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An overview of *Radix* species of the Kamchatka Peninsula (Gastropoda: Lymnaeidae)[1]

O.V. Aksenova[1], M.V. Vinarski[2], I.N. Bolotov[1], Yu.V. Bespalaya[1], A.V. Kondakov[1], I.S. Paltser[1]

[1]Federal Center for Integrated Arctic Research, Russian Academy of Sciences, Arkhangelsk 163000, Russia
e-mail: aksyonova.olga@gmail.com

[2]St. Petersburg State University, St. Petersburg 199034, Russia

In the present review, we compiled data about lymnaeid snails of the genus *Radix* Montfort, 1810 inhabiting waterbodies of the Kamchatka Peninsula (northeastern Russia), with a concise historical survey of previous investigations. Brief accounts for each species and information on their distribution in the Kamchatka Peninsula are given. The results of a taxonomic study of some endemic species of *Radix* are summarized. It is shown that the integrative taxonomic approach, based on combined use of molecular and morphological data, brings new results, including re-evaluation of taxonomic status of some alleged species of *Radix*. We found that several nominal species of *Radix* thought to be endemic to Kamchatka should not be considered as valid taxa. Thus, the overall species richness of *Radix* of the studied region is lower than it was assumed by previous workers.

Key words: *Radix*, freshwater molluscs, species richness, Kamchatka Peninsula, integrative taxonomy.

Обзор видов рода *Radix* (Gastropoda: Lymnaeidae) полуострова Камчатка

О.В. Аксёнова[1], М.В. Винарский[2], И.Н. Болотов[1], Ю.В. Беспалая[1], А.В. Кондаков[1], И.С. Пальцер[1]

[1]Федеральный исследовательский центр комплексного изучения Арктики РАН, Архангельск 163000, Россия
e-mail: aksyonova.olga@gmail.com

[2]Санкт-Петербургский государственный университет, С.-Петербург 199034, Россия

В настоящей работе обобщены сведения о моллюсках рода *Radix* Montfort, 1810, населяющих водоемы Камчатского полуострова. Коротко рассмотрена история изучения этой группы из водоемов Камчатки. Приведены краткие описания для каждого вида и информация об их распространении на полуострове. Представлены результаты таксономической ревизии двух эндемичных видов. Показано, что применение интегративного таксономического подхода, основанного на синтезе молекулярно-генетических и морфолого-анатомических данных, позволяет получить новые результаты при оценке таксономического статуса моллюсков рода *Radix*. Нами установлено, что два вида данного рода, ранее считавшиеся эндемиками Камчатки, не могут рассматриваться в качестве валидных таксонов. Таким образом, общее видовое богатство моллюсков рода *Radix* исследуемой территории оказывается ниже, чем это принималось предшествующими исследователями.

Ключевые слова: *Radix*, пресноводные моллюски, видовое богатство, Камчатка, интегративная таксономия.

[1] This paper was presented at the **3rd Symposium of the Benthological Society of Asia** (BSA–2016) held in Vladivostok, Russia on 24–26 August, 2016.

Molluscs of the genus *Radix* Montfort, 1810 are distributed almost worldwide (except of South America and Australia where no indigenous species of the genus are known). The type species of the genus is *Radix auricularia* (Linnaeus, 1758), the ear-shaped pond snail, that inhabits Europe, Northern and Central Asia as well as North America [Burch, 1989; Kruglov, Starobogatov, 1993a]. Eurasia maintains the highest species diversity of *Radix*, though it is very difficult to say exactly how many valid species of the genus are there. In the lymnaeid taxonomy of the 20th century two extremely opposite views on *Radix* diversity have been developed. The first one is that of Hubendick [1951], a prominent Swedish malacologist, who tried to classify Lymnaeidae on the basis of extensive usage of anatomical data. He did not use the taxonomic name *Radix*, and all species currently placed to this genus were classified by Hubendick [1951] as belonging to the genus *Lymnaea* Lamarck, 1799. The author accepted only two species currently placed to *Radix*: *Lymnaea auricularia* (L., 1758) and *L. peregra* (O.F. Müller, 1774).

Hubendick's approach to lymnaeid taxonomy may be considered as «hyper-lumping» since this author almost totally ignored relatively small albeit stable differences in shell morphology and reproductive anatomy treating them as insignificant manifestations of intraspecific variability.

The opposite approach to systematics of lymnaeid snails was proposed in the USSR by Kruglov and Starobogatov [1989, 1993a, b]. These authors have been viewed as explicit «splitters». They considered two Hubendick's species as corresponding to two subgenera of the genus *Lymnaea*: *Radix* s.s. (type species *Helix auricularia* Linnaeus, 1758) and *Peregriana* Servain, 1881 (type species *Buccinum peregrum* Müller, 1774). Both subgenera, according to Kruglov and Starobogatov [1993a], consist of several «sections» uniting groups of closely related species. As a result, the Soviet authors could accept as many as nearly 50 nominal species of *Radix* s.s. and *Peregriana*. Many of these species were described by Kruglov and Starobogatov as new, sometimes on the basis of a few specimens.

Most modern authors choose to follow the «middle» path lying somewhere between these two extremities. Usually, several (i.e., more than two) species of *Radix* are accepted as valid both for European [Falkner et al., 2001; Glöer, 2002; Welther-Schultes, 2012] and Asian [Subba Rao, 1989] faunas. The recent molecular-genetic researches [Bargues et al., 2001, 2003; Pfenniger et al., 2006; Schniebs et al., 2011, 2013] as well as studies based on the so-called «integrative» taxonomic methodology [Vinarski et al., 2016] give support to this «middle» approach. For example, *Lymnaea peregra* sensu Hubendick, 1951 proved to be nothing but a complex of several species that can be surely distinguished by genetic means only [Schniebs et al., 2011, 2013; Vinarski et al., 2016]. The conchological and anatomical differences among these taxa are less prominent, and the ranges of variation of their phenotypical characters may overlap.

In this paper, we present an overview of *Radix* species living in waterbodies of the Kamchatka Peninsula (north-east of Asiatic Russia). This overview is based partly

on results of our own work, including molecular-genetic and morphological studies of recently collected specimens as well as examination of museum collections gathered during last 150 years. Also, the available literary sources were used in order to cover the species not studied by us. Following Vinarski [2013], we accept the genus *Radix* s.l. as consisting of two subgenera: *Radix* s.s. and *Peregriana*.

Material and methods

Initially the lymnaeid snails were identified on the basis of morphological and anatomical features with using determination keys proposed by Kruglov [2005]. For morphometric study of variation, shells of 285 specimens of *Radix* spp. were measured by means of calipers or ocular-micrometer of the stereoscopic microscope Leica M165C (Leica Microsystems, Germany) to an accuracy of 0.1 mm. The scheme of measurement included standard measures [Kruglov, 2005]: shell height, shell width, height of spire, height of aperture and width of aperture (Table 1).

Afterwards DNA was extracted from the foot tissue of each specimen [Bolotov et al., 2014]. Phylogenetic analyses were based on 62 newly produced COI sequences and 39 new ITS sequences from specimens collected in Kamchatka and other regions as well as on additional sequences obtained from the NCBI GenBank. The list of used specimens and DNA sequences is presented in Table 2.

