Chapter 3
Phylogeny and Taxonomy of the Family Lymnaeidae

Olga V. Aksenova, Ivan N. Bolotov, Irina S. Khrebtova, Alexander V. Kondakov, and Maxim V. Vinarski

Abstract A new three-locus (COI + 16S rRNA +28S rRNA) phylogeny of the living representatives of the family Lymnaeidae, which covers the majority of recent genera and subgenera, is proposed. Two living subfamilies (Lymnaeinae Rafinesque, 1815 and Amphipepleinae Pini, 1877), each divided into a series of tribes, are recognized. Four tribes (Austropepleini, Omphiscolini, Peregrianini, and Tibetoradicini), are described as new for science, however, some lymnaeid genera have not been assigned to a tribe due to scarcity of available information. An annotated list of all accepted lymnaeid taxa above the species level is provided, with short synonymies, morphological diagnoses, distributional and taxonomic remarks (when appropriate).

3.1 Introduction

Both phylogeny and taxonomic structure of the family Lymnaeidae have been a matter of hot debates during the last century (e.g., Baker 1911; Hubendick 1951; Starobogatov 1967, 1970, 1976; Inaba 1969; Jackiewicz 1993, 1998; Garbar et al. 2004; Kruglov 2005; Ponder and Waterhouse 1997; Vinarski 2013; and many others). Until the 2010s, the vast majority of such works relied on the interpretations of morphological features (those of shell, radula, reproductive anatomy) and, more rarely, available cytogenetic information. Vinarski (2013) discussed the previous attempts to reconstruct the lymnaeid phylogeny and to develop a working taxonomy based on it. According to this author, the living lymnaeids must be divided into two

O. V. Aksenova · I. N. Bolotov · I. S. Khrebtova · A. V. Kondakov
N. Laverov Federal Center for Integrated Arctic Research, The Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia

M. V. Vinarski (✉)
Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University, Saint-Petersburg, Russia

S.I. Vavilov Institute for the History of Science and Technology, St. Petersburg Branch, Russian Academy of Sciences, Saint-Petersburg, Russia

M. V. Vinarski, A. A. Vázquez (eds.), *The Lymnaeidae*, Zoological Monographs 7,
https://doi.org/10.1007/978-3-031-30292-3_3

subfamilies—Lymnaeinae Rafinesque, 1815 and Radicinae Vinarski, 2013 (which appeared to be a junior synonym of Amphipepleinae Pini, 1877; see Bouchet et al. 2017). The phylogenetic relationships and taxonomic position of the extinct lymnaeids, including the fossil subfamily Valencienninae Gorjanović-Kramberger, 1923, were discussed neither by Vinarski (2013) nor by most other experts in the field (see, for example, Jackiewicz 1998; Kruglov 2005). In this publication, we avoid any questions concerning the fossil representatives of the family as well, focusing instead on the reconstruction of the lymnaeid phylogeny based on a molecular genetic study of the recent pond snails. Since 2010, genetic methods have become the mainstream in the lymnaeid taxonomy and phylogeny, and all most recent attempts to reveal the taxonomic structure for this family heavily relied on molecular phylogenetic information (Puslednik et al. 2009; Correa et al. 2010; Campbell et al. 2017; Aksenova et al. 2018; Saadi et al. 2020).

According to all phylogenetic reconstructions of the recent time, the Lymnaeidae form a well-resolved monophyletic clade among the Hygrophila (Dayrat et al. 2011; Saadi et al. 2020) that evolved, presumably, in the mid-Mesozoic. This clade includes both Lymnaeidae s. str. and Lancidae (ranked as a separate family by Taylor and Sohl 1962 and followed by Starobogatov 1967, 1970). Despite having a set of morphological features absent in the rest of the Lymnaeidae, the latter group proved to be nested within the subfamily Lymnaeinae in our phylogenetic reconstruction (see below) and cannot be ranked even a subfamily (contrary to Campbell et al. 2017). Starobogatov (1976) and Kruglov (2005) supposed that the family evolved from certain "*Chilina*-like" ancestors (Fig. 3.1) though the fossil forms which would support this hypothesis are unknown. The nearest living relatives of the Lymnaeidae belong to the clade comprising the families Bulinidae P. Fischer & Crosse, 1880, Burnupiidae Albrecht, 2017, and Planorbidae Rafinesque, 1815 (= Planorboidea auct.) [Saadi et al. 2020].

This chapter consists of two main parts. The first one provides a new phylogenetic hypothesis for the living representatives of the family, based on a multi-locus approach (COI, 16S rRNA, and 28S rRNA). This hypothesis then becomes a backbone for a new taxonomic structure of the living Lymnaeidae proposed here for the first time. As compared with the previous versions of the system (Vinarski 2013; Campbell et al. 2017), this one is more complicated, with the two recent subfamilies each divided into several tribes. The rank and phylogenetic position of the lancine group (= Lancinae Hannibal, 1914; = Lancidae auct.) is clarified. The second (systematic) part of the chapter provides an annotated list of all recent taxa of the Lymnaeidae between the family and species rank (i.e., subfamilies, tribes, genera, subgenera), with remarks on their taxonomic content, distribution, ecology, etc.

It should be noted that our phylogenetic reconstruction cannot be seen as an ultimate one. Firstly, it does not comprise the extinct taxa, and, that is more important, we still lack available genetic data on some lymnaeid groups of high phylogenetic interest (the genera *Acella*, *Pseudisidora*, *Lantzia*, and some others). Inevitably, the future phylogenetic work, based on an extended set of taxa and more advanced technologies (such as mitogenomics) will shed new light on some

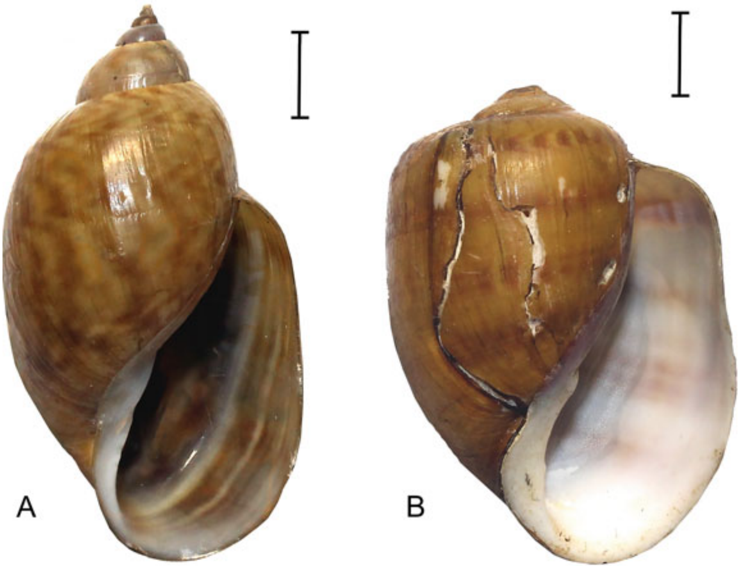

Fig. 3.1 Shells of living *Chilina* that possibly resemble shells of the direct ancestors of the Lymnaeidae (see text for explanation). (**a**) *Chilina parchappii* (D'Orbigny, 1835). (**b**) *Ch. ampullacea* G.B. Sowerby I, 1838. Both shells from the collection of the Natural History Museum, London, UK. Scale bars 5 mm. Photos: Maxim Vinarski

unresolved problems in the Lymnaeidae phylogeny, and the system of the family will change accordingly.

3.2 Material and Methods

Our phylogenetic reconstruction is based on DNA sequences of 124 lymnaeid specimens, representing 27 genera and 116 species, and two outgroup taxa, belonging to the family Physidae (Table 3.1). Here, we used a combined alignment with partial sequences of the mitochondrial *cytochrome c oxidase subunit I* (*COI*), *small ribosomal RNA* (*16S rRNA*), and the nuclear *large ribosomal RNA* (*28S rRNA*) genes. New sequences were generated using the sequencing approach and primer pairs as described in our earlier work (Aksenova et al. 2018). Each gene sequence dataset was aligned separately using the MUSCLE algorithm of MEGA7 (Kumar et al. 2016). Absent sites were treated as missing data. The maximum likelihood phylogeny was reconstructed with IQ-TREE v. 1.6.12 (Nguyen et al. 2015). The analysis was run using an automatic identification of the best evolutionary models for each partition (Kalyaanamoorthy et al. 2017) and an ultrafast bootstrap algorithm

Table 3.1 List of the *COI*, *16S rRNA*, and *28S rRNA* gene sequences used in the multi-locus phylogenetic reconstruction of the Lymnaeidae

Genus	Species	Region	Code	*COI*	*16S rRNA*	*28S rRNA*
Racesina Vinarski & Bolotov, 2018	*R. luteola* (Lamarck, 1822)	Nepal	RacLut	JN794496	JN794322	N/A
	R. oxiana (Boettger, 1889)	Tajikistan	RacOxi	MH189935	**ON620112**	MH168046
	R. siamensis (Sowerby, 1873)	Myanmar	RacSia	MH190023	**ON620118**	MH168050
Radix Montfort, 1810	*R. rubiginosa* (Michelin, 1831)	Indonesia	RadRub	MH189925	**ON620106**	MH168042
	R. brevicauda (Sowerby, 1873)	China: Tibet	RadBre	JN794435	JN794210	N/A
	R. auricularia (Linnaeus, 1758)	Russia: Kamchatka	RadAu1	MH189923	**ON620105**	**ON620444**
	R. auricularia (Linnaeus, 1758)	China: Tibet	RadAu2	MH189863	**ON620099**	MH168033
	R. makhrovi Bolotov, Vinarski & Aksenova, 2018	China: Tibet	RadMak	MH189861	**ON620098**	MH168032
	R. plicatula (Benson, 1842)	China: Tibet	RadPl1	MH190049	**ON620130**	**ON620458**
	R. plicatula (Benson, 1842)	Russian Far East	RadPl2	**ON603571**	**ON620155**	N/A
	R. cf. *swinhoei* (Adams, 1866)	Laos	RadSwi	MT344026	MT345558	N/A
	R. sp. Lake Lugu A	China: Lake Lugu	RadSpA	MT344013	MT345554	N/A
	R. sp. Lake Lugu B	China: Lake Lugu	RadSpB	MT344008	MT345557	N/A
	R. sp. Lake Lugu C	China: Lake Lugu	RadSpC	MT344011	MT345556	N/A
	R. sp. Lake Lugu D	China: Lake Lugu	RadSpD	MT344012	MT345555	N/A
	R. coreana (Martens, 1886)	South Korea	RadCor	**ON603572**	**ON620156**	N/A
	R. japonica (Jay, 1857)	Japan	RadJap	BFMN059–18	N/A	N/A
	R. hamadai Habe, 1968 [=*Radix* sp. Ra-03 Ohari et al., 2020]	Japan	RadShi	LC360961	**ON552481**	**ON552516**
	R. sp. Japan	Japan	RadHon	**ON603567**	**ON620151**	N/A
	R. alticola (Izzatullaev, Kruglov & Starobogatov, 1983)	Tajikistan	RadAlt	MH189949	**ON620113**	MH168047

	R. sp. Trichonis Lake	Greece	RadTri	EU818805	N/A	N/A
	R. euphratica (Mousson, 1874)	Tajikistan	RadEuf	MH189976	**ON620114**	MH168048
	R. dgebuadzei Aksenova, Vinarski, Bolotov & Kondakov, 2019	China: Gansu	RadDge	MN718571	**ON620131**	MN719901
	R. sp. Turkey	Turkey	RadTur	**ON603537**	**ON620108**	ON620445
	R. exsertus (Martens, 1866)	Uganda: Nile Basin	RadExs	**ON603553**	**ON620137**	ON620464
	R. debaizei (Bourguignat, 1887)	Uganda: Lake Victoria	RadDeb	**ON603552**	**ON620136**	ON620463
	R. natalensis (Krauss, 1848)	Cabo Verde	RadNat	HG977206	N/A	N/A
	R. rufescens (Gray, 1822)	Myanmar	RadRuf	MH190025	**ON620119**	MH168051
Ampullaceana Servain, 1881	*A. ampla* (Hartmann, 1821)	European Russia	AmpAmp	MH190044	**ON620124**	MH168052
	A. balthica (Linnaeus, 1758)	European Russia	AmpBal	MH190000	**ON620115**	**ON620447**
	A. sp. Italy	Italy	AmpIta	**ON603562**	**ON620146**	ON620472
	A. intermedia (Lamarck, 1822)	France	AmpInt	KP242511	N/A	N/A
	A. lagotis (Schrank, 1803)	European Russia	AmpLag	MH189858	**ON620096**	MH168030
	A. relicta (Poliński, 1929)	Macedonia	AmpRel	EU818821	JN794307	N/A
	A. fontinalis (Studer, 1820)	European Russia	AmpFon	MH189903	**ON620104**	MH168040
	A. sp. Ohrid	Albania	AmpSp1	EU818833	N/A	N/A
	A. cf. *dipkunensis* (Gundrizer & Starobogatov, 1979)	European Russia	AmpDip	MH189854	**ON620095**	MH168029
Peregriana Servain, 1881	*P. dolgini* (Gundrizer & Starobogatov, 1979)	European Russia	PerDol	MH189886	**ON620101**	MH168036
	P. peregra (O.F. Müller, 1774)	Slovakia	PerPer	MH189931	**ON620109**	MH168044
Kamtschaticana Kruglov & Starobogatov, 1984	*K. kamtschatica* (Middendorff, 1850)	Russia: Kamchatka	KamKam	**ON603574**	**ON620158**	MH168041
	K. sp. Japan [=*Radix* sp. Ra-c2 Ohari et al., 2020]	Japan	KamNip	**LC360970**	**ON552506**	**ON552540**
	K. sp. Kamchatka.	Russia: Kamchatka	KamSp1	**ON603575**	**ON620159**	ON620483

