87-1.19	-	
	-	1.77±0.36	1.96±0.20	1.08±0.10	-	-	1.51±0.13	1.03±0.12	-	

*Sample studied genetically.

as *Lymnaea (Peregriana) tumida* Held, 1836 sensu Kruglov and Starobogatov (1983b, 1993b) and showed that it is a valid species, distinct from *A. ampla*. However, to use this species name is hardly acceptable. This taxon is usually considered as an intraspecific morph of *Radix auricularia* living in large Alpine lakes (Geyer 1927; Glöer 2002). Examination of the topotypes (dried shells) of *L. tumida*, kept in different European museums (NHMW, NMG, ZMUC), allowed Aksenova et al. (2018a) to agree with this opinion. Therefore, the authors used the next oldest available name, *Lymnaea dipkunensis* Gundrizer et Starobogatov, 1979, to designate this clade. The identity of this taxon was revealed by means of the inspection of the type series (see also Sitnikova et al. 2014). The records of *Lymnaea tumida* sensu Kruglov and Starobogatov in the Lower Yenissei Basin (Gundrizer 1984), the type region of *L. dipkunensis*, give indirect evidence in favour of their identity. However, this taxonomic hypothesis is in need of future integrative research using the topotypes of *L. dipkunensis*.

13. *Ampullaceana fontinalis* (Studer, 1820)

Figs 7G, H; 8D; Table 2

Limneus fontinalis Studer 1820: 27.

Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).

Lymnaea (Peregriana) fontinalis – Kruglov and Starobogatov 1983b: 146, fig. 2(16), 1993b: 166, fig. 6B; Khokhutkin et al. 2009: 92, fig. 40; Andreeva et al. 2010: 135, fig. 70.

Ampullaceana fontinalis – Aksenova et al. 2018a: 4.

TL. Switzerland (Studer 1820).

Lectotype. Naturhistorisches Museum der Burgergemeinde Bern, Switzerland (see Forcart 1957).

Shell ovate-conical, with prominent, but relatively-low spire and moderately-inflated body whorl. Praeputium and penis sheath light-coloured, their lengths are almost equal, though the praeputium is typically slightly longer (see Fig. 8D). The mean values of ICA slightly exceed 1.0 (Kruglov 2005; see also Table 2). According to genetic data, *A. fontinalis* is distributed in Europe, from Switzerland eastward to south of the European Russia, as well as in Turkey (Aksenova et al. 2018a). The previous recordings of this species from the Urals and Siberia (Kruglov and Starobogatov 1993b; Khokhutkin et al. 2009; Andreeva et al. 2010) require molecular confirmation.

Taxonomic remark. This European species of radicine snails was not listed as valid by most authors (Hubendick 1951; Glöer 2002; Welter-Schultes 2012), except by the Russian malacologists (Kruglov and Starobogatov 1983b, 1993b; Khokhutkin et al. 2009; Andreeva et al. 2010). Aksenova et al. (2018a) have shown that specimens identified as *Lymnaea (Peregriana) fontinalis* sensu Kruglov & Starobogatov, 1993 form a species-rank clade, sister to *A. lagotis*. Shells of *A. fontinalis* sensu Kruglov and Starobogatov (1993b), stud-

ied by us, were similar to the lectotype shell illustrated by Forcart (1957) [see Fig. 7G, H]. The presence of *A. fontinalis* in Switzerland (where its type locality lies) has been confirmed molecularly (Aksenova et al. 2018). This species is morphologically similar to *A. lagotis*, but may be distinguished by a lower spire and more inflated body whorl.

14. *Ampullaceana intermedia* (Lamarck, 1822)

Fig. 7I; Table 2

Lymnaea intermedia Lamarck 1822: 162.

Limnaea intermedia – Michaud 1831: 86, pl. XVI, figs 17, 18.

Limnaeus intermedius – Küster 1862: 12, Taf. 2, figs 21, 22.

Limnaea intermedia – Sowerby 1872: pl. III, fig. 16; Kobelt 1912: 18, Taf. CCCCLXXXVIII, fig. 2602.

Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).

Lymnaea (Peregriana) intermedia – Kruglov and Starobogatov 1983b: 146, fig. 2(9); 1993b: 165, fig. 4B; Khokhutkin et al. 2009: 85, fig. 36; Andreeva et al. 2010: 125, fig. 64.

Radix (Peregriana) intermedia – Vinarski and Kantor 2016: 331.

Ampullaceana intermedia – Aksenova et al. 2018a: 4.

TL. France, Quercy Plateau.

Types. Most probably lost (Mermod 1952).

Aksenova et al. (2018a) used the binomen *Lymnaea intermedia* Lamarck, 1822 to designate a radicine species, sister to *A. balthica*, which is widely distributed in France and Spain. Since the type specimen, mentioned by Lamarck (1822), is probably lost, we based our understanding of this taxon on examination of both historical samples of it (see, for example, specimen of *L. intermedia* collected in Lyon, France, in the first half of the 19th century: Fig. 7I) and some old literary sources, dealing with lymnaeids of Western Europe (Michaud 1831; Küster 1862; Sowerby 1872; Kobelt 1912).

Conchologically, shells of *A. intermedia* resemble those of *A. balthica*, but can be distinguished from the latter by higher spire and less inflated body whorl. Modern European authors do not accept *A. intermedia* as a valid species (Glöer 2002; Welter-Schultes 2012), whereas malacologists of the former USSR still mention this taxon as a species closely allied to *A. balthica* (Kruglov and Starobogatov 1993b; Khokhutkin et al. 2009; Andreeva et al. 2010; Vinarski and Kantor 2016). The concept of this species proposed by Kruglov and Starobogatov (1983b, 1993b) coincides with that of old European authors (Michaud 1831; Küster 1862; Sowerby 1872). However, we still do not possess any sequence of *A. intermedia* from the countries lying east of France and the actual range of this species remains unknown. The Russian authors repeatedly recorded this species from different regions of Russia, including the Urals and Siberia (Kruglov and Starobogatov 1993b; Khokhutkin et al. 2009; Andreeva et al. 2010), but all these records were based solely on morphological data and need to be confirmed molecularly.

15. *Ampullaceana lagotis* (Schränk, 1803)

Figs 7J, K; 8E; Table 2

Buccinum lagotis Schränk 1803: 290.*Lymnaea peregra* – Hubendick 1951: 146, figs 1, 9 (partim).*Radix lagotis* – Glöer 2002: 219, fig. 246; Welter-Schultes 2012: 53, textfig.; Schniebs et al. 2015: 35, figs 3–5; Glöer 2019: 241, fig. 300.*Lymnaea (Peregriana) lagotis* – Kruglov and Starobogatov 1983b: 1469, fig. 2(15); 1993b: 166, fig. 6A; Khokhutkin et al. 2009: 90, fig. 39; Andreeva et al. 2010: 134, fig. 69.*Radix (Peregriana) lagotis* – Vinarski and Kantor 2016: 334.*Ampullaceana lagotis* – Aksenova et al. 2018a: 4.**TL.** Germany, Bavaria, Danube River.**Types.** Lost (Vinarski and Kantor 2016).