We used samples of snails stored in the collections of the Russian Museum of Biodiversity Hotspots of the Federal Center for Integrated Arctic Research of the Russian Academy of Sciences (RMBH FCIARactic RAS, Arkhangelsk, Russia). The molecular analysis was performed in the Laboratory of Molecular Ecology and Biogeography, FCIARctic RAS and the Engelhardt Institute of Molecular Biology, Russian Academy of Sciences (EIMB RAS, Moscow, Russia). Also, we studied samples of *Radix* from the Kamchatka waterbodies kept in the malacological collection of the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (hereafter, ZIN) and a photo of a syntype of *R. zazurnensis* kept in the National Museum of Natural History, Smithsonian Institution in Washington (hereafter, USNM).

A history of study of the Kamchatka *Radix*

A.Th. von Middendorff [1850, 1851], a brilliant Russian traveller and zoologist, was the first author to publish data on freshwater molluscs of Kamchatka. Although Middendorff himself did not manage to reach Kamchatka during his famous travel through Siberia, 1842–1845 [Sukhova, Tammiksaar, 2015], he could study malacological materials collected by I.G. Voznesenskiy (1816–1871), a naturalist who widely travelled in North America and the Russian Far East. As a result, Middendorff [1851] recorded two species of the genus *Limnaeus* (=*Lymnaea*) that actually belong to *Radix*: *L. ovatus* Draparnaud, 1805 and *L. kamtschaticus* Middendorff, 1850. The latter was

Table 1

Morphometric characteristics (mm) of studied specimens

Character/index	Shell width (SW)	Shell height (SH)	Spire height	Aperture height (AH)	Aperture width (measured with columellar lip)	Aperture width (measured without columellar lip) (AW)	SH/SW	AH/AW
Radix thermokamtschatica from the ZIN collection (n=70)	3–9.5 6.28±0.18	4.7–12.7 9.3±0.23	1.5–4.1 2.65±0.05	3.2–10.3 6.65±0.19	2.1–7.5 4.62±0.15	1.8–6.3 3.88±0.13	1.29–1.69 1.49±0.01	1.44–2.1 1.73±0.01
R. hadutkae from the ZIN collection (n=87)	2.9–12.6 4.88±0.18	4.4–17 7.08±0.24	1–4.1 1.8±0.05	3.2–13.1 5.28±0.19	2–9.5 3.4±0.14	1.7–8 2.95±0.12	1.28–1.65 1.46±0.01	1.53–2.0 1.81±0.01
R. auricularia from thermal lake Khodutka (our data) (n=26)	5–10.41 6.7±0.27	7.3–14.5 9.94±0.36	1.5–3.3 2.56±0.07	5–11.78 7.37±0.34	3.3–8.21 4.97±0.25	2.8–6.4 4.1±0.19	1.31–1.6 1.48±0.15	1.65–1.97 1.80±0.01
R. auricularia from Verkhne-Paratunskie Hot Springs (our data) (n=28)	2.9–6.7 4.83±0.19	4.3–9 6.96±0.23	1.2–2.5 1.73±0.06	3.1–6.9 5.23±0.19	1.9–5.2 3.58±0.15	1.7–4.1 2.95±0.12	1.32–1.61 1.45±0.02	1.60–2.04 1.77±0.02
R. auricularia from Plotnikova River (our data) (n=4)	7.5–13.7	10.53–17.12	3.55–4.79	6.98–13.29	3–10.14	4.5–8.49	1.25–1.55	1.55–1.73
R. kamtschatica from thermal springs of the Valley Geysers (our data) (n=20)	2.35–6.3 3.98±0.25	3.6–8.3 5.45±0.31	1.05–2.0 1.41±0.06	2.55–6.5 4.05±0.13	1.95–4.8 3.15±0.27	1.3–3.8 2.47±0.16	1.27–1.53 1.38±0.01	1.46–1.96 1.64±0.03
R. kamtschatica from Nalychevskie Hot Springs (our data) (n=26)	3.8–7.0 5.03±0.14	5.0–9.4 6.62±0.19	1.3–2.4 1.62±0.05	3.7–7.3 5.01±0.16	2.7–5.3 3.68±0.12	2.2–4.3 3.02±0.10	1.20–1.48 1.32±0.01	1.48–2.0 1.67±0.02
R. kamtschatica from Karymshinskie Hot Springs (our data) (n=24)	3.4–5.3 4.3±0.10	5.0–7.3 6.31±0.14	1.2–1.8 1.53±0.04	3.8–5.8 4.77±0.12	2.6–4.0 3.20±0.08	2.0–3.2 2.48±0.06	1.32–1.56 1.46±0.01	1.64–2.15 1.92±0.03

N o t e. Above line – minimum and maximum values; below line – mean value ± standard error of the mean.

Table 2

List of specimens of the Lymnaeidae used in the molecular genetic analysis

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
*Galba truncatula**	MTD Moll S1130	Bulgaria: Kyustendil	FR797873	FR797845
*Lymnaea stagnalis**	SNSD Moll S3436	Germany: Mecklenburg-Vorpommern	HG932257	HG931966
Radix ampla	SNSD Moll S2924	Switzerland: Bielersee Lake	HG932231	HG931945
R. ampla	SNSD Moll 53083	Germany: Baden-Wuerttemberg	HG932229	HG931944
R. ampla	SNSD Moll 53082	Germany: Baden-Wuerttemberg	HG932228	HG931943
R. ampla	isolate 5097	Montenegro: Niksic, Brezovik, Zeta River	EU818804	N/A**
R. auricularia	SNSD Moll S5211	Italy: Sicily, National Park Bosco della Ficuzza	HG932219	HG931935
R. auricularia	SNSD Moll S5210	Italy: Sicily, National Park Bosco della Ficuzza	HG932218	HG931934
R. auricularia	SNSD Moll 53087	Switzerland: Lake Constance near Güttingen	HG932217	HG931933
R. auricularia	MTD Moll S1313	Germany: Mecklenburg-Western Pomerania, Plauer See Lake	FR797878	N/A
Radix sp. clade 1	PVVO-2011 isolate 12673	China: Tibet, pond in Shigatse	JN794471	N/A
Radix sp. clade 1	PVVO-2011 isolate 12036	China: Qinghai, small river west of Budongquan	JN794427	N/A
R. auricularia	MlymB-107.1*	Russia: Republic of Buryatia, Lake Baikal	KT867317	KT867282
R. auricularia	INEP-231.1*	Russia: Kamchatka, Plotnikova River (Bolshaya Basin)	KM067612	KT867282
R. auricularia	INEP-231.3*	Russia: Kamchatka, Plotnikova River (Bolshaya River Basin)	KM067613	KT867288
R. auricularia	INEP-241*	Russia: Kunashir Island, Aliger Lake	KM067614	KY091886
R. auricularia	INEP-498*	Russia: Sakhalin Island, Tym River	KM067615	KT867289
R. auricularia	INEP-499.1*	Russia: Primorye, Ussuri River (Amur Basin)	KM067616	KT867290