(continued)

Table 3.1 (continued)

Genus	Species	Region	Code	*COI*	*16S rRNA*	*28S rRNA*
Myxas G. B. Sowerby I, 1822	*M. glutinosa* (O. F. Müller, 1774)	European Russia	MyxGlu	**ON603541**	**ON620121**	**ON620450**
Tibetoradix Bolotov, Vinarski & Aksenova, 2018	*T. hookeri* (Reeve, 1850)	China: Tibet	TibHoo	MH189865	**ON620100**	MH168034
	T. kozlovi Vinarski, Bolotov & Aksenova, 2018	China: Tibet	TibKoz	MH190045	**ON620129**	**ON620457**
	T. kruglovi Bolotov, Vinarski & Oheimb, 2021	China: Tibet	TibSp1	JN794395	JN794169	N/A
	T. imitator Vinarski, Bolotov & Oheimb, 2021	China: Tibet	TibSp2	JN794441	JN794216	N/A
	T. khamensis Oheimb, Vinarski & Bolotov, 2021	China: Tibet	TibSp3	JN794384	JN794158	N/A
	T. transhimalayensis Oheimb, Bolotov & Vinarski, 2021	China: Tibet	TibSp4	JN794436	JN794211	N/A
Orientogalba Kruglov & Starobogatov, 1985	*O. ollula* (Gould, 1859)	China: Tibet	OriOll	**ON603547**	**ON620128**	ON620456
	O. bowelli (Preston, 1909)	China: Tibet	OriBow	JN794473	JN794248	N/A
	O. viridis (Quoy & Gaimard, 1833)	Indonesia	OriVir	MH189927	**ON620107**	MH168043
	O. sp. Hokkaido [=*Austropeplea ollula* Ohari et al., 2020]	Japan	OriHok	**LC360950**	**ON552480**	**ON552515**
	O. sp. Uzbekistan	Uzbekistan	OriUzb	**ON603548**	**ON620132**	ON620459
Austropeplea Cotton, 1942	*A. tomentosa* (L. Pfeiffer, 1855)	Australia	AusTom	AY227365	AF485645	HQ156217
	A. hispida (Ponder & Waterhouse, 1997)	Tasmania	AusHis	N/A	EU556268	N/A
Bullastra Bergh, 1901	*B. lessoni* (Deshayes, 1830)	Australia	BulLes	N/A	EU556252	N/A
	B. cumingiana (L. Pfeiffer, 1855)	Philippines	BulCum	N/A	U82068	N/A
Lymnaea Lamarck, 1799	*L. stagnalis* (Linnaeus, 1758) [Asian subclade: European Russia]	European Russia	LymSt1	MH189887	**ON620102**	MH168037
	L. stagnalis (Linnaeus, 1758) [Asian subclade: European Russia]	European Russia	LymSt2	**ON603550**	**ON620134**	ON620461

	L. fragilis (Linnaeus, 1758) Siberia	Russia: Siberia	LymFra	HG932266	N/A	N/A
	L. sorensis B. Dybowski, 1912 [Asian subclade: Western China, Kamchatka, Krasnoyarsk, Kemerovo]	China: Xinjiang	LymEx1	**ON603546**	**ON620127**	ON620455
	L. sorensis B. Dybowski, 1912 [Asian subclade: Western China (Tarim basin), Kamchatka, Krasnoyarsk, Kemerovo]	Russia: East Siberia (Krasno-yarsk Region)	LymEx2	**ON603570**	**ON620154**	ON620479
	L. sp. France [Asian subclade: Iberia]	France	LymAlt	HG932252	N/A	N/A
	L. appressa Say, 1821 [Nearctic subclade: North America]	Canada	LymApp	**ON603557**	**ON620141**	ON620467
	L. sp. Kazakhstan [Asian subclade: Kazakhstan]	Kazakhstan	LymKaz	**ON603559**	**ON620143**	ON620469
	L. sp. Rostov [Nearctic subclade: Rostov]	European Russia	LymRos	**ON603560**	**ON620144**	ON620470
	L. sp. Baltic Sea [Nearctic subclade: Novgorod]	European Russia	LymNov	**ON614717**	**ON620111**	ON620446
	L. sp. Arkhangelsk [East European subclade: Arkhangelsk, Karelia, NAO, KhMAO]	European Russia	LymArk	**ON603554**	**ON620138**	ON620465
	L. sp. Crimea [East European subclade: Crimea]	Crimea	LymCri	**ON603539**	**ON620117**	**ON620448**
Kazakhlymnaea Kruglov & Starobogatov, 1984	*K. taurica* (Clessin, 1880)	Russia:Western Siberia	KazTau	HG932240	N/A	N/A
	K. sp. Italy	Italy	KazIta	HG932245	N/A	N/A
Stagnicola Jeffreys, 1830	*S. fuscus* (C. Pfeiffer, 1821)	Germany	StaFus	HG932234	N/A	N/A
	S. corvus (Gmelin, 1791)	European Russia	StaCo1	MH189932	**ON620110**	MH168045
	S. palustris (O. F. Müller, 1774)	European Russia	StaPal	MH189888	**ON620103**	MH168038
	S. montenegrinus Glöer & Pešič, 2009	Ukraine	StaMon	**ON603555**	ON620139	N/A
		European Russia	StaArc	**ON603540**	**ON620120**	**ON620449**

(continued)

Table 3.1 (continued)

Genus	Species	Region	Code	*COI*	*16S rRNA*	*28S rRNA*
	S. archangelica (Kruglov & Starobogatov, 1986)					
	S. sp. Italy	Italy	StaIta	**ON603563**	**ON620147**	ON620473
	S. sp. Rostov	European Russia	StaRos	**ON603551**	**ON620135**	ON620462
	S. sp. Kyrgyzstan	Russia: Krasnodar Region	StaKyr	**ON603576**	**ON620160**	ON620484
	S. sp. Krasnodar	Russia: Krasnodar Region	StaKra	**ON603579**	**ON620163**	ON620487
	S. turricula (Held, 1836)	Poland	StaTur	KP070778	N/A	N/A
Lanx Clessin, 1880	*L. alta* (Tryon, 1865)	USA: Oregon	LanAlt	HM230361	N/A	HM230318
	L. patelloides (Lea, 1856)	USA: California	LanPat	HM230363	KT267276	HM230322
Idaholanx Clark, Campbell & Lydeard, 2017	*I. fresti* Clark, Campbell & Lydeard, 2017	USA: Idaho	IdaFre	HM230356	KT267273	HM230308
Bulimnea Haldeman, 1841	*B. megasoma* (Say, 1824)	Canada	BulMeg	**ON603556**	**ON620140**	**ON620466**
Hinkleyia Baker, 1928 [=*Sphaerogalba* Kruglov & Starobogatov, 1985 **syn. nov.**]	*H. caperata* (Say, 1829)	USA: New Mexico	HinCap	MF962229	MF962327	N/A
	H. bulimoides (Lea, 1841) **comb. nov.**	USA: Colorado	SphBul	EU038362	EU038315	N/A
Walterlymnaea Starobogatov & Budnikova, 1976	*W. catascopium* (Say, 1817)	USA: Yellowstone National Park	LadCa1	**ON603543**	**ON620123**	**ON620452**
	W. catascopium (Say, 1817)	Russia: Kamchatka	LadCa3	KP830105	**ON620097**	**ON620443**
	W. emarginata (Say, 1821)	USA	LadEma	N/A	U82081	AY465069
	W. bonnevillensis (Call, 1884)	USA: Utah	LadBon	N/A	AF485655	N/A
	W. elrodi (Baker & Henderson, 1933)	USA: Montana	LadElr	N/A	AF485656	N/A
	W. exilis (Lea, 1834)	Canada	LadExi	MG421226	N/A	N/A
	W. sp. Ontario	Canada	LadOnt	MG421900	N/A	N/A

	W. arctica (Lea, 1864)	USA: Alaska	LadArc	**ON603545**	**ON620126**	ON620454
Ladislavella B. Dybowski, 1913	*L. liogyra* (Westerlund, 1897)	Russia: Khanka Lake	LadLio	**MH190007**	**ON620116**	MH168049
	L. terebra (Westerlund, 1885)	Russia: Western Siberia	LadTer	**ON603568**	**ON620152**	ON620477
	L. sp. Altai [*terebra*-group]	Russia: Altai Mts.	LadAlt	**ON603577**	**ON620161**	ON620485
	L. occulta (Jackiewicz, 1959)	Poland	LadOcc	KP070796	N/A	N/A
Dallirhytis Kruglov & Starobogatov, 1989 **stat. rev.**	*D. atkaensis* (Dall, 1884) **comb. rev.**	Russia: Chukchi Peninsula	DalAt1	**ON603573**	**ON620157**	ON620481
	D. atkaensis (Dall, 1884) **comb. rev.**	USA: Alaska	DalAt2	**ON603544**	**ON620125**	**ON620453**
Galba Schrank, 1803	*G. obrussa* (Say, 1825)	North America	GalObr	N/A	AF485658	N/A
	G. parva (Lea, 1841)	Canada	GalPar	KM612176	N/A	N/A
	G. truncatula (O. F. Müller, 1774)	Georgia	GalTru	**ON603566**	**ON620150**	**ON620476**
	G. neotropica (Bargues, Artigas, Mera y Sierra, Pointier & Mas-Coma, 2007)	Uruguay	GalNeo	KX781342	KX712144	N/A
	G. cubensis (L. Pfeiffer, 1839)	USA: South Carolina	GalCub	FN182205	FN182204	N/A
	G. meridensis (Bargues, Artigas, Khoubbane & Mas-Coma, 2011)	Venezuela	GalMer	JN614389	HQ283237	N/A
	G. sp. Cyprus	Cyprus	GalCyp	**ON603565**	**ON620149**	ON620475
	G. humilis (Say, 1822)	USA: Yellow-stone National Park	GalHum	**ON603542**	**ON620122**	**ON620451**
	G. schirazensis (Küster, 1862) [=*Galba* sp. Gt-14 Ohari et al., 2020]	Iran	GalSch	JF272607	JF272605	N/A
	G. viator (Orbigny, 1835)	Argentina	GalVia	JN872451	JN872461	N/A
	G. mweruensis (Connolly, 1929)	Ethiopia	GalMwe	MN601410	MN602707	N/A

(continued)

Table 3.1 (continued)

Genus	Species	Region	Code	*COI*	*16S rRNA*	*28S rRNA*
	G. cousini (Jousseaume, 1887)	Columbia	GalCou	KJ495741	N/A	N/A
	G. sp. Japan. [=*Galba* sp. Gt-c1 Ohari et al., 2020]	Japan	GalPa1	**LC360899**	**ON552492**	**ON552527**
	G. sp. Japan. [=*Galba* sp. Gt-c1 Ohari et al., 2020]	Russia: Kamchatka	GalPa2	**ON603549**	**ON620133**	**ON620460**
Omphiscola Rafinesque, 1819	*O. glabra* (O. F. Müller, 1774)	France	OmpGla	**ON603564**	**ON620148**	**ON620474**
Aenigmomphiscola Kruglov & Starobogatov, 1981	*A. europaea* Kruglov & Starobogatov, 1981	European Russia	AenEur	**ON603569**	**ON620153**	ON620478
	A. cf. *kazakhstanica* Kruglov & Starobogatov, 1981	Russia: Altai Mts.	AenAlt	**ON603578**	**ON620162**	ON620486
Pectinidens Pilsbry, 1911	*P. diaphanus* (King, 1832)	Argentina	PecDia	JN872456	JN872475	N/A
Pseudosuccinea F. C. Baker, 1908	*P. columella* (Say, 1817)	Canada	PseCo1	**ON603561**	**ON620145**	ON620471
	P. columella (Say, 1817)	Canada	PseCo2	**ON603558**	**ON620142**	ON620468
Fisherola Hannibal, 1912	*F. nuttallii* (Haldeman, 1841)	USA: Idaho	FisNut	HM230359	HM230355	HM230315
Erinna H. Adams & A. Adams, 1855	*E. aulacospira* (Ancey, 1899)	USA: Hawaii	EriAul	AY150091	N/A	N/A
Physella Haldeman, 1843[a]	*P. acuta* (Draparnaud, 1805)[a]		PhyAcu	AY651174	AY651213	EF489368
Aplexa J. Fleming, 1820[a]	*A. elongata* (Say, 1821)[a]		AplElo	EU038377	EU038330	AY465071

[a]Outgroup (Physidae). N/A – not available. New sequences generated in this study are in bold

(Hoang et al. 2017) through an online server (http://iqtree.cibiv.univie.ac.at) (Trifinopoulos et al. 2016).

Morphological studies of various lymnaeid snails have been conducted in a number of zoological depositories of Russia and Western Europe that are listed below. During this work, we were able to familiarize ourselves with representatives of all living genera and subgenera of the Lymnaeidae except for *Idaholanx* Clark, Campbell & Lydeard, 2017 and *Kutikina* Ponder and Waterhouse, 1997.

Museum Acronyms:
LMBI – Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University (Saint-Petersburg, Russia); MHNH – Museum national d'Histoire naturelle (France, Paris); NHMUK – Natural History Museum of the United Kingdom (London, UK); NHMW – Natural History Museum of Vienna, Austria; SMF – The Naturmuseum Senckenberg, Frankfurt am Main, Germany; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; ZIN – Zoological Institute of the Russian Academy of Sciences (Saint-Petersburg, Russia); ZMB – Natural History Museum of Berlin (Germany).

3.3 Phylogenetic Relationships Within the Family Lymnaeidae

A new multi-locus phylogenetic hypothesis obtained as a result of this study is presented in Fig. 3.2. Though not all recovered branches have equally high statistical support, the basic division of the living Lymnaeidae into two large monophyletic clades corresponding to the two subfamilies delineated by Vinarski (2013)—Lymnaeinae and Amphipepleinae—receives full support. The lancine snails of North America (genera *Lanx*, *Idaholanx*, *Fisherola*) do not constitute a separate clade and, instead, are clustered within the subfamily Lymnaeinae. It corresponds to the earlier findings of Aksenova et al. (2018) and Saadi et al. (2020).