This species is characterised conchologically by a relatively oblong shell, with high and narrow spire and moderately-inflated body whorl (see Fig. 7J, K). The structure of the copulatory apparatus in *A. lagotis* is typical for the genus. Praeputium is relatively long, its length is about 1.5 times larger than the length of the penis sheath (see Fig. 8E; Table 2). The range of *A. lagotis* covers, almost entirely, Europe, Siberia and some parts of Central Asia, including Tajikistan and western China (Glöer 2002, 2019; Andreeva et al. 2010; Welter-Schultes 2012; Vinarski and Kantor 2016). The molecularly-confirmed records of this species were reported from different countries of northern, central and southern Europe, as well as from Tajikistan and Siberia (Schniebs et al. 2015; Aksenova et al. 2018a).

Shell proportions of *A. lagotis* resemble those of *A. intermedia*; however, *A. lagotis* typically has a much narrower spire than the latter species (compare Fig. 7I and 7J, K).

16. *Ampullaceana relicta* (Poliński, 1929)

Note. This species is endemic to the large ancient lakes of the Balkans (Albrecht et al. 2008; Welter-Schultes 2012; Glöer 2019). *A. relicta* is phylogenetically close to *A. ampla* and, most probably, represents a local derivative of the latter originating as a consequence of its ancient invasion into large lakes. As Aksenova et al. (2018a) have shown, this species is polytypic and includes two subspecies, which are separately discussed below.

16a. *Ampullaceana relicta relicta* (Poliński, 1929)

Figs 8M; 9A.

Radix relicta Poliński 1929: 158.*Lymnaea peregra* – Hubendick 1951: 146, figs 1, 9 (partim).*Lymnaea (Peregriana) relicta* – Kruglov and Starobogatov 1983b: 1469, figs 2(12), 3(12); 1993b: 166, fig. 5C.*Radix relicta* – Albrecht et al. 2008: 160, fig. 1; Welter-Schultes 2012: 54, textfig.; Glöer 2019: 244, fig. 305*Ampullaceana relicta relicta* – Aksenova et al. 2018a: 4.**TL.** Lake Ohrid.**Types.** Whereabouts unknown.

This subspecies has been characterised both morphologically and genetically by Albrecht et al. (2008). We examined the copulatory apparatus of two specimens and found that its structure is typical for the genus. Both praeputium and penis sheath are light-coloured; praeputium is substantially larger than the penis sheath (see Fig. 8M), the ratios between their lengths are 1.42 and 1.46, respectively.

A. r. relicta inhabits Ohrid Lake (Albania and Macedonia), as well the Drin system, at least upstream to the dam Globočičko, approximately 15 km N of the lake (Albrecht et al. 2008).

16b. *Ampullaceana relicta pinteri* (Schütt, 1974)

Fig. 9B.

Radix pinteri Schütt 1974: 471, pl. 1.*Radix pinteri* – Albrecht et al. 2008: 160, fig. 2; Welter-Schultes 2012: 54, textfig.; Glöer 2019: 244, fig. 304.*Ampullaceana relicta pinteri* – Aksenova et al. 2018a: 4.**TL.** North Macedonia, Lake Prespa near village of Perovo.

Types. Holotype – SMF; paratypes were placed in NHMW and in a series of private collections in Germany and Hungary (Schütt 1974); currently, specimens from these private collections are kept in the Hungarian Natural History Museum (Budapest) and in the Natural History Museum of Bern (Switzerland). We examined the paratypes kept in NHMW and in the Budapest museum (see Fig. 9B).

This subspecies has been characterised both morphologically and genetically in a series of papers (Schütt 1974; Albrecht et al. 2008; Welter-Schultes 2012). Most authors regard this taxon as a separate species. For example, Albrecht et al. (2008) considered *A. r. relicta* and *A. r. pinteri* as two sister species from two ‘sister’ lakes, Ohrid and Prespa (but see Aksenova et al. 2018a). According to the anatomical data presented in Albrecht et al. (2008), the morphology of the copulatory apparatus in *A. r. pinteri* is virtually identical with that of the nominative subspecies.

A. r. pinteri is endemic to Prespa Lake (Albania, Greece and Macedonia).

Genus *Peregriana* Servain, 1882*Peregriana* Servain 1882: 56.**Type species.** *Buccinum peregrum* O.F. Müller, 1774.**17. *Peregriana peregra* (O.F. Müller, 1774)**

Figs 7M; 8G; Table 2

Buccinum peregrum O.F. Müller 1774: 130.*Lymnaea peregra* – Hubendick 1951: 146, figs 1, 9 (partim).*Lymnaea (Peregriana) peregra* – Kruglov and Starobogatov 1983b: 1465, fig. 2(2); 1993b: 161, fig. 1B.