Table 2 (Continued)

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
R. auricularia	INEP-500*	Russia: Primorye, small pond near Razdolnaya River	KM067618	KT867291
R. auricularia	INEP-375.1*	Russia: Kamchatka, Khodutka geothermal area	KM067602	KT867292
R. auricularia	INEP-385.2*	Russia: Kamchatka, Khodutka geothermal area	KM067603	KT852375
R. auricularia	INEP-385.3*	Russia: Kamchatka, Khodutka geothermal area	KM067604	KY091887
R. auricularia	INEP-491.1*	Russia: Kamchatka, Khodutka geothermal area	KM067605	N/A
R. auricularia	INEP-379.1*	Russia: Kamchatka, Verkhne-Paratunskie Hot Springs	KM067597	KY091888
R. auricularia	INEP-386.2*	Russia: Kamchatka, Verkhne-Paratunskie Hot Springs	KM067599	KT867287
R. auricularia	INEP-378.1*	Russia: Kamchatka, Verkhne-Paratunskie Hot Springs	KM067596	N/A
R. auricularia	INEP-393.1*	Russia: Kamchatka, Verkhne-Paratunskie Hot Springs	KM067598	N/A
R. auricularia	INEP-117.1*	Russia: Kamchatka, Malkinskie Hot Springs	KM067607	N/A
R. auricularia	INEP-117.3*	Russia: Kamchatka, Malkinskie Hot Springs	KM067608	N/A
R. auricularia	INEP-119.3*	Russia: Kamchatka, Malkinskie Hot Springs	KM067609	N/A
R. auricularia	INEP-119.4*	Russia: Kamchatka, Malkinskie Hot Springs	KM067610	N/A
R. kamtschatica	INEP-381.1*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067572	N/A

Table 2 (Continued)

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
R. kamtschatica	INEP-381.4*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067573	KP272173
R. kamtschatica	INEP-381.5*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067574	N/A
R. kamtschatica	INEP-381.6*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067575	KP272174
R. kamtschatica	INEP-381.7*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067576	N/A
R. kamtschatica	INEP-381.8*	Russia: Kamchatka, Karymshinskie Hot Springs	KM067577	N/A
R. kamtschatica	INEP-108*	Russia: Kamchatka, Nalychevskie Hot Springs, anabranch of the Goryachaya River	KM067578	KP272175
R. kamtschatica	INEP-112.1*	Russia: Kamchatka, Nalychevskie Hot Springs, anabranch of the Goryachaya River	KM067581	N/A
R. kamtschatica	INEP-112*	Russia: Kamchatka, Nalychevskie Hot Springs, anabranch of the Goryachaya River	KM067582	N/A
R. kamtschatica	INEP-118*	Russia: Kamchatka, Nalychevskie Hot Springs, anabranch of the Goryachaya River	KM067583	KP272176
R. kamtschatica	INEP-110*	Russia: Kamchatka, Talovskie Hot Springs	KM067579	KP272177
R. kamtschatica	INEP-110.1*	Talovskie Hot Springs	KM067580	KP272178
R. kamtschatica	INEP-366.1*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067584	KP272171
R. kamtschatica	INEP-366.2*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067585	N/A

Table 2 (Continued)

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
R. kamtschatica	INEP-366.3*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067586	N/A
R. kamtschatica	INEP-366.4*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067587	N/A
R. kamtschatica	INEP-367.1*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067588	KP272172
R. kamtschatica	INEP-368.1*	Russia: Kamchatka, Nizhne-Semyachikskie Hot Springs, warm stream	KM067589	N/A
R. kamtschatica	INEP-369.1*	Russia: Kamchatka, Valley of Geysers	KM067590	KP272169
R. kamtschatica	INEP-369.2*	Russia: Kamchatka, Valley of Geysers	KM067591	N/A
R. kamtschatica	INEP-369.3*	Russia: Kamchatka, Valley of Geysers	KM067592	N/A
R. kamtschatica	INEP-370.1*	Russia: Kamchatka, Valley of Geysers	KM067593	N/A
R. kamtschatica	INEP-371.1*	Russia: Kamchatka, Valley of Geysers	KM067594	N/A
R. kamtschatica	INEP-373.1*	Russia: Kamchatka, Valley of Geysers	KM067595	KP272170
R. kamtschatica	Mlym-84*	Russia: Republic of Buryatia, Baunt Hot Spring	KX056245	KX056256
R. kamtschatica	Mlym-84/1*	Russia: Republic of Buryatia, Baunt Hot Spring	KX056246	KX056257
R. kamtschatica	Mlym-85*	Russia: Republic of Buryatia, Bagdarinka River	KX056247	KX056258
R. kamtschatica	Mlym-101*	Russia: Khabarovsk Krai, Chegdomynka River	KX056248	KX056259
R. kamtschatica	Mlym-101/1*	Russia: Khabarovsk Krai, Chegdomynka River	KX056249	KX056260

Table 2 (Continued)

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
R. kamtschatica	Mlym-101/2*	Russia: Khabarovsk Krai, Chegdomynka River	KX056250	KX056261
R. kamtschatica	Mlym-102*	Russia: Kamchatka, Plotnikova River	KX056251	KX056262
R. balthica	SNSD Moll S334	Germany: Mecklenburg-Western Pomerania, Oberbek south of Fleeth	HG932224	HG931940
R. balthica	SNSD Moll 51139	Russia: Tomsk Region, Motshishtshe Lake	HG932222	HG931938
R. balthica	isolate SnUK7	United Kingdom: Norfolk, Pensthorpe Park	KT337572	KT337593
R. balthica	isolate SnUK19	United Kingdom: Surrey, Ham Dip	KT337582	KT337603
R. labiata	SNSD Moll S6139	Slovenia: Žalec, Velika Reka near Prebold	HG932227	HG931942
R. labiata	INEP-409/1*	Russia: Arkhangelsk Region, a pond near Guzhovo Village	KX056252	KX056263
R. labiata	Mlym-117/3*	Slovakia: Low Tatras, river near Vihodna	KX056253	KX056264
R. labiata	Mlym-120/3*	Slovakia: Eastern Carpathians	KX056254	KX056265
R. labiata	isolate 5812	France: Corsica, Corte, Tavignano River	EU818829	N/A
R. dolgini	MlymB-61*	Russia: Republic of Buryatia, Kiron Lake	KT030067	KT030049
R. dolgini	MlymB-87*	Russia: Republic of Buryatia, Verkhnyaya Angara River	KT030070	KT030052
R. dolgini	MlymB-88*	Russia: Republic of Buryatia, Verkhnyaya Angara River	KT030071	KT030053
R. dolgini	MlymB-91*	Russia: Republic of Buryatia, Verkhnyaya Angara River	KT030074	KT030056
R. relicta	isolate 5818	Macedonia: Radoszda, Lake Ohrid	EU818830	N/A
R. relicta	isolate 5416	Macedonia: artificial lake of Sum Spring	EU818820	N/A

Table 2 (Continued)