The deep split of the family into two large clades corresponding to subfamilies is based mainly on the molecular phylogenetic data. The only non-molecular character allowing to distinguish between the two taxa is their chromosome numbers: 16 or (most often) 17 chromosome pairs in Amphipepleinae and 18 (rarely 19) pairs in Lymnaeinae (Vinarski, 2013).

Each lymnaeid subfamily comprises several internal clades of different rank and volume (see Fig. 3.2). Within the subfamilies, we recovered a number of groups of closely related genera that may be characterized geographically. Each of these groups, that we ranked here as tribes, is distributed in a more or less well-defined region of the world which can be rather small (e. g., the Tibetan Plateau). The practice of division of a large and speciose family (or subfamily) in a series of tribes has been applied to such families of freshwater molluscs as Unionidae (Lopes-Lima et al. 2017; Bolotov et al. 2018; Froufe et al. 2020) and Planorbidae (Albrecht et al. 2007; Saadi et al. 2020). Unfortunately, a substantial portion of genera within the

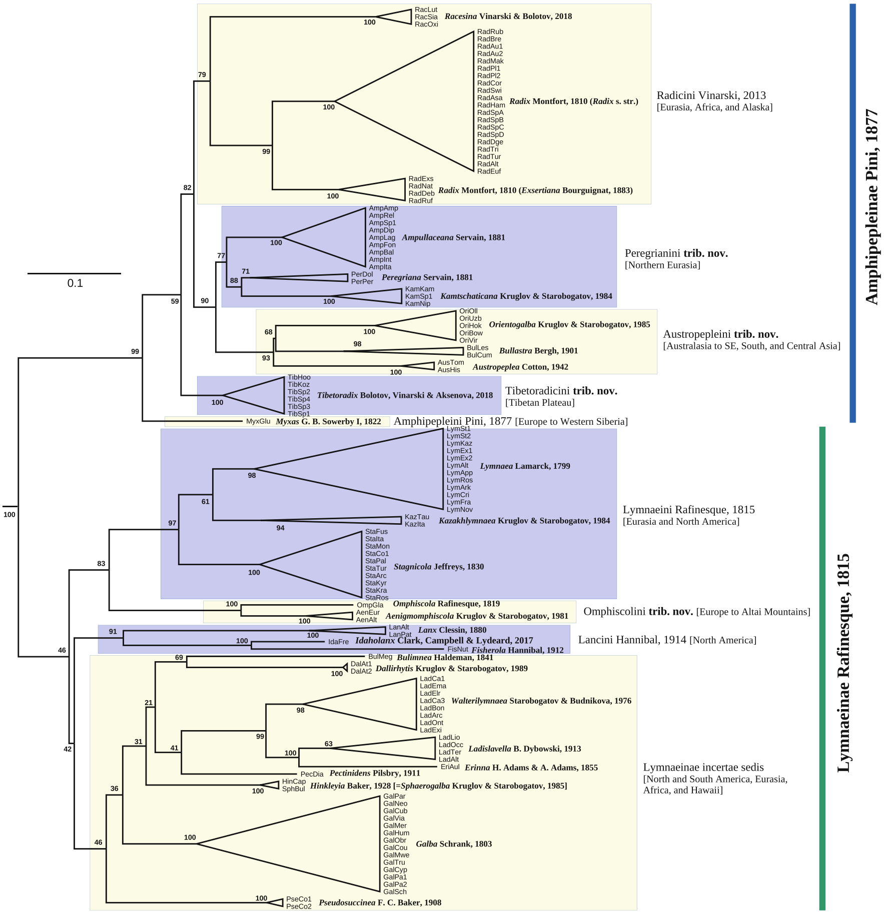

Fig. 3.2 Maximum likelihood consensus phylogeny of the family Lymnaeidae recovered from IQ-TREE analysis and obtained for the complete data set of mitochondrial and nuclear sequences (five partitions: three codons of *COI* + *16S rRNA* + *28S rRNA*). Black numbers near nodes are ultrafast bootstrap support values. The species branches are collapsed to the genus-level clades. The tribe-level clades are highlighted in color. The scale bar indicates the branch lengths. The codes, sequence accession numbers, and sampling regions for each species are given in Table 3.1

Lymnaeinae remains unassigned to tribes owing to the insufficiently high statistical support of the respective clades (see Fig. 3.2). The intergeneric relationships within this subfamily require further research with an expanded set of included genera and taxa. Thus, only three tribes may be surely defined within the subfamily: Lymnaeini Rafinesque, 1815; Omphiscolini **trib. nov.**, and Lancini Hannibal, 1914. Five tribes, including three having no available names, were recovered within the Amphipepleinae (see Fig. 3.2).

As a conclusion, we accept among the recent Lymnaeidae two subfamilies, eight tribes, and 30 genera, which are briefly characterized in the following section.

3.4 Taxonomy (Systematic Part)

The earlier morphology-based works on the taxonomy of the recent Lymnaeidae include, among others, those of W. Dybowski (1903), Baker (1911, 1915), Hubendick (1951), Jackiewicz (1993, 1998), Kruglov and Starobogatov (1993a, b), Ponder and Waterhouse (1997), Kruglov (2005), and Vinarski (2013). Since the late-2000s, most works aiming to construct a system of the family rely chiefly on the molecular genetic evidence (see Bargues et al. 2006; Puslednik et al. 2009; Correa et al. 2010; Campbell et al. 2017; Aksenova et al. 2018, and some others). The working taxonomic system for the living lymnaeids based primarily on the multi-locus phylogeny presented above may be summarized as follows.

Class Gastropoda Cuvier, 1875
Subclass Heterobranchia Burmeister, 1837
Infraclass Euthyneura Spengel, 1881
Subterclass Tectipleura Schrödl, Jörger, Klussmann-Kolb & N. G. Wilson, 2011
Superorder Hygrophila Férussac, 1822 (= Lymnaeiformes Minichev & Starobogatov, 1975)
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815

(Rafinesque 1815, p. 144)

[= Limnophysidae W. Dybowski, 1903; = Acellinae Haldeman, 1912; = Fossariinae B. Dybowski, 1913].

Type genus: *Lymnaea* Lamarck, 1799.

The family comprises two extant subfamilies—Lymnaeinae Rafinesque, 1815 and Amphipepleinae Pini, 1877.

Subfamily Lymnaeinae Rafinesque, **1815**

Diagnosis. Shell helicoid or patelliform, of different size (shell height varies from 5–6 to almost 70 mm) and shape (from subulate or turriculate to ovate conical, auriculate, or even neritiform). Prostate with one or several (2–10) internal folds or unfolded. Haploid chromosome number 18–19. Copulatory apparatus simple or with a so-called preputial organ. Spermathecal duct long, its length several times exceeds that of spermatheca.

The distribution of this subfamily is almost cosmopolitan, with an exception to Australia and other large Pacific islands (excluding Hawaii), where no aboriginal representatives of the Lymnaeinae are known.

Tribe Lymnaeini Rafinesque, **1815**

Diagnosis. Shell helicoid, large or medium-sized (up to 70 mm height), typically more or less slender, with 5 to 7 whorls and relatively small aperture. Prostate with one or several (2–10) internal folds (branched or unbranched). Copulatory apparatus simple. Penis with or without fixatory ring-like swelling.

1. ***Lymnaea*** **Lamarck**, 1799 (Fig. 3.3a)

(Lamarck 1799, p. 75)

[= *Helix* Linnaeus, 1758 (partim); = *Lymnaeus* Cuvier, 1816; = *Limnaeus* Pfeiffer, 1821; = *Limnea* Sowerby, 1822 = *Limneus* Sandberger, 1875; = *Limnoturgida* Chiamenti, 1899; = *Limnaea* Germain, 1903, non Poli, 1791 (Bivalvia); = *Eulimneus* Sandberger, 1875; = *Psiliana* Servain, 1882; = *Stagnaliana* Servain, 1882; = *Limnoturgida* Chiamanti, 1899; = *Omphalolimnus* W. Dybowski, 1903; = *Lymnoëa* Suter, 1913; = *Kobeltilymnaea* Kruglov & Starobogatov, 1993].[1]

Type species. *Helix stagnalis* Linnaeus, 1758 = *Lymnaea stagnalis* [M].[2]

Taxonomic content. Two subgenera have been assigned to this genus (Vinarski et al. 2012): *Lymnaea* s. str., and *Kazakhlymnaea* Kruglov and Starobogatov, 1984; the latter is considered below as a separate genus. Traditionally, a single recent species, *Lymnaea stagnalis* (Linnaeus, 1758), is assigned to *Lymnaea* (Glöer 2002; Welter-Schultes 2012; but see Kruglov and Starobogatov 1985c, 1993a; Glöer 2019). The latest molecular genetic data (Aksenova et al., submitted), however, reveals a cryptic genetic diversity within *Lymnaea stagnalis* s. lato, which represents a complex of more than 10 species, one of them—*Lymnaea appressa* (Say, 1821)—is endemic to North America (note that these putative species do not correspond to those delineated by Kruglov and Starobogatov 1985c, 1993a).

Distribution and ecology. The native range of *Lymnaea* lies in the Holarctic. *L. stagnalis* s. lato was introduced into Australia, New Zealand, and tropical Africa (Hubendick 1951; Tchakonté et al. 2014). *L. stagnalis* is a generalist snail inhabiting a very wide range of biotopes and demonstrating an enormous conchological variability (see Vinarski 2015 for review and discussion).

2. *Kazakhlymnaea* **Kruglov and Starobogatov, 1984** (Fig. 3.3b)

(Kruglov and Starobogatov 1984b, p. 66)

Type species. *Lymnaea palustris kazakensis* Mozley, 1934 = *Kazakhlymnaea taurica kazakensis* [OD].

Taxonomic content. The genus includes the type species, with two subspecies (Vinarski et al. 2012; Vinarski and Kantor 2016), and one undescribed species in South Europe.

Distribution and ecology. South Europe to North Kazakhstan and southwest Siberia. *Kazakhlymnaea* snails are living in ephemeral steppe waterbodies (Beriozkina and Starobogatov 1988; Vinarski et al. 2012).

3. *Stagnicola* **Jeffreys,** 1830 (Fig. 3.3c)

(Jeffreys 1830, p. 376)

[1]This list of generic synonyms is, most probably, not exhaustive.

[2]Here and below, the following abbreviations are used. M – type species designated by monotypy; OD – type species designated in the original description; SD – subsequent designation of the type species; SM – designated by subsequent monotypy.

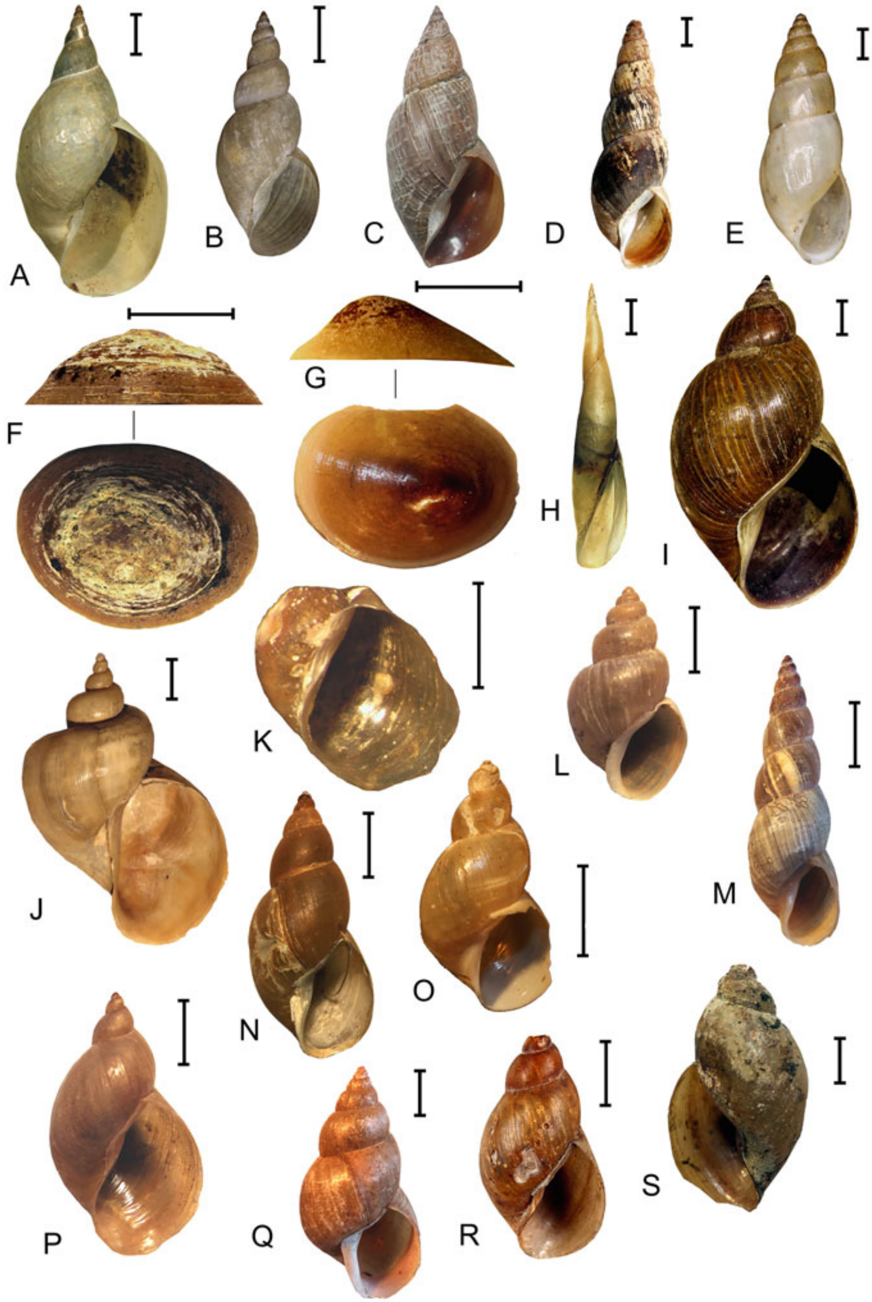

Fig. 3.3 Shells of representatives of genera and species of the Lymnaeinae. (**a**) *Lymnaea stagnalis*. Central Kazakhstan, Sholak Lake [LMBI]. (**b**) *Kazakhlymnaea taurica kazakensis* [a syntype of *Lymnaea palustris kazakensis* Mozley, 1934; USNM]. (**c**) *Stagnicola corvus*. Ukraine, Zhitomir Region, Romanov settlement [LMBI]. (**d**) *Omphiscola glabra*. Germany, Nassau [ZIN] (**e**) *Aenigmomphiscola uvalievae* [holotype; ZIN]. (**f**) *Lanx patelloides*. USA, Oregon [SMF]. (**g**) *Fisherola nuttalli*. USA, Oregon, Deschutes River [NHMUK]. (**h**) *Acella haldemani*. USA, Illinois,

[= *Limnophysa* Fitzinger, 1833; = *Fenziana* Servain, 1882; = *Ligericiana* Servain, 1882; = *Palustrisiana* Servain, 1882; = *Costolymnaea* B. Dybowski, 1913; = *Entochilius* Sandberger, 1880; = *Berlaniana* Kruglov et Starobogatov, 1986; = *Kuesterilymnaea* Vinarski, 2003].