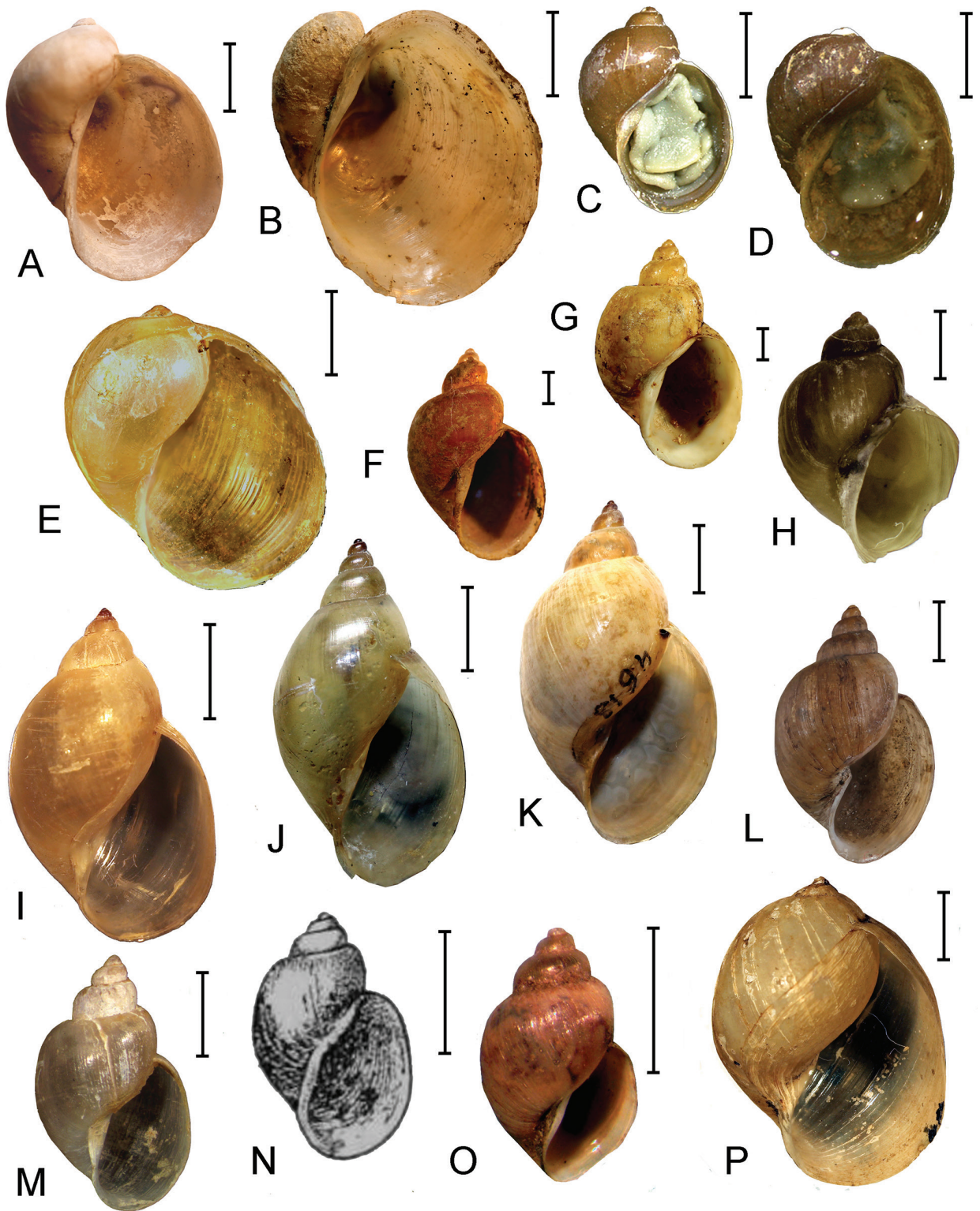


Figure 9. Shells of species of the genera *Ampullaceana*, *Kamtschaticana*, *Myxas*, *Tibetoradix*, *Racesina*, *Orientogalba* and *Bullastra*. **A.** *Ampullaceana relicta relicta* (05.1975, Macedonia, a spring near St. Naum monastery, Ohrid Lake region; NHMW). **B.** *A. r. pinteri*, a paratype (05.06.1973, Macedonia, Prespa Lake near Perovo; MHMW). **C, D.** *Kamtschaticana kamtschatica* (Russia, Kamchatka Peninsula, Valley of Geysers; RMBH). **E.** *Myxas glutinosa* (14.09.1963, Kazakhstan, floodplain of the Tobol River near Kustanay City; ZISP). **F, G.** *Tibetoradix hookeri*, two syntypes (NHMUK). **H.** *T. kozlovi*, the holotype (ZISP). **I.** *Racesina luteola* (India, Bengal, Paksay, Pabna; NHMUK). **J.** *R. oxiana* (04.07.2016, Tajikistan, a roadside ditch near Kurban-Shakhid village; LMBI). **K.** *R. siamensis* (“Thailand”; ZMB). **L.** *Orientogalba viridis*, a syntype (Guam Island; NMNH). **M.** *O. ollula* (1883, Japan, Yokohama; NHMUK). **N.** *Limnaea bowelli*, a type (after Preston 1909). **O.** *Orientogalba* cf. *bowelli* (30.06.1924, China, Tibet, Lingka, 14,500 feet a.s.l.; NHMUK). **P.** *Bullastra cumingiana* (Philippine, Cebu Island; NHMUK). Scale bars: 2 mm (C, D, F–H, L, M, O), 5 mm (A, B, E, J–K, N, P).

Radix labiata – Falkner et al. 2002: 94; Glöer 2002: 216, fig. 244; Welter-Schultes 2012: 53, textfig.; Schniebs et al. 2013: 59, figs 4–8.; Glöer 2019: 240, fig. 299.

Radix (Peregriana) peregra – Vinarski and Kantor 2016: 326.

Peregriana peregra – Aksenova et al. 2018a: 4.

TL. Denmark, Copenhagen, Frederiksberg Park, in swamps (Vinarski and Kantor 2016).

Types. Lost (Nekhaev et al. 2015).

For morphological and molecular characterisation of this species, see Schniebs et al. (2013) and Vinarski et al. (2016). *P. peregra* inhabits Europe (except of the northern part), the Urals and the southwest part of Western Siberia (Glöer 2002, 2019; Khokhutkin et al. 2009; Andreeva et al. 2010; Schniebs et al. 2013; Vinarski et al. 2016). In many recent publications, this species has been referred to as *Radix labiata* (Rossmässler, 1835).

Nomenclatorial note. Falkner et al. (2002) argued that the lymnaeid species, which had been commonly named *Radix* (or *Lymnaea*) *peregra* by the European authors, does not occur in Denmark, the type country of Müller's *Buccinum peregrum*. These authors treated *B. peregrum* as a junior synonym of *Helix balthica* Linnaeus, 1758 and proposed the name *Radix labiata* for designation of *R. peregra* auct. Such authors as Glöer (2002, 2019) and Welter-Schultes (2012) followed it, but Vinarski (2017) doubted this decision. According to him, Falkner et al. (2002) did not present the *total evidence* for the absence of *R. peregra* auct. from Denmark and their assumption still needs strong confirmation. The type specimens of *Limnaeus pereger* var. *labiatus* (kept in NHMW) were considered by Vinarski (2017) as juvenile individuals of *R. balthica*. Therefore, it was unnecessary to replace a well-established taxonomic name *R. peregra* with a long-forgotten one, *R. labiata*.

18. *Peregriana dolgini* (Gundrizer & Starobogatov, 1979)

Figs 7L; 8F; Table 2

Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).

Lymnaea dolgini Gundrizer and Starobogatov 1979: 1132, figs 1(2); 2(2).

Lymnaea kurejkae Gundrizer and Starobogatov 1979: 1131, fig. 1(1).

Lymnaea gundrizeri Kruglov and Starobogatov 1983a: 141.

Lymnaea napasica Kruglov and Starobogatov 1983a: 140.

Lymnaea ulaganica Kruglov and Starobogatov 1983a: 141.

Lymnaea (Peregriana) dolgini – Kruglov and Starobogatov 1993b: 170, fig. 7G.

Lymnaea (Peregriana) gundrizeri – Kruglov and Starobogatov 1993b: 164, fig. 5A.

Lymnaea (Peregriana) kurejkae – Kruglov and Starobogatov 1993b: 170, fig. 7F.

Lymnaea (Peregriana) napasica – Kruglov and Starobogatov 1993b: 169, fig. 7C.

Lymnaea (Peregriana) ulaganica – Kruglov and Starobogatov 1993b: 164, fig. 5B.

Radix (Peregriana) dolgini – Vinarski and Kantor 2016: 332 (partim).

Radix (Peregriana) gundrizeri – Vinarski and Kantor 2016: 333 (partim).

Radix (Peregriana) ulaganica – Vinarski and Kantor 2016: 333 (partim).

Radix dolgini – Vinarski et al. 2016: 26, figs 2, 3; Glöer 2019: 239, fig. 297.

Peregriana dolgini – Aksenova et al. 2018a: 4.

TL. Russia, Krasnoyarsk Territory, a lake in the floodplain of the Kureika River, 20 km upstream of its mouth.

Type series. ZISP (see Sitnikova et al. 2014).

Vinarski et al. (2016) presented a full morphological and molecular account for this species, as well as the data on its range and a comparison with conchologically similar radicine taxa. *P. dolgini* is a species sister to *P. peregra* and, probably, represents its vicariant taxon in Northern Asia (Siberia). The molecularly-confirmed recordings of *P. dolgini* are also known from the north-eastern part of Europe – the Pechora River basin (Aksenova et al. 2018b).

Genus *Kamtschaticana* Kruglov & Starobogatov, 1984

Kamtschaticana Kruglov and Starobogatov 1984: 30.

Type species. *Limnaeus kamtschaticus* Middendorff, 1850.

This taxon was introduced as a 'section' of the subgenus *Peregriana* (Kruglov and Starobogatov 1984). Aksenova et al. (2018a) elevated it to the genus level.

19. *Kamtschaticana kamtschatica* (Middendorff, 1850)

Figs 8H; 9C, D; Table 3

Limnaeus kamtschaticus Middendorff 1850: 110; 1851: 295, pl. 30, figs 11, 12.