Species name	Voucher number	Locality	NCBI accession number	
			COI	ITS
Radix sp. clade 2	PVVO-2011 isolate 10052	China: Tibet, Yamdrok Yumtso	JN794366	N/A
Radix sp. clade 2	PVVO-2011 isolate 10056	China: Tibet, Yamdrok Yumtso	JN794371	N/A
Radix sp. clade 2	PVVO-2011 isolate 12318	China: Tibet, Lang Tso	JN794434	N/A
Radix sp. clade 2	PVVO-2011 isolate 12321	China: Tibet, pond near Sangsang	JN794439	N/A
Radix sp. clade 2	PVVO-2011 isolate 12325	China: Tibet, small stream west of Baryang	JN794451	N/A
Radix sp. clade 2	PVVO-2011 isolate 12066	China: Tibet, stream north of Senge Tsangpo	JN794463	N/A
Radix sp. clade 3	PVVO-2011 isolate 12312	China: Yunnan, Lake Yangzong	JN794487	N/A
Radix sp. clade 3	PVVO-2011 isolate 9370	Vietnam: Kon Tum Province, rice fields south of Dak Glei	JN794514	N/A
Radix sp. clade 5	PVVO-2011 isolate 12660	Nepal: Seti Zone, Bajhang District, ponds	JN794504	N/A
Radix sp. clade 5	PVVO-2011 isolate 11245	Nepal: Mahakali Zone, Kanchanpur District, Chandara River	JN794503	N/A
R. lagotis	isolate 10953	Russia: Altai Republic, Teletskoye Lake	JN794510	N/A
R. lagotis	INEP-138.1*	Russia: Chernyshev Hill Ridge, Pymvashor Valley	KM067625	KT852376
R. lagotis	MlymB-108.1*	Russia: Irkutsk Region, Irkut River	KT867320	KT867285
R. rubiginosa	IEPN-G360.9*	Thailand	KM067685	KX056266
R. rubiginosa	MlymB-63*	Thailand	KX056255	KX056267
R. rubiginosa	isolate RADIX01	Thailand: Udonthanee	GU451737	N/A
R. rubiginosa	Lnat2	France: La Réunion, Bras de Pontho	JN614403	HQ283270
R. natalensis	isolate 6120	Malawi	EU818835	N/A
R. natalensis	Rnh2.6	Egypt	LC015519	N/A

* Our data.
** N/A – not available.

described by him as a new species, with type locality designated as «See Kainytschin, ohnfern Nizhne-Kamtschatsk» [Middendorff, 1851, p. 296]. Kruglov and Starobogatov [1984] believed that the true type locality is situated somewhere in the floodplain of the Kamchatka River.

Westerlund, a Swedish malacologist, devoted several papers to description of freshwater and terrestrial malacofauna of Northern Asia. In 1887, he published a short list of continental Mollusca of Kamchatka based primarily on Middendorff's data [Westerlund, 1887, p. 161]. Later on, Westerlund [1897] described a new variety, *Limnaea ovata* var. *aberrans* Westerlund, 1897, from the Kamchatka River.

Dybowski [1903] published the first comprehensive review of the Kamchatka malacofauna. This author could add several new taxa to the list of lymnaeids known from this region. In addition to *L. kamtschaticus* and *L. ovata* var. *aberrans* described by previous researchers, Dybowski introduced such taxa as: *Limnaea auricularia* var. *lanuginosa* Dybowski, 1903, *L. peregra* var. *pseudo-elongata* Dybowski, 1903, and *L. peregra* var. *middendorffi* Dybowski, 1903. The first of them was the most remarkable. Dybowski [1903] described its shell surface as covered by rows of small hairs visible only by means of magnifying glass. Subsequent authors, such as Zhadin [1933] erected the rank of this taxon regarding it as a species (not a variety of *L. auricularia*).

In 1908 and 1909, the expedition of F.P. Ryabushinskiy worked in Kamchatka. Among others, freshwater molluscs were collected by its participant, A.N. Derzhavin. These samples were studied by Rosen [1926], who published a list of Mollusca that included five taxa of *Radix*: *L. auricularia* var. *lanuginosa*, *L. lagotis* (Schrank, 1803), *L. lagotis* var. *patula* Westerlund, 1877, *L. ovata* var. *aberrans*, and *L. peregra*.

In 1925 and 1928, American amateur conchologist W.G. Eyerdam sampled freshwater shells near Ust-Kamchatsk Town and in southern Kamchatka [Eyerdam, 1938]. Some of these shells were identified by Dr. C. Goodrich as *Lymnaea ovata* (Draparnaud, 1805) and *Lymnaea aberrans* Westerlund, 1897. The identifications were based mostly on Westerlund's descriptions.

Ioganzen [1949] became the first author to revise some previously described taxa of Kamchatka snails by means of re-examination of their type series. Having examined the type series of *Limnaea auricularia* var. *lanuginosa*, Ioganzen revealed [1949] that so-called «hairs» on the shell surface of this variety are nothing but dried green and yellow-green algae of the genera *Oedogonium* and *Vaucheria*.

All authors quoted above studied their snails only conchologically and did not use morphometry and statistical analysis to substantiate the taxonomic distinctness of species and varieties accepted by them.

Since Hubendick's [1951] work, the examination of the anatomy of reproductive system has became almost standard method of taxonomic studies of *Radix* and other lymnaeid taxa. In the 1960s, a new generation of taxonomists started revisions of the Northern Asian freshwater snails, including lymnaeids. Several important works were published [Starobogatov, Streletzkaja, 1967; Starobogatov, Budnikova, 1976;

Bogatov, Zatrawkin, 1990]. The results of these studies were summarized by Kruglov and Starobogatov [1993a, b] and Kruglov [2005]. These authors accepted *L. kamtschatica*, *L. aberrans*, and *L. middendorffi* as valid species of the subgenus *Peregriana* and, in addition, described three new species with type localities situated in Kamchatka: *Lymnaea* (*Radix*) *chereshnevi* Kruglov et Starobogatov, 1989; *L.* (*R.*) *hadutkae* Kruglov et Starobogatov, 1989; *L.* (*R.*) *thermokamtschatica* Kruglov et Starobogatov, 1989. The two latter species are dwellers of thermal springs, whereas the former one was found in a lake. Later one more species *R. schelechovi* Kruglov et Starobogatov, 1989 described by Kruglov and Starobogatov [1989] from Magadan Region was found in Kamchatka [Prozorova, Shed'ko, 2003].

The survey of the literature showed that at least 10 species of lymnaeid snails belonging to the genus *Radix* (including *Peregriana*) have been recorded from waterbodies and rivers of the Kamchatka Peninsula (Fig. 1). Below we present a brief account for each of these species. Additional information on the *Radix* species described by Kruglov and Starobogatov may be found in Sitnikova et al. [2014].

Radix (*Radix*) *auricularia* (Linnaeus, 1758)
Figs. 1F, G; 2

Helix auricularia Linnaeus, 1758: p. 774.

Limnaea auricularia (Linnaeus, 1758): Westerlund, 1885, p. 29.

Radix auricularia (Linnaeus, 1758): Zhadin, 1952, p. 168, fig. 63; Bolotov et al., 2014, p. 586, fig. 1–4.