Type species. *Limneus communis* Jeffreys, 1830 = *Stagnicola palustris* (O.F. Müller, 1774) [M].

Taxonomic content. Two morphologically-defined subgenera: *Stagnicola* s. str., and *Corvusiana* Servain, 1882 (type species *Helix corvus* Gmelin, 1791) have been delineated (Vinarski 2013; Vinarski and Kantor 2016). Though the latter subgenus has some unique cytogenetic and anatomic differences from *Stagnicola* s. str. (Kruglov and Starobogatov 1984b; Garbar et al. 2004; Vinarski 2013), our results, as well as the results obtained by other workers (Pieńkowska et al. 2015; Pieńkowska and Lesicki 2018), give no strong evidence of its independent phylogenetic position. Possibly, the latter taxon should be treated as a full synonym of *Stagnicola*. Kruglov and Starobogatov (1986, 1993a) and Burch (1989) listed dozens of nominal species of *Stagnicola* living in North Eurasia and North America, but the actual number of valid species is not known yet since some nominal taxa remain unassessed genetically. Perhaps, there are no more than 10–15 living members in this genus.

Distribution and ecology. Palearctic. Numerous species of *Stagnicola* recorded from North America (Burch 1989; Johnson et al. 2013) belong to either *Hinkleyia* or *Ladislavella*. Most species of *Stagnicola* inhabit minor waterbodies as well as shallow zones of large lakes and streams.

Tribe Omphiscolini Bolotov, Vinarski & Aksenova *trib. nov.*

Diagnosis. Shell slender, turriculate, small to medium-sized (up to 20 mm height), with 6 to 8 whorls and diminutive aperture. Prostate with a single internal fold or unfolded. Copulatory apparatus simple or with a so-called preputial organ. Penis without fixatory ring-like swelling.

Type genus. *Omphiscola* Rafinesque, 1819.

4. ***Omphiscola* Rafinesque,** 1819 (Fig. 3.3d)

(Rafinesque 1819, p. 423)

[= *Leptolimnea* Swainson, 1840; = *Glabriana* Servain, 1882]

Type species: *Buccinum glabrum* O.F. Müller, 1774 = *Omphiscola glabra* [SM].

Fig. 3.3 (continued) Lake Cedar [LMBI]. (**i**) *Bulimnea megasoma*. Canada, Ontario, Cart Lake [LMBI]. (**j**) *Dallirhytis atkaensis*. Canada, Yukon Territory [ZIN]. (**k**) *Erinna newcombi*. Hawaii Islanda, Kenda River [NHMUK]. (**l**) *Galba viator*. Peru, Huaura River [SMF]. (**m**) *Ladislavella* (*Ladislavella*) *liogyra*. Russia, Nikol'sk-Ussuriysky [ZIN]. (**n**) *Ladislavella* (*Walterigalba*) *catascopium*. Greenland [LMBI]. (**o**) *Pectinidens diaphana*. Magellan Strait, King Cape [holotype, NHMUK]. (**p**) *Pseudosuccinea columella*. Germany, Tübingen, invasive [SMF]. (**q**) *Hinkleyia caperata*. USA, Colorado [ZIN]. (**r**) *Pseudisidora* (*Pseudisidora*) *rubella* (the lectotype of *Limnaea oahuensis* Souleyet, 1852]. Hawaii, Oahu [MHNH]. (**s**) *Pseudisidora* (*Pseudobulinus*) *reticulata*, Hawaii, Kauai [ZMB]. Scale bars 2 mm (D, E, H, K–L, N–S), 5 mm (A–C, F–G, I–J, M). Photos: Maxim Vinarski. See "Material & methods" section for museum acronyms

Taxonomic content, distribution, and ecology: A monotypic genus restricted to northwestern Europe in its distribution (Welter-Schultes 2012). *Omphiscola glabra* inhabits shallow, still waters with dense vegetation (Jackiewicz 1998). Jackiewicz (1998, p. 38) characterizes it as "a rare, even very rare species."

5. ***Aenigmomphiscola*** **Kruglov and Starobogatov**, 1981 (Fig. 3.3e)

(Kruglov and Starobogatov 1981, p. 966)

Type species: *Aenigmomphiscola europaea* Kruglov and Starobogatov, 1981 [OD].

Taxonomic content, distribution, and ecology: Two species endemic to European Russia, Western Siberia, and Northern Kazakhstan (Vinarski et al. 2011; Vinarski and Grebennikov 2012). The snails typically live in ephemeral habitats such as wetland and floodplain pools, wet meadows (Beriozkina and Starobogatov 1988; Vinarski and Grebennikov 2012).

Tribe Lancini Hannibal, **1914**
(Hannibal, 1914, p. 24)

Type genus. *Lanx* Clessin, 1882.

Diagnosis. Shell patelliform, small to medium-sized (shell width up to 20 mm), aperture broad, ovoid. Two prostatic glands of different structure and the secondarily enlarged columellar muscle (C-shaped or almost circular) constitute the anatomical synapomorphies of this tribe (Hubendick 1951; Campbell et al. 2017).

Remarks. This group of patelliform lymnaeids was ranked as a separate family within Hygrophila by some authors (Pilsbry 1925; Taylor and Sohl 1962; Starobogatov 1967; Gray 1988), while other systematists treated it as a subfamily of the family Lymnaeidae (Burch 1989; Bouchet et al. 2017; Campbell et al. 2017) or even as merely a genus of lymnaeid snails (Hubendick 1951). According to Campbell et al. (2017), the subfamily includes only three genera and four extant species distributed in the Pacific Northwest USA and Canada. The finding of lancine snails in the Cretaceous deposits of Nevada (MacNeil 1939) superficially indicates it is a very ancient taxon, but one cannot exclude the repeated origin of the limpet form in independent clades of lymnaeids as a result of convergent evolution (Vermeij 2017). The absence of a profound genetic distance between the recent lancines and the rest of the Lymnaeinae assumes a relatively young geological age of this tribe. Ecologically, these snails may be characterized as dwellers of well-oxygenated lotic waterbodies such as rivers and streams, living under and on the sides of submerged stones (Gray 1988; Campbell et al. 2017). The genus *Lanx* is also occurring in lakes (Gray 1988).

6. ***Lanx*** **Clessin,** 1880 (Fig. 3.3f)

(Clessin, 1880, p. 10)
[= *Ancylus* O.F. Müller, 1774 (partim); = *Walkerola* Hannibal, 1912]

Type species. *Ancylus patelloides* I. Lea, 1856 = *Lanx patelloides* [SD, Hubendick, 1951, p. 114].

Taxonomic content and distribution. Two extant species, inhabiting the western USA (California and Oregon).

7. ***Fisherola* Hannibal, 1912** (Fig. 3.3g)

(Hannibal, 1912, p. 10)
[= *Ancylus* O.F. Müller, 1774 (partim)]
Type species. *Fisherola lancides* Hannibal, 1912 = *Fisherola nuttallii* (Haldeman, 1841) [OD].
Taxonomic content and distribution. The genus is known from the west of the USA (California, Oregon) and Canada (British Columbia) [Burch 1989; Campbell et al. 2017].

8. ***Idaholanx* Clark, Campbell & Lydeard, 2017**

(Campbell et al. 2017, p. 121)
Type species. *Idaholanx fresti* Clerk, Campbell & Lydeard, 2017 [OD].
Taxonomic content and distribution. A monotypic genus found exclusively in Idaho, USA.

Genera of the Lymnaeinae still unassigned to tribes
The genera listed below in alphabetic order have been unassigned to a particular tribe owing either to the low statistical support of corresponding clades or to the lack of available molecular information on their representatives.

9. ***Acella* Haldeman, 1841** (Fig. 3.3h)

(Haldeman 1841, p. 6)
Type species. *Lymnaea gracilis* Jay, 1839 = *Acella haldemani* (Binney, 1867) [M].
Taxonomic content, distribution, and ecology. A single extant species, the spindle pond snail, *Acella haldemani* (Binney, 1867), is included. It is distributed in the USA and south of Canada (Baker 1911; Burch 1989; Johnson et al. 2013), lives in large perennial lakes and streams (Baker 1911; Taylor et al. 1963).

10. ***Bulimnea* Haldeman, 1841** (Fig. 3.3i)

(Haldeman 1841, p. 6)
Type species. *Lymnaea megasoma* Say, 1824 = *Bulimnea megasoma* [M].
Taxonomic content, distribution, and ecology. A monotypic genus endemic to North America: inhabits Great Lakes and St. Lawrence river drainage area and parts of the Canadian Interior Basin (Burch 1989). Lives in large perennial rivers and lakes (Taylor et al. 1963), registered from sloughs and ponds (Baker 1911).

11. ***Dallirhytis* Kruglov & Starobogatov, 1989** (Fig. 3.3j)

(Kruglov and Starobogatov, 1989, p. 15)
Type species. *Lymnaea petersi* Dall, 1905 = *Dallirhytis atkaensis* (Dall, 1884) [OD].

Taxonomic remark. Established as a "section" of the subgenus *Polyrhytis* Meek, 1876 of the genus *Lymnaea* s. lato (Kruglov and Starobogatov 1989, 1993a). The use of the generic name *Polyrhytis*, with a fossil *Lymnaea kingi* Meek, 1876 as its type species, is, in our opinion, unwarranted especially since we have no data on the real phylogenetic relationship between *L. kingi* and the recent lymnaeids of North America (see Vinarski 2012 for further discussion of the meaning and applicability of the name *Polyrhytis*). Walter (cited after Clarke 1973, p. 310) once characterized the type species of this genus as "a chimaera having marked advanced and primitive stagnicoline anatomical features, and in this it looks like a hybrid between *Lymnaea stagnalis* and *L. catascopium*." The independent generic position of this species proposed here allows us to explain this observation.

Taxonomic content, distribution, and ecology. A single species included, *Dallirhytis atkaensis*, is a "glacial" relict of the Beringian freshwater malacofauna (Clarke 1973); now it is distributed in Alaska, north-western Canada, and eastern Chukotka (Clarke 1973, 1981; Kruglov and Starobogatov 1993a). The ecological information on this snail is relatively scarce. In British Columbia it lives in "clear, cold, oligotrophic lakes" (Clarke 1981, p. 128); in Chukotka it is registered from lakes and "large lentic waterbodies" (Kruglov 2005, p. 177).

12. ***Erinna* H. Adams & A. Adams in A. Adams, 1855 (Fig. 3.3k)**

(A. Adams 1855, p. 120)

[= *Pelagolimnaea* Germain, 1928]

Type species. *Erinna newcombi* H. & A. Adams, 1855 [M].

Taxonomic content, distribution, and ecology. This taxon includes two species endemic to Hawaii (Johnson et al. 2013). One of these species, *E. aulacospira* (Ancey, 1899), is, probably, extinct now (Cowie et al. 2017). *Erinna* snails were reported from rivers and waterfalls, as well as from the wet surface rocks of a precipice (Baker 1911; Hubendick 1952).

Remark. Our phylogeny recovered *Erinna* as a part of *Ladislavella*, which makes the latter a paraphyletic taxon (see Fig. 3.2). Possibly, *Ladislavella* s. lato must be divided into several genera.

13. ***Galba* Schrank, 1803** (Fig. 3.3l)

(Schrank 1803, p. 262)

[= *Buccinum* O.F. Müller, 1774 (partim); = *Truncatuliana* Servain, 1882; = *Fossaria* Westerlund, 1885; = *Microlimnaea* W. Dybowski, 1908; = *Palustria* W. Dybowski, 1908; = *Turrilimnaea* W. Dybowski, 1908; = *Simpsonia* F.C. Baker, 1911; = *Pseudogalba* F.C. Baker, 1913; = *Nasonia* F.C. Baker, 1928; = *Montigalba* Izzatullaev, Kruglov et Starobogatov, 1983; = *Afrogalba* Kruglov et Starobogatov, 1985].

Type species. *Buccinum truncatulum* O.F. Müller, 1774 = *Galba truncatula* [SD: ICZN, 1998].