Limnaea ovata var. *aberrans* Westerlund 1897: 125.

Limnaea peregra var. *middendorffi* W. Dybowski 1904: 52, fig. 7.

Lymnaea peregra – Hubendick 1951: 146, figs 1, 9 (partim).

Lymnaea (Peregriana) kamtschatica – Kruglov and Starobogatov 1984: 30, figs 1(18), 2(7); 1993b: 164, fig. 3A.

Lymnaea (Peregriana) aberrans – Kruglov and Starobogatov 1984: 31, figs 1(21), 2(3); 1993b: 164, fig. 3E.

Lymnaea (Peregriana) middendorffi – Kruglov and Starobogatov 1984: 31, figs 1(19), 2(5); Kruglov and Starobogatov 1993b: 164, fig. 3D.

Radix (Peregriana) kamtschatica – Vinarski and Kantor 2016: 334; Aksenova et al. 2016: 20, fig. 1I.

Radix (Peregriana) aberrans – Vinarski and Kantor 2016: 327; Aksenova et al. 2016: 19, fig. 1H.

Radix (Peregriana) middendorffi – Vinarski and Kantor 2016: 335; Aksenova et al. 2016: 21, fig. 1D.

Kamtschaticana kamtschatica – Aksenova et al. 2018a: 4.

TL. Russia, Kamchatka Peninsula, Kamchatka River (Kruglov and Starobogatov [1984] suggest that the type specimens were collected from the floodplain of the river).

Lectotype. ZISP (see Kruglov and Starobogatov 1984 for details).

Aksenova et al. (2016) presented a detailed description of morphology of this snail, accompanied by a molecular analysis of its phylogenetic and taxonomic affinities.

Table 3. Morphological characterisation of shells and copulative apparatuses of several species in the genera *Kamtschaticana*, *Myxas*, *Racesina*, *Orientogalba* and *Bullastra*

Character / index	Species / locality											
	<i>Kamtschaticana kamtschatica</i>		<i>Myxas glutinosa</i>		<i>Racesina luteola</i>		<i>Racesina siamensis</i>		<i>Orientogalba ollula</i>		<i>Bullastra cumingiana</i>	
	Russia, Kamchatka Peninsula, Valley of Geysers*	Russia, Khabarovsk Territory, Polina Osipenko settlement	Germany, Magdeburg, a channel	Tajikistan, a roadside ditch near Kurbonshakhid settlement*	India, Dharwad	Myanmar, a reservoir on the Yetho River*	China, Shaanxi Province, a roadside ditch near Yandi village	Philippines, Mindoro Island				
	LMBI 50 (16)	ZISP 38 (0)	SNSD 30(0)	LMBI 6(4)	NHMKUK 8(0)	LMBI 11(11)**	LMBI 21(12)	NHMKUK 14(0)				
Repository												
Number of specimens measured (dissected)	2.50–3.50	3.25–4.12	3.00–3.50	4.75–5.25	4.00–5.00	4.00–4.25	4.00–5.00	2.50–3.25				
Whorls number	2.96±0.19	3.66±0.21	3.24±0.12	5.08±0.20	4.61±0.30	4.14±0.11	4.36±0.29	3.00±0.20				
Shell height, mm (SH)	4.8–8.1	6.9–12.9	12.6–18.0	15.4–21.6	16.6–20.1	9.9–14.0	7.1–11.0	18.0–26.4				
Shell width, mm (SW)	6.2±0.7	8.6±1.2	15.9±1.3	18.4±2.2	17.9±1.1	11.9±1.2	8.9±1.0	22.0±3.0				
Spire height, mm (SpH)	3.6–5.7	5.0–9.4	10.6–18.0	8.7–12.2	9.5–10.8	6.4–8.3	4.4–6.7	13.8–27.0				
	4.5±0.5	6.0±0.8	15.4±1.4	10.3±1.3	10.2±0.4	7.3±0.7	5.8±0.6	17.0±2.4				
	1.0–2.5	2.2–4.0	1.0–2.2	5.3–8.5	6.1–7.4	3.5–5.2	2.5–5.1	0.5–2.2				
	1.7±0.3	2.8±0.5	1.5±0.3	6.8±1.1	6.7±0.5	4.0±0.5	3.2±0.7	1.2±0.6				
Body whorl height, mm (BWH)	4.4–7.3	6.0–11.5	12.4–17.6	12.6–17.5	14.3–17.3	8.5–11.8	5.8–8.5	17.6–26.0				
	5.6±0.7	7.6±1.1	15.6±1.2	15.0±1.8	15.5±0.9	10.2±1.0	7.4±0.7	21.6±3.0				
Aperture height, mm (AH)	3.5–5.9	4.5–9.4	11.0–16.6	10.3–13.8	11.6–13.7	6.5–9.1	4.5–6.8	17.3–24.8				
	4.6±0.5	5.9±0.9	14.4±1.2	12.0±1.3	12.5±0.6	8.1±0.8	5.7±0.5	21.1±2.8				
Aperture width, mm (AW)	2.4–4.0	3.4–5.8	11.0–16.0	6.3–8.0	6.6–7.8	4.3–5.8	3.2–5.0	10.8–16.4				
	3.2±0.4	4.0±0.5	13.1±1.5	7.2±0.7	7.2±0.4	5.1±0.5	4.2±0.4	13.6±1.7				
Praeputium length, mm (PP)	1.55–2.35	–	–	5.3–6.9	–	3.0–3.4	1.75–2.8	–				
	1.80±0.19	–	–	6.2±0.8	–	3.3±0.2	2.45±0.3	–				
Penis sheath length, mm (PS)	1.20–1.95	–	–	4.4–7.7	–	2.4–3.1	1.6–2.6	–				
	1.5±0.18	–	–	5.6±1.5	–	2.7±0.3	2.0±0.3	–				
SW/SH	0.59–0.82	0.61–0.77	0.84–1.06	0.54–0.58	0.54–0.58	0.56–0.65	0.58–0.72	0.76–0.80				
	0.72±0.05	0.70±0.04	0.97±0.05	0.56±0.01	0.57±0.02	0.61±0.03	0.66±0.04	0.77±0.01				
SpH/SH	0.20–0.33	0.29–0.40	0.06–0.12	0.34–0.39	0.35–0.40	0.30–0.37	0.29–0.46	0.03–0.09				
	0.27±0.03	0.33±0.03	0.09±0.02	0.37±0.02	0.37±0.02	0.34±0.02	0.38±0.04	0.05±0.02				
BWH/SH	0.85–0.94	0.85–0.92	0.93–0.99	0.80–0.85	0.83–0.88	0.84–0.89	0.68–0.88	0.97–0.99				
	0.90±0.02	0.88±0.02	0.98±0.01	0.82±0.02	0.86±0.01	0.85±0.02	0.83±0.05	0.98±0.01				
AH/SH	0.64–0.80	0.58–0.73	0.86–0.95	0.62–0.67	0.67–0.72	0.65–0.72	0.56–0.72	0.94–0.99				
	0.73±0.03	0.68±0.03	0.90±0.02	0.65±0.02	0.70±0.02	0.69±0.03	0.65±0.03	0.96±0.02				
AW/AH	0.60–0.80	0.62–0.82	0.75–1.05	0.58–0.63	0.56–0.62	0.57–0.74	0.63–0.80	0.60–0.70				
	0.70±0.04	0.68±0.05	0.91±0.07	0.61±0.02	0.58±0.02	0.62±0.05	0.73±0.04	0.65±0.03				
ICA	0.97–1.35	–	–	0.90–1.30	–	1.10–1.36	1.00–1.39	–				
	1.24±0.09	–	–	1.13±0.17	–	1.22±0.12	1.19±0.12	–				

*Sample studied genetically. ** Five out of 11 dissected individuals were aphyllid (see species account for *C. stamensis*).