Lymnaea auricularia (Linnaeus, 1758): Starobogatov, 1977, p. 160, fig. 361; Dvoryadkin, 1987, p. 484; Kruglov, Starobogatov, 1989, p. 19, figs. 1.1, 2.1; Bogatov, Zatrawkin, 1990, p. 109, fig. 27.3; Kruglov, Starobogatov, 1993a, p. 82, fig. 10E.

Lymnaea thermokamtschatica Kruglov et Starobogatov, 1989: p. 22, figs. 1.9, 2.9; Kruglov, Starobogatov, 1993a, p. 85, fig. 11E; Kruglov, 2005, p. 265, figs. 146.4, 153, 154; Sitnikova et al., 2014, p. 25, fig. 8E.

Lymnaea thermakamtschatica Kruglov et Starobogatov, 1989: Bogatov, Zatrawkin, 1990, p. 111, fig. 28b.

Lymnaea hadutkae Kruglov et Starobogatov, 1989: p. 22, figs. 1.12, 2.7; Kruglov, Starobogatov, 1993a, p. 85, fig. 11D; Kruglov, 2005, p. 261, figs. 146.2, 149, 150; Sitnikova et al., 2014, p. 25, figs. 8F; 8G.

Lymnaea hodutkae Kruglov et Starobogatov, 1989: Khmeleva et al., 1985: p. 231; Giginyak, Baichorov, 1987, p. 327; Bogatov, Zatrawkin, 1990, p. 110, fig. 28a.

This very variable species is widespread across Eurasia (Fig. 2). It inhabits different types of stagnant waterbodies and streams. In Kamchatka Peninsula, we found it in Kamchatka, Amchagacha and Plotnikova rivers. Also, we revealed *R. auricularia* in samples taken from several thermal springs (Nizhne-Paratunskie, Verkhne-Paratunskie, Malkinskie and Khodutka Thermal Springs), where it lives in warm water at 22–36°C.

Two species of *Radix* described by Kruglov and Starobogatov [1989] – *R. hadutkae* and *R. thermokamtschatica* – were considered endemics to this peninsula [Kruglov, Starobogatov, 1993a; Kruglov, 2005]. As it was found by Bolotov et al. [2014], these two species should be considered as junior synonyms of *R. auricularia*. Possibly, they should be treated as the «local races» of the latter [Vinarski, 2016].

In Khodutka Hot Springs, *R. auricularia* s.l. is found on stones, sand, leaflets of plants and algal mats, at water temperature 13–27°C [Khmeleva et al., 1985; Sitnikova et al., 2014 and our data]. The optimum water temperature for reproduction of these snails is 22–27°C [Giginyak, Baichorov, 1987].

Several samples from Kamchatka identified by Ya.I. Starobogatov as *R. auricularia* are kept in the ZIN collection: 1) west Kamchatka, Maloye Lake, Bol'shaya River basin (I.A. Chereshnev leg., 1983); 2) west Kamchatka, Tigil'skii District, Napana River, 6–7 km downstream from the Sedanka Village (A.E. Oleynik leg., 1989); 3) Esso settlement, warm swamp (O.A. Chernyagina leg., 1990); 4) Kamchatka River (V.I. Zhadin leg., 1930); 5) Krasikovo Lake and Azabach'ye Lake, vicinity of the former Nizhne-Kamchatsk (A.N. Derzhavin leg., 1909 and I.M. Moskvicheva leg., 1978) and 6) Komandorskie Islands, Bering Island (E.A. Strelezkaja leg., 1963 and Kolotovkina leg., 1964).

Radix (*Radix*) *chereshnevi*
(Kruglov et Starobogatov, 1989)
Fig. 1E

Lymnaea chereshnevi Kruglov et Starobogatov, 1989: p. 27, figs. 1.24, 2.22; Bogatov, Zatrawkin, 1990, p. 118, figs. 29e, 29g; Kruglov, Starobogatov, 1993a, p. 92, fig. 15B; Kruglov, 2005, p. 293, figs. 186.2, 188; Sitnikova et al., 2014, p. 29, fig. 10D.

The type locality of this species is Maloye Lake, basin of the Bol'shaya River, west Kamchatka. Also, the species has been recorded in the Kvachikha River. Additional findings in Canada (Kluane Lake; ZIN collection). It lives in permanent waterbodies on the sandy and muddy bottoms [Bogatov, Zatrawkin, 1990; Prozorova, Shed'ko, 2003]. Kruglov [2005] allocated *R. chereshnevi* into *Nipponiradix* section.

Fig. 1. Shells of *Radix* species recorded from waterbodies of Kamchatka Peninsula by previous researchers: **A** – *Radix schelechovi*, the holotype (ZIN); **B** – *R. parapsilia*; **C** – *R. zazurnensis*, a syntype (USNM); **D** – *R. middendorffi* (ZIN); **E** – *R. chereshnevi*, the holotype (ZIN); **F** – *R. hadutkae*, the holotype (ZIN); **G** – *R. thermokamtschatica*, the holotype (ZIN); **H** – *R. aberrans*, lectotype (ZIN); **I** – *R. kamtschatica*, lectotype (ZIN). Scale bars – 2 mm.