Taxonomic content and nomenclature. Vinarski (2013) considered this genus as including three morphologically-defined subgenera: *Galba* s.str., *Bakerilymnaea* Weyrauch, 1964 (type species *Limnaea cubensis* Pfeiffer, 1839), and *Sibirigalba*

Kruglov & Starobogatov, 1985 (type species *Limnaea truncatula* var. *sibirica* Westerlund, 1885). Our phylogenetic analysis recovered *Galba* as a compact monophyletic clade not subdivided into subgenera (see also Alda et al. 2021). The actual number of valid species in the genus is difficult to define, since many nominal species (especially numerous representatives of *Galba* occurring in North America; see Burch 1989; Johnson et al. 2013; Alda et al. 2021) have yet not been studied molecularly. Possibly, there are 15–20 valid species in this genus. Some recent malacologists, especially those working beyond Europe, prefer to use the generic name *Fossaria* instead of *Galba* (Burch 1989; Ponder and Waterhouse 1997). The reason is that the taxonomic identity of the type species of *Galba* has been thought to be unidentifiable (Ponder and Waterhouse 1997). In this case, however, the generic name *Truncatuliana* Servain, 1882 takes precedence before *Fossaria*.

Distribution and ecology. Most species of *Galba* s. str. inhabit the Americas (Burch 1989; Artigas et al. 2011; Standley et al. 2013), two representatives of the genus, *G. truncatula* (O.F. Müller, 1774) and *G. schirazensis* (Küster, 1862), are broadly distributed in the Palearctic (van Damme 1984; Kruglov 2005; Bargues et al. 2011; Mahulu et al. 2019). Possibly, both of them are of American origin and were introduced to the Old World in the historical time (see Correa et al. 2010; Lounnas et al. 2018), however, this conclusion has been disputed (Artigas et al. 2011; Bargues et al. 2011; Mahulu et al. 2019). The fossil records of *G. truncatula* (or closely related species) in the Neogene and Quaternary deposits of Eastern Europe (Danilovsky 1955; Ložek 1964; Sanko 2007), Siberia (Popova 1981), and the Late Pleistocene and Holocene of North Africa (van Damme 1984) contradict the hypothesis on the recent introduction of this species from the New World. *G. truncatula* has been introduced to New Zealand (Climo and Pullan 1972). Recently, Mahulu et al. (2019) demonstrated that *G. mweruensis* (Connolly, 1929), which is widely distributed through Sub-Saharan Africa, is a distinct species, possibly sister to *G. truncatula*; the status of *G. robusta* Vinarski, 2018 (type locality situated in Yemen) is unclear because of the lack of molecular data.

Most representatives of *Galba* are semi-amphibious or truly amphibious snails living in seasonal pools, ditches, wet shores of lakes, streams and springs, on wet surfaces of stones (Frömming 1956; Beriozkina and Starobogatov 1988; Jackiewicz 1998).

14. ***Hinkleyia* F.C. Baker, 1928** (Fig. 3.3q)

(Baker 1928, p. 259)

[= *Sphaerogalba* Kruglov & Starobogatov, 1985]

Type species. *Lymnaeus caperatus* Say, 1829 = *Hinkleyia caperata* [OD].

Taxonomic content, distribution, and ecology. Three species of *Hinkleyia* were listed by North American malacologists as being distributed in the Nearctic (Taylor et al. 1963; Burch 1989). They may live in seasonal bodies of water (sloughs, irrigation ditches, shallow ponds) as well as in small springs and mountain streams (Taylor et al. 1963). Taylor et al. (1963) and Burch (1989) treated *Hinkleyia* as a subgenus of *Stagnicola*. Kruglov and Starobogatov (1985b) separated *H. montanensis* in a subgenus of its own, *Walterigalba* Kruglov and Starobogatov,

1985. Due to the lack of molecular data, it is difficult to decide if *Walterigalba* represents a valid subgenus, or it is merely a synonym of *Hinkleyia*. The genus *Sphaerogalba* Kruglov & Starobogatov, 1985 (type species *Lymnea bulimoides* I. Lea, 1841), with more than 10 species distributed in North and South America (Kruglov and Starobogatov 1985b), according to our phylogenetic hypothesis (see Fig. 3.2) must be treated as a junior synonym of *Hinkleyia*. At least one of the species included by Kruglov and Starobogatov (1985b) to *Sphaerogalba*, the South American *Lymnaea viator* (d'Orbighy, 1835), belongs to the genus *Galba* (Artigas et al. 2011). The habitats of *Sphaerogalba* are very similar to these of *Hinkleyia* (Kruglov and Starobogatov 1985b).

15. ***Ladislavella* B. Dybowski, 1913 (**Fig. 3.3m, n**)**

(B. Dybowski 1913, p. 179)

[= *Polyrhytis* Meek, 1876 sensu Kruglov et Starobogatov, 1989 (partim); = *Catascopia* Meier-Brook et Bargues et, 2002].

Type species. *Ladislavella sorensis* B. Dybowski, 1913 = *Ladislavella terebra* (Westerlund, 1885) [SD, Hubendick 1951, p. 116].

Taxonomic content and nomenclature. Vinarski (2012) assigned two subgenera to this genus: *Ladislavella* s. str. (two species), and *Walterlymnaea* Starobogatov & Budnikova, 1976 (type species: *Lymnaea catascopium* Say, 1817). The latter group corresponds to the *L. emarginata/catascopium* and *L. elodes* species groups (sensu Burch 1989). Our multi-locus phylogeny recovered *Walterigalba* as a sister group to *Ladislavella* s. str. + *Erinna* clade. Possibly, *Walterlymnaea* has to be assigned to a genus of its own, but the absence of molecular data on two lymnaeid taxa which are endemic to Hawaii (i.e., *Pseudisidora* s.str. and *Pseudobulinus*) do not allow us to resolve this question here. *Ladislavella* sensu Vinarski (2012) embraces approximately 20 nominal taxa (Burch 1989; Johnson et al. 2013), but it is not clear yet how many valid species are there in *Walterlymnaea*.

Distribution and ecology. *Ladislavella* s. str. is a Palearctic subgenus broadly distributed in Central and Eastern Europe as well as in Asiatic Russia (Vinarski 2012); it includes not less than three recent species. Another subgenus is confined almost exclusively to North America and Greenland, with a single subspecies in the Asiatic part of Beringia (Vinarski et al. 2016b, 2017). *Ladislavella* may occupy a wide range of habitats, from perennial large lakes to seasonal pools and thermal springs (Vinarski et al. 2016b, 2023).

16. ***Pectinidens* Pilsbry, 1911** (Fig. 3.3o)

(Pilsbry 1911, p. 522)

Type species. *Lymnaea diaphana* King, 1832 = *Pectinidens diaphanus* [OD].

Taxonomic content, distribution, and ecology. This genus, whose validity has recently been supported by a molecular study (Bargues et al. 2012), includes 1–2 species inhabiting southernmost parts of South America and the Falkland Islands (Paraense 1984; Bargues et al. 2012). The snails dwell in small waterbodies—ponds, ditches, in wetlands (Paraense 1984; Bargues et al. 2012).

17. ***Pseudisidora* Thiele, 1931** (Fig. 3.3r,s)

(Thiele 1931, p. 476)

Type species: *Lymnaea rubella* Lea, 1844 = *Pseudisidora rubella* [M].

Taxonomic content, distribution, and ecology: A small group comprising a few (2–3) species distributed in Hawaii. Kruglov and Starobogatov (1989, 1993a) included three species described from the Kamchatka Peninsula (eastern Asiatic Russia) there, but this opinion is very doubtful from the zoogeographic point of view and needs a confirmation. Two subgenera are recognized (Vinarski 2013): *Pseudisidora* s. str., and *Pseudobulinus* Kruglov & Starobogatov, 1993 (type species—*Physa reticulata* Gould, 1847). The snails of the genus have been reported from streams, artificial pools, waterfalls, ditches, and springs (Hubendick 1952).

18. ***Pseudosuccinea* F.C. Baker, 1908** (Fig. 3.3p)

(Baker, 1908, p. 943)

Type species: *Lymnaea columella* Say, 1817 = *Pseudosuccinea columella* [OD].

Taxonomic content, distribution, and ecology: The genus is distributed in both Americas (Baker 1911; Roszkowski 1927; Burch 1989). From 1927 onward, *Pseudosuccinea columella* has been reported from glasshouses and aquaria of different countries of Europe where it is broadly distributed now (Schlesch 1930; Madsen and Frandsen 1989; Lounnas et al. 2017); also it has been registered as a non-indigenous species in Sub-Saharan Africa (van Eeden and Brown 1966; Brown 1994; Tchakonté et al. 2014), South America (Davies et al. 2014; Martín et al. 2016), and in the Pacific Region—Hawaii, Australia, and New Zealand (Climo and Pullan 1972; Madsen and Frandsen 1989). All indigenous species of China and India classified by some authors as belonging to *Pseudosuccinea* (Yen 1939; Subba Rao 1989) are, actually, members of the genus *Radix*. *P. columella* is a generalist species with the highest invasive potential. It has been reported from waterbodies of a different sort (Roszkowski 1927; Welter-Schultes 2012), though it clearly prefers lotic habitats and is rarely registered from streams and brooks (Baker, 1911).

Subfamily Amphipepleinae Pini, **1877**
(Pini, 1877, p. 174)

[? = Valencienninae Kramberger-Gorjanovic, 1923]

Type genus. *Amphipeplea* Nillson, 1822 = *Myxas* G.B. Sowerby I, 1822.

Diagnosis. Shell helicoid, small to medium-sized (shell height varies from 5–6 to around 35 mm), of various shape (from ovate-conical to auriculate or neritiform). Prostate with one internal fold or unfolded. Haploid chromosome number 16–17. Copulatory apparatus simple. Penis without fixatory ring-like swelling. The spermathecal duct may be long, short, or virtually absent.

Remark. The only synapomorphy characteristic of this subfamily is the reduced haploid chromosome number (n = 16–17) [Vinarski 2013]. The Amphipepleinae are distributed almost worldwide, with most genera and species native to the Old World (Starobogatov 1970; Kruglov and Starobogatov 1993a; Vinarski 2013; Aksenova et al. 2018; Vinarski et al. 2020).

Tribe Amphipepleini Pini, **1877**

Diagnosis. Shell of moderate size, broad, almost ovoid, very fragile, with extremely expanded body whorl and almost invisible spire. The mantle of a living animal is reflected over its shell. Prostate with a single internal fold. The spermathecal duct is relatively short, its length is roughly equal to that of spermatheca or slightly exceeds it.

The tribe is endemic to Europe.

19. ***Myxas* G.B. Sowerby I, 1822** (Fig. 3.4a)

(Sowerby 1822: part VI)

[= *Amphipeplea* Nilsson, 1822; = *Lutea* T. Brown, 1827; = *Cyclolimnea* Dall, 1905].

Type species. *Buccinum glutinosum* O.F. Müller, 1774 = *Myxas glutinosa* [M].

Taxonomic content, distribution, and ecology. 1–2 species distributed in the north-western part of Palearctic westward to south-western Siberia (Jackiewicz 1998; Glöer 2002, 2019; Welter-Schultes 2012; Vinarski and Kantor 2016). Other *Myxas*-similar lymnaeids of the world have been classified within separate taxa showing no close affinity to this genus (Kruglov and Starobogatov 1985a; Vinarski et al. 2021). *Myxas* usually inhabit stagnant, permanent, and well-oxygenated waterbodies (Feliksiak 1939; Jackiewicz, 1998; Glöer 2002).

Tribe Austropepleini Bolotov, Vinarski & Aksenova trib. nov.

Type genus. *Austropeplea* Cotton, 1942.

Diagnosis. Shell of moderate size, conical to almost round. Penis simple, prostate with a single unbranched fold. The spermathecal duct relatively short. This tribe has no morphological synapomorphies and is delineated solely on the basis of molecular evidence.

20. ***Austropeplea* Cotton,** 1942 (Fig. 3.4e)

(Cotton 1942, p. 80)

[= *Glacilimnea* Iredale, 1943; = *Simlimnea* Iredale, 1943]

Type species: *Lymnaea aruntalis* Cotton & Godfrey, 1938 = *Austropeplea papyracea* (Tate, 1880) [OD].

Taxonomic content, distribution, and ecology. The genus comprises a few (6–7) species distributed in Australia, New Guinea, Tasmania, and New Zealand (Starobogatov 1970; Ponder and Waterhouse 1997). Two subgenera are recognized (Ponder et al. 2020): *Austropeplea* s. str., and *Kutikina* Ponder and Waterhouse, 1997, with *Kutikina hispida* Ponder and Waterhouse, 1997 as its type species. Ecologically, the representatives of this genus may be characterized as dwellers of ponds, springs, and wetlands (Boray 1964).

21. ***Bullastra* Bergh,** 1901 (Fig. 3.4f)

(Bergh 1901, p. 254)

[=? *Peplimnea* Iredale, 1943]

Type species. *Bullastra velutinoides* Bergh, 1901 = *Bullastra cumingiana* (L. Pfeiffer, 1855) [M].

Taxonomic content, distribution, and ecology. Five species, inhabiting Australia, the Philippines, and the Moluccas (Kruglov and Starobogatov, 1985a; Ponder et al. 2020; Vinarski et al. 2020). The ecology of *Bullastra* is similar to that of the previous genus.

22. ***Orientogalba*** **Kruglov & Starobogatov, 1985** (Fig. 3.4g)

(Kruglov and Starobogatov 1985b, p. 28)

[= *Lenagalba* Kruglov & Starobogatov, 1985; = *Viridigalba* Kruglov & Starobogatov, 1985]

Type species. *Lymnaea heptapotamica* Lazareva, 1967 = *Orientogalba heptapotamica* [OD].