Conchologically and anatomically, *K. kamtschatica* is very similar to other members of the genera *Ampullacea* and *Peregriana* and it is virtually impossible to propose a differential diagnosis for this genus. *K. kamtschatica* is widely distributed throughout north-eastern Asia, including Kamchatka and Chukotka peninsulas, Transbaikalia and the Amur River basin (Kruglov and Starobogatov 1993b; Aksenova et al. 2016). Possibly, this snail is endemic to Asiatic Russia, though we cannot exclude that it also inhabits Alaska. In Kamchatka, it forms stable populations in the geothermal sites (e.g. the Valley of Geysers) and may live in warm water up to +39.9 °C (Aksenova et al. 2016).

Genus *Tibetoradix* Bolotov, Vinarski & Aksenova, 2018

Tibetoradix Aksenova et al. 2018a: 11.

Type species. *Lymnaea hookeri* Reeve, 1850.

Von Oheimb et al. (2011) have shown that the Tibetan Plateau is a hotspot of lymnaeid diversity in High Asia, with several species-level clades of the genus *Radix* s. lato restricted to this region. Aksenova et al. (2018a) established a new radicine genus, *Tibetoradix*, to contain six species endemic to Tibet, four of which remain undescribed.

20. *Tibetoradix hookeri* (Reeve, 1850)

Figs 8I; 9F, G

Lymnaea hookeri Reeve 1850: 49.

Limnaea hookeri – G.B. Sowerby II 1872: pl. XI, fig. 74.

Limnaea hookeri – Annandale and Rao 1925: 167, figs V(7), IX (6).

Lymnaea (Galba) hookeri – Subba Rao 1989: 132.

Tibetoradix hookeri – Aksenova et al. 2018a: 12, figs 6F; 7E, H.

TL. “Thibetan or north side of Sikkim Himalaya, at 18,000 feet elevation” [Reeve, 1850: 49].

Syntypes. NHMUK (examined by us). A syntype shell was illustrated by Hubendick (1951) and Aksenova et al. (2018a).

Shell medium-sized (the largest of the two syntypes is 16.9 mm high), with high spire and moderately-inflated body whorl. The shell proportions of *T. hookeri* resemble those of *A. lagotis*. The copulatory apparatus is typical for radicles: broad and relatively compact praeputium and very thin and narrow penis sheath (see Fig. 8I); the ratio of their lengths ranges from 1.25–1.50.

T. hookeri is endemic to China. It occurs in Tibet, known from the upstream section of the Lhasa River and a single additional locality (Brahmaputra River basin), altitude range: 4,540–4,980 m. (Aksenova et al. 2018a).

Taxonomic remark. Kruglov and Starobogatov (1993b) classified this species as belonging to the (sub) genus *Orientogalba* Kruglov et Starobogatov, 1985 and treated it as a senior synonym of *Lymnaea heptapotamica* Lazareva, 1967, described from southern Kazakhstan.

The examination of the syntypes of *L. hookeri* has shown that *L. heptapotamica* should not be synonymised with the former species and may well represent a separate taxon, not related to the genus *Tibetoradix*.

21. *Tibetoradix kozlovi* Vinarski, Bolotov & Aksenova, 2018

Figs 8J; 9H.

Tibetoradix kozlovi Aksenova et al. 2018a: 11, fig. 7A–D.

TL. China, Central Tibet, the floodplain of the Requ Qu River, Yellow River basin, 33°35'20.7"N, 103°05'30.2"E, alt. 3,470 m.

Types. ZISP (holotype, paratypes), RMBH (paratypes).

This snail, endemic to Tibet, is fully described in our previous paper (Aksenova et al. 2018a), therefore, we give here only pictures of its shell and copulatory organ.

Genus *Myxas* G. B. Sowerby I, 1822

Myxas G.B. Sowerby I 1822: part vii.

Amphipeplea Nilsson 1822: 58.

Type species. *Buccinum glutinosum* O.F. Müller, 1774.

22. *Myxas glutinosa* (O.F. Müller, 1774)

Fig. 9E; Table 3.

Buccinum glutinosum O.F. Müller 1774: 129.

Amphipeplea dupuyi Locard 1893: 30.

Amphipeplea mabiliei Locard 1893: 30.

Lymnaea glutinosa – Hubendick 1951: 148, fig. 333.

Lymnaea (Myxas) dupuyi – Kruglov and Starobogatov 1985b: 74, figs 1(3), 2(3); 1993b: 171, fig. 9D (partim).

Lymnaea (Myxas) glutinosa – Kruglov and Starobogatov 1985b: 73, figs 1(2), 2(2); 1993b: 171, fig. 9B (partim).

Lymnaea (Myxas) mabiliei – Kruglov and Starobogatov 1985b: 71, figs 1(1), 2(1); 1993b: 171, fig. 9A (partim).

Myxas glutinosa – Glöer 2002: 220, fig. 248; Welter-Schultes 2012: 50, textfig.; Vinarski and Kantor 2016: 316; Glöer 2019: 249, fig. 310.

TL. Not stated in the original description. Most probably, the type locality should be quoted as Fridrichsdal, a suburb of Copenhagen, Denmark (see Nekhaev et al. 2015 for details).

Types. Lost (Nekhaev et al. 2015).

The taxonomic position and identity of this morphologically-peculiar species have not raised many doubts and most authors treated it more or less identically (Hubendick 1951; Glöer 2002; Welter-Schultes 2012; but see Kruglov and Starobogatov 1993b). The results of our study well correspond to the commonly-accepted concept of *M. glutinosa*. Shell of this species is very fragile, semi-pellucid and, in a living animal, it is completely

covered by the reflected mantle. Shell shape is almost globose, with greatly expanded aperture and very diminished spire (in some specimens, it is almost invisible).

The structure of the copulatory apparatus of *M. glutinosa*, as is described by various authors (Hubendick 1951; Kruglov and Starobogatov 1985b; Jackiewicz 1998), is virtually indistinguishable from that of the genera *Ampullaceana* and *Peregriana*. However, the length of the spermathecal duct is different (long in *Myxas*, very short or almost absent in *Ampullaceana* and *Peregriana*).

The range of *M. glutinosa* covers Europe (except of the southern and northern parts), the Urals, Western and Central Siberia (Khokhutkin et al. 2009; Welter-Schultes 2012; Vinarski et al. 2013).

Genus *Racesina* Vinarski & Bolotov, 2018

Racesina Vinarski and Bolotov 2018: 332.

Type species. *Lymnaea luteola* Lamarck, 1822.