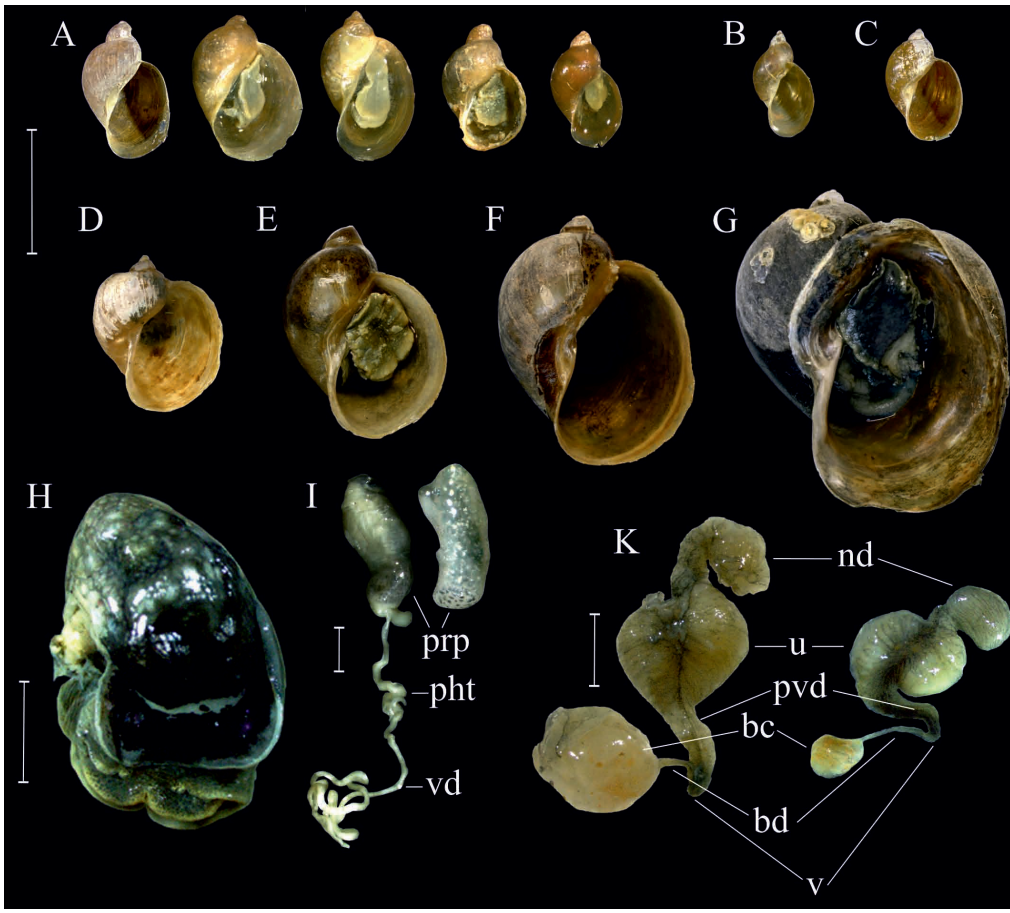

Fig. 2. Variation in conchological and anatomical characters of *Radix auricularia* s. lato from the Russian Far East: **A** – Khodutka Thermal Lake (Kamchatka); **B** – Nizhne-Paratunskie Hot Springs (Kamchatka); **C** – Verkhne-Paratunskie Hot Springs (Kamchatka); **D** – Malkinskie Hot Springs (Kamchatka); **E –** Plotnikova River (Kamchatka); **F –** Tym' River (Sakhalin Island); **G –** Razdol'naya River (Sakhalin Island); **H** – body extracted from the shell, mantle pigmentation of soft body and freckles on the foot; **I** – male copulatory organ and freckles on the preputium (lateral and dorsal view) (*prp* – praeputium, *pht* – phallotheca, *vd* – vas deferens); **K** – fragment of female genital tract with different bursa duct length (*nd* – nidamental gland, *u* – uterus, *pvd* – provaginal duct, *v* – vagina, *bd* – bursa duct, *bc* – bursa copulatrix). Scale bars: A–G – 10 mm; H–K – 2 mm.

Radix (*Radix*) *parapsilia* Vinarski et Glöer, 2009
Fig. 1B

Radix parapsilia Vinarski et Glöer, 2009: p. 132, figs. 2C, 2D, 8, 9.
Lymnaea psilia (Bourguignat, 1862): Bogatov, Zatrawkin, 1990, p. 109, fig. 27.4 (non Bourguignat, 1862).
Lymnaea psilia psilia (Bourguignat, 1862): Kruglov, Starobogatov, 1989, p. 19, figs. 1.2, 1.3, 2.4; Kruglov, Starobogatov, 1993a, p. 85, figs. 10G, 11B; Kruglov, 2005, p. 256, figs. 137.5, 144, 145, Sitnikova et al., 2012, p. 98, figs. 4F–H (non Bourguignat, 1862).

The type locality of this species and most of currently known localities of it are situated in Siberia [Vinarski, Glöer, 2009] and Russian Far East [Kruglov, Starobogatov, 1993; Prozorova, 1998; Prozorova, Shed'ko, 2003; Kantor et al., 2010; Sitnikova et al., 2012; Vinarski, Kantor, 2016]. Additionally, it was registered from western Mongolia [Prokin, 2014]. Vinarski and Glöer [2009] gave a description of its morphology alongside with data on taxonomy and distribution. Kruglov [2005] recorded it from waterbodies of both western and eastern parts of the peninsula. Two samples of this species from Kamchatka are stored in ZIN collection: 1) Napana River in western Kamchatka; and 2) «a warm swamp» near Esso settlement. Both samples were identified by Ya.I. Starobogatov as «*Lymnaea psilia*». This species was found in the Azabach'ya River opposite of Diakonovskoye Lake [Prozorova, Shed'ko, 2003]. It inhabits permanent waterbodies of different type and regime being found on the vegetation and bottom. Prozorova and Shed'ko [2003] note that it is a thermophilic species.

Radix (*Radix*) *schelechovi* (Kruglov et Starobogatov, 1989)
Fig. 1A

Lymnaea schelechovi Kruglov et Starobogatov, 1989b: p. 28, figs. 1.25, 2.16; Bogatov, Zatrawkin, 1990, p. 119, fig. 29k; Kruglov, Starobogatov, 1993a, p. 92, fig. 15G; Kruglov, 2005, p. 298, figs. 193, 194; Sitnikova et al., 2014, p. 29, fig. 10C.

The type locality of this species is the Yagel'noye Lake in the floodplain of the Yama River, coast of Okhotsk Sea, Shelikhov Bay, Magadan Region [Kruglov, 2005]. In Kamchatka, this species was recorded from the Penzhina River basin, the Verkhne-Penzhinskoe Lake (I.A. Chereshnev leg., 1988), and in the Azabach'ye Lake [Prozorova, Shed'ko, 2003]. Also, samples from Kluane Lake (Yukon, Canada) collected by D.I. Berman in 1993 were identified by Ya.I. Starobogatov as *R. shelechovi* (ZIN collection). *R. schelechovi* lives in floodland lakes on sand and silt [Bogatov, Zatrawkin, 1990; Sitnikova et al., 2014].

Radix (*Peregriana*) *aberrans* (Westerlund, 1897)
Fig. 1H

Limnaea ovata var. *aberrans* Westerlund, 1897: p. 125.
Lymnaea aberrans (Westerlund, 1897): Eyerdam, 1938, p. 58; Kruglov, Starobogatov, 1984, p. 31, figs. 1.21, 2.3; Bogatov, Zatrawkin, 1990, p. 97, figs. 24.2a, 24.2b; Kruglov, Starobogatov, 1993b, p. 164, fig. 3E; Starobogatov et al., 2004, p. 320, fig. 135.4; Kruglov, 2005, p. 331, figs. 213.5, 218; Vinarski et al., 2013, p. 89, figs. 5A, 5B.

The type locality of this species is situated in the eastern part of Kamchatka Peninsula. The Kamchatka River is the sampling site of the lectotype (I.G. Voznesenskiy leg., 1847) that was designated by Kruglov and Starobogatov [1984]. Also, the species was recorded from western coast of the Sea of Okhotsk [Kruglov, 2005], around Magadan, in the Kolyma and Kamchatka rivers basins. It is also noted by Prozorova

and Shed'ko [2003] in the Azabach'ye Lake. W.G. Eyerdam identified samples found in August 1928 in Malka Hot Springs as *Lymnaea aberrans* [Eyerdam, 1938]. According to Kruglov and Starobogatov (1984), the original description of this species [Westerlund, 1897] was probably based on the materials used by Middendorff [1851] to describe another lymnaeid species, *Limnaeus kamtschaticus* Middendorff, 1851. In this situation, Kruglov and Starobogatov [1984] designated lectotypes for both *L. aberrans* and *L. kamtschaticus*. The type series of *Limnaea ovata* var. *aberrans* includes the lectotype and two paralectotypes (see Vinarski et al. [2013]). The shell height of the lectotype is 5.1 mm [Kruglov, 2005; Bogatov, Zatrawkin, 1990], whereas the largest specimen from ZIN collection is of 13.4 mm height [Bogatov, Zatrawkin, 1990]. Prozorova and Shed'ko [2003] reported unusually large shell size in populations of *R. aberrans* in the Azabach'ye Lake. Snails from this locality are almost twice large as compared with their conspecifics from other populations that was explained by Prozorova and Shed'ko [2003] as a result of trematode infestation (parasitic sterilisation of a mollusc hosts that may enhance their growth).