Taxonomic content, distribution, and ecology. A small group consisting of 3–4 species widely distributed in Asia (except for its western and northern parts) and in some Pacific islands (Kruglov and Starobogatov 1993b; Aksenova et al. 2018; Vinarski et al. 2020), introduced into southwest Europe (*O. viridis*; see Schniebs et al. 2017). Most species are semi-amphibious and inhabit small ponds, pools, and wetlands (Kruglov and Starobogatov 1985b).

Tribe Peregrianini Bolotov, Vinarski & Aksenova trib. nov.

Type genus. *Peregriana* Servain, 1882.

Diagnosis. Shell of moderate size (shell height up to 20 mm), conical or ovate-conical. Penis simple, prostate with a single unbranched fold. The spermathecal duct is typically short or virtually absent. This tribe has no morphological synapomorphies and is delineated solely on the basis of molecular evidence.

23. ***Peregriana*** **Servain,** 1882 (Fig. 3.4j)

(Servain 1882, p. 56)

Type species. *Buccinum peregrum* O.F. Müller, 1774 = *Peregriana peregra* [SD; Kobelt 1883, p. 14].

Taxonomic content, distribution, and ecology. According to Aksenova et al. (2018), the genus comprises two species. The range of *Peregriana* covers Europe and Siberia (Vinarski et al. 2016a; Aksenova et al. 2018). The snails of this genus are inhabitants of non-permanent waterbodies of various types; sometimes may occur in small permanent wetlands (Vinarski et al. 2016a).

24. ***Ampullaceana*** **Servain,** 1882 (Fig. 3.4i)

(Servain 1882, p. 53)

[= *Biformiana* Servain 1882; = *Bouchardiana* Servain, 1882; = *Caenisiana* Servain 1882; = *Effusiana* Servain 1882; = *Limosiana* Servain, 1882; = *Nivalisiana* Servain 1882; = *Ohridlymnaea* Kruglov & Starobogatov 1993]

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

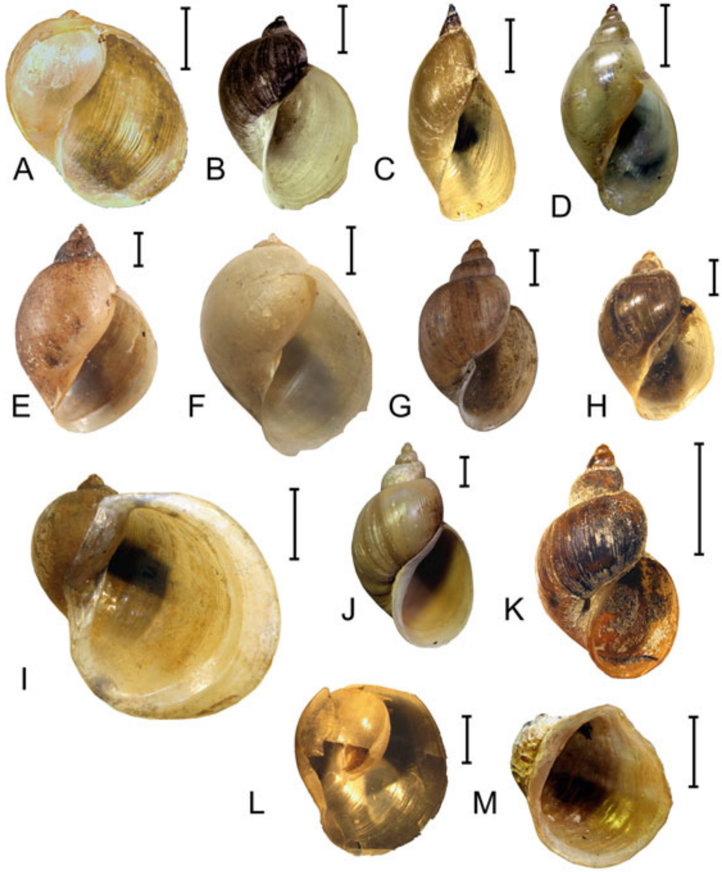

Fig. 3.4 Shells of representatives of genera and species of the Amphipepleinae. (**a**) *Myxas glutinosa*. North Kazakhstan, the Tobol River floodplain [ZIN]. (**b**) *Radix* (*Radix*) *makhrovi*. Tibet, west of the Lhasa River mouth [holotype, ZIN]. (**c**) *Radix* (*Exssertiana*) *rufescens*. Myanmar, Yeto River [LMBI]. (**d**) *Racesina oxiana*. Tajikistan, Kurban-Shakhid [LMBI]. (**e**) *Austropeplea papyracea*. Australia, Torrens River at Adelaida [MHNH]. (**f**) *Bullastra lessoni*. Australia, Brisbane [ZMB]. (**g**) *Orientogalba viridis*, Guam Island [syntype, MHNH]. (**h**) *Kamtschaticana kamtschatica*. Russia, Kamchatka, Esso River [ZIN]. (**i**) *Ampullaceana ampla*. Ukraine, Transkarpatian Region [LMBI]. (**j**) *Peregriana peregra*. Austria, South Tirol [NHMW]. (**k**) *Tibetoradix imitator*, Tibet, pond near Drongpa Tradun [holotype, ZIN]. (**l**) *Limnobulla peculiaris.* Falkland Islands [holotype, damaged; NHMUK]. (**m**) *Lantzia carinata*. Réunion Island [NHMW]. Scale bars 2 mm (B, C, E, G, H, J, L, M), 5 mm (A, D, F, I, K). Photos: Maxim Vinarski. See "Material & methods" section for museum acronyms

Taxonomic content, distribution, and ecology. Aksenova et al. (2018) include in this genus seven genetically defined species, some of them, such as *A. lagotis* (Schrank, 1803), are widely distributed throughout Europe, Siberia, and Central Asia. The species *A. relicta* (Poliński, 1929), with its two subspecies, is endemic to large Balkan lakes, Ohrid and Prespa (Aksenova et al. 2018). The native range of the genus is Palearctic; at least one species, *A. balthica*, has recently been introduced to eastern Canada (Vinarski et al. 2022b).

Most representatives of *Ampullaceana* live in small stagnant waterbodies and slowly running streams, though some species are known to inhabit the shallow zones of large lakes or thermal springs and pools (Kruglov 2005; Bolotov et al. 2017; Vinarski et al. 2020). A series of nominal species belonging to this genus remains unassessed genetically, and their validity, as well as proper generic position, are unknown.

25. ***Kamtschaticana* Kruglov & Starobogatov, 1984** (Fig. 3.4h)

(Kruglov & Starobogatov 1984a, p. 30)
[= *Lymnaea* (*Pacifimyxas*) Kruglov & Starobogatov, 1985]
Type species. *Limnaeus kamtschaticus* Middendorff, 1850 [OD].

Taxonomic content, distribution, and ecology. A single species, *K. kamtschatica* (Middendorff, 1850), is included, and two more species living in Kamchatka and Japan are not formally described yet (Aksenova, Bolotov, Vinarski, unpublished). *K. kamtschatica* inhabits the northeastern part of Eurasia and has not been found outside Russia, except for Alaska (Kruglov and Starobogatov 1984a, 1993b; Aksenova et al. 2018; Vinarski et al. 2021). *K. kamtschatica* lives in waterbodies of different type, including wet shores of lakes and rivers, and the geothermal sites (e.g., the Valley of Geysers, Kamchatka), where it can form sustainable populations in warm water up to +39.9 °C (Aksenova et al. 2016).

Tribe Radicini Vinarski, 2013
(Vinarski, 2013, p. 51)

Type genus. *Radix* Montfort, 1810.

Diagnosis. Shell of medium size (shell height up to 35 mm), high-conical to broadly ear-shaped. Penis simple, prostate one-folded or (in *Racesina*) with several internal folds. Spermathecal duct long. This tribe has no morphological synapomorphies and is delineated solely on the basis of molecular data.

26. ***Radix* Montfort,** 1810 (Fig. 3.4b,c)

(Montfort, 1810, p. 266)
[= *Helix* Linnaeus, 1758 (partim); = *Xymorus* Gebler, 1829; = *Gulnaria* Turton, 1831; = *Neritostoma* Adams & Adams, 1855; = *Cerasina* Kobelt, 1881; = *Auriculariana* Servain, 1882; = *Raffrayana* Bourguignat, 1883; = *Desertiradix* Kruglov & Starobogatov, 1989; = *Iraniradix* Kruglov & Starobogatov, 1989; = *Okhotiradix* Kruglov & Starobogatov, 1989; = *Pamiriradix* Kruglov & Starobogatov, 1989; = *Thermoradix* Kruglov & Starobogatov, 1989; = *Ussuriradix* Kruglov & Starobogatov, 1989].[3]

[3]The full synonymy of this genus is too extensive to be given here in full.

Type species. *Radix auriculatus* Montfort, 1810 = *Radix auricularia* (Linnaeus, 1758) [OD].

Taxonomic content. The genus contains two subgenera: *Radix* s.str. and *Exsertiana* Bourguignat, 1883 [type species *Limnaeus natalensis* var. *exsertus* Martens, 1866 = *Radix natalensis* (Krauss, 1848)]. The latter subgenus in its distribution is restricted to the tropical regions of the Old World (Vinarski et al. 2020). According to different authors, the genus includes 2 (Jackiewicz 1998) to more than 40 (Kruglov 2005) species, but the validity of many nominal species of *Radix* accepted by the latter author has recently been rejected as a result of the integrative taxonomic studies (Bolotov et al. 2014; Aksenova et al. 2016, 2017). The exact number of valid species of *Radix* is unknown, it may be 15–20.

Distribution and ecology: *Radix* is widely distributed in Eurasia and Africa but absent from Australia and South America (Starobogatov 1970; Aksenova et al. 2018; Vinarski et al. 2020). One species (*R. auricularia*) was introduced into North America (Burch 1989). Most representatives of *Radix* live in streams and permanent lakes, reservoirs, and quarries. They are phytophilic snails, usually restricted to shallow zones of waterbodies (Jackiewicz 1998).

27. ***Racesina* Vinarski & Bolotov,** 2018 (Fig. 3.4d)

(Vinarski and Bolotov 2018, p. 332)

Type species: *Lymnaea luteola* Lamarck, 1822 [OD].

Taxonomic content, distribution, and ecology: The genus contains not less than 3 species distributed in Central and South Asia, from Tajikistan and Uzbekistan southwards to Ceylon, Thailand, and south China (Brandt 1974; Kruglov 2005; Aksenova et al. 2018; Vinarski and Bolotov 2018; Vinarski et al. 2020). The molluscs dwell in small bodies of water, often in non-permanent ones (Subba Rao 1989; Kruglov 2005).

Remark: Three species included in *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. 2018). 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.

Tribe Tibetoradicini Bolotov, Vinarski & Aksenova trib. nov.

Type genus. *Tibetoradix* Bolotov, Vinarski and Aksenova, 2018.

Diagnosis. Shell of medium size (shell height up to 23 mm), high-conical to almost ear-shaped. Penis simple, prostate with a single unbranched fold. Spermathecal duct long. This tribe has no morphological synapomorphies and is delineated solely on the basis of molecular evidence.

A single genus is included. This tribe is endemic to the Tibetan Plateau and thus is characterized by the narrowest range among all lymnaeid tribes.

28. ***Tiberoradix* Bolotov, Vinarski & Aksenova, 2018** (Fig. 3.4k)

(Aksenova et al., 2018, p. 11)

Type species. *Lymnaea hookeri* Reeve, 1850 [OD].

Taxonomic content. The genus comprises not less than six species (Aksenova et al. 2018; Vinarski et al. 2022a). *Tibetoradix* is endemic to the Tibetan Plateau in China, where the crown group of this genus evolved in the Miocene (Vinarski et al. 2022a). The snails of this genus are known to live in streams, wetlands, and floodplain waterbodies. *Tibetoradix* is a unique genus among freshwater snails completely consisting of high-mountain species adapted to live at heights between 3500 and 5000 m a.s.l.

Genera of the Amphipepleinae still unassigned to tribes

Two nominal genera, on which no molecular genetic information is accessible, are provisionally classified here within the Amphipepleinae, however, their placement to particular tribes stays unclear.

29. ***Lantzia* Jousseaume,** 1872 (Fig. 3.4m)

(Jousseaume 1872, p. 5)

Type species. *Lantzia carinata* Jousseaume, 1872 [M].

Taxonomic content, distribution, and ecology. The monotypic genus which is found exclusively in the Réunion Island lying in the Indian Ocean (Brown 1994; Ponder and Waterhouse 1997). Lives in waterfalls (Brown 1994). Cowie et al. (2017) mention *Lantzia carinata* as probably an extinct species.

30. ***Limnobulla* Kruglov & Starobogatov, 1985** (Fig. 3.4l)

(Kruglov and Starobogatov 1985a, p. 71)

Type species. *Lymnaea peculiaris* Hubendick, 1951 = *Limnobulla peculiaris* [OD].

Taxonomic content, distribution, and ecology. A single species of *Limnobulla* inhabits the Falkland Islands. It is unknown both anatomically and ecologically (Kruglov and Starobogatov 1985a; Ponder and Waterhouse 1997) and has been provisionally included in the Amphipepleinae.

Acknowledgments The authors thank the Russian Science Foundation for the financial support of our research on the phylogeny and systematics of the Lymnaeidae (projects Nos. 19-14-00066/P and 21-74-10155).