Three species included into *Racesina* by Vinarski and Bolotov (2018), were previously treated as members of the (sub-) genus *Cerasina* Kobelt, 1881 (Subba Rao 1989; Kruglov 2005; Aksenova et al. 2018a). As Vinarski and Bolotov (2018) have shown, the genus *Cerasina* sensu Kobelt is a junior synonym of *Radix* and a new generic name was proposed by these authors for *Cerasina* sensu auct. non Kobelt. The type species of the genus inhabits India and some adjacent countries. Despite some serious morphological peculiarities of *Cerasina* sensu Kruglov and Starobogatov (1993b), the validity of this taxon was rejected by most authors dealing with the South Asian malacofauna (Annandale and Rao 1925; Hubendick 1951; Brandt 1974; Subba Rao 1989). Vinarski (2013; Vinarski and Kantor 2016) classified *Cerasina* as a separate genus within his subfamily Radicinae (see also Zhadin 1952). The results of the Aksenova et al. (2018a) molecular taxonomic study confirmed this opinion. The prostate with numerous (5–8) internal folds (Hubendick 1951; Kruglov 2005) and a single synapomorphy to sharply distinguish *Racesina* from all other genera of radicine snails are discussed in this paper.

23. *Racesina luteola* (Lamarck, 1822)

Fig. 9I

Lymnaea luteola Lamarck 1822: 160.

Limnaeus cerasum Troschel 1837: 170.

Limnaeus impurus Troschel 1837: 172.

Limnaeus nucleus Troschel 1837: 171.

Limnaeus prunum Troschel 1837: 170.

Limnaea tigrina Dohrn 1858: 134.

Limnaea ovalior Annandale et al. 1921: 572, 573, fig. 13A; pl. VII, figs 4–6; Annandale and Rao 1925: 186.

Limnaea (Pseudosuccinea) luteola – Annandale and Rao 1925: 183, fig. IV(1–7), IX.

Limnaea (Pseudosuccinea) luteola f. *impura* – Annandale and Rao 1925: 184, fig. IV(7).

Limnaea (Pseudosuccinea) luteola f. *australis* – Annandale and Rao 1925: 184, fig. IV(3).

Limnaea (Pseudosuccinea) luteola f. *ovalis* – Annandale and Rao 1925: 184, fig. IV(4).

Limnaea (Pseudosuccinea) luteola f. *succinea* – Annandale and Rao 1925: 184, fig. IV(2).

Lymnaea (Radix) luteola – Brandt 1974: 232, pl. 16, fig. 98 (partim).

Lymnaea (Pseudosuccinea) luteola – Subba Rao 1989: 128, figs 275–287.

Lymnaea (Pseudosuccinea) ovalior – Subba Rao 1989: 129, fig. 285.

Lymnaea (Cerasina) luteola – Kruglov and Starobogatov 1993a: 85, fig. 10C.

Lymnaea (Cerasina) impura – Kruglov and Starobogatov 1993a: 85, fig. 10D, non Troschel 1837 (partim).

Cerasina luteola – Aksenova et al. 2018a: 4.

Racesina luteola – Vinarski and Bolotov 2018: 331.

TL. India, Bengalalia.

Types. Not traced, probably in Muséum d’Histoire Naturelle, Genève, Switzerland.

A highly-variable species, with several intraspecific ‘morphs’ differing from each other by their shell shape and proportions (Annandale and Rao 1925; Subba Rao 1989). The typical morph (see Fig. 9I) has ovate shell with more or less prominent and wide spire and weakly-inflated body whorl. Aperture is moderately expanded. Shell surface is smooth and glossy. We had no fixed specimens of *R. luteola* for dissection; however, according to Hubendick (1951) and Kruglov (2005), the genital morphology of this species generally corresponds to that of the genus *Radix*, except for the drastically different internal structure of the prostate. Penis sheath is very narrow as compared to thick and oblong praeputium, ICA > 1.00 (Hubendick 1951).

R. luteola inhabits India and Nepal (Aksenova et al. 2018a). The recordings of this species from other countries such as China (south), Sri Lanka and the Andamanes (Brandt 1974; Subba Rao 1989) need a molecular re-evaluation. The findings of “*Lymnaea luteola*” in Thailand and Myanmar (Brandt 1974) belong most probably to *R. siamensis* (Sowerby).

24. *Racesina oxiana* (Boettger, 1889)

Figs 8K; 9J; Table 3

Limnaeus impurus var. *oxiana* Boettger 1889: 961, Taf. 27, figs 4, 5.

Cerasina luteola var. *oxiana* – Zhadin 1952: 177, fig. 79.

Lymnaea (Cerasina) impura – Kruglov and Starobogatov 1993a: 85, fig. 10D, non Troschel 1837 (partim).

Cerasina impura – Vinarski and Kantor 2016: 338, non Troschel 1837.

Cerasina oxiana – Aksenova et al. 2018a: 4.

Racesina oxiana – Vinarski and Bolotov 2018: 332.

TL. Turkmenistan, middle Amu-Darya River, ‘Tschardschui’ (nowadays Türkmenabat).

Types. Not traced.

As compared to *R. luteola*, this snail is characterised by a higher spire and ovate-conical shape of shell. In all other respects, it is conchologically very similar to the type species of the genus. The copulatory apparatus of *R. oxiana* specimens from Tajikistan, dissected by us, was virtually identical with that of *R. luteola* from India studied and illustrated by Hubendick (1951). Penis sheath is very narrow, its length is almost equal to length of praeputium or slightly less (see Fig. 8K).

This species of *Racesina* is distributed in Central Asia (within the ex-USSR boundaries) and Nepal (Aksenova et al. 2018a). The oldest available name, based on a type locality situated within this area, is *Limnaeus impurus* var. *oxiana* Boettger, 1889. Though Kruglov and Starobogatov (1993b) treated this taxon as identical with *Lymnaea impura*, the type locality of the latter species is in India, where *R. oxiana* does not occur. *L. impura* is, most probably, a junior synonym of *R. luteola* (Hubendick 1951; Brandt 1974).

25. *Racesina siamensis* (G.B. Sowerby II, 1872)

Figs 8L; 9K; Table 3

Limnaea siamensis G.B. Sowerby II 1872: pl. X, fig. 63.

Limnaea luteola f. *siamensis* – Annandale and Rao 1925: 185, fig. IV(5, 6).

Lymnaea (Radix) luteola – Brandt 1974: 232, pl. 16, fig. 98 (partim).

Cerasina siamensis – Aksenova et al. 2018a: 4.

Racesina siamensis – Vinarski and Bolotov 2018: 332.

TL. “Siam” (= Thailand).

Types. Not traced.

Aksenova et al. (2018a) used this name as the oldest one applicable to a species of *Racesina* which is distributed in Myanmar and Thailand. Though Brandt (1974) considered *L. siamensis* as a junior synonym of *Radix rubiginosa*, our data show it is untenable. Despite the substantial genetic distance separating *Racesina siamensis* and *R. luteola*, we were not able to find prominent morphological differences between them, either in conchological or in anatomical characters. It allows us to treat *R. siamensis* as a ‘cryptic’ taxon. Note, however, that we had only a limited number of specimens from Myanmar and some stable morphological differences between the two species will probably be found in future after a thorough study of their intraspecific variation. There is a strong need for a detailed study of genetic diversity and phylogeography of the *Racesina luteola* species complex.

Morphological note. In a sample of eleven individuals of *R. siamensis* from Myanmar, dissected by us, five snails had under-developed copulatory apparatuses or lacked them altogether. No signs of a heavy parasite load were seen, thus the hypothesis of the parasitic castration may be rejected. Such a state (aphally) has been registered in different families of freshwater pulmonates, including Physidae, Planorbidae and Lymnaeidae (see Vinarski and Palatov 2018 and references therein). For the radicles, aphally was reported by Arutyunova (1977).