R. aberrans is known to dwell in large waterbodies and shallow waters of floodplains [Kruglov, 2005; Bogatov, Zatrawkin, 1990].

The taxonomic validity of *R. aberrans* has been not studied genetically. We could not find specimens of this species in our samples from Kamchatka.

Radix (*Peregriana*) *kamtschatica* (Middendorff, 1851)
Fig. 1I

Limnaeus kamtschaticus Middendorff, 1851: p. 295, pl. 30, figs. 11, 12.
Lymnaea kamtschatica Middendorff, 1851: Starobogatov, Budnikova, 1976, p. 79, figs. 3, 11; Kruglov, Starobogatov, 1984, p. 30, figs. 1.18, 2.7; Bogatov, Zatrawkin, 1990, p. 96, figs. 24.1a, 24.1b; Kruglov, Starobogatov, 1993b, p. 164, fig. 3A; Kruglov, 2005, p. 326, fig. 213.1.
Lymnaea peregra kamtschatica (Middendorff, 1851): Starobogatov, Streletzkaja, 1967, p. 231, fig. 17.

Type locality – Kamchatka River floodplain (I.G. Voznesenskiy leg., 1847). It is a relatively small snail. The shell height of the lectotype is 5.1 mm [Kruglov, 2005]. The largest specimen from ZIN collection is of 11.7 mm height [Bogatov, Zatrawkin, 1990]. This species is distributed in Kamchatka, eastern Chukotka, Magadan Region and northern part of Eastern Siberia [Bogatov, Zatrawkin, 1990; Kruglov, 2005 and our data]. The samples of *R. kamtschatica* stored in ZIN were collected from lakes Azabach'ye and Nerpich'ye in the eastern part of Kamchatka, Yavinskoe Lake, Paratunskie Cold Springs (Derzhavin leg., 1908–1909) and unknown hot springs of the southern Kamchatka (W.G. Eyerdam leg., 1928), Kamchatka River and Apuka River basins in the north-eastern Kamchatka Peninsula (former Koryak Autonomous Area) (I. Likharev leg., 1960). Several samples of this species were taken from the Valley of Geysers, the Kronotsky Nature Reserve. Those from the warm mainstream at the foot of the «Vitrazh» («Stained Glass»), Kirevka River, hot springs of the Elovka River basin (+18°C) (O.A. Chernyagina leg., 1989–1990) and Nalychevskie Hot Springs

(+23°C) (V.P. Smaznova leg., 1989) were identified by Ya.I. Starobogatov as *L. hadutkae* and *L. thermokamtschatica* (see below). Samples from the Geyzernaya River and from Geyzernoye Lake in the Valley of Geysers were identified by L.E. Lobkova as *L. thermokamtschatica* [Lobkova et al., 2012]. Lobkova [l.c.] noted their high density (up to 8000 ind./m^2).

According to our data, this species occupies most of the thermal springs of eastern Kamchatka, including streams, ponds and wetlands of the Valley of Geysers, Nizhne-Semyachikskie, Nalychevskie, Karymshinskie and Nachikinskie Hot Springs [Aksenova et al., 2015, 2016]. It lives in warm water up to +39.9°C, on the stones and sand. Also, we found *R. kamtschatica* in the Plotnikova River near Nachikinskie Hot Springs.

Prozorova and Shed'ko [2003] noted that *R. kamtschatica* from the Azabach'ye Lake are characterized by unusually large size as compared to their conspecific from other populations. Possibly, it was due to trematode infestation.

The status of *R. kamtschatica* as a valid species has been confirmed by molecular-genetic method in our studies (see below).

Radix (*Peregriana*) *middendorffi* (W. Dybowski, 1903)
Fig. 1D

Limnaea peregra var. *middendorffi* W. Dybowski, 1903: p. 52, fig. 7.
Lymnaea middendorffi (W. Dybowski, 1903): Kruglov, Starobogatov, 1984, p. 31 figs. 1.19, 2.5; Bogatov, Zatrawkin, 1990, p. 99, figs. 25.2a, 25.2b; Kruglov, Starobogatov, 1993b, p. 164, fig. 3D; Kruglov, 2005, p. 330, figs. 213.4, 217.

The valley of the Kamchatka River is the type locality of *R. middendorffi* [Bogatov, Zatrawkin, 1990; Kruglov, 2005]. Also it was found in rivers of Kamchatka, Magadan Region and Kolyma River basin [Bogatov, Zatrawkin, 1990]. *R. middendorffi* dwells in temporary and permanent waterbodies, on the silty bottom. Samples of this species from Kamchatka are stored in the ZIN collection: 1) right bank of the Kamchatka River, a lake 35 kilometers upstream of the river (I.M. Moskvicheva leg., 1978); and 2) Esso settlement, warm swamp (O.A. Chernyagina leg., 1990). Prozorova and Shed'ko [2003] reported unusually large individuals of *R. middendorffi* from the Azabach'ye Lake.

Kruglov [2005] described *R. middendorffi* as a species closely related to *R. kamtschatica* and living sympatrically with the latter. Possibly, *R. middendorffi* represents a junior synonym of *R. kamtschatica*.

Radix (*Peregriana*) *zazurnensis* (Mozley, 1934)
Fig. 1C

Lymnaea zazurnensis Mozley, 1934: p. 6, pl. 1, fig. 2; Kruglov, Starobogatov, 1993b, p. 164, fig. 2D; Kruglov, 2005, p. 323, figs. 201.6, 209, 210; Khokhutkin et al., 2009, p. 79, fig. 32.
Lymnaea zazurensis Mozley, 1934: Starobogatov, Strelezkaja, 1967, p. 231, fig. 19.
Lymnaea zazurniensis Mozley, 1934: Kruglov, Starobogatov, 1984, p. 25, figs. 1.1, 2.1; Bogatov, Zatrawkin, 1990, p. 90, figs. 21.4a, 21.4b.

Mozley [1934, p. 6] stated that the type locality of this species is «Lake Zazurnia, in the mountain range known as Khamar Daban, eastern shore of Lake Baikal». However, no lake in the Baikal Region bears such a name. In opinion of Kruglov and Starobogatov [1984; Kruglov, 2005], the true type locality of *R. zazurnensis* is Snezhnoye Lake situated near Vydrino Station in the Republic of Buryatia (southern Siberia). This species is distributed from Kamchatka and Chukotka in the east to the Polar Urals in the west, and from shores of the Arctic Ocean in the north to the Amgun' River and mountain lakes of Khamar Daban and Teletskoye Lake in the south [Kruglov, 2005]. It inhabits stagnant waterbodies and typically lives among vegetation near to the water surface, sometimes – at the bottom [Bogatov, Zatrawkin, 1990; Khokhutkin et al., 2009]. Several samples from Kamchatka identified by Ya.I. Starobogatov as *R. zazurnensis* are stored in the ZIN: 1) Esso settlement, warm swamp (O.A. Chernyagina leg., 1990); and 2) southern Kamchatka, hot spring (W.G. Eyerdam leg., 1928).