References

Adams A (1855) Descriptions of two new genera and several new species of Mollusca, from the collection of Hugh Cummings, Esq. P Zool Soc Lond 23:119–124

Aksenova OV, Vinarski MV, Bolotov IN et al (2016) An overview of *Radix* species of the Kamchatka Peninsula (Gastropoda: Lymnaeidae). Bulletin of the Russian Far Eastern Malacological Society 20:5–27

Aksenova O, Vinarski M, Bolotov I et al (2017) Two *Radix* spp. (Gastropoda: Lymnaeidae) endemic to thermal springs around Lake Baikal represent ecotypes of the widespread *Radix auricularia*. J Zool Syst Evol Res 55(4):298–309. https://doi.org/10.1111/jzs.12174

Aksenova OV, Bolotov IN, Gofarov MY et al (2018) Species richness, molecular taxonomy and biogeography of the radicine pond snails (Gastropoda: Lymnaeidae) in the Old World. Sci Rep-UK 8:11199. https://doi.org/10.1038/s41598-018-29451-1

Albrecht C, Kuhn K, Streit B (2007) A molecular phylogeny of Planorboidea (Gastropoda: Pulmonata): insights from enhanced taxon sampling. Zool Scr 36:27–39. https://doi.org/10.1111/j.1463-6409.2006.00258.x

Alda P, Lounnas M, Vázquez AA et al (2021) Systematics and geographical distribution of *Galba* species, a group of cryptic and worldwide freshwater snails. Molec Phyl Evol 157:107035. https://doi.org/10.1016/j.ympev.2020.107035

Artigas P, Bargues MD, Mera y Sierra RL et al (2011) Characterisation of fascioliasis lymnaeid intermediate hosts from Chile by DNA sequencing, with emphasis on *Lymnaea viator* and *Galba truncatula*. Acta Trop 120:245–257. https://doi.org/10.1016/j.actatropica.2011.09.002

Baker FC (1908) Suggestions for a natural classification of the family Lymnæidæ. Science 27(703): 942–943

Baker FC (1911) The Lymnaeidae of North and Middle America. Special publication of the Chicago Academy of Sciences 3:1–539. https://doi.org/10.5962/bhl.title.20500

Baker FC (1915) On the classification of the Lymnaeids. The Nautilus 29(2):20–24

Baker FC (1928) The fresh water Mollusca of Wisconsin. Part I. Gastropoda. Bulletin of the Wisconsin Geological and Natural History Survey 70(1):xx+1–x507

Bargues MD, Mera y Sierra RL, Artigas P (2012) DNA multigene sequencing of topotypic specimens of the fascioliasis vector *Lymnaea diaphana* and phylogenetic analysis of the genus *Pectinidens* (Gastropoda). Mem I Oswaldo Cruz 107(1):111–124. https://doi.org/10.1590/s0074-02762012000100016

Bargues MD, Artigas P, Jackiewicz M et al (2006) Ribosomal DNA ITS-1 sequence analysis of European stagnicoline Lymnaeidae (Gastropoda). Heldia 6(1–2):57–68

Bargues MD, Artigas P, Khoubbane M et al (2011) *Lymnaea schirazensis*, an overlooked snail distorting fascioliasis data: genotype, phenotype, ecology, worldwide spread, susceptibility, applicability. PLoS One 6:e24567. https://doi.org/10.1371/journal.pone.0024567

Bergh R (1901) Bullacea. In: Reisen in Archipel der Philippinen von Dr. C. Semper. C.W. Kreidel, Wiesbaden 7(4):209–256

Beriozkina GV, Starobogatov YI (1988) Reproductive ecology and egg clusters of freshwater Pulmonata. Trudy Zoologicheskogo Instituta AN SSSR 174:1–306. [in Russian]

Bolotov I, Bespalaya Y, Aksenova O et al (2014) A taxonomic revision of two local endemic *Radix* spp. (Gastropoda: Lymnaeidae) from Khodutka geothermal area, Kamchatka, Russian Far East. Zootaxa 3869:585–593. https://doi.org/10.11646/zootaxa.3869.5.9

Bolotov IN, Aksenova OV, Bespalaya YV et al (2017) Origin of a divergent mtDNA lineage of a freshwater snail species, *Radix balthica*, in Iceland: cryptic glacial refugia or a postglacial founder event? Hydrobiologia 787:73–98. https://doi.org/10.1007/s10750-016-2946-9

Bolotov IN, Pfeiffer JM, Konopleva ES et al (2018) A new genus and tribe of freshwater mussel (Unionidae) from Southeast Asia. Sci Reps-UK 8:10030. https://doi.org/10.1038/s41598-018-28385-y

Boray JC (1964) Studies on the ecology of *Lymnaea tomentosa*, the intermediate host of *Fasciola hepatica*: I. History, geographical distribution, and environment. Aust J Zool 12(2):217–230. https://doi.org/10.1071/ZO9640217

Bouchet P, Rocroi JP, Hausdorf B et al (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2):1–526. https://doi.org/10.4002/040.061.0201

Brandt RAM (1974) The non-marine aquatic Mollusca of Thailand. Arch Molluskenkd 105:1–423

Brown DS (1994) Freshwater snails of Africa and their medical importance. Taylor and Francis, London. https://doi.org/10.1201/9781482295184

Burch JB (1989) North American freshwater snails. Malacological Publications, Hamburg, MI

Campbell DC, Clark SA, Lydeard C (2017) Phylogenetic analysis of the Lancinae (Gastropoda, Lymnaeidae) with a description of the U.S. federally endangered Banbury Springs lanx. Zookeys 663:107–132. https://doi.org/10.3897/zookeys.663.11320

Clarke AH (1973) The freshwater molluscs of the Canadian Interior Basin. Malacologia 13:1–509

Clarke AH (1981) The freshwater molluscs of Canada. National Museum of Natural Sciences, Ottawa

Clessin S (1880) Die Familie der Ancylinen. Systematisches Conchylien-Cabinet von Martini und Chemnitz. Bauer und Raspe, Nürnberg 1(6):1–40

Climo FM, Pullan NB (1972) A taxonomic review of the family Lymnaeidae (Mollusca: Gastropoda) in New Zealand. J Roy Soc New Zeal 2:5–13. https://doi.org/10.1080/03036758.1972.10423300

Correa AC, Escobar JC, Durand P et al (2010) Bridging gaps in the molecular phylogeny of the Lymnaeidae (Gastropoda: Pulmonata), vectors of fascioliasis. BMC Evol Biol 10:381. https://doi.org/10.1186/1471-2148-10-381

Cotton BC (1942) Some australian freshwater Gasteropoda. Trans R Soc S Aust 66(1):75–82

Cowie RH, Régnier C, Fontaine R et al (2017) Measuring the sixth extinction: what do mollusks tell us? The Nautilus 131(1):3–41

Danilovsky IV (1955) Scandinavian glaciation deposits key site of the Russian plain and index quaternary molluscs. Gosgeoltekh Publishers, Moscow. [in Russian]

Davies D, Nieva L, Choke LA et al (2014) First record of *Pseudosuccinea columella* (Say, 1817) from Salta province, Northwest Argentina (Mollusca: Gastropoda: Lymnaeidae). CheckList 10(3):597–599. https://doi.org/10.15560/10.3.597

Dayrat B, Conrad M, Balayan S et al (2011) Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): new insights from increased taxon sampling. Mol Phylogenet Evol 59: 425–437. https://doi.org/10.1016/j.ympev.2011.02.014

de Montfort PD (1810) Conchyliologie Systématique et classification Méthodique des coquilles, vol 2. Coquilles Univalves, Non Cloisonées. F. Schoell, Paris, pp 1–676. https://doi.org/10.5962/bhl.title.10571

Dybowski W (1903) Bemerkungen über die gegenwärtige Systematik der Süsswasserschnecken. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 35(9–10):130–145

Dybowski B (1913) Bemerkungen und Zusatze zu der Arbeit von Dr. W. Dybowski "Molluscen aus der Uferregion des Baicalsees". Ezhegodnik Zoologicheskogo muzeya Imperatorskoy Akademii nauk 17:165–218

Feliksiak S (1939) Über Biologie und Morphologie der Mantelschnecke, *Radix glutinosa* (O.F. Müller). Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geografie der Tiere 72:17–70

Frömming E (1956) Biologie der mitteleuropäischen Süßwasserschnecken. Dunker-Humblot, Berlin

Froufe E, Bolotov I, Aldridge DC et al (2020) Mesozoic mitogenome rearrangements and freshwater mussel (Bivalvia: Unionoidea) macroevolution. Heredity 124:189–196. https://doi.org/10.1038/s41437-019-0242-y

Garbar AV, Manilo VV, Korniushin AV (2004) Probable directions of evolution of karyotypes of the European Lymnaeidae (Mollusca, Gastropoda, Pulmonata) in the light of modern concepts of phylogeny of the family. Vestnik zoologii 38(2):29–37. [in Russian]

Glöer P (2002) Die Sußwassergastropoden Nord- und Mitteleuropas: Bestimmungschlussel, Lebenweise, Verbreitung. Die Tierwelt Deutschlands. Conchbooks, Hackenheim 73:1–327

Glöer P (2019) The freshwater gastropods of the west-Palaearctis. Volume 1. Fresh- and brakish waters except spring and subterranean snails. Identification key, anatomy, ecology, distribution. The author, Hetlingen

Gray J (1988) Evolution of the freshwater ecosystem: the fossil record. Palaeogeogr Palaeocl 62:1–214. https://doi.org/10.1016/0031-0182(88)90054-5

Haldeman SS (1841) A monograph of the Limniades and other fresh-water univalve shells of North America. J Dobson, Philadelphia 3:1–16. https://doi.org/10.5962/bhl.title.11226

Hannibal HA (1912) A synopsis of the recent and tertiary freshwater Mollusca of the California Province, based upon an ontogenetic classification. Proc Malac Soc London 10(2):112–165. https://doi.org/10.1093/oxfordjournals.mollus.a063488

Hannibal HA (1914) Note on the classification of Ancylidae. The Nautilus 28(2):23–24

Hoang DT, Chernomor O, von Haeseler A et al (2017) UFBoot2: improving the ultrafast bootstrap approximation. Mol Biol Evol 35:518–522. https://doi.org/10.1093/molbev/msx281

Hubendick B (1951) Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature and distribution. Kungliga Svenska Vetenskapsakademiens Handlingar Fjärde Serien 3(1): 1–223

Hubendick B (1952) Hawaiian Lymnaeidae. Occasional Papers of Bernice P, vol 20(19). Bishop Museum, Honolulu, Hawaii, pp 307–328

ICZN (1998) Opinion 1896. *Galba* Schrank, 1803 (Mollusca: Gastropoda): *Buccinum truncatulum* designated as the type species. Bull Zool Nomencl 55(2):123

Inaba A (1969) Cytotaxonomic studies of lymnaeid snails. Malacologia 7(2/3):143–168

Jackiewicz M (1993) Phylogeny and relationships within the European species of the family Lymnaeidae. Folia Malacologica 5:61–95

Jackiewicz M (1998) European species of the family Lymnaeidae (Gastropoda, Pulmonata, Basommatophora). Genus 9(1):1–93

Jeffreys JG (1830) A synopsis of the testaceous pneumobranchous Mollusca of Great Britain. Trans Linn Soc Lond 16:323–392

Johnson PD, Bogan AE, Brown KM et al (2013) Conservation status of freshwater gastropods of Canada and the United States. Fisheries 38(6):247–282

Jousseaume F (1872) Description de quatre mollusques nouveaux. Revue et Magasin de Zoologie Pure et Appliquée, series 2(23):5–15

Kalyaanamoorthy S, Minh BQ, Wong TKF et al (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nat Methods 14:587–589. https://doi.org/10.1038/nmeth.4285

Kobelt W (1883) Erster Nachtrag zur zweiten Auflage des Catalogs der im europäischen Faunengebiet lebenden Binnenconchylien. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 15(1/2):1–25

Kruglov ND (2005) Lymnaeid snails of Europe and Northern Asia. Smolensk State Pedagogical University Press, Smolensk. [in Russian]

Kruglov ND, Starobogatov YI (1981) A new genus of the Lymnaeidae and taxonomy of the subgenus *Omphiscola* (*Lymnaea*) (Pulmonata, Gastropoda). Zool Zh 60(7):965–977. [in Russian]

Kruglov ND, Starobogatov YI (1984a) A contribution to the morphology and taxonomy of the subgenus *Peregriana* (*Lymnaea,* Gastropoda, Pulmonata) of the Asiatic part of the USSR and adjacent regions. Zool Zh 63:22–33. [in Russian]

Kruglov ND, Starobogatov YI (1984b) Morphological peculiarities and taxonomy of mollusks of the subgenus *Corvusiana* of the genus *Lymnaea* (Gastropoda, Pulmonata, Lymnaeidae). Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, otdel biologicheskiy 89(2):58–70. [in Russian]

Kruglov ND, Starobogatov YI (1985a) *Myxas*-similar Lymnaeidae (Gastropoda, Pulmonata), their origin and specific composition. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, otdel biologicheskiy 90(2):69–78. [in Russian]

Kruglov ND, Starobogatov YI (1985b) The volume of the subgenus *Galba* and of other similar subgenera of the genus *Lymnaea* (Gastropoda, Pulmonata). Zool Zh 64(1):24–35. [in Russian]

Kruglov ND, Starobogatov YI (1985c) Methods of experimental hybridization and some results of its applications in the taxonomy of Lymnaeidae. Malacol Rev 18:21–35

Kruglov ND, Starobogatov YI (1986) Mollusks of the subgenus *Stagnicola* of the genus *Lymnaea* of the USSR fauna. Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, otdel biologicheskiy 91(2):59–72. [in Russian]

Kruglov ND, Starobogatov YI (1989) Mollusks of the subgenus *Polyrhytis* of the genus *Lymnaea* in the fauna of the USSR (Pulmonata, Lymnaeidae). Zool Zh 68(3):14–20. [In Russian]

Kruglov ND, Starobogatov YI (1993a) Annotated and illustrated catalogue of species of the family Lymnaeidae (Gastropoda Pulmonata Lymnaeiformes) of Palaearctic and adjacent river drainage areas. Part I Ruthenica: Russian Malacol J 3(1):65–92