Aphally in aquatic pulmonates is often viewed as an indirect sign of obligate self-fertilisation (autogamy), which may facilitate their introduction into new habitats and rapid establishment of new populations (Beriozkina and Starobogatov 1991; Jarne et al. 1993). Due to a limited sample size, it is unclear whether our finding indicates that *R. siamensis* is a species prone to self-fertilisation. However, it is a remarkable fact that the aphally was not found during this research in the rest of the radicine species studied anatomically.

Genus *Orientogalba* Kruglov & Starobogatov, 1985

Orientogalba Kruglov and Starobogatov 1985a: 28.

Viridigalba Kruglov and Starobogatov 1985a: 29.

Type species. *Lymnaea heptapotamica* Lazareva, 1967.

Kruglov and Starobogatov (1985a) established their subgenus *Lymnaea (Orientogalba)* to embrace five nominal lymnaeid species distributed in a vast Pacific Region, stretching from north-eastern Asia to the Guam and Hawaii. Though, conchologically, these snails resemble representatives of the genus *Galba*, their genital morphology is typical for the radicles (Kruglov 2005). The molecular analysis conducted by Aksenova et al. (2018a) has shown that there are at least three biological species within *Orientogalba*, which are presumably allopatric: *O. viridis* (Indonesia and Pacific Islands), *O. ollula* (Far East and, probably, some regions of Central Asia) and *O. cf. bowelli* (known from Sichuan, China and, probably, also inhabiting Tibet). The actual range of these species remains unknown since only a limited set of sequences has been available. The true species content of *Orientogalba* is unknown as well, because some nominal species of this genus, such as *Orientogalba heptapotamica* (Lazareva) and *O. lenaensis* (Kruglov et Starobogatov, 1985) have not been studied molecularly. The true taxonomic position of “*Austropeplea viridis*”, recently recorded from Spain as an alien species (Schniebs et al. 2017), must also be clarified.

In our opinion, the genus *Orientogalba* is not a junior synonym of the genus *Austropeplea* Cotton, 1942, as was suggested by some authors (Ponder and Waterhouse 1997; Schniebs et al. 2017).

26. *Orientogalba viridis* (Quoy & Gaimard, 1832)

Fig. 9L

Lymnaea viridis Quoy and Gaimard 1832: 204, pl. 58, figs 16–18.

Lymnaea viridis – Hubendick 1951: 162, fig. 351 (partim).

Lymnaea (Radix) viridis – Brandt 1974: 231, pl. 16, fig. 97.

Lymnaea (Orientogalba) viridis – Kruglov and Starobogatov 1993b: 174, fig. 10C.

Orientogalba viridis – Aksenova et al. 2018a: 4; Glöer 2019: 246, fig. 307.

TL. The Pacific, Marian Archipelago, Guam Island.

Syntypes. MNHN (examined by us).

Our concept of this species is based on the type series of *O. viridis* (see Fig. 9L). Shell is almost globose, with relatively wide and short spire and heavily-inflated body whorl. Aksenova et al. (2018a) recorded *O. viridis* from Indonesia. Numerous recordings of this species from other areas, including China, Mongolia, Thailand, Siberia, Spain and some others (Hubendick 1951; Brandt 1974; Kruglov and Starobogatov 1985a, 1993b; Schniebs et al. 2017; Vinarski et al. 2017), were based chiefly on morphological evidence and, therefore, the actual range of *O. viridis* sensu Aksenova et al. (2018a) is unclear.

27. *Orientogalba ollula* (Gould, 1859)

Figs 8M; 9N; Table 3

Limnaea ollula Gould 1859: 40.

Limnaeus pervius von Martens 1867: 221.

Limnaea viridis – Hubendick 1951: 162, fig. 351 (partim).

Galba pervia – Zhadin 1952: 176, fig. 77.

Limnaea (Orientogalba) ollula – Kruglov and Starobogatov 1993b: 175, fig. 10C.

Orientogalba ollula – Vinarski and Kantor 2016: 357; Aksenova et al. 2018a: 4.

TL. China, streams and marshes of Hong Kong Island.

Lectotype. National Museum of Natural History, Smithsonian Institution, Washington, USA (Johnson 1964).

Though the type material of *L. ollula* Gould is extant, we were unable to study it. Instead, we examined a small series of shells of this species collected in Yokohama, Japan (NHMUK). Shell is ovoid, with shortened spire and strongly-inflated body whorls. Generally, it much resembles the shell of *O. viridis* and we could not delimit these two taxa by means of conchology. Like most species of radicles discussed above, *O. ollula* is characterised by the disproportion in sizes between the penis sheath and praeputium, the latter being much larger and broader (see Fig. 8M).

Taxonomic remark. This species, described from eastern China, has usually been considered as a junior synonym of *O. viridis* (Hubendick 1951; Brandt 1974); however, Kruglov and Starobogatov (1993b) regarded it as a separate taxon. The results of our study allowed us to accept their opinion and use the name *O. ollula* to label a species of *Orientogalba*, widely distributed in China (found also in South Korea and Nepal). Perhaps, all recordings of “*Limnaea viridis*” from Siberia, Russian Far East and Mongolia (Kruglov and Starobogatov 1985a, 1993b; Vinarski and Kantor 2016; Vinarski et al. 2017) should also be referred to as *O. ollula*.

28. *Orientogalba cf. bowelli* (Preston, 1909)

Fig. 9N, O

Limnaea bowelli Preston 1909: 115, fig. 1.

Limnaea bowelli – Annandale and Rao 1925: 169, fig. V(6).

Limnaea (Galba) bowelli – Subba Rao 1989: 131, figs 298, 299.

Orientogalba cf. bowelli – Aksenova et al. 2018a: 4.

TL. Tibet, “Te-ring Gompa, in a small hill stream arising from a spring, 14,000 feet; also from Mangtsa, 14,500 feet; High Hill, Gompa, Gyantse valley in a small hill stream, among moss and stones, 14,500 feet; and Gyantse, 13,120 feet”.

Types. Zoological Survey of India, Kolkata (fide Subba Rao 1989).

This poorly-studied species inhabits China: Tibet, Sichuan Province (Subba Rao 1989; Aksenova et al. 2018a) and possibly lives in other parts of the High Asia (Kruglov and Starobogatov 1985a; Kruglov 2005). Conchologically, it represents a typical *Orientogalba* and the traits allowing one to distinguish it surely from the two above-mentioned species of this genus are unknown. A special study of intraspecific variation in *O. cf. bowelli* and allied species is needed to delineate them on the basis of morphological data. The data on anatomy of *O. cf. bowelli* are scarce. Though Kruglov (2005) gave a rather detailed description of its genital morphology, the picture provided by this author (Kruglov 2005: fig. 90) illustrates an animal belonging to the genus *Galba*, not *Orientogalba*.

Taxonomic remark. The application of the binomen *Limnaea bowelli* Preston is difficult. Recent authors tend to consider it as a member of the (sub)genus *Galba*, whose distribution is restricted to High Asia (Subba Rao 1989; Kruglov 2005; Vinarski and Kantor 2016). On the other hand, Hubendick (1951) hypothesised that *Limnaea bowelli* is identical with *Radix auricularia*, whereas Brandt (1974) synonymised *L. bowelli* with *L. viridis*. The type series was unavailable for Aksenova et al. (2018a) and the authors conditionally attached the Preston’s taxon name to a species of *Orientogalba* found in Sichuan Province of China. Having examined several small samples of this species kept in NHMUK and NHMN, we found that these shells may belong to *Orientogalba*; some of them are very similar to shells of *O. viridis*, whereas others were more or less like Preston’s original drawing (see Fig. 9N, O).