Conchologically, *R. zazurnensis* much resembles *R. lagotis* (Schrank, 1803) and may represent a junior synonym of the latter. The taxonomic validity of this species needs to be checked by molecular genetic methods.

Results and discussion

All *Radix* species described above had been separated on the basis of the shell morphology and reproductive system anatomy. During our research we added molecular data to clarify the taxonomic validity and phylogenetic relationships of some species of *Radix* considered endemic to Kamchatka.

As a result, two local endemic lymnaeid species, *R. hadutkae* and *R. thermokamtschatica*, described from the Khodutka geothermal area of Kamchatka [Kruglov, Starobogatov, 1989; Kruglov, 2005] were re-classified as junior synonyms of *R. auricularia* [Bolotov et al., 2014]. Also, specimens from the Valley of Geysers identified by Lobkova as *Lymnaea thermokamtschatica* and by Starobogatov as *Lymnaea hadutkae* proved to belong to *R. kamtschatica* [Aksenova et al., 2015 and present study] (Fig. 3).

Thus, two of the ten species that were recorded from the Kamchatka Peninsula have been recognized as synonyms *R. auricularia*. In addition, all samples collected by us in various parts of the Kamchatka Peninsula belonged to only two species of *Radix* genus. There is a strong need to revise the rest of species on the basis of the integrative taxonomic approach [Vinarski et al., 2016]. It is possible that some other *Radix* species from Kamchatka (*R. parapsilia*, *R. chereshnevi*, *R. schelechovi*, *R. middendorffi* and *R. aberrans*) [Kruglov, 2005] may also represent morphotypes of *R. auricularia* or *R. kamtschatica*, not independently evolving units. The observed diversity of phenotypical traits in the *Radix* of Kamchatka may be caused by the influence of some environmental factors such as differences in hydrological properties of waterbodies. Their modifying impact on lymnaeid shell size and proportions has been well documented [Hubendick, 1951; Stift et al., 2004; Bolotov et al., 2012; Vinarski et al., 2013; Vinarski, 2016].

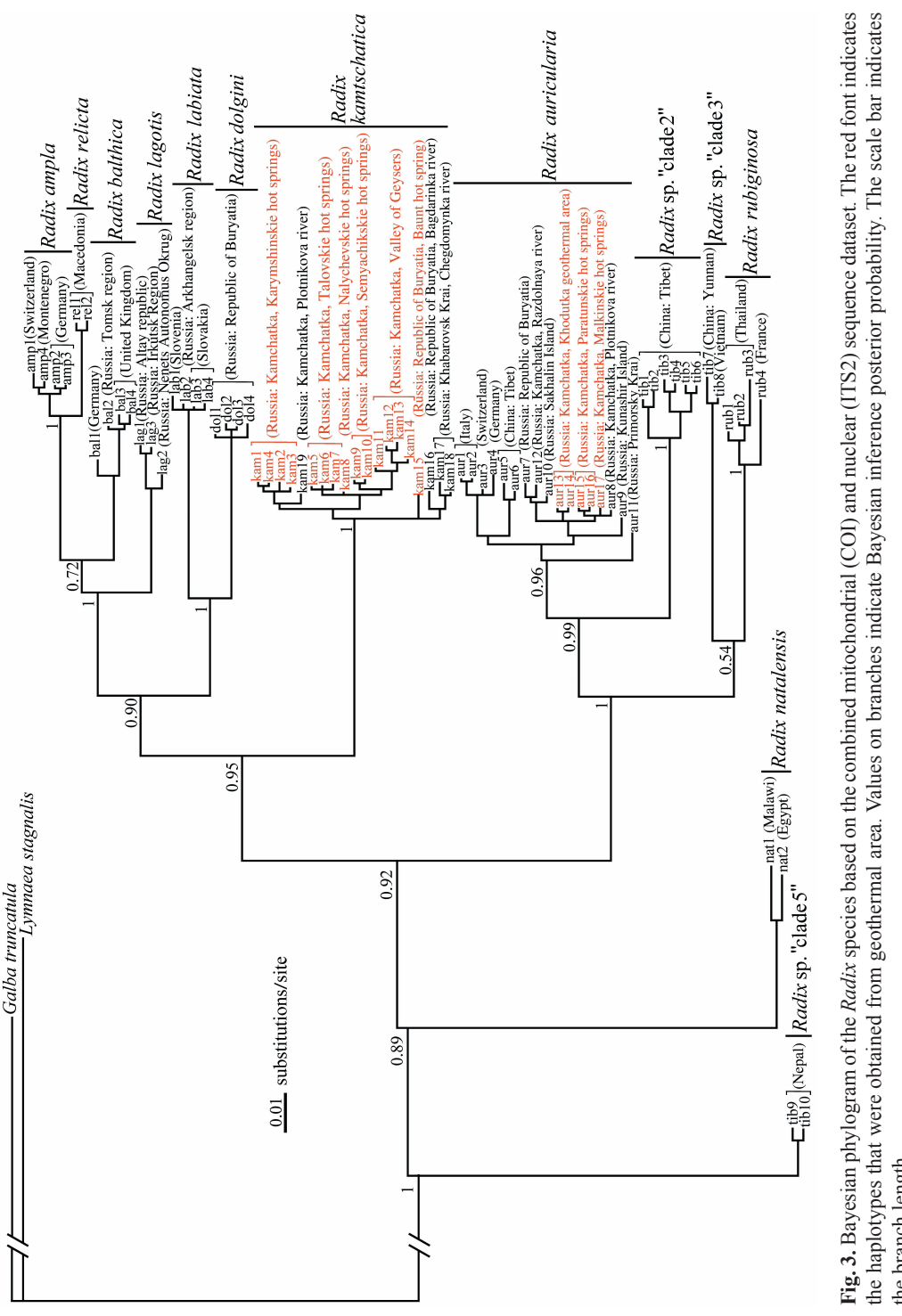

Fig. 3. Bayesian phylogram of the *Radix* species based on the combined mitochondrial (COI) and nuclear (ITS2) sequence dataset. The red font indicates the haplotypes that were obtained from geothermal area. Values on branches indicate Bayesian inference posterior probability. The scale bar indicates the branch length.

American naturalist Walter J. Eyerdam noted that the fauna of the Kamchatka Peninsula is meager in species and consists mostly of forms having a wide range in the circumboreal regions [Eyerdam, 1938]. In his opinion, through glacial and volcanic destruction very few refugia or glacial islands have persisted down to the present, so there are not many relict biotic species to be found in the peninsula. As a result of unfavorable conditions one cannot expect to find an abundance of molluscan species.

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