Kruglov ND, Starobogatov YI (1993b) Annotated and illustrated catalogue of species of the family Lymnaeidae (Gastropoda Pulmonata Lymnaeiformes) of Palaearctic and adjacent river drainage areas. Part II Ruthenica: Russian Malacol J 3(1):161–180

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33(7):1870–1874. https://doi.org/10.1093/molbev/msw054

Lamarck JB (1799) Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. Lu à l'Institut national, le 21 frimaire an VII. Mémoires de la Société d'Histoire Naturelle de Paris 1:63–91

Lopes-Lima M, Froufe E, Do VT et al (2017) Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): defining modern subfamilies and tribes. Mol Phylogenet Evol 106:174–191. https://doi.org/10.1016/j.ympev.2016.08.021

Lounnas M, Correa AC, Vázquez AA et al (2017) Self-fertilization, long-distance flash invasion and biogeography shape the population structure of *Pseudosuccinea columella* at the worldwide scale. Mol Ecol 26:887–903. https://doi.org/10.1111/mec.13984

Lounnas M, Correa AC, Alda P et al (2018) Population structure and genetic diversity in the invasive freshwater snail *Galba schirazensis*. Can J Zool 96(5):425–435. https://doi.org/10.1139/cjz-2016-0319

Ložek V (1964) Quartärmollusken der Tschechoslowakei. Rozpravy Ústředního Ústavu Geologického 31:1–374

MacNeil FS (1939) Fresh-water invertebrates and land plants of Cretaceous age from Eureka, Nevada. J Paleontol 13:355–360

Madsen H, Frandsen F (1989) The spread of freshwater snails including those of medical and veterinary importance. Acta Trop 46:139–146. https://doi.org/10.1016/0001-706x(89)90030-2

Mahulu A, Clewing C, Stelbrink B et al (2019) Cryptic intermediate snail host of the liver fluke *Fasciola hepatica* in Africa. Parasite Vectors 12:573. https://doi.org/10.1186/s13071-019-3825-9

Martín PR, Ovando XMC, Seuffert ME (2016) First record of the freshwater snail *Pseudosuccinea columella* (Gastropoda: Lymnaeidae) in southern Pampas (Argentina) and assessment of future spread. Mollusc Res 36(3):213–221. https://doi.org/10.1080/13235818.2015.1128602

Nguyen LT, Schmidt HA, Haeseler VA et al (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol Biol Evol 32:268–274. https://doi.org/10.1093/molbev/msu300

Paraense WL (1984) *Lymnaea diaphana*: a study of topotypic specimens (Pulmonata: Lymnaeidae). Mem I Oswaldo Cruz 79:75–81. https://doi.org/10.1590/S0074-02761984000100009

Pieńkowska JR, Lesicki A (2018) A note on the status of *Galba occulta* Jackiewicz, 1959 (Gastropoda: Hygrophila: Lymnaeidae). Folia Malacologica 26(4):231–247. https://doi.org/10.12657/folmal.026.02

Pieńkowska JR, Rybska E, Banasiak J et al (2015) Taxonomic status of *Stagnicola palustris* (O.F. Müller, 1774) and *S. turricula* (Held, 1836) (Gastropoda: Pulmonata: Lymnaeidae) in view of new molecular and chorological data. Folia Malacologica 23(1):3–18. https://doi.org/10.12657/folmal.023.003

Pilsbry HA (1911) Non-marine Mollusca of Patagonia. Reports of the Princeton University expeditions to Patagonia, 1896–1899. Princeton, New York, The University; Stuttgart, Schweizerbart 3(5):513–633. https://doi.org/10.5962/bhl.title.12486

Pilsbry HA (1925) The family Lancidae distinguished from the Ancylidae. The Nautilus 38:73–75

Pini N (1877) Molluschi terrestri e d'acque dolce viventi nel territorio d'Esino. Bullettino della Società Malacologica Italiana 2(2):67–205

Ponder WF, Waterhouse J (1997) A new genus and species of Lymnaeidae from the lower Franklin River, south western Tasmania. J Mollus Stud 63:441–468. https://doi.org/10.1093/mollus/63.3.441
Ponder WF, Hallan A, Shea ME et al (2020) Australian freshwater molluscs. Revision 1. https://keys.lucidcentral.org/keys/v3/freshwater_molluscs/
Popova SM (1981) The Cenozoic continental malacofauna of southern Siberia and adjacent territories. Nauka Publishers, Moscow. [in Russian]
Puslednik L, Ponder WF, Dowton M et al (2009) Examining the phylogeny of the Australasian Lymnaeidae (Heterobranchia: Pulmonata: Gastropoda) using mitochondrial, nuclear and morphological markers. Mol Phylogenet Evol 52(3):643–659. https://doi.org/10.1016/j.ympev.2009.03.033
Rafinesque CS (1815) Analyse de la nature ou Tableau de l'Univers et des corps organisés. de l'Auteur, Palerme. https://doi.org/10.5962/bhl.title.106607
Rafinesque CS (1819) Prodrome. De 70 nouveaux genres d'animaux découverts dans l'intérieur des Etats-Unis d'Amérique, durant l'année 1818. Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts 88:417–429
Roszkowski W (1927) Contributions to the study of the family Lymnaeidae VIII. The genus *Pseudosuccinea* from South Brazil. Annales Zoologici Musei Polonici Historiae Naturalis 6(1):1–33
Saadi AJ, Davison A, Wade CM (2020) Molecular phylogeny of freshwater snails and limpets (Panpulmonata: Hygrophila). Zool J Linnean Soc 190(2):518–531. https://doi.org/10.1093/zoolinnean/zlz177
Sanko AF (2007) Quaternary freshwater mollusks of Belarus and neighboring regions of Russia, Lithuania, Poland (field guide). Institute of Geochemistry and Geophysics, National Academy of Sciences, Belarus, Minsk. [in Russian]
Schlesch H (1930) *Pseudosuccinea peregrina* Clessin, espèce d'Amérique du Sud, introduite dans les jardins des plantes de l'Europe. Bulletin de la Sociéte Zoologique de France 55(5):425–426
Schniebs K, Glöer P, Vinarski MV et al (2017) A new alien species in Europe: first record of *Austropeplea viridis* (Quoy & Gaimard, 1833) in Spain. J Conchol 42(5):357–370
Schrank von Paula F (1803) Fauna Boica. Durchgedachte Geschichte der in Baiern einheimischen und zahmen Thiere, vol 3(2). Philipp Krull, Landshut, pp 1–372
Servain G (1882 ["1881"]). Histoire malacologique du lac Balaton en Hongrie. S. Lejay et Co., Poissy. https://doi.org/10.5962/bhl.title.10458
Sowerby GBI (1822) The genera of recent and fossil shells, for the use of students in conchology and geology, vol 1. G.B. Sowerby, London, pp 1–274. https://doi.org/10.5962/bhl.title.86281
Standley CJ, Prepelitchi L, Pietrokovsky SM et al (2013) Molecular characterization of cryptic and sympatric lymnaeid species from the *Galba*/*Fossaria* group in Mendoza Province, Northern Patagonia, Argentina. Parasit Vectors 6:304. https://doi.org/10.1186/1756-3305-6-304
Starobogatov YI (1967) On the systematization of freshwater pulmonate molluscs. Trudy Zoologicheskogo Instituta AN SSSR 42:280–304. [in Russian]
Starobogatov YI (1970) Molluscan fauna and zoogeographic zonation of continental freshwater bodies of the world. Nauka, Leningrad. [in Russian]
Starobogatov YI (1976) The system and phylogeny of the Lymnaeidae. Problemy Zoologii. Zoologicheskiy Institut AN SSSR, p 79–81 [in Russian]
Subba Rao MV (1989) Handbook: freshwater molluscs of India. Zoological Survey of India, Calcutta
Taylor DW, Sohl NF (1962) An outline of gastropod classification. Malacologia 1(1):7–32
Taylor DW, Walter HJ, Burch JB (1963) Freshwater snails of the subgenus *Hinkleyia* (Lymnaeidae: Stagnicola) from the Western United States. Malacologia 1(2):237–281
Tchakonté S, Ajeagah GA, Diomandé C et al (2014) Diversity, dynamic and ecology of freshwater snails related to environmental factors in urban and suburban streams in Douala-Cameroon (Central Africa). Aquat Ecol 48:379–395. https://doi.org/10.1007/s10452-014-9491-2

Thiele J (1931) Handbuch der Systematischen Weichtierkunde, vol 2. Gustav Fischer Verlag, Jena, pp 377–778

Trifinopoulos J, Nguyen LT, von Haeseler A et al (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Res 44:W232–W235. https://doi.org/10.1093/nar/gkw256

van Damme D (1984) The freshwater Mollusca of northern Africa: distribution, biogeography and paleoecology. Dev Hydrobiol 25:1–164

van Eeden JA, Brown DS (1966) Colonization of fresh waters in the Republic of South Africa by *Lymnaea columella* Say (Mollusca: Gastropoda). Nature 210:1172–1173

Vermeij G (2017) The limpet form in gastropods: evolution, distribution, and implications for the comparative study of history. Biol J Linn Soc 120:22–37. https://doi.org/10.1111/bij.12883

Vinarski MV (2012) The lymnaeid genus *Catascopia* Meier-Brook et Bargues, 2002 (Mollusca: Gastropoda: Lymnaeidae), its synonymy and species composition. Invertebr Zool 9(2):91–104

Vinarski MV (2013) One, two, or several? How many lymnaeid genera are there? Ruthenica Russian Malacol J 23(1):41–58

Vinarski MV (2015) Conceptual shifts in animal systematics as reflected in the taxonomic history of a common aquatic snail species (*Lymnaea stagnalis*). Zoosyst Evol 91(2):91–103. https://doi.org/10.3897/zse.91.4509

Vinarski MV, Bolotov IN (2018) *Racesina*, a new generic name for a group of Asian lymnaeid snails (Gastropoda: Hygrophila: Lymnaeidae). Zoosystematica Rossica 27:328–333. https://www.zin.ru/journals/zsr/content/2018/zr_2018_27_2_Vinarski.pdf

Vinarski MV, Grebennikov ME (2012) An overview of species of the genus *Aenigmomphiscola* Kruglov et Starobogatov, 1981 (Gastropoda: Pulmonata: Lymnaeidae). Ruthenica The Russian Malacol J 22(2):159–170. [in Russian]

Vinarski MV, Kantor YI (2016) Analytical catalogue of fresh and brackish water molluscs of Russia and adjacent countries. A.N. Severtsov Institute of Ecology and Evolution of RAS, Moscow

Vinarski M, Schniebs K, Glöer P et al (2011) The taxonomic status and phylogenetic relationships of the genus *Aenigmomphiscola* Kruglov and Starobogatov, 1981 (Gastropoda: Pulmonata: Lymnaeidae). J Nat Hist 45(33–34):2049–2068. https://doi.org/10.1080/00222933.2011.574800

Vinarski M, Schniebs K, Glöer P et al (2012) The steppe relics: taxonomic study on two lymnaeid species endemic to the former USSR (Gastropoda: Pulmonata: Lymnaeidae). Arch Molluskenk 141(1):67–85. https://doi.org/10.1127/arch.moll/1869-0963/141/067-085

Vinarski MV, Aksenova OV, Bespalaya YV et al (2016a) *Radix dolgini*: the integrative taxonomic approach supports the species status of a Siberian endemic snail (Mollusca, Gastropoda, Lymnaeidae). C R Biol 339(1):24–36. https://doi.org/10.1016/j.crvi.2015.11.002

Vinarski MV, Aksenova OV, Bespalaya YV et al (2016b) *Ladislavella tumrokensis*: the first molecular evidence of a Nearctic clade of lymnaeid snails inhabiting Eurasia. Syst Biodivers 14(3):276–287. https://doi.org/10.1080/14772000.2016.1140244

Vinarski MV, Bolotov IN, Schniebs K et al (2017) Endemics or strangers? The integrative re-appraisal of taxonomy and phylogeny of the Greenland Lymnaeidae (Mollusca: Gastropoda). C R Biol 340:541–557. http://dx.doi.org/10.1016/j.crvi.2017.09.005

Vinarski MV, Aksenova OV, Bolotov IN (2020) Taxonomic assessment of genetically-delineated species of radicine snails (Mollusca, Gastropoda, Lymnaeidae). Zoosyst Evol 96(2):577–608. https://doi.org/10.3897/zse.96.52860

Vinarski MV, Aksenova OV, Bespalaya YV et al (2021) One Beringian genus less: a re-assessment of *Pacifimyxas* Kruglov & Starobogatov, 1985 (Mollusca: Gastropoda: Lymnaeidae) questions the current estimates of Beringian biodiversity. J Zool Syst Evol Res 59:44–59. https://doi.org/10.1111/jzs.12411

Vinarski MV, von Oheimb PV, Aksenova OV et al (2022a) Trapped on the roof of the world: taxonomic diversity and evolutionary patterns of Tibetan plateau endemic freshwater snails

(Gastropoda: Lymnaeidae: *Tibetoradix*). Integr Zool 17:825–848. https://doi.org/10.1111/1749-4877.12600

Vinarski MV, Aksenova OV, Bolotov IN (2022b) A new alien snail *Ampullaceana balthica* for the Canadian fauna, with an overview of transatlantic malacofaunal exchange in the Anthropocene. Aquat Invasions 17(1):21–35. https://doi.org/10.3391/ai.2022.17.1.02

Vinarski MV, Aksenova OV, Bespalaya YV et al (2023) How an ecological race is forming: Morphological and genetic disparity among thermal and non-thermal populations of aquatic lymnaeid snails (Gastropoda: Lymnaeidae). Diversity 15:548. https://doi.org/10.3390/d15040548

Welter-Schultes F (2012) European non-marine molluscs: a guide for species identification. Planet Poster Editions, Göttingen

Yen TC (1939) Die Chinesische Land- und Süsswasser-Gastropoden in Natur-Museums Senckenberg. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 444:1–233