Genus *Bullastra* Bergh, 1901

Bullastra Bergh 1901: 254.

Type species. *Bullastra velutinoides* Bergh, 1901.

A genus with South Asian – Australasian distribution. It includes several nominal species living in Philippines, Indonesia and mainland Australia (Kruglov and Starobogatov 1993a; Puslednik et al. 2009). Aksenova et al. (2018a) have studied one of these species.

28. *Bullastra cumingiana* (L. Pfeiffer, 1845)

Figs 8N; 9P; Table 3

Amphipeplea cumingiana Pfeiffer 1845: 68.

Amphipeplea cumingi Pfeiffer 1854–1860: 5, pl. II, figs 3, 4.

Bullastra velutinoides Bergh 1901: 254, pl. 20, figs 22–34.

Limnaea cumingiana – Hubendick 1951: 162, fig. 355.

Bullastra cumingiana – Aksenova et al. 2018a: 4.

TL. Philippines, island of Luzon, Naga, province of South Camerines.

Probable syntypes. ZMB (see Vinarski 2016a for details).

Hubendick (1951) provided a description of shell, radula and genital morphology of this peculiar species. By its almost globose shell, with extremely reduced spire and extended and reflected mantle border, *B. cumingiana* superficially resembles *M. glutinosa*; however, the alleged phylogenetic affinity between the two snails has been rejected by Hubendick (1951) and Kruglov (2005).

Two specimens of *B. cumingiana* originated from Lake Sampaloc (Philippines, Luzon Island; LMBI collection) were dissected during this study. The structure of the copulatory apparatus is typical for radicines. Praeputium is enlarged and widened, its length is around twice that of the penis sheath length (see Fig. 8N). Penis sheath is short and narrow. The ICA values of the two dissected individuals were 2.11 and 2.13. Both parts of the copulatory apparatus are light-coloured.

B. cumingiana is endemic to the Philippine Islands (Hubendick 1951).

Discussion

In this article, we attempted to present the taxonomic accounts for all species of the Old World radicines genetically delineated up to now. The 35 biological species of radicine snails recovered during our molecular taxonomic study (Aksenova et al. 2018a) by no means exhaust the overall diversity of extant species in this group. There are morphologically-distinct species of the radicines still not studied genetically and their actual taxonomic status and phylogenetic affinities remain unclear. Such species of Central Asia as *Radix obliquata* (Martens, 1864) and *R. cucunorica* (Möllendorff, 1902) may be mentioned here as two examples. In our opinion, the actual glob-

al taxonomic richness of the radicines may approach 50 valid species.

These molluscs exhibit an impressive variation in their shell characters, including shell size, shape, number of whorls, aperture proportions and so on (see Figs 2, 4). Strikingly, this wide repertoire of shell forms is not accompanied by any substantial anatomical diversity. As we tried to show, the structure of the copulatory apparatus remains virtually the same within the Old World radicines (see Figs 3, 7). Although the species slightly differ from each other by the ICA values, the overall morphological scheme of this organ is identical within the group. Though Kruglov (2005) used the ICA as a tool for delineation and identification of radicine species, the usefulness of this ratio for lymnaeid systematics is sometimes questioned. Some authors considered its intraspecific variation too high to provide significant and reproducible results (Schniebs et al. 2011, 2013). Our results have shown that there are no hiatuses in the ICA values of sister species (see Tables 1–3) and, thus, this ratio is almost useless for species diagnostics. Though the species may differ by some qualitative characters, such as pigmentation of praeputium (compare colouration of this organ in two sister species, *A. fontinalis* and *A. lagotis*: Fig. 8D, E), we do not have information how widely this trait varies amongst populations of the same species.

A comparison of conchological, anatomical and karyological traits of the radicine genera discussed in Aksenova et al. (2018a) and this paper is given in Table 4. The structure of the copulatory organ within radicines is so uniform that it led some researchers to a drastic reduction of the number of valid species they agreed to accept (see, for example, Hubendick 1951; Jackiewicz 1998). On the other hand, there were malacologists with a strong inclination to species splitting. For example, Kruglov and Starobogatov (1993a, b) delineated more than 90 nominal radicine species within the Northern Eurasia alone. The recent works,

Table 4. A comparison of conchological, anatomical and caryological features of the genera and subgenera of the Old World radicines*.

Genus (Subgenus)	Shell height	Shell shape	Shell surface	Spire	Spermathecal duct	Mantle border	Haploid chromosome number	Number of prostate folds
<i>Racesina</i>	Up to 25 mm	Ovoid to ovate-conical	Smooth	High and relatively wide	Long	?Reflected	?17	5–8
<i>Myxas</i>		Globose		Flattened, very low		Reflected		
<i>Radix</i> s. str.	Up to 35 mm	Ear-shaped to ovate-conical	Sculptured	Low and acute	Short	Not reflected	?17	1
<i>Exsertiana</i>								
<i>Ampullaceana</i>	Up to 25 mm	Ear-shaped to conical		Low to relatively high and obtuse				
<i>Peregriana</i>	Up to 25 mm	Ovate-conical to conical		Medium-sized and obtuse				
<i>Kamtschaticana</i>	Up to 20 mm	Ovate-conical to almost globose		Low and obtuse			?17	
<i>Tibetoradix</i>	Up to 15 mm	Ovate-conical		High to medium-sized, narrow and obtuse	Long		?17	
<i>Orientogalba</i>		Ovate-conical to almost globose		High to low, obtuse				
<i>Bullastra</i>	Up to 30 mm	Globose	Smooth	Very low, reduced, obtuse	Long	Reflected	16	

*After Aksenova et al. (2018a), modified.

based on the integrative taxonomic approach, have shown that many of these nominal taxa lack molecular support and should be synonymised (Aksenova et al. 2016, 2017; Vinarski et al. 2016). The ratio between valid and non-valid species in this group may be around 1:4 (Vinarski et al. 2016).

Unfortunately, due to overlap of morphological traits, including both shell and soft body characters, between closely allied species of radicles (Schniebs et al. 2011, 2013), to develop a dichotomous key for identification of snails is next to impossible. The molecular methods are most reliable for species determination in this group (Schniebs et al. 2011, 2013; Vinarski et al. 2016), though there are morphologically-distinct taxa (such as *Myxas glutinosa*), whose correct identification is possible on the basis of shell characters alone. The use of the reproductive anatomy characters, such as the ICA, is very limited due to the relative uniformity of the copulatory organ structure within the radicles.

Though the evolutionary processes in this group have rarely been studied and discussed, the high species richness and endemism of Radicinae in the mountain part of Central Asia is remarkable. This region forms an obvious hotspot of diversity of this group, with at least one endemic genus (*Tibetoradix*), which includes not less than six narrow-range species. In addition, at least four species of the genus *Radix* (*R. alticola*, *R. brevicauda*, *R. makhrovi*, *Radix dgebuadzei*) are restricted in their distribution to High Asia. This highlights the significance of the region for evolution of the current diversity of the subfamily Amphipepleinae and the probable role of mountain refugia for speciation in lymnaeid snails (see Aksenova et al. 2018a for details).

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